TAXONOMIC AND PHYLOGENETIC REVISION OF THE FAMILY

CHIASMODONTIDAE (PERCIFORMES: ACANTHOMORPHA)

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CHIASMODONTIDAE (PERCIFORMES: ACANTHOMORPHA)

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VITA

Marcelo Roberto Souto de melo, son of Abraão Cavalcanti de Bessa and Amélia Souto de Melo, was born in Brasília, Brazil, on July 9, 1976. He received a Bachelor of Science in Biology in 1999 from Universidade Federal de Goiás (Brazil). In 2001, Marcelo earned a Master in Science degree in Biology at the Brazilian Museu Nacional, Universidade Federal do Rio de Janeiro. In 2004 he was awarded with a fellowship from the Brazilian government to join the Graduate School at Auburn University. Marcelo finished his degree requirements for a Doctor of Philosophy in Biological Sciences in August 10, 2009.

TAXONOMIC AND PHYLOGENETIC REVISION OF THE FAMILY

CHIASMODONTIDAE (PERCIFORMES: ACANTHOMORPHA)

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Doctor of Philosophy, August 10, 2009
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The family Chiasmodontidae, commonly known as swallowers, comprises four genera and 33 species distributed in the meso and bathypelagic regions of the Atlantic, Pacific, Indian and Southern Oceans. The species of *Chiasmodon* and *Pseudoscopelus* have disjunct distribution, and those of *Dysalotus* and *Kali*, wide distributions.

The genus *Chiasmodon* is composed of seven species, two of them new: *C. niger*; *C. subniger*; *C. braueri*; *C. microcephalus*; *C. pluriradiatus*; *C. asper* n. sp.; and *C. harteli* n. sp. *Pseudoscopelus* has 16 species, five of them new: *P. scriptus*; *P. sagamianus*; *P. altipinnis*; *P. cephalus*; *P. obtusifrons*; *P. scutatus*; *P. aphos*; *P. parini*; *P. astronesthidens*; *P. australis*; *P. pierbartus*; *P. bothrorrhinos* n. sp.; *P. lavenbergi* n. sp.; *P. paxtoni* n. sp.; *P. cordilluminatus*, n. sp.; and *P. odontoglossum* sp. n. *Dysalotus* has only three species, one new: *D. alcocki*; *D. oligoscolus*; and *D. acanthobrychos*. *Kali* has

seven species, two of them new: *K. indica*; *K. kerberti*; *K. macrodon*; *K. macrura*; *K. parri*; *K. colubrina*, n. sp.; and *K. falx*, n. sp.

The chiasmodontids have several morphologic adaptations related to life in the deep-sea and swallowing of enlarged preys. Those characteristics include the reduction of some bones and muscles, diverse dentition, enlarged mouth, a very distensible stomach and body walls, photophores, and the presence of superficial neuromasts on head and body. One of the most remarkable characteristics is the innumerous superficial neuromasts, which are present in all chiasmodontids. The superficial neuromasts are more concentrated in the head, but are also present on body along the trunk lateral-line canal, on upper and lower lobes of the caudal fin, and dorsal part, anterior and to the first-dorsal fin. The distribution of neuromasts is described, as well as their innervation.

A phylogenetic analysis was made based on 161 morphological characters obtained from osteology, myology, lateral line system, dentition and miscellaneous. The monophyly of the Chiasmodontidae is corroborated by 24 synapomorphies. Within the chiasmodontids, two major clades are formed: the *Chiasmodon* clade is composed of *Chiasmodon* and *Pseudoscopelus*, and supported by 18 synapomorphies; and the *Kali* clade is composed by *Dysalotus* and *Kali*, and supported by 22 synapomorphies. The monophyly of the genus *Chiasmodon* is supported by 16 synapomorphies; *Pseudoscopelus*, by 12 synapomorphies; *Dysalotus*, by 18 synapomorphies; and *Kali*, by 23 synapomorphies.

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Style manual or journal used: Zootaxa.

Computer software used: Microsoft Word 2003 (text), Microsoft Excel 2003 (tables), Corel Draw Graphics Suite 12 (figures), Adobe Photoshop CS2 (figures), JMP version 5 (statistic analysis); PAUP* version 4.0b10 (maximum parsimony reconstructions, genetic distance calculations, hypothesis testing), MacClade 4 (dataset handling, ancestral character reconstructions), Mesquite 2.6 (ancestral character reconstructions), TreeRot version 2b2 (produce commands for performing Decay analysis).

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CHAPTER 1 – INTRODUCTION TO THE FAMILY CHIASMODONTIDAE

General Introduction

The fishes of the family Chiasmodontidae are commonly known as swallowers because they can swallow prey larger than themselves. It is also one of the few families of perciforms that inhabits the meso- and bathypelagic regions of the oceans, being found between depths of 500 to 3,000 meters. The family contains 28 valid species distributed across four recognized genera: *Chiasmodon* Johnson, 1864, *Kali* Lloyd, 1909, *Pseudoscopelus* Lütken, 1892; and *Dysalotus* MacGilchrist, 1905 (Eschmeyer, 1998).

The chiasmodontids are small fishes (to 26 cm SL) with a bizarre appearance: They have a cylindrical body, dark skin, and some species have photophores. The head is very well-developed and has dorsal ridges and large sensorial canal pores. The mouth is enlarged, terminal and non-protractile. Long fang-like teeth are present on the dentary, premaxillary and maxillary bones; and the stomach and the lateral muscles of body are greatly distensible (Mooi and Paxton, 2001).

The type species of the family is *Chiasmodon niger* Johnson 1864, collected off Madeira Island, Atlantic Ocean. In the description, Johnson (1864) referred to his new genus only as a member of the Malacopterygii Order [sic], not placing it in any family. Nearly 20 years later, Jordan and Gilbert (1882) erected the family Chiasmodontidae.

Based on the number of scientific publications, the history of species descriptions can be divided into four different time periods. The first begins 25 years after the description of *Chiasmodon niger* and is represented by three years at the end of the nineteenth century. Three species described were: *C. subniger* Garman 1889, *Ponerodon vastator* Alcock 1890, and *Pseudoscopelus scriptus* Lütken 1892. *Ponerodon vastator* is now considered species inquirenda.

The second ranges from the beginning of the twentieth century to the mid-1930's. An additional 17 species and subspecies were described: *Dysalotus alcocki* MacGilchrist 1905, *Pseudoscopelus sagamianus* Tanaka 1908, *P. scriptus sagamianus* Tanaka 1908, *Chiasmodon bolangeri* Osório 1909, *Kali indica* Lloyd 1909, *C. braueri* Weber 1913, *Odontonema kerberti* Weber 1913, *Dysalotus macrodon* Norman 1929, *C. microcephalus* Norman 1929, *Dolichodon normani* Parr 1931, *P. stellatus* Beebe 1932, *Hemicyclodon macrurus* Parr 1933, *P. altipinnis* Parr 1933, *C. niger pluriradiatus* Parr 1933, *Myersiscus obtusifrons* Fowler 1934, *P. cephalus* Fowler 1934, *P. microps* Fowler 1934. Norman (1929) provided the first revision for Chiasmodontidae, diagnosing the family and giving the first species key available. However, he did not include several species (such as those described in the genus *Kali*), and he considered *Odontonema* as a valid genus (today it is recognized as a junior synonym of *Kali*), as well as *Kali macrodon* as a *Dysalotus*. He also considered *C. braueri*, *C. microcephalus*, *C. niger*, and *C. subniger* as valid *D. alcocki*, and *Pseudoscopelus scriptus* as valid, and placed *Ponerodon vastator* in synonymy of *C. niger*.

From 1965 to 1974 three additional species were described: *Gargaropteron pterodactylops* Smith 1965, *Pseudoscopelus scutatus* Krefft 1971, *Kali parri* Johnson and Cohen 1974 and *Dysalotus oligoscolus* Johnson and Cohen 1974. The most important contributions in this period were the revisions of *Kali* by Johnson (1969) and Johnson and Cohen (1974), and the revision of *Pseudoscopelus* by Lavenberg (1974). Johnson (1969) placed *Dolichodon, Hemicyclodon* and *Odontonema* in synonymy with *Kali*, and considered five species as valid: *K. indica*; *K. macrodon*; *K. macrura*; and *K. normani*. Johnson and Cohen (1974) also placed *G. pterodactylops* in synonymy of *K. indica*.

Lavenberg (1974) placed *Myersiscus* in synonymy of *Pseudoscopelus* and considered *P. altipinnis*, *P. obtusifrons*, *P. sagamianus*, *P. scriptus*, *P. scutatus*, and *P. stellatus* as valid, and listed five additional species, which were never described according to the International Code of Zoological Nomenclature (1999).

In the last three years several contributions increased the knowledge about the taxonomy of the chiasmodontids with several descriptions. Prokofiev and Kukuev (2006a, b, c) described *Pseudoscopelus aphos*, *P. astronesthidens*, *P. australis* and *P. parini* –the latter three species were previously mentioned by Lavenberg (1974); Spitz et al. (2007) described *P. pierbartus*; Melo et al. (2007) described *P. bothrorrhinos* and *P. lavenbergi*, two other species listed by Lavenberg (1974), and Prokofiev and Kukuev (2008) described *P. albeolus* and *P. vityazi*. Melo (2008) described *K. colubrina* and *K. falx*, and Prokofiev and Kukuev (2008) described *K. caribbea* and *Chiasmodon lavenbergi*.

In terms of numbers of revisions, the past three years were also very prolific. Prokofiev and Kukuev (2005, 2006a, 2008) published a series of revisions for the genus *Pseudoscopelus*; however, they included several misidentifications. In their earlier works, Prokofiev and Kukuev (2006a, b) misidentified *P. altipinnis*, *P. scriptus*, *P. sagamianus, P. microps* and *P. stellatus*. In (2006c), Prokofiev and Kukuev corrected the identification of *P. altipinnis*, regarding *P. microps* as a junior synonym, and describing *P. astronesthidens* and *P. australis*. In (2008), Prokofiev and Kukuev were unable to establish the validity of *P. pierbartus*, did not include the species described by Melo et al. (2008), retained the misidentifications of *P. stellatus* and *P. sagamianus*, and described two species with questionable status: *P. albeolus* and *P. vityazi*. Prokofiev (2009) also confused *P. sagamianus* with *P. scriptus*.

Objectives

This dissertation is divided into seven chapters. The chapters were organized in the format of scientific papers; therefore, each chapter is independent from the other. Chapters 2 to 5 resulted in four manuscripts which were already published or submitted for publication: Melo et al. (2007); Melo (2008); Melo (accepted); Melo (submitted). The content of each Chapter is summarized below:

- Chapter 2: the revision of *Chiasmodon* Johnson. This chapter resulted in a single publication: Melo (in press). The genus *Chiasmodon* is revised, with the validation of seven species, two of them new: *Chiasmodon braueri*, *C. microcephalus*, *C. niger*, *C. subniger*, *C. pluriradiatus*, *C. asper* n. sp. and *C. harteli*, n. sp. *Chiasmodon lavenbergi* is placed in the synonymy of *C. pluriradiatus*. A key to the genera of Chiasmodontidae, with diagnosis, maps of distributions and a key for the species of *Chiasmodon* is provided.

- Chapter 3: the revision of *Kali* Lloyd. This chapter resulted in a single publication: Melo (2008). The genus *Kali* is revised, with the validation of seven species, two of them new: *K. indica*, *K. kerberti*, *K. macrura*, *K. macrodon*, *K. parri*, and *K. colubrina* n. sp. and *K. falx* n. sp. The genera *Dolichodon, Hemicyclodon*, *Odontonema* and *Gararopteron* are confirmed as synonyms of *Kali*; *Kali normani* is placed in the synonymy of *K. kerberti*, *K. pterodactylops* of *K. macrodon*, and *K. caribbea* of *K. colubrina*. The status of *Ponerodon vastator* is discussed and it is regarded as species inquirenda. Diagnosis, maps of distributions and a key for the species of *Kali* are provided.

- Chapter 4: the revision of *Pseudoscopelus* Lütken. This chapter resulted in two publications: Melo et al. (2007) and Melo (submitted). The genus *Pseudoscopelus* is revised with the validation of 16 species, five of them new: *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. obtusifrons*, *P. pierbartus*, *P. parini*, *P. sagamianus*, *P. scutatus*, *P. scriptus*, and *P. odontoglossum*, n. sp., *P. lavenbergi*, n. sp.; *P. paxtoni*, n. sp., *P. bothrorrhinos*, n. sp., *P. cordilluminatus*, n. sp. The genus *Myersiscus* is confirmed as a junior synonym of *Pseudoscopelus*, and *P. microps* of *P. altipinnis*. *Pseudoscopelus stellatus* is placed in synonymy of *P. scriptus*, *P. albeolus* of *P. australis* and *P. vityazi* of *P. parini*. Diagnosis, maps of distributions and a key for the species of *Pseudoscopelus* are provided.

- Chapter 5: a new species of *Dysalotus*. This chapter has not been submitted for publication. *Dysalotus acanthobrychos* is described. *Dysalotus alcocki* and *D. oligoscolus* are considered valid. A key and an updated map of distribution for the species of Dysalotus are given.

- Chapter 6: gross morphology and innervation of the neuromasts in the family Chiasmodontidae. This chapter has not been submitted. The gross morphology, distribution and innervation of the canal and superficial neuromasts are described and compared in the genus *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*.

- Chapter 7: the phylogenetic relationships of the family Chiasmodontidae. This chapter has not been submitted. A phylogenetic hypothesis is proposed based on morphological characters obtained from osteology, myology, innervation, sensorial system, photophores and miscellaneous other characteristics. The monophyly of the family Chiasmodontidae and the four genera is examined using cladistics, and the relationships of the species explored.

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CHAPTER 2 – REVISION OF THE GENUS CHIASMODON JOHNSON

Publication:

Melo, M. R. S. (in press) Revision of the Genus *Chiasmodon* (Acanthomorpha: Chiasmodontidae), with the Description of Two New Species. *Copeia*, 71 pages MS.

Abstract

Chiasmodon is a genus of meso- and bathypelagic fishes, commonly known as swallowers. The genus has a wide distribution in the Atlantic, Pacific, Indian and Southern Oceans. Five species previously described are considered valid and two are being described as new: *C. niger*, from tropical North Atlantic, including the Gulf of Mexico and Caribbean; *C. subniger* from the eastern Pacific; *C. braueri* from the Indian, western and Central Pacific and western South Atlantic; *C. microcephalus*, from southern parts of the Atlantic, Indian and Pacific, and the Southern Ocean; *C. pluriradiatus* from tropical Atlantic, Indian, and Pacific; *C. asper* n. sp., from the temperate North Pacific; and *C. harteli* n. sp., from the temperate North Atlantic. *Chiasmodon bolangeri* is considered a junior synonym of *C. niger*, and *C. lavenbergi* a junior synonym of *C. pluriradiatus*. Taxonomic keys to the family Chiasmodontidae and to the species of *Chiasmodon*, as well as updated maps of distribution are provided.

Introduction

Chiasmodon Johnson 1864 is a genus of meso- and bathypelagic fishes with a world-wide distribution. The species of this genus are commonly known as swallowers because of the capacity to swallow prey larger than their own bodies. All nominal species of the genus *Chiasmodon* known to date were described between the second half of the nineteenth and the first half of the twentieth centuries. *Chiasmodon niger*, the type species of the genus and family Chiasmodontidae, was described by Johnson (1864a) based on a specimen collected off Madeira Island, in the eastern North Atlantic. Garman (1899) described *C. subniger* based on a juvenile obtained off the Pacific coast of

Mexico. Alcock (1890) described *Ponerodon vastator* from a single specimen obtained off India in the Indian Ocean. Osorio (1909) described *Chiasmodon bolangeri* based on a single specimen collected off the coast of Portugal, eastern North Atlantic. Weber (1913) obtained a single specimen from the Banda Sea, Indonesia and described it as *C. braueri*. Norman (1929) described *C. microcephalus* from a series of four specimens obtained in the South Atlantic. Parr (1933) described the subspecies *C. niger pluriradiatus* from six specimens obtained in the Bahamas, western North Atlantic. Recently, Prokofiev (2008) described *C. lavenbergi* from 13 specimens obtained in several parts of the Pacific Ocean.

Norman (1929) provided the only thorough revision available for the genus until the present, in which he recognized four species: *Chiasmodon niger* from the Atlantic, Caribbean Sea and Gulf of Bengal; *C. braueri* from Sierra Leone in the Atlantic coast of Africa, and Malay Archipelago in the Indo-Pacific; *C. subniger* from the Gulf of California; and *C. microcephalus* from South Atlantic. Norman (1929) considered *Ponerodon vastator* as a junior synonym of *C. niger*, but made no mention of *C. bolangeri*. Johnson and Keene (1986) recognized *C. niger* and *C. bolangeri* from South Africa and referred to *C. microcephalus* as a junior synonym of *C. bolangeri*. Johnson and Keene (1990) considered *C. microcephalus* as a junior synonym of *C. bolangeri*, and questioned the status of *C. braueri* and *C. subniger*. Prokofiev (2008) only considered *C. niger* and *C. subniger* valid and placed all other species in the synonymy of *C. niger*. None of the previous works were based on direct examination of types, but mainly on comparison of few specimens with the characteristics given in the original diagnosis of the species.

Herein, seven species of *Chiasmodon* are considered valid, two of which are described as new: *C. niger*, *C. subniger*, *C. braueri*, *C. microcephalus*, *C. pluriradiatus*, *C. harteli* n. sp., and *C. asper* n. sp. *Chiasmodon bolangeri* is considered a junior synonym of *C. niger*, and *C. lavenbergi* a junior synonym of *C. pluriradiatus*. The status of *Ponerodon vastator* is impossible to verify, and it is being regarded as *species inquirenda*. Taxonomic keys to the genera of Chiasmodontidae and the species of *Chiasmodon* are provided, with updated maps of distribution.

Material and Methods

Morphometric and meristic data were obtained following the protocol described by Melo et al. (2007). Measurements were recorded to the nearest 0.1 mm using digital calipers; size range of lots given in SL. Terminology for the sensory system of the head follows Webb (1989). Counts of dorsal-, anal-, caudal-, and pelvic-fin rays are indicated as follows: true spines (*sensu* Johnson and Patterson 1993) in uppercase Roman numerals, soft unbranched rays in lowercase Roman numerals, and soft branched rays in Arabic numerals. Pectoral-fin rays are listed as the total number of rays, rather than branched/unbranched, because rays were frequently broken. Counts of the caudal-fin rays were made ventral to dorsal, with the first principal caudal-fin ray as the most anteroventral ray, and the last as the most dorsal ray according to McDowall (2003). Vertebral counts were made from cleared and stained or x-rayed specimens. Counts listed in the text are followed by their frequency in parenthesis with an asterisk indicating values for the holotype. Total number of specimens listed may vary because some specimens have poorly preserved or completely destroyed structures.

Terminology for major ocean regions follows Tomczack and Godfrey (2003); biogeographic zones of the Atlantic follow Backus et al. (1977) with the addition of Atlantic Subantarctic to the region between the South Atlantic Subtropical and Guinean Provinces, and the Southern Ocean; classification for Indian and Pacific Oceans follows Springer (1982). Institutional abbreviations are as listed at http://www.asih.org/codons.pdf, with the addition of ZMH for Zoologisches Museum Hamburg (former ISH), Germany; SAIAB for South African Institute for Aquatic Biology (former JLB), South Africa; and NMNZ now refers to the Museum of New Zealand Te Papa Tongerewa, New Zealand.

Terminology for tooth attachment follows Fink (1981). Due to the heterodont and great diversity of teeth shape and size among the chiasmodontids, a specific terminology is introduced: cone tooth, long, sharp, unicuspid, triangular shaped tooth; flange, sharp, cutting edge on tooth crown that transverses the tooth apex; fang, remarkably elongated, unicuspid, triangular shaped tooth, easily distinguished from other teeth because of its enlarged size; and canine an enlarged, well-developed unicuspid tooth, with a type 1 attachment. The canines differ from fangs by their function and position: canines seem to function to hold the prey, are completely ankylosed to bone, and remain exposed when mouth is closed; fangs seem to be used to perforate prey, are loosely attached with the type 4 ligament in *Chiasmodon*, or ventral attachment to bone in *Kali* (Melo 2008). Dentition is presented followed by the number of specimens counted, mode or median, when mode is not possible to be obtained. The sensory system of head is summarized in figure 2.1.A; gill arches in figure 2.1.B, and premaxilla in figure 2.1.C and dentary in figure 2.1.D.

List of abbreviations

ang – angular

bh – basihyal

bb basibranchial

cb – ceratobranchial

ch – ceratohyal

den – dentary

dst – dermosphenotic

eh – epihyal

ESC – epiphyseal branch of supraorbital sensory canal

ext – extrascapular

fr – frontal

hh – hypohyal

IO – infraorbital canal

io 1-6 – infraorbitals 1–6

lls – lateral-line scale

lp – lower pharyngeals.

MD – mandibular canal

mst – mesethmoid

mx – maxilla

na – nasal

OT – otic canal

pa – parietal

pmx – premaxilla

pop – preopercle

PrO – preopercular canal

pto – pterotic

ptt – posttemporal

SO – supraorbital canal

so – supraoccipital

ST – supratemporal canal

T temporal canal

TR – trunk canal

Results

Key to the genera of Chiasmodontidae

1a. Bones forming the skull weak, with apparent trabeculae; nasal weakly calcified, circular but not spoon-shaped, located dorsally, and covered by pigmented skin; parietals poorly developed, less than half the length of supraoccipital; caudal fin rays ii+6+7+ii or ii+6+6+ii; last pored lateral line scale contiguous with penultimate scale, at fork of caudal fin; large elongated neuromasts absent on top of the head, cheek or snout, small circular neuromasts present or absent on cheek and in two rows between supraoccipital and dorsal fin; pre- and postzygapophyses absent. 2

1b. Bones forming the skull dense, trabeculae not easily distinguished; nasal strongly calcified, spoon-shaped, located anterolaterally, and covered by thin transparent skin; parietals well-developed, of same length or a little smaller than supraoccipital; caudal fin rays usually i+7+8+i; last pored scale of lateral line well separated from the penultimate scale and positioned over the lower lobe of the caudal fin; numerous large, elongated neuromasts present on surface of the head, over supraoccipital, parietals, frontals and pterotic cranial bones, face, snout, lower jaw, and on body as two parallel rows anterior to first dorsal fin; parietals well-developed, of same length or a little smaller than supraoccipital; pre- and postzygapophyses present on vertebrae 3

2a. Body naked, dermal spinules absent; premaxillary and dentary teeth in two rows, those of internal row recurved, flanged, with ventral attachment to bone; teeth of external row variable, recurved, flanged, with ventral attachment to bone, needle-like and/or caniniform with type 4 attachment; extremely elongate fangs present or not; total premaxillary teeth 9–42, total dentary teeth 9–40; branchiostegal rays six; bony projection at tip of chin absent; total vertebrae 33–40, precaudal 20–26. ....*Kali*

2b. Well developed dermal spinules present on posterior part of body, above and below lateral line, in one to four rows; premaxillary and dentary teeth needle-like, without flange, with type 4 attachment, arranged in three rows with three to seven series; fangs absent; total premaxillary teeth 60–198, total dentary teeth 67–199; branchiostegal rays seven; bony projection at tip of chin present; total vertebrae 39–

40, precaudal 15–16. .... *Dysalotus*

3a. Premaxillary teeth in three rows [lateral, middle and mesial], and dentary in two rows of one to five series of needle-like teeth, without a flange, with type 4 attachment, premaxillary and dentary canines, lateral accessory teeth, and fangs absent; total vertebrae 31–38, precaudal 14–19; photophores usually present on head and ventral part of body (absent in *P. aphos*) .... *Pseudoscopelus*

3b. Premaxillary and dentary teeth in two rows of single series; well developed type 1 canines present at anterior edge of premaxilla, and anterior portion of dentary, exposed when mouth is closed, remaining teeth type 4; one or two lateral accessory to the premaxillary canine; teeth one or two fangs in ventral margin of premaxillary head, and first two teeth of internal series of dentary; total vertebrae 41–48, precaudal 19–25; photophores always absent. .... *Chiasmodon*

Key to the species of *Chiasmodon*

1a. Pectoral-fin rays 15–16; fangs on premaxillary head two (Fig. 2.4); numerous and minute dermal spinules on body in specimens larger than 48.0 mm SL. 2

1b. Pectoral-fin rays 12–14; fangs on premaxillary head one (Fig. 2.4); dermal spinules absent in specimens larger than 48.0 mm SL 3

2a. Supraorbital pores nine (Fig. 2.2). .... *Chiasmodon asper*

2b. Supraorbital pores eight (Fig. 2.2). .... *Chiasmodon pluriradiatus*

3a. Supraorbital pores six (Fig. 2.2), vertebrae 47–48......................... *Chiasmodon harteli*

3b. Supraorbital pores seven or eight (Fig. 2.2), vertebrae 44–46..................................... 4

4a. Infraorbital pores 11–13 (mode = 12), infraorbital 1 pores five to six (Fig. 2.2); snout short and blunt; upper jaw 63.9–72.7 % HL; lower jaw not projecting beyond anterior tip of premaxilla, 63.9–72 % HL; teeth on first basibranchial always absent. .... *Chiasmodon subniger*

4b. Infraorbital pores 13–15 (mode = 14), infraorbital 1 pores seven to eight (Fig. 2.2); snout elongated; upper jaw 68.3–84.2 % HL; lower jaw prognathous, 76.8–86.7 % HL; teeth on first basibranchial present or absent. 5

5a. Teeth on second basibranchial usually absent (rarely one to three small teeth). .... *Chiasmodon microcephalus*

5b. Teeth on second basibranchial always present, strong, three to 18. 6

6a. Teeth on second ceratobranchial absent (Fig. 2.3), supraorbital canal pores seven (fig. 2.2). ....*Chiasmodon niger*

6b. Teeth on second ceratobranchial present (three to 16, modally six, Fig. 2.3), supraorbital canal pores eight (Fig. 2.2). .... *Chiasmodon braueri*

Chiasmodon Johnson 1864

Black swallowers

Chiasmodon Johnson 1864a: 408 [type species *Chiasmodon niger* Johnson 1864a; type by original designation; gender: Masculine].

Chiasmodus Günther 1887: 99, misspelled, and invalid.

Diagnosis. The genus *Chiasmodon* can be diagnosed from all other chiasmodontids by dentition pattern: head of premaxilla with a well-developed canine, one to two lateral accessory teeth, and well-developed fangs (vs. premaxillary head lacking canine and fangs in *Dysalotus* and *Kali*, and not remarkably developed in *Pseudoscopelus*; lateral accessory teeth always absent); lateral series of dentary with well-developed canine followed by a diastema (canine and diastema of lateral series of dentary absent in *Dysalotus*, *Kali*, and *Pseudoscopelus*); mesial series in single row, two anteriormost teeth specialized as fangs and much enlarged than following teeth (vs. mesial series of dentary in one to four rows of needle-like teeth, two anterior teeth not specialized as fangs in *Dysalotus* and *Pseudoscopelus*; and strikingly recurved, with ventral attachment to bone, and if developed as fangs, not much more enlarged than following teeth in *Kali*).

Chiasmodon is further distinguished from *Dysalotus* and *Pseudoscopelus* by premaxillary teeth in two series, lateral and mesial, consisting of a single row each (vs. premaxillary teeth in three series, lateral, middle and mesial, with lateral and mesial consisting of one to seven rows), teeth in mesial series conical, with flange, needle-like teeth absent (vs. teeth in middle and mesial series needle-like and without flanges); teeth in mesial series of dentary in one to four rows, conical or fangs, with flange, needle-like teeth absent (vs. teeth in mesial series of dentary in one to multiple rows, needle-like and without flanges); total vertebrae 42 to 48, precaudal vertebrae 19 to 22 (vs. total vertebrae 39 to 40, precaudal vertebrae 15 to 16 in *Dysalotus*; 33 to 40, 20 to 26 in *Kali*; and 31 to 38, 14 to 19 in *Pseudoscopelus*).

Chiasmodon is further distinguished from *Kali* and *Dysalotus* by having well calcified bones forming the neurocranium (vs. bones forming neurocranium poorly calcified with trabeculae easily distinguishable with the naked eye); nasal strongly calcified, spoon-shaped, located anterolaterally, and covered by thin transparent skin (vs. nasal weakly calcified, circular but not spoon-shaped, located dorsally, and covered by pigmented skin); parietals well-developed, of same length or a little smaller than supraoccipital (vs. parietals poorly developed, less than half the length of supraoccipital); pre- and postzygapophyses present on vertebrae (vs. pre- and postzygapophyses absent); large, elongated neuromasts present on surface of head, over supraoccipital, parietals, frontals and pterotic cranial bones, cheek, snout, lower jaw, and in body as two parallel rows anterior to first dorsal fin (vs. large elongated neuromasts absent; small circular neuromasts present or absent on cheek and in two rows between supraoccipital and dorsal fin); last pored scale of lateral line well separated from the penultimate scale and positioned over the lower lobe of the caudal fin (vs. last pored lateral line scale contiguous with penultimate scale); and caudal fin rays i+7+8+i (vs. caudal fin rays ii+6+7+ii). Furthermore, *Chiasmodon* differs from *Kali* by the absence of the strikingly recurved teeth with ventral attachment in the mesial series of the premaxilla and dentary (vs. teeth in mesial series of premaxilla and dentary straight or slightly curved, with types 1 or 4 attachment), and by branchiostegal rays seven (vs. branchiostegal rays six in *Kali*).

Description. Largest specimen examined 270.0 mm. Body elongate, laterally compressed. Greatest body depth at origin of first dorsal fin. Scales absent, except for lateral-line scales, embedded in skin. Small dermal spinules present on body and head of all juveniles less than 45.0 mm SL, and present or absent on body of adults (see species account).

Anterior profile of head elongate in lateral view, tip of snout protruding, with gentle curve at level of nasal bone. Mouth terminal, oblique, and enlarged, reaching ventral edge of preopercle. Orbit circular. Nares distinctly separated, anterior naris circular, anteriorly pointed, lateral to third supraorbital pore; posterior naris crescent shaped, closer to anterodorsal margin of eye than to anterior naris. Bones of head compact and well calcified.

Pectoral fin well-developed. Pelvic-fin origin slightly posterior to level of pectoral-fin base. Dorsal fins two, first dorsal-fin insertion slightly posterior to level of pelvic-fin insertion; second dorsal-fin origin at level of anal-fin origin. Anal fin opposite to second dorsal fin. Caudal fin forked. True spines present in first dorsal fin, and first ray of pelvic fin. Lateral line complete, with pores opening between each scale; last scale of lateral line separate from anterior, in lower lobe of caudal fin, with two pores. Head bones and sensory system of head illustrated in figure 2.1 A.

Gill arches four; pseudobranchia present, ventral elements of gill arch summarized in figure 2.1 B. Epibranchial of first arch dorsally connected to opercle to midline; ceratobranchial and hypobranchial of first arch free. Epibranchials of second, third and fourth arches connected distally to each other and to the pharyngobranchials; ceratobranchial of second arch free. Hypobranchial and basibranchial of second, third and four arches connected medially. Ceratobranchial of third arch connected anteriorly to fourth arch; ceratobranchial of fourth arch connected medially to body wall at anterior half. Basihyal, elongated, free anteriorly, with posterior and ventral connection to first basibranchial; first basibranchial small, triangular, connected to basihyal and second basibranchial; second basibranchial elongated; third basibranchial extremely elongated, extending posteriorly beyond fourth basibranchial, posterior half cartilaginous and ventrally curved; four basibranchial small, diamond-shaped, cartilaginous. Hypohyals with dorsal and ventral elements, attached to first basibranchial; first hypobranchial attached immediately posterior to basihyal, between joint of first and second basibranchials; second hypobranchial connected to joint between second and third basibranchials; third hypobranchial proximally connected to anterior edge of fourth basibranchial, distal tip of fourth hypobranchial ventrally pointed; fourth hypobranchial absent or fused to ceratobranchial, fourth ceratobranchial connected to posterior edge of fourth basibranchial; ventral pharyngobranchials connected posteriorly to fourth ceratobranchial.

Dentition. General arrangement of premaxilla summarized in figure 2.1 C and dentary in figure 2.1 D. Premaxilla divided into head, neck, body, and caudal process. Premaxillary head with three specialized types of teeth: canine, single tooth positioned at anterior edge of premaxilla, projecting outside of mouth, strong, type 1, conical, with flange, slightly sigmoid; lateral accessory teeth, one to two, lateral to base of canine, small, type 1, conical, with flange, slightly curved; premaxillary fang, inserted in ventral shelf of head of premaxilla, one to two, type 4, moderately elongated, conical, with flange, slightly curved. Premaxillary neck toothless, forming diastema. Premaxillary body elongated and expanded medially by flat process, with two series of teeth: lateral and mesial. Lateral series in single row, extending laterally along body of premaxilla to end of caudal process, teeth nine to 41, type 4, conical, with flange, slightly curved; mesial series in single row, extending along and restricted to mesial shelf of premaxilla, teeth one to six, type 4, conical, flanged, slightly curved.

Dentition of dentary arranged in two series: lateral and mesial. Lateral series in single row, extending from symphysis to posterior tip of bone; teeth at anterior edge two to four, small, type 4, conical, with short flange, slightly curved; dentary canine next, largest tooth in series, type 1, conical, with flange, curved, exposed when mouth closed via insertion through diastema in premaxillary neck; short diastema immediately posterior to canine of dentary, followed by six to 32 teeth, type 4, conical, with flange, slightly curved. Mesial series in single row, four to nine: anterior two teeth fangs of dentary, opposite positioned to fang of premaxilla, type 4, conical, with flange, moderately elongated, first fang smaller than second, inserted slightly medial to diastema of dentary; next teeth type 4, conical, with flange, slightly curved, extending to posterior fourth of dentary.

Teeth on palatine in single row, three to 10, conical, with flange, slightly curved; first tooth at anterior third of palatine followed by diastema; next teeth in posterior half of palatine. Upper pharyngobranchial teeth in one to two rows, type 4, conical, without flange, slightly curved; lower pharyngobranchial teeth in single row, type 4, conical, without flange, slightly curved; teeth on second and third basibranchials present or absent, if present small, type 1, conical, without flange, individually attached to bone or in small patches of few teeth. Teeth present or absent on second hypobranchial and ceratobranchial, if present type 1, conical, without flange, straight; teeth in second pharyngobranchial in single row, type 4, conical, without flange, slightly curved; teeth on third ceratobranchial in single row, type 1, conical, without flange, curved. Teeth absent on remaining branchial elements.

Color. Recently collected specimens of all known species dark brown, darker in dorsum and lighter in belly. Preserved specimens fade quickly, becoming faded brown, or even completely bleached white.

Distribution. In temperate and tropical regions of the Atlantic, Indian, Pacific, and Southern Oceans, from 67° N to 54° S (Fig. 2.5).

Etymology. From the Greek, chiasmos, means diagonally arranged, and odous, tooth or teeth.

Ontogenetic changes and identification of juveniles. Development of *Chiasmodon* cf. *niger* was described by Shiganova (1990a, b). Juveniles of all species have tiny dermal spinules along body and head, and coloration is pale with dark spots in dorsal and ventral areas. Spots disappear at 35.2 mm SL and color pattern becomes dusky, but not as dark as in adults; at 50.0 mm SL *Chiasmodon* has the adult color pattern (personal observation). Adults of five species completely lack dermal spinules: *Chiasmodon braueri*, *C. harteli*, *C. microcephalus*, *C. niger* and *C. subniger*. Smallest individuals of each species lacking dermal spinules were, respectively, 35.8 mm SL (USNM 288986), 56.5 mm SL (ZMUC P. 6595), 35.1 mm SL (AUM I. 20315069), 45.2

mm SL (UF 219999), and 48.7 mm SL (LACM 30475). The fact that specimens with 45.6 mm SL (ZMUC P. 6589) of *C. harteli* and 44.7 mm SL (UF 219999) of *C. niger* still keep dermal spinules (vs. 35.1 mm SL of *C. microcephalus*) may imply that size when spinules disappear varies in each species. Two species retain dermal spinules on body when adults: *C. pluriradiatus* and *C. asper*.

The development of dentition in *Chiasmodon* differs from the other genera in the family by the fact that dentition is fully developed in very small specimens, as small as 20.0 mm SL. The genus *Kali* has a distinctive gargaropteron larval stage, which undergoes a drastic transformation before acquiring the very different characteristics of adults at about 50.0 mm SL (Hardy 2005, 2007; Melo 2008). Juveniles of *Pseudoscopelus* and *Dysalotus* resemble the adults externally, except that tooth rows are not completely formed until specimens reach about 45.0 mm SL (Melo, pers. obs.). In both cases, the species diagnoses cannot be made with precision until they reach the mature form. Juveniles of *Chiasmodon* can be identified based on the counts of pectoral-fin rays, dentition, and presence of teeth on the gill arches.

Chiasmodon niger Johnson 1864

Figure 2.6, Tables 2.1 and 2.2

Chiasmodon niger Johnson 1864a: 408–410 [type by original designation; type locality Madeira Island, eastern North Atlantic, approx. 22°30’ N, 107°00’ W, J. Johnson col.; holotype BMNH 1863.12.12.4]; Johnson 1864b: 76–78 [repeated description]; Osorio

1909: plate 2, figure 2 [comparison with *C. bolangeri*]; Norman 1929: 338–339 [in part, taxonomic revision of the genus, species account, key to the species, records in the Atlantic, Caribbean (questionable), and Bay of Bengal (questionable)]; Parr 1933 [record from Bermudas, western North Atlantic]; Séret and Andreata 1992: 93 [record from off Brazil, western South Atlantic, reported lot apparently lost]; Johnson and Keene 1990: 899–901 [record in the eastern tropical Atlantic]; Reiner 1990: 236 [record at Cabo Verde Archipelago, eastern North Atlantic]; Shiganova 1990, a, b: 143–151, figures 1–3 [larval development]; McEachran and Sutton 2003: 1742–1743 [list of species in the Atlantic]; Moore et al. 2003: 227 [in part, records from off New England, western North Atlantic].

Chiasmodon subniger (not Garman) McEachran and Sutton 2003: 1742–1743 [list of species from western Central Atlantic].

Chiasmodus niger Günther 1887: 99 [original name misspelled, records for Mid-Atlantic].

Chiasmodon bolangeri Osorio 1909: 22–27, plate II, figure 1 [original description; type locality off Setubal, Portugal, eastern North Atlantic, aprox. 38°20' N, 8°55' W, 800 m; holotype MB T135 (1506), destroyed in 1978 fire]. New synonym.

Diagnosis. *Chiasmodon niger* can be distinguished from its congeners by a combination of characteristics: from *C. braueri* by the teeth on second ceratobranchial absent (vs. present in *C. braueri*) and supraorbital canal pores seven (vs. eight); from *C. harteli* by total vertebrae 43–45 (vs. total vertebrae 47–48), supraorbital canal pores seven (vs. six); from *C. microcephalus* by teeth on basibranchials well-developed, three to 18, always present on second basibranchial and often on third basibranchial and second hypobranchial (vs. teeth on basibranchials usually absent, rarely one to three, small, restricted to second basibranchial); from *C. pluriradiatus* and *C. asper*, by pectoral-fin rays 13–14 (vs. pectoral-fin rays 15–16), tiny dermal spinules on body of specimens larger than 45.0 mm absent (vs. spinules present), fang in premaxillary head one (vs. two), and supraorbital pores seven (vs. eight in *C. pluriradiatus*, and nine in *C. asper*) and from *C. pluriradiatus* by lateral-line pores 86–93 (vs. 91–94) from *C. subniger*, by teeth on second basibranchial present (vs. absent), infraorbital pores 14 (vs. 12–13, modally 13), snout elongate and pointed, 22.2–26.6 % HL (vs. snout short and blunt, 21.4–23.9 % HL), upper jaw 72.2–80.0 % HL (vs. 63.9–72.7 % HL), and lower jaw 80.0–86.7 % HL (vs. 69.0–76.7 % HL).

Description. Largest specimen examined 205.7 mm. Morphometric data summarized in table 2.2. General body pattern as described for genus. Skin naked; dermal spinules absent in individuals larger than 45.2 mm SL.

First dorsal-fin rays X (5), XI (7*), XII (1); second dorsal-fin rays iii+22 (1), iii+23 (2), iii+24 (3), iv+24 (1), iii+25 (2), iv+25 (1), iii+26 (3*); anal-fin rays iv+22 (1), iv+23 (2), iii+24 (1), iv+24 (6*), v+24 (1), iv+25 (1), v+25 (1); pectoral-fin rays 13 (6*), 14 (7); pelvic-fin rays I+5 (13*); caudal-fin rays i+7+8+i (13*). Branchiostegal rays seven (13*). Pre-caudal vertebrae 20 (4*), 21 (2), 22 (2); total vertebrae 43 (1), 44 (5*), 45 (5).

Lateral line complete, pore counts summarized in table 2.1. Sensory system of head as illustrated in figure 2.2. Pores in temporal canal 2 (13*); supratemporal canal 3 (13*); otic canal 2 (13*); supraorbital canal 7 (13*); epiphyseal branch 2 (1), 3 (10); infraorbital canal 14 (13*); preopercular canal five (13*); mandibular canal 6 (13*);

fourth pore of mandibular canal 1 (1), 2 (12*); fifth pore of mandibular canal 1 (13*).

Dentition. Teeth present on premaxilla, dentary, palatine, second and third basibranchials, second hypobranchial, upper and lower pharyngobranchials, and rarely on second hypobranchial; sometimes absent on third basibranchial, and absent on other branchial elements. Ventral elements of gill arches illustrated in figure 2.3; premaxilla, in figure 2.4. Teeth on premaxilla: canine 1 (10), at anterior tip of head; accessory anterior tooth 1 (10), lateral to canine; fang 1 (10), at ventral part of head; lateral series 15–25 (10, mode = 22), equally spaced between neck and posterior tip of caudal process; mesial series 2–4 (10, mode = 3), at medial shelf of body. Teeth on dentary: lateral series 9–23 (10, mode = 18), teeth at anterior edge 1–2 (10, mode = 1), canine 1 (10), diastema, remaining teeth uniformly distributed between diastema and posterior tip of dentary; mesial series 5–10 (10, mode = 9), first and second anteriormost teeth developed as fangs. Palatine teeth 4–10 (11, mode = 8). Teeth on basibranchials 3–18 (12, mode = 4), individually attached to bone or in small plates of two to three teeth, always present on second basibranchial and sometimes on third basibranchial. Teeth on second hypobranchial frequently absent, 0–6 (12, mode = 0).

Distribution. Throughout the tropical and temperate eastern and western North Atlantic and Gulf of Mexico, from 95° W to 5° E, 46° N to 5° S (Fig. 2.5).

Bathymetric distribution. Meso- to bathypelagic zones. Specimens larger than 45.0 mm are more frequently collected between 730 and 1900 m; the shallowest record is 150 m and the deepest, 3900 m (mean 1390 m). Juveniles are found in shallower water, between the zero and 1050 m (mean 542 m), with the smallest specimens (>10.0 mm) collected nearest to the surface.

The status of *Chiasmodon bolangeri*. Osorio (1909) described *C. bolangeri* based on a single specimen obtained off Portugal, in the eastern North Atlantic. The specimen was deposited at Museu Bocage, Portugal, and was destroyed in a 1978 fire. The only diagnostic characteristic used was the "little capacity of dilatation that the abdomen skin seems to be capable" (p. 22, translation by the author) compared to the holotype of *C. niger*. Such characteristics, however, is extremely variable depending on the stomach fullness. Norman (1929) revised the genus and described *C. microcephalus* from the South Atlantic, but ignored the description of *C. bolangeri*. Johnson and Keene (1986 1990) considered *C. bolangeri* a senior synonym of *C. microcephalus*.

Chiasmodon bolangeri is being placed in the synonymy of *C. niger* because of the lack of good characteristics to diagnose it, and the fact that *C. niger* was the only species identified around the its type locality, off the coast of Portugal at about 38°20' N and 8°55' W. *Chiasmodon niger* is by far the most common species in the eastern North Atlantic and its type locality is only 1000 km away from the type locality of *C. bolangeri*. *Chiasmodon pluriradiatus* is common in the tropical and equatorial regions of the Atlantic, Indian and Pacific, but has never been recorded north to 32° N. *Chiasmodon harteli* is a common species in temperate waters of the North Atlantic, and although its southern limit of distribution is about 35° N, it is very uncommon at that latitude. *Chiasmodon asper*, *C. braueri*, *C. microcephalus* and *C. subniger* were not recorded in the North Atlantic.

Chiasmodon subniger Garman 1899

Figure 2.7, Tables 2.1 and 2.2

Chiasmodon subniger Garman 1899: 73–74 [type by original designation; type locality off the Pacific coast of Mexico, 22°30'30" N, 107°01'00" W, 1682 m, 19–IV–1891, holotype MCZ 28744].

Chiasmodon subniger Norman 1929: 541 [key to species of *Chiasmodon* and a brief diagnosis of the species]; Johnson and Keene 1986: 900 [report of the holotype and a questionable specimen from western North Atlantic].

Diagnosis. *Chiasmodon subniger* can be diagnosed from its congeners by total infraorbital pores 11–13, infraorbital 1 pores five to six (vs. 13–14, rarely 11, infraorbital 1 pores seven to eight); and lower jaw short, not extending beyond upper jaw, 63.9–72.7 % HL (vs. lower jaw elongated, extending beyond upper jaw, 73.3–77.1 % HL in *C. asper*; 76.0–83.8 % HL in *C. braueri*, 80.8–89.9 % HL in *C. harteli*; 76.8–85.2 % HL in *C. microcephalus*; 72.2–80.0 % HL in *C. niger*; and 72.2–77.0 % HL in *C. pluriradiatus*). It further differs from other species by snout blunt, short, 21.4–23.9 % HL (vs. snout elongated and pointed 23.0–26.6 % HL in *C. harteli*; 23.7–28.0 % HL in *C. microcephalus*; and 22.2–26.6 % HL in *C. niger*); upper jaw 63.9–72.7 % HL (vs. 70.0–77.1 % HL in *C. braueri*; 74.3–84.2 % HL in *C. harteli*; and 72.2–80.0 % HL in *C. niger*); from *C. braueri*, by the teeth on second ceratobranchial absent (vs. present); from *C. harteli*, by the total vertebrae 43–44 (vs. total vertebrae 47–48), and supraorbital pores seven to eight (vs. six, rarely seven); from *C. pluriradiatus* and *C. asper*, by pectoral-fin rays 12–13 (vs. 15–16), tiny dermal spinules on body in specimens larger than 48.7 mm absent (vs. spinules present), and fang on premaxillary head one (vs. two).

Description. Largest specimen examined 235.7 mm. Morphometric data summarized in table 2.2. General body pattern as described for genus. Skin naked; dermal spinules absent in individuals larger than 48.7 mm SL.

First dorsal-fin rays X (6), XI (9), XII (4); second dorsal-fin rays iii+21 (3), iv+21 (4), iii+22 (5), iv+22 (1), ii+23 (1), iii+23 (3), iv+23 (2); anal-fin rays iv+20 (2), iv+21 (4), v+21 (5), iv+22 (2), v+22 (1), iv+23 (5); pectoral-fin rays 12 (4), 13 (15); pelvic-fin rays I+5 (19); caudal-fin rays i+7+8+i (18), i+8+8+i (1). Branchiostegal rays 7 (19). Pre-caudal vertebrae 20 (5), 21 (5); total vertebrae 43 (3), 44 (7).

Lateral line complete, pore counts summarized in table 2.1. Sensory system of head as illustrated in figure 2.2. Pores in temporal canal 2 (19); supratemporal canal 3 (19); otic canal 2 (19); supraorbital canal 7 (16), 8 (3); epiphyseal branch 1 (1), 2 (8), 3 (8), 4 (2); infraorbital canal 11 (7), 12 (6), 13 (5); preopercular canal 5 (19); mandibular canal 6 (19); fourth pore of mandibular canal 1 (5), 2 (13), 3 (1); fifth pore of mandibular canal 1 (19).

Dentition. Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials; absent on other branchial elements. Ventral elements of gill arches illustrated in figure 2.3; premaxilla, in figure 2.4. Teeth on premaxilla: canine 1 (19), at anterior tip of head; accessory anterior teeth 1–2 (18, mode = 1), lateral to canine; fang 1 (19), at ventral part of head; lateral series 12–41 (19, mode = 14), equally spaced between neck and posterior tip of caudal process; mesial series 2–4 (19, mode = 4), at medial shelf of body. Teeth on dentary: lateral series 10–34 (19, mode = 16), teeth at anterior edge 1–5 (18, mode = 1), canine 1 (19), diastema, remaining teeth uniformly distributed between diastema and posterior tip of dentary; mesial series 4–9 (19, mode = 4), first and second anteriormost teeth developed as fangs. Palatine teeth 1–8 (19, mode = 5).

Distribution. Eastern Pacific, from Hawaii 155°30' W to the west coast of North, Central and northern South America; from 48° N to 29° S (Fig. 2.5).

Bathymetric distribution. Meso- to bathypelagic zones, from 245 to 4568 m (mean 1920 m).

Remarks. Diagnosis and validation of *Chiasmodon subniger* is a difficult task. Garman (1899: 73) described *C. subniger* based on a specimen of about 40.0 mm, diagnosed by "skin thickly beset with fine spinuloid scales presenting a pilose appearance." This, however, is a common characteristic of the juveniles of *Chiasmodon* (Kotthaus 1972; Shiganova 1990a, b; Hardy 2005). Because of that, Johnson and Keene (1990) questioned the validity of *C. subniger*. The presence of prickles on the body of adults is actually a diagnostic feature of *Chiasmodon pluriradiatus* and *C. asper*. Those species, however, can also be distinguished from *C. subniger* by two other characteristics, which can be identified even in the juveniles: 15–16 pectoral-fin rays (vs. 12–13); and two fangs on premaxillary head (vs. one).

Extensive material of *Chiasmodon* was examined from the Pacific Ocean, including samples from the type locality of *C. subniger*, off the Pacific coast of Mexico and surrounding areas. *Chiasmodon subniger* as diagnosed herein, lacks spinules on its body as an adult. The holotype of *C. subniger* is in very poor condition and the main diagnostic characteristic of the species, the number of infraorbital pores, could not be verified. Other characteristics, such as pectoral fin rays, dentition and absence of teeth on branchial elements, largely agree with those used to diagnose the species. This conclusion is supported by the distribution of *C. subniger* along the western coast of the Americas from Canada to northern Chile and the fact that no other species occurs in that same area. Four additional species occur in the Pacific, *C. asper*, *C. braueri*, *C. microcephalus* and *C. pluriradiatus*, but none of these were found off the western coast of Mexico, or even close to the type locality of *C. subniger*.

Prokofiev (2008: 214–213) considered *C. subniger* as valid, but diagnosed it from *C. lavenbergi* incorrectly "by the better development of gill rakers and presence of two rows of teeth on copula between the bases of the first and the second gill arches." Chiasmodontids lack true gill rakers (pers. obs.), and all specimens of *C. subniger* examined, including the holotype, lack teeth on branchial elements.

Chiasmodon braueri Weber 1913

Figure 2.8, Tables 2.1 and 2.3

Chiasmodon braueri Weber 1913: 147–148 [type by original designation; type locality Banda Sea, Indonesia, 5°39' S, 122°12' E, 1886 m, 22–IX–1899, R/V *Siboga*, holotype ZMA 112.462].

Chiasmodon braueri de Beaufort and Chapman 1951: 9–10 [records of fishes from Australia]; Johnson and Keene (1990) [records of holotype and one questionable specimen from eastern North Atlantic].

Chiasmodon niger (not Johnson) Mooi and Paxton 2001: 3496 [list of species in the western Central Pacific]; Matsuda et al. 1984: 221 [questionable, list of species from

Japan].

Chiasmodon subniger (not Garman) Mooi and Paxton 2001: 3496 [list of species in the western Central Pacific].

Diagnosis. *Chiasmodon braueri* can be diagnosed from its congeners by a unique characteristic: teeth on second ceratobranchial three to 16 (vs. teeth absent). It further differs from *C. harteli* by total vertebrae 42–44 (vs. total vertebrae 47–48); from *C. microcephalus* and *C. subniger* by teeth present on second and third basibranchials, four to 11 (vs. teeth on basibranchial absent, rarely one to three on second basibranchial); from *C. subniger*, by infraorbital pores 13-15, modally 14, infraorbital 1 pores seven to eight (vs. infraorbital pores 11–13, infraorbital 1 pores five to six), snout elongate and pointed (vs. snout blunt), upper jaw 70.0–77.1 % HL (vs. 63.9–72.7 % HL); lower jaw 76.0–83.8 % HL (vs. 69.9–76.7 % HL); from *C. harteli*, *C. niger* and *C. microcephalus* by supraorbital pores eight (vs. six to seven); from *C. pluriradiatus* and *C. asper*, by pectoral-fin rays 12–13 (vs. 15–16); tiny dermal spinules on body of specimens larger than 35.8 mm absent (vs. spinules present), fang on premaxillary head one (vs. two).

Description. Largest specimen examined 183.9 mm. Morphometric data summarized in table 2.3. General body pattern as described for genus. Skin naked; dermal spinules absent in individuals larger than 35.8 mm SL.

First dorsal-fin rays IX (1), X (11), XI (4*); second dorsal-fin rays iii+22 (1), iii+24 (3*), iii+25 (7), iv+25 (3), iii+26 (1), iv+26 (1); anal-fin rays iv+17 (1), iv+23 (4*), iv+24 (5), iv+25 (3), v+25 (2), iv+26 (1); pectoral-fin rays 12 (1), 13 (15*); pelvic-fin rays I+5 (16*); caudal-fin rays i+7+8+i (14), i+8+7+i (2*). Branchiostegal rays 7 (16).

Pre-caudal vertebrae 20 (3*), 21 (4); total vertebrae 42 (2), 43 (3*), 44 (3).

Lateral line complete, pore counts summarized in table 2.1. Sensory system of head as illustrated in figure 2.2. Pores in temporal canal 2 (16*); supratemporal canal 3 (16*); otic canal 2 (16*); supraorbital canal 8 (16*); epiphyseal branch 2 (2*), 3 (8), 4 (6); infraorbital canal 13 (2), 14 (13), 15 (1); preopercular canal 5 (16*); mandibular canal 6 (16*); fourth pore of mandibular canal 2 (16*); fifth pore of mandibular canal 1 (4), 2 (12*).

Dentition. Teeth present on premaxilla, dentary, palatine, second and, often, third basibranchial, upper and lower pharyngobranchials, second hypobranchial and second ceratobranchial; absent on remaining branchial elements. Ventral elements of gill arches illustrated in figure 2.3; premaxilla, in figure 2.4. Teeth on premaxilla: canine 1 (16), at anterior tip of head; accessory anterior teeth 1–2 (14, mode = 1), lateral to canine; fang 1 (16), at ventral part of head; lateral series 20–41 (16, mode = 27), equally spaced between neck and posterior tip of caudal process; mesial series 4–7 (16, mode = 4), at medial shelf of body. Teeth on dentary: lateral series 15–32 (16, mode = 21), teeth at anterior edge 1–2 (15, mode = 1), canine 1 (16), diastema, remaining teeth uniformly distributed between diastema and posterior tip of dentary; mesial series 9–16 (15, mode = 9), first and second anteriormost teeth developed as fangs. Palatine teeth 5–12 (15, mode = 9). Teeth on second and third basibranchials 4–11 (16, mode = 9), individually attached to bone or in small plates of two to three teeth. Teeth present on second arch, hypobranchial teeth 3–9 (16, mode = 7), ceratobranchial teeth 3–16 (16, mode = 6).

Distribution. Throughout the tropical and temperate regions of the Pacific plate, western Pacific from 31° N to 8° S; 119° E to 136° W; in both sides of the Indian Ocean, in the Indo-Pacific, 122° E, and off eastern Africa, 39° E, from 5° to 8° S; and in the Atlantic, off eastern South America, 13° to 21° S, around 39° W (Fig. 2.5).

Bathymetric distribution. Meso- to bathypelagic zones, from 150 to 2326 m (mean 1189 m).

Remarks. *Chiasmodon braueri* was diagnosed by Weber (1913) as having nine pectoral-fin rays, a character that was used by some authors (Norman 1929; de Beaufort and Chapmann 1951). Johnson and Keene (1990: 890) noticed that the holotype of *C. braueri* actually has more pectoral-fin rays than previously reported and listed 12 rays. The holotype is a very delicate, bleached specimen, making fin-ray counts difficult, but there are in fact 13 pectoral-fin rays. The species is being validated herein by the presence of a novel characteristic: the presence of teeth on the second ceratobranchial.

Chiasmodon microcephalus Norman 1929

Figure 2.9, Tables 2.1 and 2.4

Chiasmodon microcephalus Norman 1929: 539–540, figure 8 [type by original designation, type locality western South Atlantic, 39°50’30” S, 36°23’00” W, 0–1500 m, 5–VI–1926, R.R.S. *Discovery*; holotype BMNH 1930.1.12.1060].

Diagnosis. *Chiasmodon microcephalus* can be diagnosed from its congeners by a combination of characteristics: from *C. niger* and *C. braueri* by teeth on basibranchials frequently absent, if present two to three small, restricted to second basibranchial, absent on other gill elements (vs. teeth on second basibranchial always present and enlarged, often present on third basibranchial and second hypobranchial, three to 18; teeth on second ceratobranchial present in *C. braueri*); from *C. harteli* by the total vertebrae 43–45 (vs. total vertebrae 47–48); from *C. pluriradiatus* and *C. asper* by pectoral-fin rays 12–14 (vs. 15–16), tiny dermal spinules on body of specimens larger than 35.1 mm absent (vs. spinules present), fang on premaxillary head one (vs. two); from *C. subniger*, by infraorbital pores usually 13–14, rarely 11 or 12, infraorbital 1 pores seven to eight (vs. infraorbital pores 11–13, infraorbital 1 pores five to six), snout elongate and pointed, 23.7–28.0 % HL (vs. snout short and blunt, 21.4–23.9 % HL), upper jaw 69.3–77.7 % HL (vs. 63.9–72.7 % HL); and lower jaw 76.8–85.2 % HL (vs. 69.0–76.7 % HL). *Chiasmodon microcephalus* further differs from other species by supraorbital pores seven (vs. six in *C. harteli*, eight in *C. braueri* and *C. pluriradiatus*, and nine in *C. asper*).

Description. Largest specimen examined 225.5 mm. Morphometric data summarized in table 2.4. General body pattern as described for the genus. Skin naked; dermal spinules absent in individuals larger than 35.1 mm SL.

First dorsal-fin rays X (8), XI (14*), XII (5); second dorsal-fin rays iv+21 (1), iv+22 (2), v+22 (2), i+25 (1), iii+23 (9*), iv+23 (1), iii+24 (3), iv+24 (2), iii+25 (4), iii+26 (1), viii+19 (1); anal-fin rays v+15 (1) , iii+20 (1), iv+20 (1), iii+22 (2), iv+22 (2), iv+23 (9), v+23 (1), iii+24 (3), vi+ 22 (1*), iv+24 (2), vi+23 (1), iii+25 (1), iv+25 (2); pectoral-fin rays 12 (9), 13 (17*), 14 (1); pelvic-fin rays I+5 (27*); caudal-fin rays i+7+6+i (1), i+7+7+i (4), i+7+8+i (18*), i+8+7+i (1), i+8+8+i (2). Branchiostegal rays 6 (2), 7 (21*). Pre-caudal vertebrae 19 (2), 20 (2*), 21 (7), 22 (1); total vertebrae 44 (1), 45 (7*), 46 (6).

Lateral line complete, pore counts summarized in table 2.1. Sensory system of head as illustrated in figure 2.2. Pores in temporal canal 2 (27*); supratemporal canal 3 (27*); otic canal 2 (27*); supraorbital canal 7 (26*), 8 (1); epiphyseal branch 2 (1), 3 (16*), 4 (10); infraorbital canal 11 (1), 12 (2), 13 (8*), 14 (16); preopercular canal 5 (27*); mandibular canal 6 (27*); fourth pore of mandibular canal 2 (27*); fifth pore of mandibular canal 1 (23*), 2 (4).

Dentition. Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials, rarely on second basibranchial; absent on other branchial elements. Ventral elements of gill arches illustrated in figure 2.3; premaxilla, in figure 2.4. Teeth on premaxilla: canine 1 (22), at anterior tip of head; accessory anterior teeth 1–2 (22, mode = 1), lateral to canine; fang 1 (22), at ventral part of head; lateral series 9–22 (21, mode = 15), equally spaced between neck and posterior tip of caudal process; mesial series 1–6 (10, mode = 3), at medial shelf of body. Teeth on dentary: lateral series 8–19 (21, mode = 10), teeth at anterior edge 1–3 (21, mode = 1), canine 1 (21), diastema, remaining teeth uniformly distributed between diastema and posterior tip of dentary; mesial series 3–10 (21, mode = 6), first and second anteriormost teeth developed as fangs. Palatine teeth 3–9 (22 mode = 6). Teeth on second basibranchial often absent, 0–3 (22, mode = 0).

Distribution. Circumglobal in the southern parts of the Atlantic, Indian and Pacific, and the Southern Ocean; from 32° S to 54° S (Fig. 2.5).

Bathymetric distribution. Meso- to bathypelagic zones, from 150 to 2500 m (mean 1062 m).

Remarks. Norman (1929: 540) listed four specimens between 48.0 and 115.0 mm in total length and selected the largest as holotype. Only three specimens were found at the BMNH collection, being the largest 99.1 mm SL and probably the same specimen selected as holotype.

Chiasmodon pluriradiatus Parr 1933

Figure 2.10, Tables 2.2 and 2.4

Chiasmodon niger pluriradiatus Parr 1933: 34 [type by original designation, type locality Bahamas, 23°48’ N, 76°58’ W, 9–III–1927, R/V *Pawnee*, holotype YPM 2827]. New status.

Chiasmodon lavenbergi Prokofiev, 2008: 209–213, figure 1 [in part, type by original designation, type locality Coral Sea, 25°57’00” S, 162°06’00” E, 1240 m, R/V *Mys Tikhii*, holotype ZMMU 21661]. New Synonym.

Diagnosis. *Chiasmodon pluriradiatus* can be distinguished from all species of *Chiasmodon* except *C. asper* by pectoral-fin rays 15–16 (vs. 12–14); fangs on premaxillary head two (vs. one); tiny dermal spinules on body of specimens larger than 48.7 mm present (vs. spinules absent). It differs from *C. asper* by supraorbital canal pores eight (vs. nine).

Description. Largest specimen examined 220.8 mm. Morphometric data summarized in table 2.4. General body pattern as described for genus. Skin covered with dermal spinules in adults, more dense in juveniles and spaced in larger specimens.

First dorsal-fin rays IX (1), X (2), XI (4*); second dorsal-fin rays iv+23 (2), iv+24 (3*), iii+25 (1), v+24 (1); anal-fin rays iv+22 (2), iii+23 (1), iv+23 (1), iv+24 (2*), iv+25 (1); pectoral-fin rays 15 (5), 16 (2*); pelvic-fin rays I+5 (7*); caudal-fin rays i+6+7+i

(1*), i+7+7+i (3), i+7+8+i (3). Branchiostegal rays 7 (7). Pre-caudal vertebrae 21 (1), 23 (1); total vertebrae 44 (1), 45 (1).

Lateral line complete, pore counts summarized in table 2.1. Sensory system of head as illustrated in figure 2.2. Pores in temporal canal 2 (7*); supratemporal canal 3 (7*); otic canal 2 (7*); supraorbital canal 8 (7*); epiphyseal branch 2 (2*), 3 (2), 4 (4); infraorbital canal 13 (3*), 14 (4); preopercular canal 5 (7*); mandibular canal 6 (7*); fourth pore of mandibular canal 2 (6*), 3 (1); fifth pore of mandibular canal 1 (1), 2 (6*).

Dentition. Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials; often absent on second basibranchial; absent on remaining branchial elements. Ventral elements of gill arches illustrated in figure 2.3; premaxilla, in figure 2.4. Teeth on premaxilla: canine 1 (7), at anterior tip of head; accessory anterior teeth 1 (7), lateral to canine; fangs 2 (7), at ventral part of head; lateral series 12–29 (7, median = 17), equally spaced between neck and posterior tip of caudal process; mesial series 1–2 (7, mode = 1). Teeth on dentary: lateral series 11–19 (7, mode = 14), teeth at anterior edge 1 (7), canine 1 (7), diastema, remaining teeth uniformly distributed between diastema and posterior tip of dentary; mesial series 2–8 (7, mode = 8), first and second anteriormost teeth developed as fangs. Palatine teeth 4–13 (7, mode = 4). Teeth on second basibranchial 0–8 (7, mode = 0).

Distribution. Widely distributed in the tropical Atlantic, including the Eastern islands of Gulf of Mexico, from 32° N to 11° S, 20° W to 77° W; in the western Indian from 12° S to 32° S, 60° E to 58° E; and in the southern part of western Pacific and Pacific Plate, from 25° S to 38° S, 167° W to 179° E (Fig. 2.5).

Bathymetric distribution. Meso- to bathypelagic zones, from 230 to 1600 m (mean 969 m); adults more frequently collected below 900 m.

Remarks. Prokofiev (2008: 211) diagnosed *C. lavenbergi* by three characteristics: "dermal spinelets in adult fishes, fixed teeth in jaws, as a rule, without gill rakers and basibranchial teeth in adult fishes." The presence of spinules on the skin of *Chiasmodon* is not restricted to a single species, as Prokofiev (2008) suggested, but the spinules are present in adults of *C. pluriradiatus* and *C. asper* and the juveniles of all species. The first to notice the presence of spinules on body was made by Garman (1899) during the description of *C. subniger*; unfortunately Prokofiev (2008) did not provide any discussion about that, and failed to identify this character in the types of *C. pluriradiatus*. Further discussion on the status of *C. subniger* is given in this species' account.

The presence of "fixed teeth as a rule" is controversial. Prokofiev (2008) does not make a proper distinction between the type of tooth attachment. All species of *Chiasmodon* have type 1 and 4 teeth in the lateral rows of premaxilla and dentary. The type 4 teeth of lateral series are not as mobile as those of mesial series, especially the fangs, but the type of attachment is obvious when a specimen is cleared and stained. All species also possess a canine in both premaxilla and dentary, which are actually the only fixed teeth, ankylosed to the bone, on those elements.

Regarding the gill rakers, they are absent in chiasmodontids (pers. obs.). Finally, Prokofiev's (2008) use of the absence of basibranchial teeth in adults is improper, because of two specimens with 137.0 and 138.0 mm described to have teeth on basibranchials (p. 212). This agrees with the results presented herein, that teeth may be present or not in the second basibranchial of *C. pluriradiatus* and *C. asper*. *Chiasmodon subniger* also lacks teeth on basibranchials, and this is a variable characteristic in *C.*

microcephalus.

The range of supraorbital pores listed by Prokofiev (2008) suggests that both *C. asper* and *C. pluriradiatus* were listed in the type series of *C. lavenbergi*. Based on the wide distribution of *C. pluriradiatus* in the Atlantic, Indian and South Pacific, a topotype (BMNH 1997.5.21.28), and the lack of evidence that *C. asper* occurs in the South Pacific, *C. lavenbergi* is being considered a junior synonym of *C. pluriradiatus*.

Chiasmodon asper, new species

Figure 2.11, Tables 2.1 and 2.5

Chiasmodon lavenbergi Prokofiev 2008: 209–213 [in part].

Holotype. SIO 68–483–60, 1, 65.2 mm, eastern North Pacific, Pacific Plate, 25°46' N, 178°19' E, 19–IX–1968, R/V *Alexander Agassiz*.

Paratypes. *Pacific Plate:* HUMZ 143753, 1, 87.6 mm, Hawaiian islands, 5691 m, 12–II–1996; HUMZ 143630, 1, 83.7 mm, 5154 m, 8–II–1996; SIO 68–447, 1, 47.2 mm, 19°17' N, 168°35' W, 29–VIII–1968, R/V *Alexander Agassiz*; SIO 97–83, 1, 60.5 mm, 24°00' N, 145°00' W, midwater trawl, 0–1000 m of wire, depth of water 5300, 22–V–1972, R/V *David Starr Jordan*; SIO 73–338–60, 1, 178.6 mm, 28°23' N, 155°29' W, 11/12–VII–1973, R/V *Thomas Washington*; FMNH 88158, 1, 41.5 mm, 21º23' N, 158º18' W, 22–VI–1971, R. E. Young col.

Non-type specimens. *Pacific Plate:* LACM 36471, 1, 36.4, 31º06' N, 135º13' W, 0–450 m, 14–IV–1966, UCSB *Swan*; LACM 36432–9, 1, 21.1 mm, 25º48' N, 148º39'

W, 0–250 m, 10–IV–1966, UCSB *Swan*; LACM 36428–1, 1, ca. 30.0 mm, 25º40’ N, 148º58’ W, 0–450 m, 10–IV–1966, UCSB *Swan*; SIO 74–51, 2, 39.8–40.9 mm, 28º20’ N, 158º51’ W, 0–180 m, 4–III–1974, R/V *Thomas Washington*; FMNH 88155, 1, 43.2 mm, 21º23’ N, 158º18’ W, 18–III–1971, R. E. Young col.; FMNH 88156, 1, 41.1 mm, 21º23’ N, 158º18’ W, 1–VII–1972, R. E. Young col.; FMNH 88159, 1, 41.8 mm, 21º23’ N, 158º18’ W, 23–VI–1971, R. E. Young col.; SAIAB 31282, 1, 69.4 mm, 27º24’ N, 155º13’ W, 30–IX–1971, R. McGowan col.

Diagnosis. *Chiasmodon asper* can be diagnosed from its congeners by a single unique characteristic: supraorbital pores nine (vs. six in *C. harteli*; seven in *C. braueri*, *C. niger*, and *C. subniger*; eight in *C. pluriradiatus*). It further differs from all species except *C. pluriradiatus* by pectoral-fin rays 15–16 (vs. 13–14); tiny dermal spinules on body in specimens larger than 48.7 mm present (vs. spinules absent); fangs on premaxillary head two (vs. one).

Description. Largest specimen 178.6 mm. Morphometric data summarized in table 2.5. General body pattern as described for genus. Skin covered with dermal spinules in adults, more dense in juveniles and spaced in larger specimens.

First dorsal-fin rays X (2), XI (2*), XII (1); second dorsal-fin rays iv+23 (1), iv+24 (1), iii+25 (1), iv+25 (2*); anal-fin rays iv+22 (1), iii+24 (1), iv+24 (1), v+23 (1*) iv+26 (1); pectoral-fin rays 15 (5*); pelvic-fin rays I+5 (5*); caudal-fin rays i+7+8+i (5*). Branchiostegal rays 7 (5*). Pre-caudal vertebrae 20 (3*), 21 (2), 22 (1); total vertebrae 44 (3*), 45 (2), 46 (1).

Lateral line continuous, as summarized in table 2.1. Sensory system of head as illustrated in figure 2.2. Pores in temporal canal 2 (5*); supratemporal canal 3 (5*); otic canal 2 (5*); supraorbital canal 9 (5*); epiphyseal branch 4 (5*); infraorbital canal 13 (1), 14 (4*); preopercular canal 5 (5*); mandibular canal 6 (5*); fourth pore of mandibular canal 2 (5*); fifth pore of mandibular canal 2 (4*), 3 (1).

Dentition. Teeth present on premaxilla, dentary, palatine, second and third basibranchials, second hypobranchial, upper and lower pharyngobranchials, rarely present on second ceratobranchial; sometimes absent on third basibranchial; absent on other branchial elements. Ventral elements of gill arches illustrated in figure 2.3; premaxilla, in figure 2.4. Teeth on premaxilla: canine 1 (5), at anterior tip of head; accessory anterior tooth 1 (5), lateral to canine; fangs 2 (5), at ventral part of head; lateral series 15–19 (5, mode = 19), equally spaced between neck and posterior tip of caudal process; mesial series 1 (5), at medial shelf of body. Teeth on dentary: lateral series 9–14 (5, mode = 9), teeth at anterior edge 1–2 (5, mode = 1), canine 1 (5), diastema, remaining teeth uniformly distributed between diastema and posterior tip of dentary; mesial series 5–6 (5, mode = 5), first and second anteriormost teeth developed as fangs. Palatine teeth 4–6 (5, mode = 4). Second basibranchial teeth 0–3 (5, median = 1), individually attached to bone.

Distribution. Pacific plate, north of Hawaii; from 135° W to 178° E, 19°30’ N to 31° S (Fig. 2.5).

Bathymetric distribution. Meso- to bathypelagic zones. Juveniles are known from 180–450 m, while adults are know from greater depths, 5154–5691 m (mean 5423 m).

Etymology. From the Latin *asper*, means asperous, rough; in a reference to its rough skin due to the presence of minute prickles in the juveniles and adults.

Chiasmodon harteli, new species

Figure 2.12, Tables 2.1 and 2.5

Chiasmodon bolangeri (not Osorio) Shinohara and Okamura 1995:218 [checklist of fishes from Greenland].

Holotype. BSKU 48914, 1, 135.5 mm, Greenland, western North Atlantic, Subartic, 64°31' N, 55°30' W, 967 m, 9–VI–1989, R/V *Shinkai-Maru*.

Paratypes. Atlantic, Subartic: BSKU 46298, 1, 146.9 mm, 65°27' N, 31°10' W, 495 m, 24–VII–1988, R/V *Shinkai-Maru*; BSKU 47582, 1, 138.4 mm, 63°26' N, 53°58' W, 495 m, 24–VII–1988, R/V *Shinkai-Maru*; BSKU 47627, 1, 172.0 mm, 63°47' N, 57°29' W, 1303 m, 3–X–1988, R/V *Shinkai-Maru*; BSKU 48749, 1, 145.4 mm, 65°29' N, 55°18' W, 547 m, 3–IV–1989, R/V *Shinkai-Maru*; BSKU 48752, 1, 190.6 mm, 65°29' N, 55°18' W, 547 m, 3–IV–1989, R/V *Shinkai-Maru*; BSKU 48912, 1, 152.5 mm, 64°22' N, 55°22' W, 1038 m, 8–VI–1989, R/V *Shinkai-Maru*; BSKU 48915, 1, 145.9 mm, 64°32' N, 55°28' W, 947 m, 9–VI–1989, R/V *Shinkai-Maru*; BSKU 48916, 1, 164.6 mm, 64°31' N, 55°33' W, 983 m, 10–VI–1989, R/V *Shinkai-Maru*; BSKU 48920, 1, 198.3 mm, 64°31' N, 55°35' W, 985 m, 11–VI–1989, R/V *Shinkai-Maru*; BSKU 48921, 1, 166.4 mm, 64°31' N, 55°35' W, 985 m, 11–VI–1989, R/V *Shinkai-Maru*; BSKU 80997, 1, 108.1 mm, 67°08' N, 56°37' W, 700 m, 19–VIII–1992, R/V *Shinkai-Maru*; BSKU 81044, 1, 127.3 mm, 67°18' N, 57°04' W, 750 m, 19–VIII–1992, R/V *Shinkai-Maru*; BSKU 81045, 1, 131.9 mm, 67°18' N, 57°04' W, 750 m, 19–VIII–1992, R/V *Shinkai-*

Maru; BSKU 81120, 1, 173.0 mm, 64°31' N, 55°35' W, 985 m, 11–VI–1992, R/V *Shinkai-Maru*; BSKU 81204~81207, 4, 127.3–144.7 mm, 63°53' N, 57°36' W, 1130 m, 19–VIII–1992, R/V *Shinkai-Maru*; BSKU 81228, 1, 136.8 mm, 63°56' N, 57°36' W, 1130 m, 19–VIII–1992, R/V *Shinkai-Maru*; HUMZ 118608, 1, 173.6 mm, 63°24' N, 54°45' W, 1146 m, 25–VI–1990, col. unknown; HUMZ 118959, 1, 179.7 mm, no data; HUMZ 118960, 1, 159.6 mm, Atlantic; HUMZ 118976, 1, 133.3 mm, 64°10' N, 54°43' W, 944 m, 16–IX–1990, col. unknown; HUMZ 119100, 1, 154.1 mm, 64°02' N, 54°35' W, 720 m, 16–IX–1990, col. unknown; HUMZ 119172, 1, 126.6 mm, 65°20' N, 55°10' W, 583 m, 6–IX–1990, col. unknown; HUMZ 124407, 1, 117.2 mm, 63°47' N, 55°19' W, 1273 m, 14–VIII–1992, col. unknown; HMUZ 124432, 1, 145.8 mm, 63°55' N, 56°04' W, 879 m, 18–VIII–1992, col. unknown; HUMZ 124466, 2, 136.1–138.6 mm, 64°07' N, 53°59' W, 740 m, 15–VII–1992, col. unknown; HUMZ 124499, 1, 170.9 mm, 64°56' N, 57°07' W, 765 m, 20–VIII–1992, col. unknown; HUMZ 124524, 1, 135.5 mm, 63°41' N, 57°26' W, 1417 m, 13–VIII–1992, col. unknown; HUMZ 126501, 1, 158.1 mm, Greenland, 12–I–1992; col. unknown; HUMZ 125643, 1, 121.7 mm, Greenland, 12–III–1992; col. unknown; ZMUC P. 6589, 1, 45.6 mm, collected with ZUMC P. 6588; ZMUC P. 6597, 1, 148.8 mm, 65°00' N, 30°00' W, 190–270 m, 15–IV–1989, R/V *E Quits*; ZMUC P. 6598, 1, 188.2 mm, collected with ZMUC P. 6597; ZMUC P. 65101, 1,180.9 mm, 66°00' N, 30°00' W, IV–1991, R/V *Tasiilaq*; ZMUC P. ZMUC P. 65102, 1, 122.1 mm, 65°13' N, 55°41' W, 804 m, 13–IX–1988, R/V *Shinkai-Maru*; ZMUC P. 65103, 1, 175.5 mm, 64°52' N, 57°15' W, 787–793 m, 28–IX–1988, R/V *Shinkai-Maru*; ZMUC P. 65104, 1, 149.9 mm, 64°22' N, 55°58' W, 964–961 m, 29–IX–1988, R/V *Shinkai-Maru*; ZMUC P. 65105, 1, 130.0 mm, 64°22' N, 56°42' W, 764–733 m, 29–IX–

1988, R/V *Shinkai-Maru*; ZMUC P. 65106, 1, 114.5 mm, collected with ZMUC P. 65106; ZMUC P. 65107, 1, 177.3 mm, 64°06' N, 55°49' W, 962–959 m, 2–X–1988, R/V *Shinkai-Maru*; ZMUC P. 65108, 1, 123.7 mm, 64°41' N, 55°43' W, 948–947 m, 1–V–1989, R/V *Shinkai-Maru*; ZMUC P. 65142, 1, 109.3 mm, 63°55' N, 57°35' W, 19–VIII–1992, R/V *Shinkai-Maru*; ZMUC P. 65143, 1, 96.9 mm, 63°20' N, 10°27' W, 1–V–1993, R/V *Magnus Heinason*; ZMUC P. 65151, 1, 156.2 mm, 64°03' N, 55°33' W, 1071–1077 m, 27–VIII–1983, R/V *Shinkai-Maru*; ZMUC P. 65152, 1, 142.3 mm, collected with ZMUC P. 65151; ZMUC P. 65166, 1, 127.9 mm, 64°27' N, 56°08' W, 30–XI–1992, R/V *Shinkai-Maru*; ZMUC P. 65167, 1, 136.9 mm, 65°08' N, 55°40' W, 25–XI–1992, R/V *Shinkai-Maru*; ZMUC P. 6588, 1, 43.8 mm, unknown locality. Slope Water: MCZ 65530, 1 (cs) aprox. 40.0 mm, 38°53' N, 71°47' W, 800–992 m, 7–VIII–1982, R/V *Oceanus*; MCZ 69698, 1, 68.8 mm, 39°27' N, 71°08' W, 1–V–1982, R/V *Oceanus*; MCZ 69739, 1, 43.4 mm, 38°48' N, 71°44' W, 30–IV–1972, R/V *Oceanus*; MCZ 163434, 3 of 4, 60.5–74.3 mm, 40°00' N, 67°23' W, 15–V–2003, R/V *Delaware*; MCZ 163437, 4, 26.3–164.5 mm, 39°56' N, 67°36' W, 18–V–2003, R/V *Delaware*; MCZ 164280, 3, 63.5–81.2 mm, 39°55' N, 67°19' W, 0–1081 m, 5–VI–2005, R/V *Delaware II*; MCZ 69693, 1, 88.5 mm, 39°33' N, 70°56' W, 0–1200 m, 1–II–1973, R/V *Chain*. Azores–Britain Province: ZMUC P. 6591, 1, 106.2 mm, 43°21' N, 25°58' W, 9–VI–1982, R/V *Walter Herwig*; ZMUC P. 6592, 1, 120.0 mm, collected with ZMUC P. 6591; ZMUC P. 6593, 1, 93.8 mm, 45°40' N, 27°48' W, 11–VI–1982, *R/V Walter Herwig*; ZMUC P. 6594, 1, 67.4 mm, collected with ZMUC P. 6593; ZMUC P. 6595, 1, 56.5 mm, collected with ZMUC P. 6593. North African Subtropical Sea: BMNH 2002.11.22.66, 1, 46.3 mm, 35°01' N, 33°00' W, 13–VI–1981, Institute of Oceanographic Sciences, col.

Diagnosis. *Chiasmodon harteli* can be diagnosed from its congeners by total vertebrae 47–48 (vs. 42–46), and supraorbital pores six (vs. seven or eight). It further differs from *C. braueri*, by teeth on the second ceratobranchial absent (vs. present); from *C. microcephalus* by teeth on second basibranchial three to 18, rarely two, often present on second hypobranchial (vs. teeth on second basibranchial usually absent, rarely one to three); from *C. niger* by lateral-line pores 89–95 (vs. 86–90); from *C. pluriradiatus* and *C. asper* by pectoral-fin rays13–14 (vs. 15–16); tiny dermal spinules on body in specimens larger than 48.7 mm absent (vs. spinules present), fang on premaxillary head one (vs. two), supraorbital pores seven (vs. eight in *C. pluriradiatus*, and nine in *C. asper*); and from *C. subniger* by infraorbital pores 13–16, usually 14, infraorbital 1 pores seven to eight (vs. infraorbital pores 11–13, infraorbital 1 pores five to six), snout elongate and pointed, 23.0–26.6 % HL (vs. snout short and blunt, 21.4–23.9 % HL), upper jaw 74.3–84.2 % HL (vs. 63.9–72.7 % HL); lower jaw 80.8–89.9 % HL (vs. 69.0–76.7% HL), and lateral-line pores 90–95 (vs. 75–87).

Description. Largest specimen 198.3 mm. Morphometric data summarized in table 2.5. General body pattern as described for genus. Skin naked; dermal spinules absent in individuals larger than 56.5 mm SL.

First dorsal-fin rays X (2), XI (15*), XII (6), XIII (1); second dorsal-fin rays iv+23 (2*), iii+24 (3), iv+24 (3), iii+25 (6), iv+25 (2), iii+26 (7), iii+27 (1); anal-fin rays iv+21 (1), iii+23 (1), v+22 (1*), iv+23 (2), iv+24 (1), iii+25 (2), v+24 (4), iv+25 (5), v+25 (1), iv+26 (2), v+26 (2), iv+27 (1), iv+28 (1); pectoral-fin rays 12 (3), 13 (18), 14 (3*); pelvic-fin rays I+5 (24*); caudal-fin rays i+8+7+i (3), i+7+8+i (21*). Branchiostegal rays 7 (24*). Pre-caudal vertebrae 21 (15), 22 (15); total vertebrae 47

(22), 48 (12).

Lateral line continuous, as summarized in table 2.1. Sensory system of head as illustrated in figure 2.2. Pores in temporal canal 2 (24*); supratemporal canal 3 (24*); otic canal 2 (24*); supraorbital canal 6 (24*); epiphyseal branch 2 (8), 3 (16*); infraorbital canal 13 (2*), 14 (19), 15 (2), 16 (1); preopercular canal 5 (24*); mandibular canal 6 (24*); fourth pore of mandibular canal 1 (5), 2 (18*); fifth pore of mandibular canal 1 (21*), 2 (2).

Dentition. Teeth present on premaxilla, dentary, palatine, second basibranchial, upper and lower pharyngobranchials; absent on remaining branchial elements. Ventral elements of gill arches illustrated in figure 2.3; premaxilla, in figure 2.4. Teeth on premaxilla: canine 1 (22), at anterior tip of head; accessory anterior teeth 0–1 (22, mode = 1), lateral to canine; fang 1 (22), at ventral part of head; lateral series 13–27 (22, mode = 23), equally spaced between neck and posterior tip of caudal process; mesial series 1 (22), at medial shelf of body. Teeth on dentary: lateral series 13–28 (21, mode = 16), teeth at anterior edge 1–3 (21, mode = 2), canine 1 (22), diastema, remaining teeth uniformly distributed between diastema and posterior tip of dentary; mesial series 6–10 (21, mode = 7), first and second anteriormost teeth developed as fangs. Palatine teeth 2–7 (22, mode = 7). Teeth on second basibranchial rarely absent, 0–13 (24, mode = 4).

Distribution. Eastern and western North Atlantic, from 11°' W to 40° W, 35° N to 37°50' N (Fig. 2.5).

Bathymetric distribution. Meso- to bathypelagic zones, between 495 and 1417 m (mean 910 m).

Etymology. This species is named in honor of Karsten Hartel (MCZ) in recognition of his lifetime contribution to ichthyology, in particular to the comprehension of deep-sea fish fauna.

Discussion

Based on general characters, the species of *Chiasmodon* can be divided into two taxonomic groups: *C. pluriradiatus* group and *C. niger* group. Sympatry is observed between those two groups; however, there is a well-defined and disjunct pattern of distribution among the species within each group. The *Chiasmodon pluriradiatus* group includes two species, *C. pluriradiatus* and *C. asper*, and is diagnosed by the adults having tiny dermal spinules on body (vs. body naked), the presence of two fangs on the premaxillary head (vs. one), and the pectoral fin with 15–16 rays (vs. 12–14). *Chiasmodon pluriradiatus* occurs sympatrically with *C. niger* throughout the tropical Atlantic, *C. microcephalus* in the Indian and south western Pacific, and *C. braueri* in the southern Pacific Plate; and *C. asper* slightly overlaps with *C. braueri* and *C. subniger*, in both cases around the Hawaiian Islands. Besides the overlap in geographical distribution, the *C. pluriradiatus* group apparently occurs at greater depths than the *C. niger* group. Within the *C. pluriradiatus* group, species differ by the number of supraorbital pores (eight in *C. pluriradiatus* vs. nine in *C. asper*) and no range overlap was observed.

The *Chiasmodon niger* group is composed of five species, externally very similar, but with conspicuous differences in dentition and vertebral count: *C. niger*, *C. braueri*, *C. microcephalus*, and *C. harteli*. *Chiasmodon harteli* in the temperate North Atlantic and its distribution slightly overlaps slightly with *C. niger* between 35° and 45° N, and they were collected together at the Slope Water in the western North Atlantic. *Chiasmodon* *niger* is widely distributed in the tropical and temperate North Atlantic; *C. subniger* is a distinctive species endemic to the eastern Pacific; *C. braueri* is widely distributed in the tropical Pacific, and is recorded from both sides of the Indian Ocean, and four lots from the western South Atlantic, off the southern coast of South America. Ranges of *C. braueri* and *C. subniger* overlap in the Pacific between 155° and 133° W, being the two species even collected together (SIO 60–229–72). *Chiasmodon microcephalus* is distributed in the Southern regions of the Atlantic, Indian, Pacific Oceans, and the northern part of the Southern Ocean, between 28° and 54° S; its range overlaps with *C. braueri* in the western South Atlantic.

Identification of juveniles. Juveniles of *Chiasmodon* are very easy recognized because of their external resemblance with adults, especially on the general body shape and dentition. To species level, however, the identification can de difficult, because of the presence of presence of spinules, reduced size of pores in sensory system of head and differences in the color pattern. They can be tentatively identified based on fin-rays counts, characteristics of dentition on the premaxilla and gill arches.

Unidentified specimen. A single specimen of *Chiasmodon* obtained from the Bermudas (USNM 254372, 1, 270.0 mm, 32°10' N, 63°53' W, 0–760 m, 21–X–1971, Ocean Acre Expeditions) does not fit on the diagnostic characteristics given above for the species on the Atlantic Ocean: it lacks dermal spinules; teeth on basihyal, basibranchials and gill arches are also absent; dentition is in poor condition and some teeth are being replaced, therefore a precise count of fangs is not possible; the total vertebrae is 44, precaudal, 20. Moreover, this is the largest specimen of *Chiasmodon* examined during this work. For now, although it seems to be very distinctive from other species found in the western North Atlantic, I prefer to regard to it as *Chiasmodon* sp., and will eventually describe the species, if more material or additional morphological characteristics becomes available.

The status of *Ponerodon vastator*. The validity of *Ponerodon vastator* as a genus or species is the topic of some debate. Norman (1929) was the first to consider *Ponerodon vastator* a junior synonym of *Chiasmodon niger* and was followed by subsequent authors (Norman 1966; Krefft 1973; Johnson and Keene 1986, 1990). This hypothesis can be rejected due to the distribution of *C. niger* versus the type locality of *P. vastator* in the Indian Ocean. Moreover, it is not clear whether or not any author mentioned above examined the holotype of *Ponerodon vastator*, or based their works on the species' general body shape according to the illustration published in the original description.

The holotype of *Ponerodon vastator* was obtained off India, in the Bay of Bengal, 15°38' N, 82°30' E, 690–920 fathoms (1262–1683 m), 4–I–1890, R/V Investigator Sta. 102. The specimen was listed by Menon and Rama-Rao (1975: 40), but recent efforts to examine it have failed and there is a concern that the specimen has been permanently lost (Shobnon Ferdous, pers. comm. 2006; Naomi Delventhal, pers. comm. 2007). Additionally, very little material is available from the Indian Ocean, particularly from the off the coast of Asia.

Alcock's (1890: 204–205) description of *Ponerodon vastator* mixes characteristics of both *Chiasmodon* and *Kali parri*, and some others that do not match any chiasmodontid species known to date. The illustration provided is inaccurate, and does not depict *Kali parri* neither any species of *Chiasmodon*. Alcock (1890) diagnosed the specimen as a chiasmodontid based on the following characteristics: "V. [pelvic-fin rays] 1/5" (p. 203), "interorbital space (…) transversed by two anteriorly-converging ridges which enclose a V-shaped groove" (p. 204); "cleft of mouth extremely wide" (p. 203), "cleft of mouth oblique, extremely wide, its angle nearly reaching the preopercular angle; the maxilla (…) is almost three fourths the length of the head; the symphyseal connexions are loose " (p. 204); "abdominal cavity enormous, (…) gape and abdomen enormously distensible"(p. 203); "the abdomen is a great elastic sac, which extends behind the normally situated vent into the tail" (p. 204); "the enormous gape, the loosely articulated jaw-bones, and the stomach would permit the deglutition of a relatively immense object" (p. 205).

The following characteristics make the identification to species doubtful. "Seven branchiostegals" (p. 203) – *Kali* is diagnosed by having six branchiostegal rays, while all other chiasmodontids have seven (Melo 2008). "Depressible hinged fangs in two rows, (…) in both jaws" (p. 204) – excludes *Dysalotus* and *Pseudoscopelus*, which have teeth in multiple rows; both *Chiasmodon* and *Kali parri* have hinged teeth, but the hinge of the internal series in all species of *Kali* is more remarkable because it allows the teeth to rotate (see Melo 2008). "(…) The most anterior and external [pre]maxillary tooth is very stout, curved, and fixed" (p. 204) – a diagnostic of *Chiasmodon*. "There are fourteen abdominal and twenty-four caudal vertebrae" (p. 205) – none of the known species of *Chiasmodon* have such low number of vertebrae; among the chiasmodontids, only some species of *Pseudoscopelus* (31–38 vertebrae; Melo, unpub. data.), and most of *Kali* (33–40, Melo 2008) would fit this count. (…) "Oral cavity, but not the peritoneum, darkly pigmented" – *Kali parri* has both oral cavity and peritoneum pigmented; *Chiasmodon* spp. have a dusky oral cavity, but the peritoneum is pale; this characteristic is variable among the species of *Pseudoscopelus*. Characteristics that do not fit any known chiasmodontid are the number of second dorsal-fin rays, 29 (p. 204); and anal-fin rays, 29 (p. 204), and "no pyloric appendages [in the stomach]" (p.205), since all chiasmodontids have pyloric appendages anterior to stomach.

The number of branchiostegal rays, shape of the anteriormost premaxillary tooth, and distensible stomach and body wall makes *Ponerodon vastator* fit *Chiasmodon*; on the other hand, the mention of hinged fangs on jaws, oral cavity darkly pigmented and, mainly, vertebral count makes this author wonder if it could be *Kali parri*, consequently making that species a junior synonym. A definitive conclusion regarding the status of this genus and species could not be made without examination of the holotype and/or further material from off India. For now this author prefers to regard to *Ponerodon vastator* as *species inquirenda*, at least until the type is recovered or more material from off India becomes available.

Comparative material

Chiasmodon niger: 113 specimens, including holotype. Atlantic Ocean, Slope Water: MCZ 69742, 1, 51.3 mm, 38°58' N, 71°29' W, 0–1291 m, 16–VI–1982, R/V *Oceanus*; MCZ 162157, 1, 78.7 mm, 39°50' N, 67°28' W, 0–1152 m, 25–VII–2002, R/V *Delaware*; MCZ 163434, 1 of 4, 102.7 mm, 40°00' N, 67°23' W, 15–V–2003, R/V *Delaware*. North Sargasso Sea: BMNH 1998.8.9.6381 1, 32.5 mm, 32°18' N, 62°10' W, 9–III–1973, Institute of Oceanographic Sciences col.; CAS–SU 43340, 1, 203.2 mm, 32°30' N, 64°30' W, 9–VI–1930, W. Beebe col.; CAS–SU 66488, 1, aprox. 40.9 mm, 32°12' N, 64°36' W, 24–VII–1929, 1463 m, W. Beebe col.; CAS–SU 66491, 1, ca. 50.0 mm, 32°12' N, 64°36' W, 1829 m, 7–IX–1929, W. Beebe col.; FMNH 49841, 1, 40.4 mm, 32°13' N, 64°37'W, 26–VIII–1948, R/V Caryn; FMNH 49844, 1, 118.4 mm, 32°08' N, 64°33'W, 20–VIII–1948, R/V *Caryn*; MCZ 69695, 2, 32.0–40.0 mm, 35°42 N, 67°21' W, 900–970 m, 30–X–1977, R/V *Knorr*; USNM 254317, 2, 29.3–28.8 mm, 32°19' N, 63°37'W, 225–235 m, 29–IV–1969, Ocean Acre Expeditions; USNM 254318, 2, 31.3–34.2 mm, 31°59' N, 63°43'W, 900 m, 27–III–1969, Ocean Acre Expeditions; USNM

254319, 1, 29.8 mm, 32°17' N, 63°46'W, 0–1050 m, 30–III–1969, Ocean Acre Expeditions; USNM 254320, 2, 32.9–33.9 mm, 31°59' N, 63°43'W, 900 m, 27–IV–1969, Ocean Acre Expeditions; USNM 254325, 1, 29.5 mm, 31°57' N, 63°37'W, 800 m, 27–III–1969, Ocean Acre Expeditions; USNM 254333, 3, 17.7–31.8 mm, 31°55' N, 63°57'W, 0–300 m, 27–IV–1969, Ocean Acre Expeditions; USNM 254342, 11, 10.2–14.5 mm, 32°17' N, 63°36'W, 0–90 m, 23–III–1970, Ocean Acre Expeditions; USNM 254348, 1, ca. 30.0 mm, 33°12' N, 64°35'W, 0–312 m, 5–VII–1968, Ocean Acre Expeditions; USNM 254350, 1, 20.1 mm, 32°31' N, 63°41'W, 0–320 m, 9–IX–1969, Ocean Acre Expeditions; USNM 254351, 1, 27.4 mm, 32°03' N, 64°05'W, 0–610 m, 19–III–1970, Ocean Acre Expeditions; USNM 254352, 1, 19.0 mm, 31°57' N, 63°37'W, 800 m, 27–III–1969, Ocean Acre Expeditions; USNM 254353, 1, 23.3 mm, 31°45' N, 63°34'W, 0–290 m, 19–III–1970, Ocean Acre Expeditions; USNM 254354, 1, 22.1 mm, 31°49' N, 63°55'W, 0–400 m, 21–III–1970, Ocean Acre Expeditions; USNM 254355, 1, 25.4 mm, 31°29' N, 64°49'W, 205 m, 5–VI–1970, Ocean Acre Expeditions; USNM 254356, 1, 30.6 mm, 32°16' N, 64°21'W, 0–970 m, 3–VI–1970, Ocean Acre Expeditions; USNM 254357, 1, 25.7 mm, 32°30' N, 64°18'W, 277 m, 5–IX–1971, Ocean Acre Expeditions; USNM 254358, 1, 32.1 mm, 32°14' N, 63°40'W, 523–533 m, 2–III–1972, Ocean Acre Expeditions; USNM 254360, 1, ca. 20.0 mm, 31°51' N, 63°55'W, 452–500 m, 8–VI–1972, Ocean Acre Expeditions; USNM 254361, 1, 31.6 mm, 32°14' N, 63°46'W, 880–913 m, 11–VI–1972, Ocean Acre Expeditions; USNM 254362, 1, 32.4 mm, 32°04' N, 63°58'W, 0–1025 m, 22–VIII–1971, Ocean Acre Expeditions; USNM 254363, 1, 55.7 mm, 32°10' N, 62°49'W, 816–875 m, 14–I–1971, Ocean Acre Expeditions; USNM 254365, 1, 37.6 mm, 33°00' N, 64°06'W, 975–1000 m, 27–VIII–1971, Ocean Acre Expeditions; USNM 254366, 1, 35.1 mm, 32°07' N, 64°19'W, 0–110 m, 20–VIII–1971, Ocean Acre Expeditions; USNM 254367, 1, 47.1 mm, 32°11' N, 64°10'W, 0–150 m, 20–VIII–1971, Ocean Acre Expeditions; USNM 254368, 1, 59.0 mm, 32°14' N, 64°00'W, 0–1000 m, 21–VIII–1971, Ocean Acre Expeditions; USNM 254369, 1, 37.8 mm, 32°09' N, 64°11'W, 0–750 m, 24–VIII–1971, Ocean Acre Expeditions; USNM 254370, 3, 39.0–35.3 mm, 32°13' N, 64°16'W, 0–950 m, 24–VIII–1971, Ocean Acre Expeditions; USNM 254373, 2, 36.2–30.4 mm, 32°13' N, 63°40'W, 0–750 m, 30–IV–1969, Ocean Acre Expeditions; USNM 254633, 1, >20.0 mm, 32°23' N, 63°45'W, 0 m, 1–IX–1971, Ocean Acre Expeditions; USNM 256710, 3, 10.0–11.2 mm, 31°58' N, 63°39'W, 25–50 m, 16–III–1973, R/V *Discovery*; USNM 256711, 1, 9.1 mm, 31°47' N, 63°37'W, 10–25 m, 16–III–1973, R/V *Discovery*; USNM 256712, 4, 19.6–34.5 mm, 31°35' N, 63°32'W, 205–300 m, 18–III–1973, R/V *Discovery*; USNM 256713, 1, 29.7 mm, 31°41' N, 63°33'W, 208–300 m, 18–III–1973, R/V *Discovery*; USNM 256715, 3, ca. 30.0 mm, 31°41' N, 64°02'W, 89–110 m, 20–III–1973, R/V *Discovery*; USNM 256716, 1, 13.6 mm, 31°59' N, 63°57'W, 190–300 m, 20–III–1973, R/V *Discovery*; USNM 254363, 1, 55.7 mm, 32°10' N, 62°49' W, 14–I–1971, Ocean Acre expedition; USNM 254368, 1, 59.0 mm, 32°14' N, 64°00' W, 0–1000 m, 21–X–1971, Ocean Acre expedition. Gulf of Mexico: FMNH 65936, 1, ca. 30.0 mm, 25°21' N, 91°02' W, 3200 m, 25–VII–2959, R/V Oregon; FMNH 65937, 1, 72.1 mm, 28°33' N, 88°48' W, 1189 m, R/V Oregon; USNM 367286, 1, 52.9 mm, 27°36' N, 94°40' W, 731 m, 22–I–1964, R/V *Oregon*; USNM 367288, 1, 44.4 mm, 28°58' N, 88°18' W, 800–990 m, 27–IX–1960, R/V *Oregon*. Amazonian Province: BMNH 1879.5.14.588, 1, 50.6 mm, 1°22' N, 26°36' W, 26–VIII–1873, R/V *Challenger*. North

African Subtropical Sea: BMNH 1863.12.12.4, 1 (holotype), 76.9 mm, approx. 22°30’ N, 107°00’ W, J. Johnson col.; BMNH 1922.5.26.1–3, 2, 97.1–104.7 mm, 33°00’ N, 16°00’ W, E. Noronha col.; BMNH 1998.8.9.6418, 1, 19.2 mm, 31°57’ N, 47°18’ W, 4–III–1973, Institute of Oceanographic Sciences; ZMH 7120, 1, 33.8 mm, 29°34’ N, 24°13’ W, 0–400 m, 13–II–1970, R/V *Meteor*; ZMUC P. 6587, 1, 99.9 mm, 35°20’ N, 30°16’ W, 30–IV–1979, R/V *Anton Dohm*; ZMH 9171, 1, 117.3 mm, 29°53’ N, 28°17’ W, 900–1000 m, 17–IX–1998, R/V *Meteor*; USNM 367284, 3, 161.7–180.0 mm, 32°47’ N, 16°24’ W, 1750–1800 m, 22–IV–1971, R/V Walter Herwig. South African Subtropical Sea: BMNH 1998.8.9.18365, 1, 101.9 mm, 29°56’ N, 23°05’ W, 5–IV–1972, Institute of Oceanographic Sciences col.; USNM 113302, 1, 34.7 mm, 28°00’ N, 15°00’ W [coordinates inferred], 19–II–1951, U.S.S. *San Pablo*. Guinean Province: BMNH 1930.1.12.1057, 1, 48.5 mm, 6°55’ N, 15°54’ W, 2–VI–1927, R/V *Discovery*; BMNH 2002.8.7.24–25, 2, 34.5–35.8 mm, 5°26’ S, 0°30’ E, 596–697 m, 01–V–1982, R.R.S. *Challenger*; MCZ 41378, 3, 38.0–44.8 mm, 11°17’ N, 30°00’ W, 230 m, 2–V–1961, R/V *Chain*; UF 216530, 1, 72.9 mm, 4°56’ N, 0°13’ E, 1605–2125 m, 27–V–1964, R/V *Pillsbury*; UF 219999, 2, 44.7–45.2 mm, 0°25’ N, 5°09’ E, 850 m, 27–V–1964, R/V *Pillsbury*. Mediterranean Outflow: ZMH H. 7123, 1, 30.7 mm, 34°02’ N, 15°18’ W, 0–3900 m, 8–III–1970, R/V *Meteor*; USNM 367204, 3, 161.7–180.0 mm, 37°47’ N, 16°24’ W, 1750–1800 m, 22–IV–1971, R/V *Walter Herwig*. Uncertain locality: CAS–SU 23553, 1, 83.1 mm, locality uncertain, probably Como de Lobos, SW of Funchall, A. C. Noronha col.

Chiasmodon subniger: 147 specimens, including holotype. Pacific Plate: LACM 44394–2, 1, 35.4 mm, 21°20’ N, 158°10’ W, 0–245, 2–III–1978R/V *Kana Keoki*; SIO 55–221, 1, 153.7 mm, 8°01’ N, 120°03’ W, 0–2639 m, 15/16–V–1965, R/V *Horizon*; SIO 56–66, 1, 109.9 mm, 32°36’ N, 117°36’ W, 1146–1237 m, 4–III–1956, R/V *Paolina–T*; SIO 60–234–60, 1, 58.9 mm, 2°21’ S, 137°16’ W, 0–2500 m, 2–VII–1960, R/V *Spencer F Baird*; SIO 60–229–60, 1, 91.6 mm, 1°39’ S, 133°35’ W, 0–2326 m, 29–VI–19,60, R/V *Spencer F Baird*; SIO 72–25, 1, 193.0 mm, 27°35’ N, 155°23’ W, 04/05–X–1971, R/V *Thomas Washington*; SIO 73–20, 1, 135.5 mm, 2°36’ N, 112°57’ W, 21–XI–1970, R/V *Thomas Washington*; SIO 73–25, 2, 40.5–63.0 mm, 0°55’ S, 112°36’ W, 23–XI–1970, R/V *Thomas Washington*; SIO 90–120, 1, 12.9 mm, 25°00’ N, 148°21’ W, 31–VII–1973, R/V *David Starr Jordan*; SIO 97–101, 1, 68.5 mm, 27°00’ N, 135°00’ W, 443 m, 8–X–1972, R/V *David Starr Jordan*; SIO 69–496–60, 1, 39.9 mm, 2°16’ S, 100°34’ W, 0–675 m, 26–XI–1969, R/V *Thomas Washington*; SIO 69–497, 2, 54.3–64.3 mm, 28°38’ S, 103°46’ W 0–675 m, 9–XII–1969, R/V *Thomas Washington*. Western Pacific: CAS–SU 66481, 1, 30.0 mm, 0°05’ S, 91°11’ W, 909 m, 13–IV–1925, W. Beebe et al. col.; CAS–SU 66484, 1, 32.6 mm, 0°10’ N, 88°22’ W, 727 m, 29–IV–2925, W. Beebe et al. col.; LACM 4609, 1, 67.3 mm, 33°10’ N, 118°30’ W, 1226 m, 18–X–1963, R/V *Velero*; LACM 30020–8, 1, 36.2 mm, 28°08’ N, 117°31’ W, 3477–3523 m, 20–VIII–1967, R/V *Velero IV*; LACM 30035–12, 2, 43.5–44.5 mm, 20°35’ N, 106°17’ W, 3294–4300 m, 08–XI–1967, R/V *Velero IV*; LACM 30037–29, 1, 41.7 mm, 21°39’ N, 106°58’ W, 2791–2818 m, 11–XI–1967, R/V *Velero IV*; LACM 30039–19, 1, 80.4 mm, 22°51’ N, 108°14’ W, 2562–2882 m, 12–XI–1967, R/V *Velero IV*; LACM 30071–5, 1, 94.1 mm, 26°34’ N, 114°48’ W, 3111–3477 m, 11–IV–1968, R/V *Velero IV*; LACM 30179–11, 1, 38.4 mm, 31°26’ N, 118°23’ W, 2196–2379 m, 29–V–1968, R/V *Velero IV*; LACM 30279–6, 1, 35.5 mm, 28°24’ N, 118°20’ W, 3569–4575 m, 24–VIII–1968, R/V

Velero IV; LACM 30284–7, 1, 38.0 mm, 28°48’ N, 118°10’ W, 3111–4575 m, 24–VIII–1968, R/V *Velero IV*; LACM 30382–5, 1, 61.4 mm, 27°49’ N, 119°16’ W, 2654–3935 m, 19–XI–1968, R/V *Velero IV*; LACM 30399–22, 1, 114.0 mm, 32°15’ N, 117°57’ W, 1830 m, 24–IV–1969, R/V *Velero IV*; LACM 30400–7, 1, 88.8 mm, 32°42’ N, 118°13’ W, 1610 m, 10–X–1968, R/V *Velero IV*; LACM 30407–12, 1, 98.5 mm, 32°51’ N, 118°59’ W, 1720 m, 26–II–1969, R/V *Velero IV*; LACM 30408–3, 1, 129.1, 33°05’ N, 119°11’ W, 1684 m, 27–II–1969, R/V *Velero IV*; LACM 30417, 1, 31.8 mm, 29°07’ N, 118°10’ W, 2562 m, 13–III–1969, R/V *Velero IV*; LACM 30424, 1, 63.8 mm, 32°09’ N, 117°55’ W, 1830 m, 16–III–1969, R/V *Velero IV*; LACM 30437–23, 1, 128.2 mm, 31°42’ N, 118°40’ W, 1830 m, 05–II–1969, R/V *Velero IV*; LACM 30440–9, 1, ca. 34.0 mm, 32°37’ N, 118°08’ W, 1931 m, 10–XII–1968, R/V *Velero IV*; LACM 30474–6, 1, 35.9 mm, 26°11’ N, 114°10’ W, 2928 m, 23–VI–1968, R/V *Velero IV*; LACM 30475, 1, 48.8 mm, 28°39’ N, 118°24’ W, 3386 m, 17–XI–1968, R/V *Velero IV*; LACM 30479–6, 1, 74.7 mm, 28°32’ N, 118°34’ W, 3843 m, 20–XI–1968, R/V *Velero IV*; LACM 30532–11, 1, 82.1 mm, 32°39’ N, 118°11’ W, 1739 m, 27–I–1968, R/V *Velero IV*; LACM 30558, 1, 65.8 mm, 32°14’ N, 117°53’ W, 1830 m, 31–I–1968, R/V *Velero IV*; LACM 30562–5, 1, 117.5 mm, 33°06’ N, 119°11’ W, 1200 m, 15–III–1968, R/V *Velero*; LACM 30608–6, 1, 50.2 mm, 27°58’ N, 119°05’ W, 3935 m, 19–XI–1968, R/V *Velero IV*; LACM 30511–2, 1, 50.8 mm, 29°15’ N, 118°09’ W, 3203–3294 m, 26–XI–1965, R/V *Velero IV*; LACM 30758–1, 1, 62.1 mm, 33°24’ N, 118°49’ W, 1281 m, 28–X–1967, R/V *Velero IV*; LACM 31127–22, 1, 39.5 mm, 22°50’ N, 109°09’ W, 2745, 22–I–1970 m, R/V *Velero IV*; LACM 31172–2, 1, 59.3 mm, 32°43’ N, 118°14’ W, 1830 m, 28–V–1970, R/V *Velero IV*; LACM 32204–20, 1, 160.2 mm, 28°20’ N, 118°18’ W, 19–VI–1969, R/V *Velero*; LACM 32205–2, 2, 89.36–121.21 mm, 33°02’N, 119°49’ W, 29–VII–1970, R/V *Velero*; LACM 35877–1, 1, 88.9 mm, 33°14’ N, 118°34’ W, 500 m, 30–VI–1976, R/V *Velero IV*; LACM 36014–1, 1, 96.2 mm, 33°10’ N, 118°24’ W, 500–700 m, 20–X–1976, R/V *Velero IV*; LACM 37466–1, 2, 31.2–31.3 mm, 29°00’ N, 117°00’ W [coordinates inferred], X–1977, boat *High Seas*; LACM 37602–1, 1, 113.7 mm, 33°00’ N, 118°00’ W [coordinates inferred], 860 m, 19–VII–1978, Boat *JJ*; LACM 37780–1, 1, 88.3 mm, 33°00’ N, 118°00’ W [coordinates inferred], 824 m, 28–VII–1978, boat *JJ*; LACM 38527, 1, 104.1 mm, 34°00’ N, 120°00’ W [coordinates inferred], 915 m, 27–VIII–1979, Boat *Val Jean*; LACM 39167–11, 1, 97.3 mm, 32°39’ N, 118°12’ W, 25–VIII–1970, R/V *Velero*; LACM 44518, 1, 96.9 mm, 33°16’ N, 118°32’ W, 1330–1350 m, 23–X–1974, R/V *Velero IV*; LACM 46020–1, 1, 69.3 mm, 33°37’ N, 118°27’ W, 16–IV–1991, R/V *Vantuna*; LACM 9253–15, 1, 133.0 mm, 32°47’ N, 12°01’ W, 3678–3752 m, 18–X–1966, R/V *Velero IV*; LACM 9497–1, 1, 66.2 mm, 29°28’ N, 119°02’ W, 08–VIII–1964, R/V *Velero IV*; LACM 9651–17, 2, 37.6–56.8 mm, 29°20’ N, 118°12’ W, 3480–3150 m, 03–VIII–1966, R/V *Velero IV*; LACM 9664–2, 2, 41.3–42.1 mm, 29°20’ N, 118°12’ W, 3480–3150 m, 03–VIII–1966, R/V *Velero IV*; LACM 9666–26, 1, 35.9 mm, 28°05’ N, 115°11’ W [coordinates inferred], 17–VI–1967, R/V *Velero*; LACM 9676–34, 1 72.6 mm, 32°20’ N, 117°50’ W, 1190–1830 m, 21–VI–1967, R/V *Velero IV*; LACM 9682–12, 1, 68.1 mm, 31°30’ N, 118°29’ W, 16–VIII–1967, 1956–2000 m, R/V *Velero*; LACM 9762–14, 1, 61.1 mm, 33°09’ N, 119°16’ W, 1684 m, 10–VI–1965, R/V *Velero IV*; LACM 9859–35, 1, 88.8 mm, 33°00’ N, 119°00’ W [coordinates inferred], 20–V–1967; R/V *Velero*; LACM 9959–30, 1, 93.4 mm, 31°45’ N, 117°58’ W, 1647–1940 m, 20–V–1967, R/V *Velero IV*; LACM 9995, 1, 94.9 mm, 33°00’ N, 119°01’ W, 1524–1714 m, 14–II–1968, R/V *Velero IV*; SIO 01–46, 1, 73.4 mm, 5°33’ N, 87°03’ W, 29–XII–1998, J. E. McCosker and D.J. Rehren col.; LACM 30399–15, 1, 114.0 mm, 32°15’ N, 117°57’ W, 24–IV–1969, R/V *Velero IV*; MCZ 28744, 1 (holotype), ca. 40.0 mm, 22°30’ N, 107°01’ W, 1681 m, 19–IV–1891, R/V *Steamer Albatross*; SIO 51–148–60A, 1, 124.8 mm, 32°43’ N, 117°38’ W, 1001 m, 20–III–1951, R/V *Paolina–T*; SIO 64–1028–60, 1, 123.2 mm, 37°38’ N, 123°18’ W, 15–III–1957, R/V *Spencer F Baird*; SIO 65–204–60, 1, 56.9 mm, 26°32’ N, 114°55’ W, 0–4586 m, 15–VI–1965, R/V Horizon; SIO 65–443–60, 1, 124.0 mm, 32°15’ N, 118°26’ W, 23/24–IX–1965, R/V *Alexander Agassiz*; SIO 66–20–60, 1, 53 mm, 28°58’ N, 117°32’ W, 0–3603 m, 1/2–IV–1966, R/V *Alexander Agassiz*; SIO 66–42–60, 1, 142.3 mm, 31°14’ N, 117°30’ W, 0–2140 m, 7/8–IV–1966, R/V *Alexander Agassiz*; SIO 67–52–60, 1, 86.2 mm, 30°46’ N, 117°00’ W, 0–2354 m, 22–IV–1967, R/V *Thomas Washington*; SIO 67–61–60, 1, 42.2 mm, 29°02’ N, 118°13’ W, 0–2782 m, 26–IV–1967, R/V *Thomas Washington*; SIO 68–316–60, 1, 104.1 mm, 23°51’ N, 112°51’ W, 1240 m, 10–IX–1963, R/V *Alexander Agassiz*; SIO 71–93, 1, 106.1 mm, 32°26’ N, 117°30’ W, 1201–1237 m, 22–VI–1971, R/V *Alexander Agassiz*; SIO 72–180–60, 1, 108.9 mm, 20°19’ S, 71°14’ W, 0–900 m, 20°19’ S, 71°14’ W, R/V *Thomas Washington*; SIO 72–182, 3, 97.8–106.9 mm, 18°36’ S, 70°37’ W, 940 m, R/V *Thomas Washington*; SIO 72–192, 1, 68.1 mm, 13°52’ S, 77°42’ W, 0–1100 m, 11–IV–1972, R/V *Thomas Washington*; SIO 72–195–60, 2, 80.8–86.0 mm, 13°51’ S–77°41’ W, 1100 m, 11/12–IV–1972, R/V *Thomas Washington*; SIO 72–71, 2, 81.7–118.8 mm 32°29’ N, 117°31’ W, 14–IX–1971, R/V *Alexander Agassiz*; SIO 79–183, 1, 76.2 mm, 32°54’ N, 117°33’ W, 27–V–1979, R/V *David Starr Jordan*; SIO 90–154, 1, 98.4 mm, 32°24’ N, 120°35’ W, 0–2100 m, 18/19–XI–1990, R/V *Robert Gordon Sproul*; SIO 91–21, 1, 42.1 mm, 32°38’ N, 123°58’ W, 600 m, 22–IX–1980, T. Bailey col.; SIO 94–67, 1, 66.4 mm, 8°59’ N, 104°22’ W, 20–II–1988, R/V *Thomas Washington*; SIO H 53–223, 1, 84.2 mm, 32°38’ N, 117°37’ W, 964 m, 11/12–XII–1953, R/V *Horizon*; UW 43302, 1, 133.0 mm, 1–XI–1995, 42°38’ N, 124°56’ W, 1034 m, R/V *Miller Freeman*; UW 43306, 1, 136.1 mm, 42°55’ N, 125°01’ W, 1110 m, 29–X–1995 R/V/ *Miller Freeman*; UW 45555, 1, 130.1 mm, 47°33’ N, 125°19 W, 891 m, 21–X–1996, R/V *Miller Freeman*; UW 46672, 1, 104.5 mm, 37°15’ N, 123°08’ W, 1054 m, 29–X–2000, R/V *Miller Freeman*; UW 46692, 1, 95.8 mm, 34°31’ N, 121°06’ W, 948 m, 3–XI–2000, R/V *Miller Freeman*; UW 47234, 2, 75.9–235.7 mm, 36°23’ N, 122°13’ W, 1149 m, 3–XI–2001, R/V *Miller Freeman*; UW 47235, 1, 143.5 mm, 39°32’ N, 124°10’ W, 1144 m, 27–X–2001, R/V *Miller Freeman*; UW 48713, 1, 122.0 mm, 36°22’ N, 122°13’ W, 1084 m, 23–X–1999, R/V *Miller Freeman*; UW 48697, 1, 103.0 mm, 35°47’ N, 121°48’ W, 1034 m, 22–X–1999, R/V *Miller Freeman*. Uncertain locality: LACM 3274, 1, 57.8 mm, no data, 17–VII–1963, R/V *Velero*; MCZ 41110, 1, 149.7 mm, 7°31’ S, 81°27 W [coordinates questionable, may be 7°31 N], 20–XII–1958, R/V *Vema*.

Chiasmodon braueri: 44 specimens, including holotype. Pacific Plate: FMNH 88152, 1, 96.8 mm, 21°23’ N, 158°18’W, 16–VI–1973, R.E. Young col.; FMNH 88153, 1, 49.3 mm, 21°23’ N, 158°18’ W, Hawaii, off Oahu, 23–IV–1971, R.E. Young col.; FMNH 88154, 1, 38.6 mm, Hawaii, off Oahu, 21°23’ N, 158°18’ W, 26–V–1972, R.E. Young col.; FMNH 88157, 1, 88.1 mm, Hawaii, off Oahu, 3–VIII–1978, R.E. Young col; LACM 31479–1, 1, 89.6 mm, 0°03’ N, 147°00’ W, R/V *Caride III*; LACM 31518–1, 1, 96.9 mm, 4°04’ S, 169°51’ E, 21–Jul–1967, R/V *Cyclone V*; LACM 31519–1, 1, 89.0 mm, 4°22’ S, 169°58’ E, 21–VI–1967, R/V *Cyclone V*; LACM 32749–7, 1, 70.4 mm, 21°20’ N, 158°20’ W, 940–1000 m, 1–III–1971, R/V *El Pescadero III*; LACM 33374–2, 1, 68.6 mm, 21°20’ N, 158°20’ W, 0–150 m, 26–27–II–1971, R/V *Townsend Cromwell*; SIO 70–306–60, 1, 149.8 mm, 32°00’ N, 136°12’ W , 0–1400 m, 28/29–VIII–1970, R/V *Melville*; SIO 73–185–60, 1, 61.1 mm, 4°38’ S, 128°14’ E, 21–XII–1972, R/V *Alpha Helix*; SIO 60–229–72, 1, 129.4 mm, 1°39’ S, 133°35’ W, 0–2326 m, R/V *Spencer F Baird*; USMN 288972, 1, 51.5 mm, 8°16’ S, 150°02’ W, 0–1000 m, 6–VI–1979, R/V *Gyre*; USNM 288986, 1, 35.8 mm, 5°53’ N, 150°01’ W, 0–850 m, 11–II–1979, R/V *Gyre*. Eastern Pacific: LACM 31507, 2, 37.8–42.3 mm, 0°26’ S, 169°45’ E, 13–VI–1967, R/V *Cyclone IV*; LACM 31508–1, 1, 85.1 mm, 0°40’ S, 169°54’ E, 13–VI–1967, R/V *Cyclone IV*; LACM 36024–2, 3, 38.92–58.54 mm, 4°56’ N, 129°59’ E, 28–IV–1975, R/V *Alpha Helix*; LACM 36039–1, 1, 27.5 mm, 5°07’ S, 130°08’ E, 650–1000 m, 13–V–1975, R/V *Alpha Helix*; LACM 36040–1, 1, 27.2 mm, 2°45’ S, 127°55’ E, 0–2000 m, 1–IV–1975, R/V *Alpha Helix*; LACM 36041–1, 1, 32.1 mm, 4°45’ S, 129°51’ E, 0–1000 m, 13–IV–1975, R/V *Alpha Helix*; LACM 36042–1, 1, 30.6 mm, 5°04’ S, 129°54’ E, 720–990 m, 19–IV–1975, R/V *Alpha Helix*; LACM 36043–1, 1, 28.2 mm, 4°09’ S, 130°50’ E, 0–840 m, 24–IV–1975, R/V *Alpha Helix*; LACM 36046–1, 1, 64.8 mm, 4°54’ S 129°42’ E, 0–850 m, 6–V–1975, R/V *Alpha Helix*; LACM 36047–1, 1, 78.9 mm, 5°03’ S 129°41’ E, 0–960 m, 1–V–1975, R/V *Alpha Helix*; LACM 36048–1, 1, 183.9 mm, 4°54’ S 129°30’ E, 830–1050 m, 11–IV–1975, R/V *Alpha Helix*; SIO 70–346–60, 1, 51.6 mm, 14°34’ N, 119°33’ E, 0–1500 m, 19–IX–1970, R/V *Melville*; ZMA 112.462, 1 (holotype), 45.0 mm, 5°39’ S, 122°12 E, 1886 m, 22–IX–1899, Siboga Expedition. Indian: SAIAB 76427, 1, 79.1 mm, 8º06’ S, 39º58’ W, 30–VII–2003, J. R. Stapley col.; South Atlantic Subtropical: MNRJ 26701, 1, 171.4 mm, 20°27’ S, 39°38’ W, 1680 m, 2–VII–2000, R/V *Thalassa*; MNRJ 26695, 1, 53.0 mm, 20°24’ S, 39°46’ W, 1209–1362 m, 2–VII–2000, R/V *Thalassa*; MNRJ 26696, 1, 68.6 mm, 21°26’ S, 39°49’ W, 1594–1614 mm, 7–VII–2000, R/V *Thalassa*; MNRJ 26706, 1, 103.7 mm, 13°19’ S, 38°19’ W, 1726–1929 m, 20–VI–2000 R/V *Thalassa*.

Chiasmodon microcephalus: 70 specimens, including holotype and paratypes. Atlantic, Subantarctic: BMNH 1930.1.12.1060, 1 (holotype), 99.1 mm, 39º50’ S, 36º23’ W, 1470 m, 5–VI–1926, R.R.S. *Discovery*; BMNH 1930.1.12.1061, 1 (paratype), 72.8 mm, collected with holotype; BMNH 1930.1.12.1062 (paratype), 1, 37.2 mm, 33º25’ S, 6º31’ W, 24–VI–1926, R.R.S. *Discovery*; SAIAB 61668, 2, 154.1–197.1 mm, 35º24’ S, 18º 42’ E, 22–I–2001, col. unknown; SAIAB 63888, 29, 42.3–141.6 mm, 35º54’ S, 15º00’ E, 22–II–2001, col. unknown; SAIAB 63772, 14, 44.7–113.95 mm, 34º49’ S, 18º07’ E, 11–II–2001, col. unknown. South Atlantic Subtropical: MNRJ 26691, 1, 188.2 mm, 21°28’ S, 39°40’ W, 1790–1806 m; 7–VII–2000, R/V *Thalassa*; MNRJ 26792, 1, 159.5 mm, 20°06’ S, 38° 40’ W, 1636–1649 m, 28–VI–2000, R/V *Thalassa*; Indian: USNM 202442, 1, 76.1 mm, 28º05’ S, 64º58’ E, 27–VI–1964, R/V *Anton Bruun*. Eastern Pacific: AMS I. 20315069, 1, 35.1 mm, 33º53’ S, 152º02’ E, 900 m, 14–XII–1977, R/V *Kapala*; AMS I. 29822002, 1, 199.5 mm, 32º52’ S, 152º49’ E, 1006–1052 m, 8–VI–1989, R/V *Kapala*; AMS I. 29812005, 1, 225.5 mm, 32º52’ S, 152º49’ E, 1060–1097 m, 3–VIII–1989, R/V *Kapala*; NMNZ P. 25871, 1, 145.4 mm, 42º38’ S, 177º11’ E, 1185–1188 m, 17–VI–1990, F/V *Cordella*; NMNZ P. 27200, 1, 186.1 mm, 44º27’ S, 179º40’ W, 1065–1092 m, 10–IX–1990; F/V *Cordella*; NMNZ P. 27201, 1, 148.8 mm, 44º17’ S, 178º55’ E, 1103–1140 m, 25–XI–1990, F/V *Cordella*; NMNZ P. 27978, 1, 151.8 mm, 49º37’ S, 168º04’ E, 625–630 m, 19–X–1991, col. unknown; NMNZ P. 27983, 1, 165.3

mm, 45º00’ S, 174º04’ E, 1171–1183 m, 15–X–1991, R/V *Tangaroa*; NMNZ P. 28980, 1, 60.1 mm, 39º 39’ S, 178º 19’ E, 825–870 m, 18–VI–1986, F/V *Galliard*; NMNZ P. 34841, 1, 150.1 mm, 44º50’ S, 173º09’ E, 953–990 m, 13–III–1997, R/V *Tangaroa*; NMNZ P. 34843, 1, 188.3 mm, 44°49’ S, 173°02’ E, 1052 m, 13–III–1997, R/V *Tangaroa*; NMNZ P. 37851, 1, 202.9 mm, 36º00’ S, 169º00’ E, 800–1200 m, II–2001, F/V *Santa Monica*; NMNZ P. 31317, 2, 122.0–127.1 mm, 42º46’ S, 176º13’ W, 1202–1225 m, 19–VII–1994, R/V *Tangaroa*; NMNZ P. 38820, 1, 132.0 mm, 42º45’ S, 179º54’ W, 1130–1138 m, 18–VII–2002, R/V *Tangaroa*; NMNZ P. 39732, 2, 60.9–91.3 mm, 35º59’ S, 170º03’ E, 0–2000 m, 05–VI–2003, R/V *Tangaroa*; NMNZ P. 39975, 2, 150.1–93.8 mm, 49º01’ S, 171º15’ W, 564–583 m, 15–IX–2003, R/V *Tangaroa*; NMNZ P. 42052, 1, 60.2 mm, 42°47’ S, 179°33’ E, 1123 m, 21–VI–2005, R/V *Tangaroa*; NMV A. 5173, 1, 40.0 mm, 40º18’ S, 149º01’ E, 0–150 m, 18–I–1982, R/V *Solea* CSIRO; NMV A. 5182, 1, 39.7 mm, 37º31’ S, 150º21’ E, 150–400 m, 19–I–1982, R/V *Solea* CSIRO; NMV A. 5933, 1, 49.4 mm, 38º19’ S, 149º24’ E, 850–880 m, 14–V–1988, R/V *Solea* CSIRO; NMV A. 25179–004, 1, 65.4 mm, 35º56’ S, 170º01’ E, 0–1975 m, 5–VI–2003, R/V *Tangaroa*. Eastern Pacific: MCZ 97611, 1, 50.7 mm, 33°58’ S, 82°20’ W, 0–2500, 15–I–1966, R/V *Anton Bruun*. Southern Ocean: USNM 372314, 1, 166.8 mm, 53º28’ S, 127º129’ E, 0–1250 m, 16–IV–2003, R/V *Eltanin*.

Chiasmodon pluriradiatus: 24 specimens, including holotype and paratypes. Atlantic, North Sargasso Sea: MCZ 41506, 1, 46.5 mm, 30º14’N, 69º17’ W (from stomach of blue fin tuna), 24–IV–1971, R/V *Crawford*; USNM 254371, 1, 47.9 mm, 31°46’ N, 64°30’ W, 0–363 m, 23–II–1972, Ocean Acre expedition; USNM 256717, 2, 43.8–52.7 mm, 31°55’ N, 63°44’ W, 21–III–19084, 990–1100 m, R.R.S. *Discovery*. South Sargasso Sea: BMNH 1998.8.9.7637–7638, 2, 23.5–34.0 mm, 32º01’ N, 50º33’ W, 5–III–1973, 0–995 m, R.R.S. *Discovery*. Straits of Florida: YPM 2827, 1, 48.5 mm (holotype), 23°49’ N, 76°58’ W, 2–III–1927, R/V *Pawnee*; YPM 18108 (former YPM 2827), 1 (paratype), 40.6 mm, collected with holotype; YPM 2829, 3 (paratypes), 30.5–47.5 mm, 23°57’ N, 77°26’ W, 9–III–1927, R/V *Pawnee*; YPM 2828, 1 (paratype), 37.2 mm, 24°29’ N, 77°29’ W, 14–III–1929, R/V *Pawnee*. South Atlantic Subtropical: BMNH 1998.8.9.10295, 1, 46.9 mm, 10º54’ N, 19º38’ W, 610–700 m, 9–III–1972, R.R.S. *Discovery*. North African Subtropical: BMNH 1998.8.9.581, 1, 62.8 mm, 29º45’ N, 34º20’ W, 1200 m, 20–VI–1981, R.R.S. *Discovery*. Guinean Province: BMNH 2002.6.20.6, 1, 46.8 mm, 3º01’ N, 22º52’ W, 905–1000 m, 31–VII–1974, R.R.S. *Discovery*; MCZ 41378, 3, 38.4–46.7 mm, 11°17’ N, 30°00’ W, 2–V–1961, 230 m, R/V Chain. Indian: USNM 202437, 1, 33.2 mm, 32°11’ S, 59°30’ E, 750 m, 8–IX–1973, R/V *Anton Bruun*; USNM 202438, 1, 30.5 mm, 28°54’ S, 60°01’ E, 1222 m, 6/7–IX–1973, R/V *Anton Bruun*; USMN 202439, 1, 87.5 mm, 12°09’ S, 58°35’ E, 1600 m, 26–IX–1963, R/V *Anton Bruun*. Pacific, western Pacific: NMNZ P. 33063, 1, 179.7 mm, 37º56’ S, 179º03’ E, 922–1218 m, 12–V–1995, R/V *Tangaroa*. Pacific Plate: BMNH 1997.5.21.28, 1, 220.9 mm, 24º44’ S, 167º43’ W, 1213– 1246 m, N. Merret col.

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TABLE 2.1. Total lateral-line pores in the species of *Chiasmodon*.

Lateral-line pores	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**
C. niger												1	1	4	3*	1			1		
C. subniger	1		2		1	1	3	1	1	2		3	1								
C. braueri									1	1	1*	1	3	3	2	1	1				
C. microcephalus					1			1	1	1	7	3	3	1	2*	5					
C. pluriradiatus																	1	2		4*	
C. asper																1	1*		1		
C. harteli															2	3*	6	5	4	2	1

TABLE 2.2. Morphometric data of *Chiasmodon niger* (n=13) and *C. subniger* (n=19).

Character	*Chiasmodon niger*			*Chiasmodon subniger*		
	Range	Mean	SD	Range	Mean	SD
Standard length (mm)	76.9–205.7	120.5	40.6	66.9–234.8	111.9	39.8
Head length (mm)	22.7–58.7	34.8	14.1	22.3–69.1	34.5	11.3
Percentage of HL						
Snout	22.2–26.6	24.1	1.4	21.4–23.9	22.6	0.7
Upper jaw	72.2–80.0	75.8	2.2	63.9–72.7	67.9	2.5
Lower jaw	80.0–86.7	83.0	2.0	69.0–76.7	72.8	2.3
Orbit width	15.3–18.5	17.0	1.0	14.5–18.5	16.2	1.1
Orbit height	12.8–16.1	14.5	1.0	12.6–16.5	13.8	1.0
Anterior nostril to eye	10.0–13.8	11.6	1.2	9.2–12.4	11.1	0.8
Posterior nostril to eye	2.5–4.8	3.6	0.7	2.8–5.1	3.8	0.6
Distance between nostrils	6.7–9.0	7.8	0.8	6.0–8.3	7.2	0.7
Interorbital distance	17.3–19.9	18.4	0.9	18.4–24.3	20.2	1.5
Head width	26.1–29.9	28.0	1.2	26.9–34.8	29.9	2.0
Cheek depth	3.5–5.8	4.6	0.8	3.5–6.7	5.3	0.9
Percentage of SL						
Head length	25.8–29.4	28.2	1.1	29.1–33.3	31.1	1.3
Body width	3.6–12.9	6.6	2.6	4.0–13.4	7.9	2.6
Insertion of pectoral fin	28.6–32.4	30.4	1.1	29.3–33.0	31.3	1.0
Insertion of pelvic fin	31.4–38.8	34.2	2.5	30.1–36.7	33.0	1.9
Pectoral-fin length	15.8–22.4	19.4	2.0	16.0–22.7	18.9	2.0
Pelvic-fin length	8.3–11.7	9.9	1.0	9.3–12.3	10.5	0.9
Origin of 1st dorsal fin	30.7–35.6	32.9	1.4	33.1–36.8	34.7	1.2
Base of 1st dorsal fin	13.9–17.9	15.6	1.4	13.6–18.9	16.8	1.2
1st dorsal-fin depth	9.0–12.2	10.2	0.8	8.4–12.9	10.7	1.5

TABLE 2.2. (cont.)

Origin of 2^{nd} dorsal fin	49.5–54.9	51.3	1.7	50.2–55.6	52.6	1.2
Base of 2^{nd} dorsal fin	35.8–40.4	38.3	1.5	34.3–41.5	38.6	2.1
2^{nd} dorsal-fin depth	13.5–19.5	16.8	2.0	14.3–20.9	16.7	1.9
Origin of anal fin	51.3–66.4	56.2	4.4	51.2–62.0	54.8	3.0
Base of anal fin	29.5–37.4	34.2	2.2	29.7–39.6	34.8	2.2
Anal-fin depth	14.2–20.0	16.4	1.6	15.3–22.7	17.5	2.0
Peduncle depth	2.8–4.3	3.8	0.4	3.2–4.9	4.0	0.4
Peduncle length	9.2–13.7	11.4	1.5	9.5–14.4	11.7	1.2

TABLE 2.3. Morphometric data of *Chiasmodon braueri* (n=16).

Character	*Chiasmodon braueri*		
	Range	**Mean**	**SD**
Standard length (mm)	39.2–183.9	86.4	43.9
Head length (mm)	11.5–53.4	26.4	12.8
Percentage of HL			
Snout	21.5–25.0	23.8	1.1
Upper jaw	70.0–77.1	72.3	2.4
Lower jaw	76.0–83.8	79.1	2.7
Orbit width	14.7–18.8	16.9	1.2
Orbit height	12.6–17.6	14.5	1.6
Anterior nostril to eye	9.4–11.9	10.5	0.8
Posterior nostril to eye	2.8–4.3	3.4	0.4
Distance between nostrils	5.6–8.9	7.3	0.9
Interorbital distance	16.2–19.5	17.9	1.1
Head width	25.4–31.7	28.4	1.7
Cheek depth	3.0–5.4	4.3	0.7
Percentage of SL			
Head length	26.4–31.7	29.4	1.5
Body width	5.1–9.4	7.0	1.4
Insertion of pectoral fin	28.3–33.2	30.9	1.6
Insertion of pelvic fin	30.3–38.4	33.7	2.5
Pectoral-fin length	17.7–25.2	21.6	2.5
Pelvic-fin length	6.4–11.5	9.7	1.5
Origin of 1st dorsal fin	31.6–35.2	33.2	1.1

TABLE 2.3. (cont.)

Base of 1st dorsal fin	13.1–18.4	16.6	1.6
1st dorsal-fin depth	9.0–12.3	10.3	1.0
Origin of 2nd dorsal fin	49.4–53.1	51.5	1.1
Base of 2nd dorsal fin	36.5–42.1	39.1	1.6
2nd dorsal-fin depth	11.7–20.3	16.0	3.6
Origin of anal fin	50.8–61.3	55.5	3.0
Base of anal fin	30.4–37.0	33.9	2.2
Anal-fin depth	14.5–21.6	17.0	2.5
Peduncle depth	3.5–4.7	4.2	0.3
Peduncle length	10.1–14.2	11.4	1.3

TABLE 2.4. Morphometric data of *Chiasmodon microcephalus* (n=26) and *C. pluriradiatus* (n=7).

Character	*Chiasmodon microcephalus*			*Chiasmodon pluriradiatus*		
	Range	Mean	SD	Range	Mean	SD
Standard length (mm)	51.0–225.5	134.9	50.3	40.6–220.8	97.5	72.9
Head length (mm)	14.4–59.4	36.2	13.2	12.0–62.3	28.2	21.3
Percentage of HL						
Snout	23.7–28.0	25.7	1.1	21.4–24.4	22.6	1.2
Upper jaw	69.3–77.7	74.7	1.8	66.4–73.5	69.8	2.4
Lower jaw	76.8–85.2	81.6	2.3	72.2–77.0	75.1	1.9
Orbit width	13.9–21.5	17.8	1.5	14.3–21.6	18.4	2.6
Orbit height	11.8–18.9	15.1	1.8	11.1–18.4	15.4	2.3
Anterior nostril to eye	10.5–15.1	126	1.1	8.9–12.1	10.3	1.1
Posterior nostril to eye	3.4–5.5	4.5	0.6	2.5–5.7	3.7	1.1
Distance between nostrils	5.8–10.7	7.9	1.3	6.3–8.2	7.1	0.7
Interorbital distance	18.0–22.2	19.8	1.0	18.0–21.8	20.0	1.3
Head width	25.7–36.4	30.2	2.3	26.5–28.7	27.8	1.0
Cheek depth	3.5–7.3	4.5	0.8	2.8–4.3	3.4	0.5
Percentage of SL						
Head length	25.1–29.0	26.9	1.0	26.4–30.5	28.9	1.3
Body width	4.0–13.9	8.1	2.6	6.6–8.9	7.8	0.9
Insertion of pectoral fin	25.7–31.7	28.7	1.6	27.2–31.0	29.3	1.4
Insertion of pelvic fin	27.6–36.2	31.5	2.4	28.8–33.7	31.0	1.9
Pectoral-fin length	13.1–23.6	17.5	2.7	18.0–22.9	20.5	1.6
Pelvic-fin length	7.2–12.6	9.7	1.2	8.9–10.3	9.9	0.6
Origin of 1st dorsal fin	30.9–35.9	33.6	1.5	31.9–34.2	33.0	0.8

TABLE 2.4. (cont.)

Base of 1st dorsal fin	12.2–19.9	16.1	1.7	14.1–16.3	15.5	1.0
1st dorsal-fin depth	7.4–13.7	8.9	1.5	8.3–11.2	9.8	2.0
Origin of 2nd dorsal fin	48.2–55.5	52.6	1.7	48.6–52.0	50.4	1.5
Base of 2nd dorsal fin	35.1–40.8	37.7	1.5	37.5–40.5	39.3	1.3
2nd dorsal-fin depth	12.1–19.0	15.7	1.7	16.1–19.1	17.5	1.5
Origin of anal fin	50.9–61.8	55.5	3.0	49.9–53.9	51.4	1.5
Base of anal fin	30.4–36.0	33.7	1.7	29.5–36.9	34.9	3.6
Anal-fin depth	11.4–17.8	15.2	1.8	12.9–16.0	14.7	1.4
Peduncle depth	3.5–5.5	4.2	0.5	3.8–4.7	4.3	0.4
Peduncle length	10.6–14.9	12.1	1.2	11.2–13.4	12.0	1.0

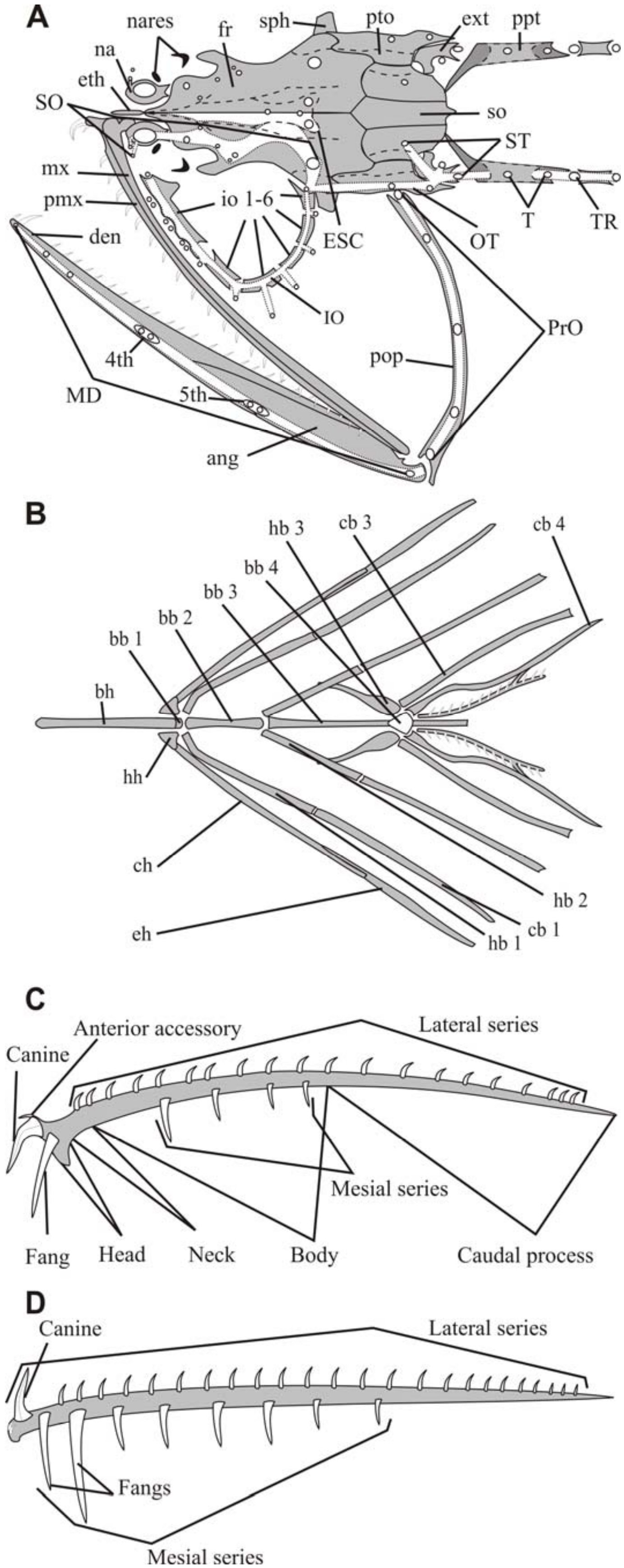
TABLE 2.5. Morphometric data of *Chiasmodon asper* (n=5) and *C. harteli* (n=24). D stands for distance, H, for holotype, and SD, standard deviation.

Character	*Chiasmodon asper*				*Chiasmodon harteli*			
	H	**Range**	**Mean**	**SD**	**H**	**Range**	**Mean**	**SD**
Standard length (mm)	64.2	60.5–178.6	94.9	48.3	133.4	46.3–198.3	137.4	39.5
Head length (mm)	18.8	18.0–56.6	28.5	16.0	35.5	12.3–50.7	36.6	10.4
Percentage of HL								
Snout	20.9	20.9–24.6	22.9	1.4	24.4	23.0–26.6	24.9	1.0
Upper jaw	70.3	69.4–70.8	70.2	0.6	77.2	74.3–84.2	77.9	2.3
Lower jaw	76.4	73.3–77.1	75.6	1.6	86.4	80.8–89.9	84.5	2.5
Orbit width	17.8	12.7–17.9	16.3	2.2	18.9	13.7–24.7	18.2	2.5
Orbit height	14.8	12.6–15.5	14.2	1.3	14.8	12.7–19.3	15.6	1.6
Anterior nostril to eye	10.0	9.5–12.9	11.2	1.5	12.5	11.2–14.8	13.0	0.9
Posterior nostril to eye	2.8	2.8–4.8	3.8	0.9	4.0	2.1–6.8	4.8	1.0
D. between nostrils	7.3	6.3–8.9	7.5	1.0	7.3	6.7–9.6	7.8	0.8
Interorbital distance	21.0	18.1–21.0	20.1	1.2	17.5	17.0–20.0	18.5	0.9
Head width	27.3	27.2–29.1	27.8	0.8	27.8	26.8–34.8	29.2	1.8
Cheek depth	4.1	4.1–6.5	5.5	1.0	6.0	3.2–6.5	4.6	1.0
Percentage of SL								
Head length	29.3	28.2–31.7	29.6	1.3	26.6	25.0–28.8	26.7	1.0
Body width	7.4	5.2–9.1	7.1	1.4	6.4	4.5–8.9	6.6	1.0
Insertion of pectoral fin	20.5	29.2–32.9	30.4	1.5	30.1	26.0–30.7	28.7	1.2
Insertion of pelvic fin	31.4	30.8–33.8	32.2	1.1	32.9	25.9–33.7	30.5	1.6
Pectoral-fin length	27.6	19.6–27.6	23.4	2.9	16.8	14.1–20.8	16.8	1.8
Pelvic-fin length	10.7	8.0–11.6	10.0	1.4	10.8	11.8–11.8	10.0	1.0
Origin of 1st dorsal fin	33.4	33.2–35.3	33.8	0.9	33.8	31.0–35.5	32.8	1.1

TABLE 2.5. (cont.)

Base of 1st dorsal fin	19.8	15.7–19.8	17.0	1.7	17.7	11.7–20.9	16.1	1.9
1st dorsal-fin depth	13.8	8.8–13.8	11.0	2.0	8.1	6.9–11.4	8.7	1.3
Origin of 2nd dorsal fin	53.5	50.3–53.5	52.0	1.4	52.0	49.0–56.3	51.2	1.7
Base of 2nd dorsal fin	41.7	38.3–41.7	39.7	1.3	37.3	33.5–41.7	38.9	1.8
2nd dorsal-fin depth	13.7	13.5–17.9	15.0	2.0	18.3	11.3–19.1	15.5	2.5
Origin of anal fin	54.8	49.8–54.8	53.1	2.0	50.6	48.9–64.0	52.7	3.4
Base of anal fin	37.6	34.8–39.4	36.9	2.0	36.1	26.2–39.1	35.9	2.4
Anal-fin depth	15.7	14.9–16.1	15.5	0.5	20.5	12.6–20.5	15.8	2.3
Peduncle depth	4.3	4.0–4.8	4.3	0.3	4.3	3.2–4.5	3.9	0.4
Peduncle length	10.4	9.3–13.3	11.6	1.8	11.6	10.2–13.8	12.1	0.8

FIGURE 2.1. Schematic of a hypothetical *Chiasmodon*: in (A) sensory system of head; (B) ventral elements of gill arch in dorsal view; (C) right premaxilla; and (D) right dentary. Some of the conditions presented may not be present at the same time in an individual specimen (for specific variation, see Figures 2.4, 2.5, and 2.6).


A
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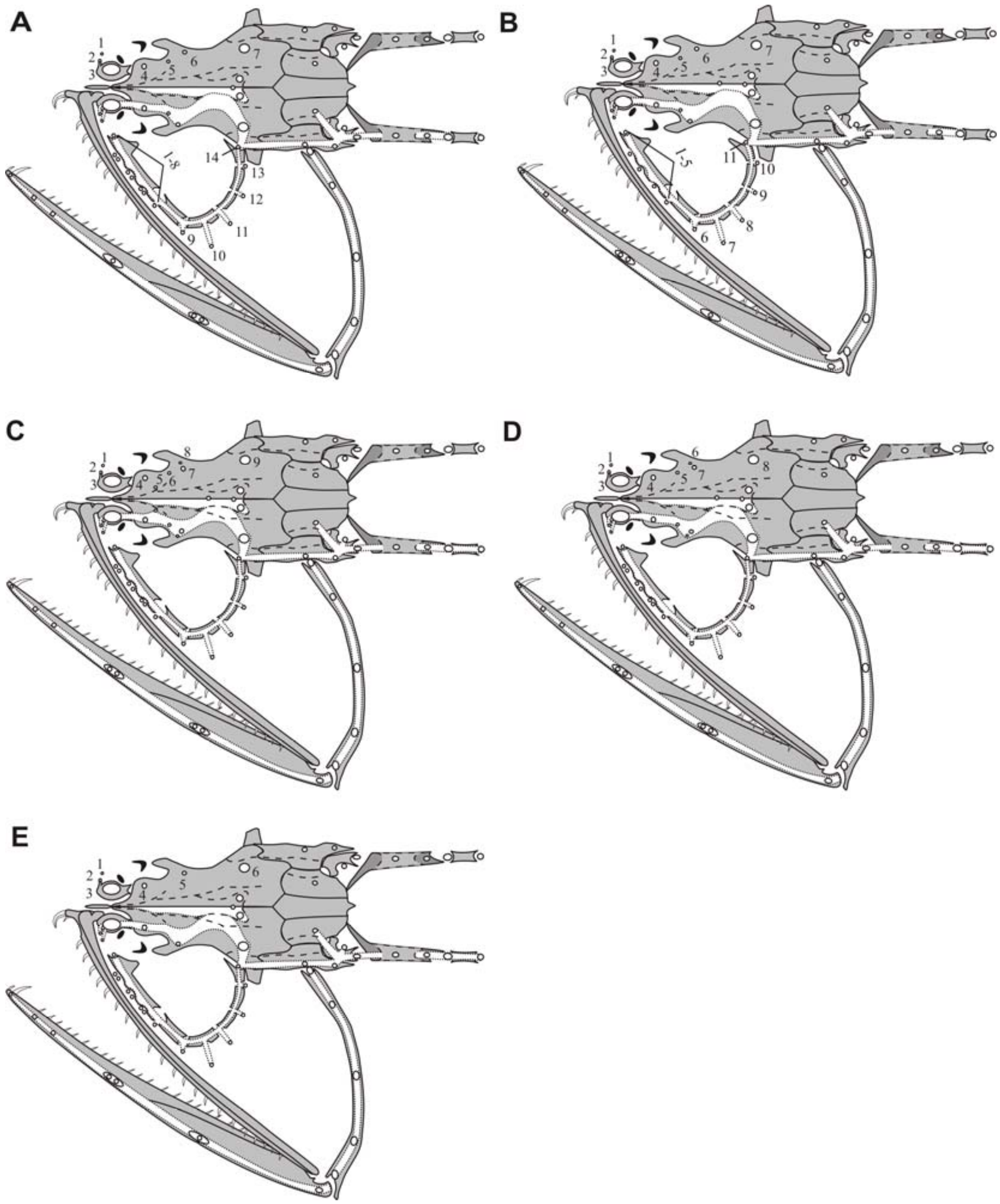
4th
MD
5th
ang
B
hb 3
cb 3
cb 4
bb 4
bb 3
bb 2
bb 1
bh
hh
ch
hb 2
cb 1
eh
hb 1
C
Anterior accessory
Lateral series
Canine
Mesial series
Fang
Head
Neck
Body
Caudal process
D
Canine
Lateral series
Fangs
Mesial series

FIGURE 2.2. Schematic of the most common configurations of sensory pores in head of *Chiasmodon* (see text for details and variation): (A) *C. niger* and *C. microcephalus*; (B) *C. subniger*; (C) *C. asper*; (D) *C. pluriradiatus* and *C. braueri*; and (E) *C. harteli*.


A
1
2
3
4
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6
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1-8
9
10
11
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13
14
B
1
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4
5
6
7
1-5
6
7
8
9
10
11
C
1
2
3
4
5
6
7
8
9
D
1
2
3
4
5
6
7
8
E
1
2
3
4
5
6

FIGURE 2.3.Schematic of teeth on ventral elements of gill arch (see text for details): (A) *C. braueri*; (B) *C. harteli* and *C. niger*; (C) *C. pluriradiatus* and *C. asper*; and (D) *C. subniger* and *C. microcephalus*.

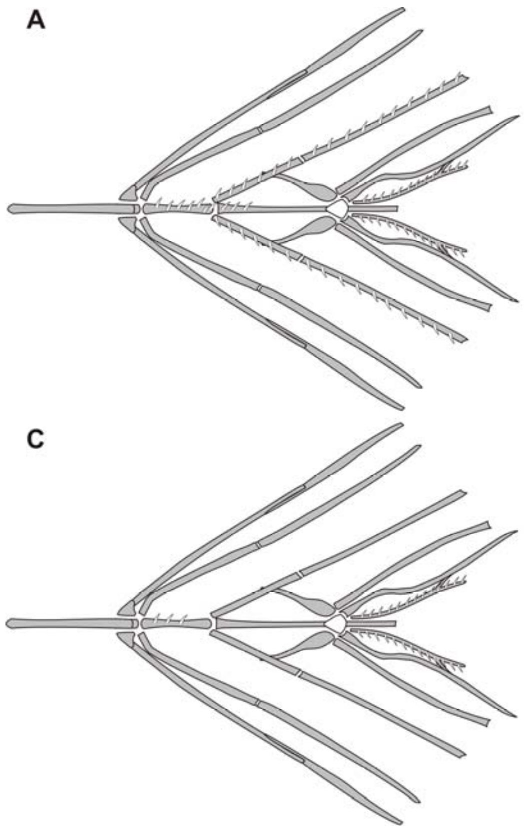
A
B
C
D

FIGURE 2.4. Schematic of dentition in premaxilla of *Chiasmodon* (see text for details): (A) *C. braueri*, *C. harteli*, *C. niger*, *C. microcephalus*, and *C. subniger*; (B) *C. pluriradiatus*, *C. asper*.

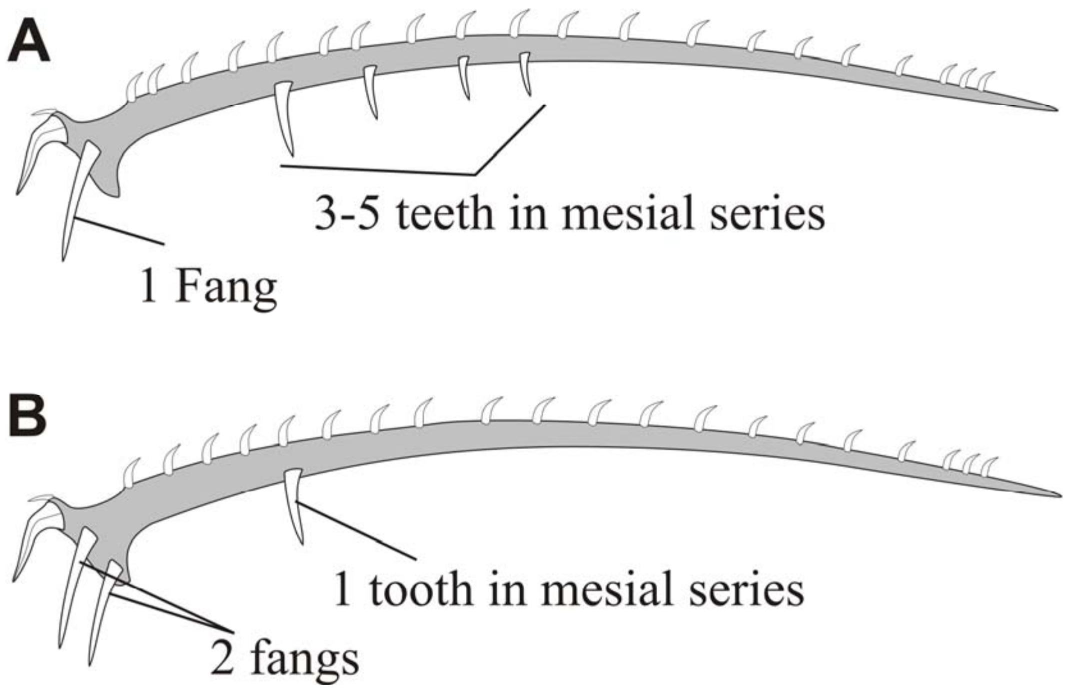
A
3-5 teeth in mesial series
1 Fang
B
1 tooth in mesial series
2 fangs

FIGURE 2.5. Distribution of *Chiasmodon*: in (A) *C. niger* (circle), *C. braueri* (asterisk), and the type locality of *C. bolangeri* (X; species valid as *C. niger*, see text); in (B) *C. pluriradiatus* (cross), and *C. subniger* (diamond); and in (C) *C. asper* (star), *C. harteli* (square), and *C. microcephalus* (triangle). Solid symbols stand for type localities, open symbols for specimens examined in this work; each symbol may represent more than one sampling locality or lot of specimens.

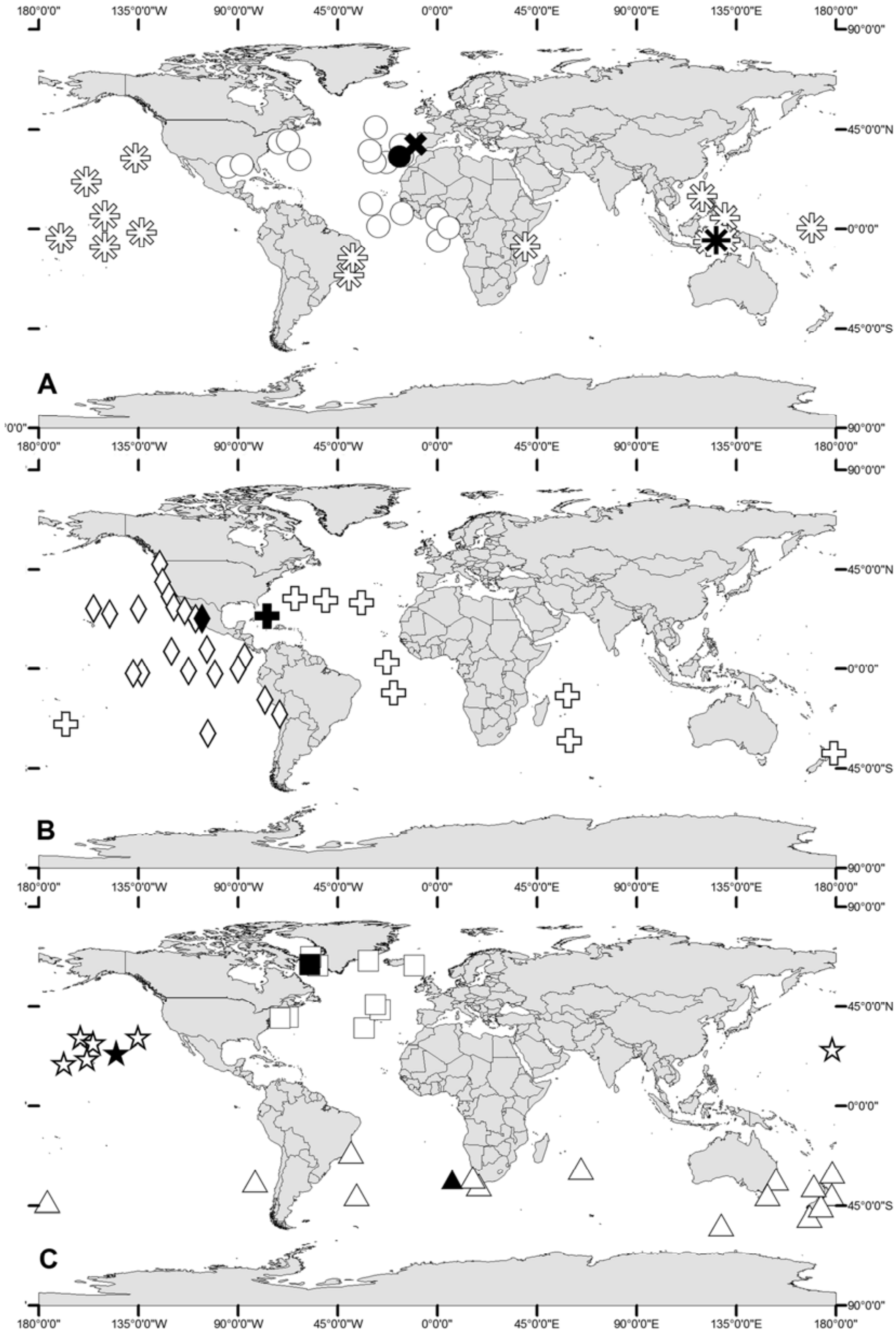
180°0'0"
135°0'0"W
90°0'0"W
45°0'0"W
0°0'0"
45°0'0"E
90°0'0"E
135°0'0"E
180°0'0"
90°0'0"
45°0'0"N
0°0'0"
45°0'0"S
90°0'0"
A
B
C

FIGURE 2.6. *Chiasmodon niger* in lateral view: (A) BMNH 1863.12.12.4, holotype; (B) ZMH 9171, 117.3 mm.

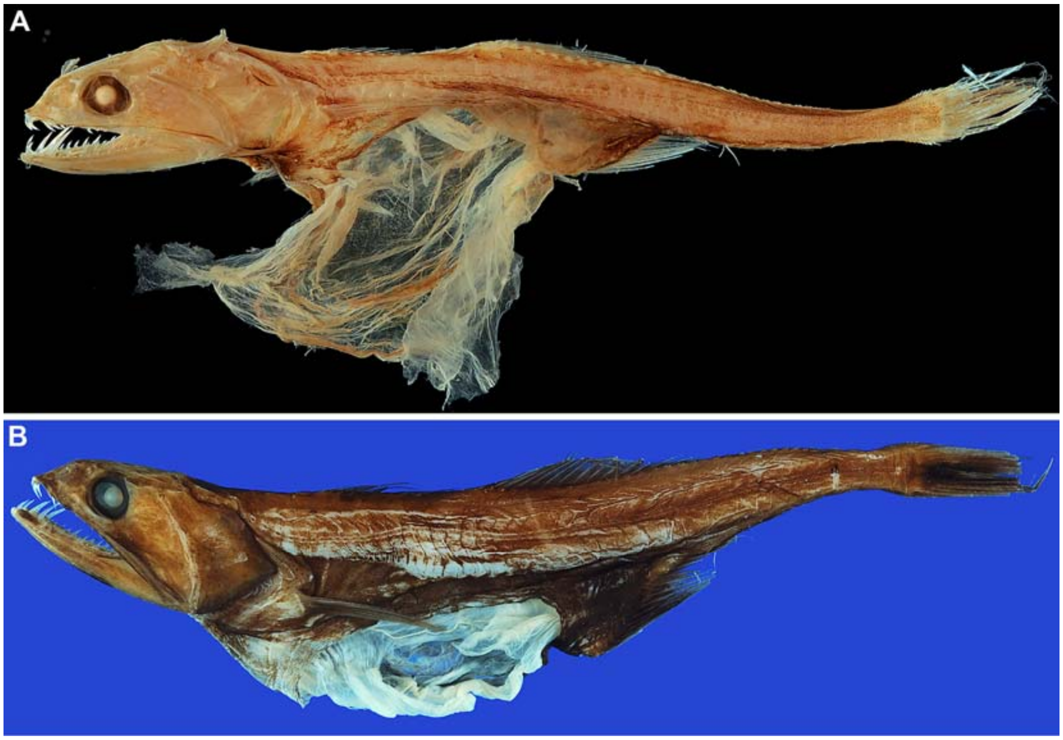
A
B

FIGURE 2.7. *Chiasmodon subniger* in lateral view: (A) MCZ 28744, holotype, ca. 40.0 mm; (B) LACM 30562–5, 117.5 mm.


A
B

FIGURE 2.8. *Chiasmodon braueri* in lateral view: (A) ZMA 112.462, holotype, 45.0 mm; (B) SIO 70–306–60, 149.8 mm.

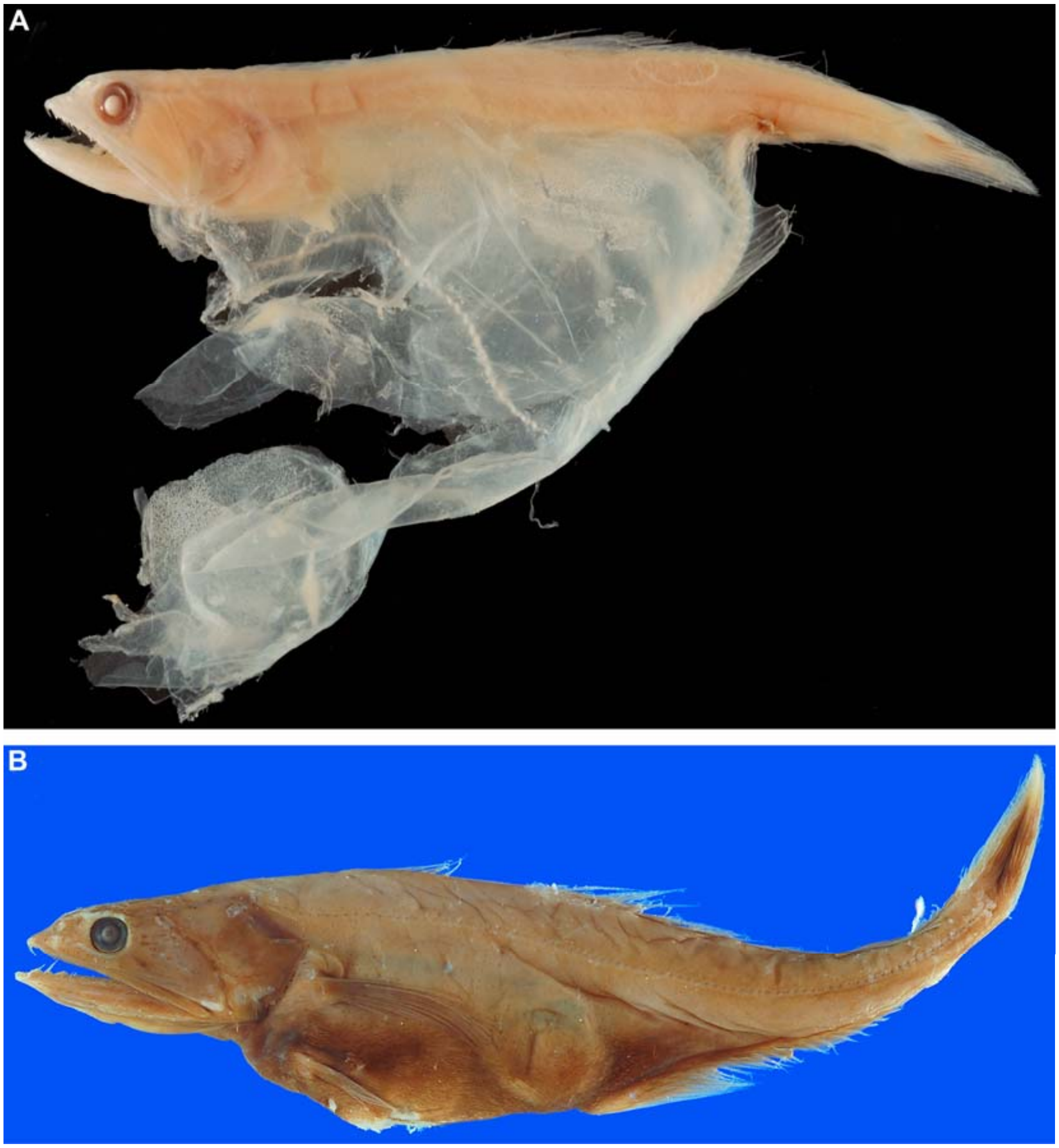
A
B

FIGURE 2.9. *Chiasmodon microcephalus* in lateral view: (A) BMNH 1930.1.12.1060, holotype; (B) NMNZ P. 34841, 150.1 mm.


A
B

FIGURE 2.10. *Chiasmodon pluriradiatus* in lateral view: (A) YPM 2827, holotype, 48.5 mm; (B) USNM 202439, 87.5 mm.


A
B

FIGURE 2.11. *Chiasmodon asper* in lateral view: (A) SIO 68–483–60, holotype, 64.2 mm, (B) HUMZ 143630, paratype, 83.7 mm.


A
B

FIGURE 2.12. *Chiasmodon harteli* in lateral view: (A) BSKU 48914, holotype, 135.5 mm; B) BMNH 2002.11.22.66, paratype, 46.3 mm.


A
B

CHAPTER 3 – REVISION OF THE GENUS *KALI* LLOYD

Publications:

Melo, M. R. S. (2008) The genus *Kali* Lloyd (Chiasmodontidae: Teleostei) with description of new two species, and the revalidation of *K. kerberti* Weber. *Zootaxa*, 1747: 1–33.

Melo, M. R. S. (submitted) *Kali colubrina* Melo 2008, a senior synonym of *Kali caribbea* Prokofiev 2008. *Zootaxa*, 3 pages MS.

Abstract

Kali Lloyd is a very distinctive group of bathypelagic fishes with fragile bones in the cranium and recurved teeth, which are remarkably enlarged in some species. The genus has a worldwide distribution, being found in the subtropical to equatorial regions of the Atlantic, Indian, and Pacific; one species is also found in the Southern Ocean. In this taxonomic revision, seven species are considered valid, two of them described herein: *K. indica*; *K. kerberti*; *K. macrodon*; *K. macrurus*; *K. parri*; *K. colubrina*, new species; and *K. falx*, new species. *Kali kerberti* is re-evaluated as valid and the senior synonym of *K. normani*. A key for the species with updated maps of distribution are also given.

Introduction

The species of *Kali* Lloyd with their recurved teeth, delicate bones and, sometimes, enlarged fangs are among of the most distinctive bathypelagic fishes. The genus includes seven valid species widely distributed in the Atlantic, Indian, Pacific, and Southern Oceans: *Kali indica* Lloyd 1909; *K. kerberti* (Weber 1913); *K. macrodon* (Norman 1929); *K. macrurus* (Parr 1933); *K. parri* Johnson and Cohen 1974; *K. colubrina*, new species; and *K. falx*, new species. Two additional nominal species were described, *K. normani* (Parr 1933), a junior synonym of *K. kerberti*, and *K. pterodactylops* (Smith 1965), of *K. macrodon*. Taxonomically, it is one of the most complexes among the Chiasmodontidae: of the seven nominal species previously described only one, other than the type species, was assigned correctly to the genus *Kali*; four genera were erected and are now recognized as synonymous of *Kali*; *K. macrodon* was described in the wrong genus; *K. gargaropteron* was described from a larva; and *K. kerberti* was described twice, and placed in a wrong synonym for more than 30 years. A taxonomic summary is given below.

Lloyd (1909) described the type species of the genus, *Kali indica*, based on a single specimen collected by the British R.I.M.S. *Investigator* off India, in the Indian Ocean. Weber (1913) erected the genus *Odontonema* while describing *O. kerberti* from a specimen collected by the Dutch Siboga Expedition in the Indonesia. Apparently Weber was not familiar with Lloyd's work, because there is no reference to it. Norman (1929) described *Dysalotus macrodon* from a specimen obtained in the eastern South Atlantic.

Parr (1931a) erected *Dolichodon* while describing *D. normani* from the Pacific coast of Mexico, and also included *K. macrodon*. Later, *Dolichodon* was replaced by *Hemicyclodon* (Parr, 1931b) because it was preoccupied. In 1933, Parr described *H. macrurus* from off the Bahamas. Smith (1965) was the first author to recognize the unnecessary proliferation of genera and to refer to Lloyd's work: he synonymized *Odontonema* and *Hemicyclodon* with *Kali*. In that same work, Smith described *Gargaropteron pterodactylops* as "an aberrant form of the Chiasmodontidae" (p. 567), and provided a very detailed redescription of *K. kerberti* based on type examination – but was unable to compare it with the types of other species.

Johnson (1969) provided the first revision of *Kali*, after examining extensive material from the Pacific, considered *K. kerberti* as a junior synonym of *K. indica*, and the remaining species as valid – but made no mention about the status of *G. pterodactylops*. Johnson and Cohen (1974) added records to the Atlantic, described *K. parri*, recognized that *K. pterodactylops* was actually a juvenile of *Kali*, and suggested it as a junior synonym of *K. macrodon*. Because of the generic name given by Smith (1965), the juveniles of all species of *Kali* are nowadays referred to as the gargaropteron stage.

Herein the genus *Kali* is reviewed, with the description of two new species: *Kali colubrina*, new species; and *Kali falx*, new species. After examination of the primary types, *K. kerberti* is re-evaluated and considered the senior synonym of *K. normani*; *K. pterodactylops* is retained as a junior synonym of *K. macrodon*. A key for the species and updated maps of distribution are also being provided.

Material and Methods

Morphometric and meristic data were obtained following the protocol described by Melo *et al.* (2007) except that, because the tip of dorsal- and anal-fins rays is frequently broken, the total number of rays is presented rather than discriminating branched to unbranched rays; the length of those fins are not presented. Measurements were recorded to the nearest 0.1 mm using digital calipers. Because of the fragile bones that are frequently destroyed, measurements were only made on well preserved specimens, and from the best preserved side – *i.e.*, not always from left side. Vertebral counts were made from cleared and stained or x-rayed specimens.

The terminology for tooth attachment follows Fink (1981) with the addition of *ventral attachment* to indicate a unique mode of attachment that connects the ventral part of the tooth to bone (see diagnosis for genus). Terms used to define dentition pattern are as follows: *conical*, triangular tooth in the shape of a cone; *caniniform*, large, pointed, conical tooth; *needle-like*, long, slender, aculeate tooth; *fang*, remarkably elongated tooth, resembling a fang of a viper (Viperidae: Serpentes); *recurved*, posteriorly or ventrally curved; *sickle-shaped*, curved like a sickle, but not curved posteriorly; *tooth crown* (cap), the distal, enamel part of tooth; *flange*, sharp, cutting edge on tooth crown that transverses the tooth apex. For description of dentition, the following measurements were taken: tooth length measured in a straight line from base to tip of tooth; tooth crown length measured in the largest tooth, in a straight line from base of crown to tip of tooth.

Major oceans terminology follows Tomczack and Godfrey (2003); biogeographic zones of the Atlantic follow Backus *et al.* (1977) with the addition of Atlantic Subantarctic to the region between the South Atlantic Subtropical and Guinean Provinces, and Southern Ocean; classification for Indian and Pacific Oceans follows Springer (1982). Institutional abbreviations are as listed by Leviton *et al.* (1985); cs stands for *cleared and stained*.

Results

Key to the Species of *Kali*

1a. Teeth with ventral ligament in mesial series and at least in posterior portion of lateral series (Fig. 2.1); second dorsal fin 18–23; anal fin 19–23... 2

1b. Teeth with ventral ligament restricted to mesial series (Fig. 2.1); second dorsal fin 21–26; anal fin 22–28 3

2a. Orobranchial chamber and gill arches pale; lateral series with needle-like, type 4 teeth at anterior portion of premaxilla (total teeth six to ten) and dentary (teeth seven to

13); recurved teeth with ventral attachment in lateral series restricted to posterior third of premaxilla (teeth seven to 10), and posterior fourth of dentary (total teeth five to 11); teeth in mesial series in premaxilla three to four, in dentary six to eight (Fig. 2.1); total vertebrae 33–34..*Kali macrura*

2b. Orobranchial chamber and gill arches dark; type 4 teeth absent in lateral and mesial series of premaxilla and dentary; recurved teeth with ventral attachment in lateral series extending along entire bone in premaxilla (total teeth 21-39) and dentary (total teeth 18-32); teeth in mesial series in premaxilla six to 15, in dentary seven to 17 (Fig. 2.1); total vertebrae 37–38 .... *Kali parri*

3a. Teeth in mesial series of premaxilla and dentary not remarkably elongated; longest tooth of premaxilla 10.1–14.2 % in premaxillary length; longest tooth in dentary 8.9–12.5 % in dentary length .... *Kali colubrina*

3b. Teeth in mesial series of premaxilla and dentary remarkably elongated, fang-like; longest tooth of premaxilla 20.1–33.5 % in premaxillary length; longest tooth in dentary 14.0–29.3 % in dentary length 4

4a. Teeth in lateral series of premaxilla and dentary few (11 or less), conical, slightly curved; first tooth of lateral series of premaxilla the largest in the series, with little or restricted movement; teeth in mesial series of premaxilla three, all fang-like; teeth in mesial series of dentary three to four; gill rakers absent; upper and lower jaws not strongly curved.. 5

4b. Teeth in lateral series of premaxilla and dentary numerous (10–33) straight, needle-like; first tooth of lateral series smaller than adjacent teeth, all teeth depressible; teeth in mesial series of premaxilla five to ten, first tooth small and conical, not fang-like; teeth in mesial series of dentary four to nine (Fig. 2.1); gill rakers present; upper and lower jaws strongly curved 6

5a. First tooth in lateral series of premaxilla slightly curved, not projecting anteriorly, 15.2–16.4% in premaxillary length; first tooth in mesial series of premaxilla anterior to level of anterior nostril, and to second tooth in lateral series; first tooth in mesial of dentary beside second tooth of lateral series (Fig. 2.1); eye enlarged, orbit width 15.4–22.7% and orbit height 12.5–18.0% in head length; basihyal not reduced and curved, tip of basihyal pointing forward... *Kali indica*

5b. First tooth in lateral series of premaxilla moderately arched, sickle-shaped, projecting anteriorly, 17.2–20.5% in premaxillary length; first tooth in mesial series of premaxilla below level of anterior nostril, beside second tooth in lateral series; first tooth in mesial series of dentary between second and third teeth of lateral series (Fig. 2.1); orbit width 11.2–16.0% and orbit height 9.7–12.4% in head length; basihyal very reduced and strongly curved, tip of basihyal pointing ventrally ....*Kali falx*

6a. Internal row of premaxillary teeth seven to ten, six to nine fangs, mesial row of dentary teeth seven to nine (Fig. 2.1); teeth in palatine five to 10 (modally seven) .... *Kali macrodon*

6b. Internal row of premaxillary teeth five to six, four to five fangs, mesial row of dentary teeth four to five (Fig. 2.1); teeth in palatine zero to six (modally three)...*Kali kerberti*

Kali Lloyd 1909

Snake-toothed swallowers

Kali Lloyd 1909: 154–155, Plate 45 [type species: *Kali indica* Lloyd 1909, by original designation; gender: Feminine].

Odontonema Weber 1913: 149 [type species: *Odontonema kerberti* Weber 1913, by original designation].

Dolichodon Parr 1931a: 45–4, not *Dolichodon* Gray 1865; not *Dolicodon* Frazango 1874 [type species: *Dolichodon normani* Parr 1931, by original designation].

Hemicyclodon Parr 1931b: 162 [substitute name for *Dolichodon*, preoccupied].

Gargaropteron Smith 1965: 569, figure 1 [type species: *Gargaropteron pterodactylops* Smith 1965, by original designation].

Diagnosis. The genus *Kali* is diagnosed from *Chiasmodon*, *Dysalotus* and *Pseudoscopelus* by three characteristics: branchiostegal rays six (*vs.* branchiostegal rays seven); the presence of strikingly recurved teeth in the mesial series of both premaxilla and dentary (*vs.* teeth in mesial series of dentary and premaxilla straight or slightly curved, never recurved); and a unique type of tooth attachment to bone, the ventral attachment, that connects the ventral basis of the tooth to the dentigerous area of denary and premaxilla, allowing the rotation on a reflex angle of up to 270^{o} on its own axis (*vs.* tooth completely ankylosed to bone, or with posterior attachment that allows deflection but not allows tooth rotation; for further discussion on other types of tooth attachment among the teleosts see Fink 1981 and Huysseune & Sire 1998). *Kali* can be further diagnosed from *Dysalotus* by dentition in two rows (*vs.* dentition in three series of several rows); and prickles on flank absent (*vs.* prickles on flank present). From *Chiasmodon* and *Pseudoscopelus*, by the cranium fragile with bone trabeculae of frontals easily distinguishable with naked eye (*vs.* bones forming cranium well calcified with trabeculae not apparent); nasal weakly calcified, circular but not spoon-shaped, positioned in the dorsal part of the snout, and covered by pigmented skin (*vs.* nasal spoon-shaped in the lateral or anterior sides of the snout, covered by thin transparent skin); parietals small, with less than half the size of supraoccipital (*vs.* parietals enlarged, of same size or little smaller than supraoccipital); pre- and postzygapophyses absent (*vs.* pre- and postzygapophyses present); elongate neuromasts in head absent (*vs.* enlarged elongated neuromasts exposed in surface of head, over supraoccipital, parietals, frontals and pterotic cranial bones, face, snout, and lower jaw); last scale of lateral line contiguous with penultimate scale (*vs.* last scale of the lateral line well separated from the penultimate scale and positioned on lower lobe of the caudal fin).

Description. Dentition and color patterns detailed in species accounts. Body elongate, laterally compressed. Greatest body depth at origin of first dorsal fin. Scales absent, except for lateral-line scales, embedded in skin.

Anterior profile of head elongate, concave in lateral view, snout pointed or slightly concave. Bones of head remarkably fragile, with bone trabecules visible by naked eye. Head with cavernous appearance, with dorsal concavity at level of braincase medially and well developed crests in frontals, extending laterally to concavity in posterior part of cranium, and converging at level of posterior naris; foramina of sensorial system of head wide. Lower jaw projecting anterior to upper jaw, slightly arched in *Kali colubrina*, *K. macrura*, and *K. parri*, and moderately arched in *K. indica*, *K. falx*, *K. kerberti*, and *K. macrodon*; upper jaw slightly arched in *K. colubrina*, *K. macrura*, and *K. parri*, and moderately arched in *K. indica*, *K. falx*, *K. kerberti*, and *K. macrodon*. Ascending process of premaxilla flat in *K. colubrina*, *K. falx*, *K. indica*, *K. parri*, *K. macrura*, and with anterior concavity in *K. macrodon* and *K. kerberti*. Orbit circular, nares oval, and distinctly separated.

Rays of fins fragile and often broken, few specimens available with fins intact; pectoral fin insertion lateral on body, posterior to angle of opercle; pelvic fin insertion ventral, below or slightly anterior to pectoral fin. Dorsal fins two, true spines (*sensu* Johnson & Patterson 1993) present only in first dorsal fin; last spine of first dorsal fin frequently embedded in skin. Anal fin opposite to second dorsal fin, lacking true spines. Caudal fin forked, lacking true spines.

Gill arches four, with poorly developed filaments; pseudobranchia present. Epibranchial of first arch attached to opercle until midline; ceratobranchial of second, third and fourth arches linked; fourth gill arch mostly attached to body wall, except for oval slit in ceratobranchial.

Distribution. World-wide, in the Atlantic, Indian, Pacific, and Southern Ocean, from 53° N to 60° S (Fig. 2.2).

Etymology. Named after Kali, a Hindu goddess.

Remarks. The skin of *Kali* is very delicate and missing in the majority of the examined specimens; in most specimens only the dermis is preserved, but the epidermis is completely gone; in others, even dermis is destroyed. With the exception of the type series of *K. parri*, no other specimen examined has the skin fully preserved on the head; therefore a precise count of pores in the dorsal part of head was not possible.

Kali indica Lloyd 1909

(Figs. 3.3; Tables 3.1, 3.3 and 3.4)

Kali indica Lloyd 1909: 154–155, plate 54, figure 6 [original description; type locality Bay of Bengal, India, 16°56’15” N, 92°33’00” E, 1343 fathoms (2458 m), R/V *Investigator* sta. 312; holotype ZSI F1054/1]; Smith 1965[reassignment of genus]; Norman 1966: 366–367 [key to genera of Chiasmodontidae and list of species]; Johnson 1969: 587–588, figure 1 [revision of the genus and key to the species]; Johnson and Cohen 1974: 39–41 [revision of the genus, diagnosis and brief description]; Novikov et al. 1981 [list of specimens collected in Jingu Seamount, Emperor chain; material not examined]; Johnson and Keene 1986: 732, figure 228.5 [key to the species]; Johnson and Keene 1990: 902 [record of eastern tropical Atlantic species]; Trunov 1998: 138–139, figure 1 [record for the Antarctic]; Smith (in press) [key to species]; Mooi and Paxton 2001: 3495–3496 [list of Pacific species]; Nakabo 2002: 1589 [key to family]; McEachran and Sutton 2003: 1742–1743 [list of Atlantic species]; Moore *et al.* 2003: 227 [checklist of deep-sea fishes from off New England, Western North Atlantic]; Mundy 2005: 455 [checklist of Hawaiian species]; Hardy 2005: 1902, 1908–1909 [identification of larvae]; Hardy 2007: 1312 [identification of larvae].

Diagnosis. *Kali indica* can be distinguished from all species of *Kali* except *K. falx* by the teeth in lateral series of premaxilla seven to 11, caniniform, elongated, slightly curved, type 4, widely spaced (*vs.* teeth in lateral series of premaxilla 13 to 33; recurved, with ventral attachment, closely spaced in *K. parri*; needle-like, closely spaced in *K. kerberti* and *K. macrodon* and anterior part fourth of *K. normani*; caniniform but not very elongated in *K. colubrina*); first tooth of lateral series of premaxilla longest, with tight type 4 attachment (*vs.* first tooth of lateral series of premaxilla not remarkably enlarged, smaller than adjacent teeth, with loose types 4 attachment or with ventral attachment to bone); teeth in mesial series of premaxilla three, fang-like (*vs.* teeth in mesial series of premaxilla four or 15; not fang-like in *K. macrura*, *K. parri*, and *K. colubrina*); teeth in lateral series of dentary six to eight, very elongated, curved, type 4, widely spaced (*vs.* teeth in lateral series of dentary 12 to 32; recurved, with ventral attachment, closely spaced in *K. parri*, needle-like, closely spaced in *K. kerberti* and *K. macrodon* and anterior part fourth of *K. normani*; recurved in *K. colubrina*).

Kali indica can be distinguished from *K. falx* by the larger eye, orbit width 15.4–22.7% and orbit height 12.5–18% in head length (*vs.* eye small, orbit width 11.2–16.0% and orbit height 9.7–12.4% in head length); basihyal elongated and straight, pointing forward (*vs.* basihyal reduced and strongly curved, pointing ventrally); first tooth in lateral series of premaxilla enlarged, 15.2–16.4 % in premaxillary length, slightly curved, not projecting anteriorly (*vs.* first tooth in lateral series of premaxilla remarkably enlarged, 17.2–20.5% in premaxillary length, sickle-shaped, projecting anteriorly); first tooth in mesial series of premaxilla anterior to level of anterior nostril, and to second tooth of lateral series (*vs.* first tooth in mesial series of premaxilla below level of anterior nostril, and beside second tooth of lateral series); first tooth in mesial series of dentary beside second tooth of lateral series (*vs.* first tooth in mesial series of dentary between second and third teeth in lateral series).

Description. Moderate-sized species of *Kali*, largest specimen examined 207.7 mm SL. Morphometric data summarized in table 3.3, and meristic in table 3.4. General body pattern as described for genus.

Dentition. Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials; premaxilla and dentary as illustrated in figure 3.1 A, and summarized in table 1. Tooth crown length 14.9–20.5% in tooth length. Premaxilla elongated, arched in lateral view, with teeth arranged in two series: lateral and mesial. Lateral series in single row; teeth type 4, caniniform, with flange, widely spaced. Anteriormost tooth longest, 15.1–16.4% in premaxillary length, slightly curved, inserted at antero-ventral tip of premaxilla; tightly attached to bone, with restricted movement. Following teeth curved, decreasing in size from anterior to posterior, at lateral edge of premaxilla; second to fourth teeth at anterior half of premaxilla, between level of anterior nostril and posterior margin of eye; posterior teeth needle-like, at posterior third of premaxilla. Mesial series in single row; teeth with ventral attachment, recurved, fang-like, largest tooth 23.4–33.5% in premaxillary length, with flange; widely spaced, decreasing in size from anterior to posterior; base of first tooth below anterior nostril, beside second tooth of lateral series; second tooth below anterior margin of eye, between third and fourth teeth of lateral series; and third tooth slightly posterior to posterior margin of eye, between fourth and fifth teeth of lateral series.

Dentary elongated, moderately arched in lateral view; teeth arranged in two series: lateral and mesial. Lateral series in single row; teeth type 4, caniniform, slightly curved, with flange, widely spaced; anterior tooth longest, remaining teeth decreasing in size from anterior to posterior, opposite to premaxillary teeth. Mesial series in single row; teeth with ventral attachment to bone, recurved, fang-like, largest tooth 20.1–29.3% in dentary length, with flange. Teeth widely spaced, decreasing in size from anterior to posterior; base of first tooth beside second of tooth of lateral series; second tooth halfway between third and fourth of teeth of lateral series, and third tooth slightly anterior to fifth tooth of lateral series. Single specimen (MNRJ 26693) with small fourth tooth in mesial series, at posterior end of dentary.

Palatine teeth type 4, conical, slender, with short flange, in single row. Lower pharyngeal teeth type 4, needle-like, without flange, in single row; upper pharyngeal teeth type 4, conical, slender, without flange, in one to two rows. Teeth absent on gill arches, basihyal and basibranchials.

Color. Skin covering body fragile, missing in most specimens, description based on MCZ 164764. Epidermis black, thin and fragile, completely destroyed or restricted to small patches in all specimens examined; dermis thin, transparent with widely spaced melanophores. Peritoneum transparent, with moderate concentration of melanophores. Orobranchial chamber pale, with few widely-spaced melanophores in sides of mouth, opercle and membranes between branchiostegal rays; gill arches and filaments pale.

Distribution. World-wide in the equatorial, tropical, subtropical, temperate and subpolar regions: in the Atlantic from 40° N to 40° S; in the Indian from the type locality, 16°56’ N, 92°33’ E; in the Pacific 31° N to 43° S; and in the Southern Ocean between

50° S and 60° S (Fig. 3.2).

Bathymetric distribution. Bathypelagic zone; more frequently recorded in depths between 1400 and 2500 m (mean 1954 m). A single record from above 1000 m (935 m); deepest record at 3300 m.

Kali kerberti (Weber 1913)

(Figs. 3.4; Tables 3.1, 3.3 and 3.4)

Odontonema kerberti Weber 1913: 149 [original description; type locality Banda Sea, Indonesia 5°39’ S, 122°12’ E, Siboga sta. 208, 1886 m; holotype ZMA 104006]; Norman 1929: 544 [key to species, distribution based on original description]; de Beaufort and Chapman 1951: 10–11 [record based on original description]; Norman 1966: 366–367 [key to genera of Chiasmodontidae and list of species].

Kali kerberti Smith 1965: 572–574, figure 2 [species validated as a member of *Kali*, redescription included].

Dolichodon normani Parr 1931a: 46–47, figure 18 [original description, type locality 16°14’ N, 99°36’ W, 3291 m, 31–VI–1926, R/V *Pawnee*, holotype YPM 2693]. NEW COMBINATION.

Hemicyclodon normani Parr 1931b: 1962 [replacement name for *Dolichodon*, preoccupied].

Kali normani Smith 1965 [species validation and synonymized *Odontonema* with *Kali*]; Johnson 1969: 589–590, figure 1 [revision of the genus and key to the species]; Johnson and Cohen 1974: 42–44 [revision of the genus, diagnosis and brief description]; Johnson and Keene 1986: 734, figure 228.8 [key to the species]; Smith (in press) [key to species]; Johnson and Keene 1990: 9030–904 [record of eastern tropical Atlantic species]; Mooi and Paxton 2001: 3495–3496 [list of Pacific species]; Figueiredo *et a*. 2003: 93 [checklist of Brazilian species]; McEachran and Sutton 2003: 1742–1743 [list of Atlantic species]; Mundy 2005: 455–456 [checklist of Hawaiian species]; Hardy 2005: 1902, 1912–1913 [identification of larvae]; Hardy 2007: 1312 [identification of larvae].

Diagnosis. *Kali kerberti* can be distinguished from all species of *Kali*, except *K. macrodon* by the ascending process of premaxilla with a strong concavity limited anteriorly by bony crest (*vs*. ascending process of premaxilla flat or with gentle concavity, anterior bony crest absent). It further differs from *K. colubrina*, *K. falx*, *K. indica*, and *K. parri* by the teeth in lateral series of premaxilla and dentary 12–25, type 4, needle-like (*vs*. teeth in lateral series of premaxilla with ventral attachment, recurved in *K. parri*; five to 11, caniniform, type 4, slightly curved in *K. indica* and *K. falx*; and recurved in *K. colubrina*); from *K. macrura*, teeth in lateral series of premaxilla and dentary type 4, needle-like, extending to the end of dentigerous area, teeth with ventral attachment absent in lateral series (*vs*. teeth in lateral series of premaxilla and dentary need-like in anterior third and fourth, respectively, followed by teeth with ventral attachment, recurved in posterior areas).

Kali kerberti can be distinguished from *K. macrodon* by the teeth in mesial series of premaxilla and dentary, four to five, modally five (*vs*. teeth in mesial series of premaxilla teeth six to nine, modally seven, of and dentary seven to nine, modally eight).

Description. Moderate-sized species of *Kali*, largest specimen examined 196.4 mm SL. Morphometric data summarized in table 3.3, and meristic in table 3.4. General body pattern as described for genus.

Dentition. Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials; premaxilla and dentary as illustrated in figure 3.1 B and summarized in table 3.1. Tooth crown length 36.5–46.7% in tooth length. Premaxilla elongated, strongly arched in lateral view, with teeth arranged in two series: lateral and mesial. Lateral series in single row; teeth small and numerous, type 4, needle-like, without flange, closely spaced, increasing in size from anterior to posterior on first half, gradually decreasing in size to posterior end. Mesial series in irregular single row; first tooth type 4, conical, slightly curved, with flange, not developed into fang; following teeth fang-like, recurved with ventral attachment, largest tooth 28.1–29.5% in premaxillary length; widely spaced, decreasing in size from anterior to posterior; base of first mesial tooth at anterior ventral portion of premaxilla, second tooth (first fang) at level of anterior nostril, third tooth at posterior nostril, fourth tooth at anterior margin of eye, fifth tooth at posterior margin of eye, and sixth tooth slightly posterior to middle of premaxilla.

Dentary elongated, moderately arched in lateral view; teeth arranged in two series: lateral and mesial. Lateral series in single row; teeth type 4, needle-like, without flange, closely spaced, increasing in size from anterior to posterior on first half, gradually decreasing in size to posterior end. Teeth in mesial series with ventral attachment, recurved, fang-like, largest tooth 23.8–25.8% in dentary, with flange; teeth widely spaced, decreasing in size from anterior to posterior. Base of first tooth opposite to gap between first and second teeth in mesial series of premaxilla; remaining teeth opposite to gaps between premaxillary fangs.

Palatine teeth type 4, conical, slender, with short flange, in single row. Lower pharyngeal teeth type 4, needle-like, without flange, in single row; upper pharyngeal teeth type 4, needle-like, without flange, in two rows. Gill rakers tooth-like, type 1, conical, slender, without flange, individually attached to bone, or in small patches of two; present on first, second and third arches; absent on first hypobranchial, basihyal and basibranchials.

Color. Skin covering body fragile, missing in most specimens, description based on USNM 207601, AMNH 225946 and an unpreserved specimen (Fig. 3.4 B, C). Epidermis black, thin and fragile, completely destroyed or restricted to small patches in all specimens examined; dermis thick and gelatinous, whitish or clear gray, with widely spaced melanophores. Peritoneum transparent, with moderate concentration of melanophores. Orobranchial chamber, gill arches and gill filaments pale, melanophores absent; red blood vessels visible in fresh specimen.

Distribution. World-wide in the equatorial, tropical, and subtropical regions: in the Atlantic from 38° N to 21° S; a single record in the western Indian at 8° S, 31° S; in the Pacific 27° N to 33° S (Fig. 3.2).

Bathymetric distribution. Meso- and bathypelagic zones; more frequently recorded in depths between 800 and 2500 m (mean 1343 m). Shallowest record at 200 m; deepest at 4465 m.

Remarks. Johnson (1969: 338) considered *Kali kerberti* to be a junior synonym of *Kali indica* without examining the holotype, based on meristic data and the "strong developed gap between the expanded apices of the premaxillaries" – a characteristic not considered to be useful herein. Johnson and Cohen (1974) after examining the holotype followed Johnson's previous conclusion. Those authors surprising ignored Smith's (1964) detailed-rich redescription of the species. Smith (1965: 573) noticed that "a few slender widely separated small tooth-like gillrakers [sic] are present on the first arch", which is also confirmed herein: the epibranchial has one tooth, the ceratobranchial four, and the hypobranchial zero (teeth-like gill rakers are absent in *K. indica*). Smith (1965: 574) description of the dentition in the holotype of *K. kerberti* also agrees with the data presented herein: "four long blunt moderately stout flexible slightly curved fangs" in the upper jaw (*vs.* three fangs in *K. indica*); "between these [fangs] are several much smaller sharp teeeth [sic]", regarding the teeth in lateral series (*vs.* teeth in lateral series not numerous and sharp, 7–11 in *Kali indica vs.* 15–33 in *K. kerberti*); and in lower jaw "four of the larger fangs, and between these a series of long slender sharp recumbent inwardly directed flexible hair-like [=needle-like] teeth" (*vs.* fangs 3, lateral series not needle-like in *K. indica*). This combination of characteristics is unique and clearly diagnostic for *K. kerberti*, therefore the species is considered as valid.

Kali macrodon (Norman 1929)

(Figs. 3.5; Tables 3.1, 3.5 and 3.6)

Dysalotus macrodon Norman 1929: 542–543, figure 10 [original description; type locality West of Cape Town, South Africa, 33°20'–33°46' S, 15°18'–15°08' E, 2000–2500 m, 4–X–1926, R/V *Discovery*; Holotype: BMNH 1930.1.12.1064].

Gargaropteron pterodactylops Smith 1965: 569–571 [original description, type locality

Beach at Seapark, Natal, South Africa, 30°42’ S, 30°29’ E G. Joliffe col.].

Dolichodon macrodon Parr 1931: 46 [reassignment of genus].

Kali macrodon Smith 1965 [species validated as a member of *Kali*]; Johnson 1969: 588–589, figure 1 [revision of the genus and key to the species]; Kotthaus 1972: 19, figure 5 [records from the Canary basin, Eastern North Atlantic]; Johnson and Cohen 1974: 41–42 [revision of the genus, diagnosis and brief description]; Johnson and Keene 1986: 733, figure 228.6 [key to the species];Smith (in press) [key to species]; Johnson and Keene 1990: 902 [record of eastern tropical Atlantic species]; Mooi and Paxton 2001: 3495–3496 [list of Pacific species]; McEachran and Sutton 2003: 1742–1743 [list of Atlantic species]; Moore *et al.* 2003: 227 [checklist of deep-sea fishes from off New England, Western North Atlantic]; Hardy 2005: 1902, 1910–1911 [identification of larvae]; Hardy 2007: 1312 [identification of larvae]

Diagnosis. *Kali macrodon* can be distinguished from all species of *Kali*, except *K. kerberti* by the ascending process of premaxilla with a strong concavity limited anteriorly by bony crest (*vs.* ascending process of premaxilla flat or with gentle concavity, anterior bony crest absent); teeth in lateral series of premaxilla and dentary 16 or more, type 4, needle-like (*vs.* teeth in lateral series of premaxilla with ventral attachment, recurved, teeth in *K. parri*; premaxilla six to 11, dentary five to eight, caniniform, slightly curved in *K. indica* and *K. falx*; premaxilla 13–22, dentary six to 10, recurved in *K. colubrina*). *Kali macrodon* further differs from *K. macrura*, by teeth in lateral series of premaxilla and dentary type 4, needle-like, extending to the end of dentigerous area, teeth with ventral attachment absent in lateral series (*vs.* teeth in lateral series of premaxilla and dentary type 4, needle-like in anterior third and fourth, respectively, followed by teeth with ventral attachment, recurved in posterior areas).

Kali macrodon can be distinguished from *K. kerberti* by the teeth in mesial series of premaxilla six to nine, modally seven, and of dentary seven to nine, modally eight (*vs.* teeth in mesial series of premaxilla and dentary four to five, modally five).

Description. Moderate-sized species of *Kali*, largest specimen examined 239.4 mm SL. Meristic data summarized in table 3.5, and morphometric in table 3.6. General body pattern as described for genus.

Dentition. Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials; premaxilla and dentary as illustrated in figure 3.1 C and summarized in table 3.1. Tooth crown length 15.5–21.0% in tooth length. Premaxilla elongate, strongly arched in lateral view, with teeth arranged in two series: lateral and mesial. Lateral series in single row; teeth small and numerous, type 4, needle-like, without flange, closely spaced, increasing in size from anterior to posterior on first half, gradually decreasing in size to posterior end. Teeth at anterior portion smaller, increasing in size until middle of premaxilla, than decreasing in size posteriorly. Mesial series in single row, irregularly arranged; first tooth type 4, conical, slightly curved, without flange, not developed as fang; following teeth with ventral attachment, recurved fang-like, largest tooth 20.1–21.1% in premaxillary length, with flange. Base of first tooth at anterior-ventral tip of premaxilla; second to last teeth (fangs) equally spaced between level of ascending process of premaxilla and posterior margin of orbit, decreasing in size from anterior to posterior.

Dentary elongate, strongly arched in lateral view; teeth arranged in two series:

lateral and mesial. Teeth in lateral series numerous and closely spaced, type 4, needle-like, without flange, increasing in size from anterior to posterior on first half, gradually decreasing in size to posterior end. Teeth in mesial series with ventral attachment, recurved, fang-like, largest tooth 14.0–16.7% in dentary, with flange; closely spaced, decreasing in size from anterior to posterior. Base of first tooth opposite to gap between first and second teeth in mesial series of premaxilla; remaining teeth opposite to gaps between premaxillary fangs, extending to end of dentigerous area of dentary.

Palatine teeth type 4, conical, slender, with short flange, in single row. Lower pharyngeal teeth type 4, needle-like, without flange, in two rows; upper pharyngeal teeth type 4, needle-like, in one to two rows. Gill rakers tooth-like, type 1, conical, slender, without flange; present on second and third arches; absent on first hypobranchial, basihyal and basibranchials.

Color. Skin covering body fragile, missing in most specimens, description based on NMNZ P. 30778. Epidermis black, thin and fragile, rarely preserved especially in head; dermis thin, transparent, with widely spaced melanophores. Peritoneum transparent, with moderate concentration of melanophores. Orobranchial chamber pale with scarce melanophores, including in gill arches and membranes between branchiostegal rays, roof of mouth dusky; gill filaments not pigmented.

Distribution. World-wide in the equatorial, tropical, subtropical and temperate regions: in the Atlantic from 53° N to 40° S; in Indian from 12° S to 29° S; in the Pacific 25° N to 43° S (Fig. 3.2).

Bathymetric distribution. Bathypelagic zone; more frequently recorded in depths between 1000 and 2500 m (mean 1808 m). A single record from above 1000 m

(325 m); deepest record at 3700 m.

Remarks. In a single specimen (NMNZ P. 30778) teeth were absent from first epibranchial and a single tooth was present on the ceratobranchial; for all other specimens examined three or more teeth were present on the first epibranchial and 10 or more on the ceratobranchial, including specimens from adjacent areas (*e.g.* AMS 25862001).

The status of *Gargaropteron pterodactylops*. *Gargaropteron pterodactylops* was described from a 45 mm specimen found on the beach, washed up by the waves. Johnson and Cohen (1974) were the first authors to identify that specimen as a juvenile of *Kali*, and considered it to be a junior synonym of *K. macrodon* based on a combination of meristic characteristics. The larval stage of *Kali* is now known as the gargaropteron stage, and substantially differs from adults by having very elongated pectoral and pelvic fins, and a relatively larger eye; the dentition is composed of two rows of conical teeth in both premaxilla and dentary. With the discovery of two new species, the characters used to fit *K. pterodactylops* with *K. macrodon* are not useful anymore. Because of the differences in dentition between the juveniles and adults, allied to the lack of a good series of larval specimens, a precise identity of juveniles can not be given. I prefer to follow Johnson and Cohen (1974), however, and regard to *K. pterodactylops* as a junior synonym of *K. macrodon* to avoid the proliferation of taxonomic problems.

Kali macrura (Parr 1933)

(Figs. 3.6; Tables 3.1, 3.7, and 3.8)

Hemicyclodon macrurus Parr 1933 [original description; type locality, off Acklins Islands, Bahamas, 22°31'15" N, 74°26'20" W, 10000 ft. (3048 m) of wire, 30–III–1927, R/V *Pawnee*; holotype YPM 2739].

Kali macrurus Johnson 1969: 589, figure 1 [revision of the genus and key to the species].

Kali macrura Johnson and Cohen 1974: 39–41 [revision of the genus, diagnosis and brief description]; Johnson and Keene 1986: 733–734, figure 228.7 [key to the species]; Johnson and Keene 1990: 902 [record of eastern tropical Atlantic species]; McEachran and Sutton 2003: 1742–1743 [list of Atlantic species]; Moore *et al.* 2003: 227 [checklist of deep-sea fishes from off New England, Western North Atlantic]; Hardy 2005: 1912 [identification of larvae]; Hardy 2007: 1902 [identification of larvae]; Smith (in press) [key to species].

Diagnosis. *Kali macrura* is diagnosed from its congeners by two unique characteristic: the low number of total vertebrae, 33–34 (*vs.* 37 or more); and by teeth in lateral series of premaxilla and dentary six to 10, needle-like at anterior fourth/third, respectively, followed by seven to 10 recurved teeth with ventral attachment in the posterior dentigerous area (*vs.* teeth in lateral series of premaxilla of premaxilla and dentary recurved or caniniform in *K. colubrina*, *K. falx*, *K. indica*; 12–31, needle-like, extending to the end of dentigerous area in *K. kerberti* and *K. macrodon*; 18–32, recurved, with ventral attachment, extending to the end of dentigerous area in *K. parri*).

Kali macrura further differs from all species of *Kali*, except *Kali parri* by a smaller number of first dorsal-fin rays, IX–XI, modally IX (*vs.* first dorsal-fin rays XI or more); smaller number of second dorsal-fin rays, 18–21, modally 21 (*vs.* second dorsal-fin rays usually 22 or more); anal-fin rays 19–21, modally 20 (*vs.* anal-fin rays usually more than 22).

Description. Smallest species of *Kali*, largest specimen examined 130.4 mm SL. Morphometric data summarized in table 3.7, and meristic in table 3.8. General body pattern as described for genus.

Dentition. Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials; premaxilla and dentary as illustrated in figure 3.1 D and summarized in table 3.1. Toot crown length 17.9–26.4% in tooth length. Premaxilla elongate, strongly arched in lateral view, with teeth arranged in two series: lateral and mesial. Lateral series in single row, divided into two groups: anterior, at anterior fourth of premaxilla, type 4, needle-like, without flange, closely spaced, increasing in size from anterior to posterior; and posterior, teeth with ventral attachment, recurved, with flange, as in teeth of mesial series, closely spaced, decreasing in size from anterior to posterior. Mesial series in single row; teeth with ventral attachment, recurved, with flange, widely spaced, decreasing in size from anterior to posterior; none developed as fang, largest tooth 14.9–18.0% in premaxillary length. Base of first tooth at anterior fourth of premaxilla, anterior to level of anterior nostril, second tooth beside first tooth of lateral series, third below anterior nostril, and fourth at level of anterior margin of eye.

Dentary elongate, moderately arched in lateral view; teeth arranged in two series: lateral and mesial. Lateral series in single row, divided into two groups: anterior, at anterior third of dentary, teeth type 4, needle-like, without flange, closely spaced, increasing in size from anterior to posterior; and posterior, teeth with ventral attachment, recurved, with flange, closely spaced, decreasing in size from anterior to posterior; none developed as fang, largest tooth 12.3–15.1% in dentary length. Mesial series in single row; teeth with ventral attachment, recurved, with flange, decreasing in size from anterior to posterior. Base of first tooth at level of last needle-like tooth of lateral series, next teeth closely spaced to end of dentigerous area of dentary.

Palatine teeth type 4, needle-like, without flange, in single row. Lower pharyngeal teeth type 4, needle-like, without flange, in small patches; upper pharyngeal teeth type 4, needle-like, without flange, in small patches. Gill rakers tooth-like, type 1, conical, slender, without flange, individually attached to bone, or in small patches of two; present on first, second, third and fourth arches; teeth absent in basihyal and basibranchials.

Color. Skin covering body very thin, missing in most specimens, description based on LACM 30428–32 and holotype. Epidermis black or dark brown, thin and fragile, completely destroyed or restricted to small patches in all specimens examined; dermis thin, transparent, with widely spaced melanophores. Peritoneum transparent, with moderate concentration of melanophores. Orobranchial chamber pale, slightly dusky in roof and lateral sides of mouth, including opercle, skin below gill arch, membrane between branchiostegal rays and over basihyal and basibranchials; gill arches and filaments pale.

Distribution. World-wide in the equatorial, tropical, and subtropical regions, except the western Pacific: in the Atlantic from 40° N to 31° S; in the western Indian from 24° S, 31° S; in the Pacific 33° N to 30° S (Fig. 3.2).

Bathymetric distribution. Bathypelagic zone; more frequently recorded in depths between 1900 and 2500 m (mean 2239 m). A single record from above 1000 m (930 m); deepest record at 2750 m.

Kali parri Johnson and Cohen 1974

(Figs. 3.7; Tables 3.1, 3.7, and 3.8)

Kali parri Johnson and Cohen 1974: 37–39, figure 13 [original description; type locality South Atlantic, 5°30'S, 16°28'W, 0–1900 m, 9–III–1971, R/V *Walther Herwig*; holotype ISH 2123a–1971]; Johnson and Keene 1986: 734, figure 228.9 [key to the species]; Smith (in press) [key to species]; Johnson and Keene 1990: 902 [record of eastern tropical Atlantic species].

Diagnosis. *Kali parri* is diagnosed from its congeners by four unique characteristics: the orobranchial chamber and gill arches black, intensively pigmented (*vs.* orobranchial chamber and gill arches pale, melanophores widely spaced or absent); teeth in lateral series of premaxilla and dentary with ventral attachment, recurved, extending along the entire dentigerous area, teeth type 4 completely absent (*vs.* teeth type 4 in lateral series of premaxilla and dentary always present, needle-like, caniniform or recurved; recurved teeth with ventral attachment in lateral series absent in *K. colubrina*, *K. falx*, *K. indica*, *K. kerberti*, *K. macrodon*, and restricted to posterior part of dentigerous area of premaxilla and dentary in *K. macrura*); tooth crown not distinguishable (*vs.* tooth crown clearly distinguishable in teeth in mesial series, 10.0–45% in tooth length). *Kali parri* can be further distinguished from all species of *Kali*, except *K. macrura* by smaller number of second dorsal-fin rays, 20–23, modally 21 (*vs.* second dorsal-fin rays usually 22 or more); anal-fin rays 20–23, modally 22 (*vs.* anal-fin rays usually more than 22).

Description. Moderate-sized species of *Kali*, largest specimen examined 235.5 mm SL. Morphometric data summarized in table 3.7, and meristic in table 3.8. General body pattern as described for genus.

Dentition. Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials; premaxilla and dentary as illustrated in figure 3.1 E. Tooth crown not distinguishable. Premaxilla elongate, slightly arched in lateral view, with teeth arranged in two series: lateral and mesial. Lateral series in single row, teeth with ventral attachment, recurved, with flange; teeth at anterior edge of premaxilla flared outwards. Mesial series in single row; teeth with ventral attachment, with flange, all except third, recurved; third tooth elongated slightly curved, largest, 10.4–12.1% in premaxillary length; none enlarged as fang. Teeth equally and closed spaced, decreasing in size from anterior to posterior.

Dentary elongate, slightly arched in lateral view; teeth arranged in two series of single row each: lateral and mesial. Lateral series in single row, teeth with ventral attachment, recurved, with flange; teeth at anterior curvature of dentary flared outwards. Mesial series in single row; teeth with ventral attachment, with flange, all except second recurved; second tooth elongated slightly curved, largest, 6.7–8.4% in dentary length; none developed as fang. Teeth equally and closely spaced, decreasing in size from anterior to posterior.

Palatine teeth type 4, conical, slender, with flange, in single row. Lower pharyngeal teeth type 4, conical, slender, without flange, in single row; upper pharyngeal teeth type 4, conical, slender, without flange, in patches. Gill rakers tooth-like, type 1, conical, slender, without flange; present on first, second, third and fourth arches; absent in basihyal and basibranchials.

Distribution. In equatorial to temperate regions; in the Atlantic from 40° N to 30° S, western Indian off Australia and in the Pacific Plate from 13° N to 25° S (Fig. 3.2).

Bathymetric distribution. Bathypelagic zone; more frequently recorded at depths around 2000 m (mean 1649 m). A single record from above 1000 m (730 m); deepest record at 2162 m.

Color. Skin covering preserved in most specimens examined, description based on ISH 2123b/1971. Epidermis black; dermis thin, dusky, melanophores not distinguishable. Peritoneum black. Orobranchial chamber, gill arches and membranes between branchiostegal rays black; gill filaments pale.

Kali colubrina Melo 2008

(Figs. 3.8; Tables 3.2, 3.9 and 3.10)

Kali colubrina Melo 2008: 24–28, figures 1F, 9 and10 [original description; type locality, Subtropical South Atlantic, off Brazil, 19°50' S, 39°10' W, 1342–1444 m, 29–VI–2000, R/V *Thalassa*, holotype MNRJ 31663, 123.0 mm].

Kali caribbea Prokofiev 2009: 213–216, figure 2 [original description; type locality Surinam, 7°52' N, 54°06'–54°15' W, 830 m, 30–VI–1980, JAMARC col., holotype NSMT-P 40343].

Kali sp. Uyeno *et al.* 1983: 402 [brief diagnosis, record from off Suriname].

Diagnosis. *Kali colubrina* is diagnosed from its congeners by the unique dentition pattern: teeth in lateral series of premaxilla 13–22, type 4, caniniform but not developed as fangs, recurved (*vs.* teeth in lateral series of premaxilla seven to 22; first tooth developed as fang in *K. falx* and *K. indica*; needle-like at least in the anterior part of dentigerous area in *K. kerberti*, *K. normani*, and *K. macrura*; recurved, with ventral attachment in the posterior dentigerous area in *K. macrura* and entire dentigerous area in *K. parri*); teeth in mesial series of premaxilla five to nine, not developed as fangs (*vs.* teeth in mesial series of premaxilla three in *K. falx* and *K. indica*; four to five in *K. kerberti*, three to four in *K. macrura*; and six to fifteen in *K. parri*; developed as fangs in *K. falx*, *K. indica*; *K. kerberti*, and *K. macrodon*); teeth in lateral series of dentary eight to 18, type 4, caniniform but not very elongated, recurved (*vs.* teeth in lateral series of dentary seven to 22, elongated in *K. falx* and *K. indica*; needle-like at least in the anterior fourth of dentigerous area in *K. kerberti*, *K. normani*, and *K. macrura*; with ventral attachment, recurved, in the posterior dentigerous area in *K. macrura*, and entire dentigerous area in *K. parri*); teeth in mesial series of dentary six to ten, not developed as fangs (*vs.* teeth in mesial series of premaxilla two to four in *K. falx* and *K. indica*; four to five in *K. kerberti*, six to eight in *K. macrura*; and seven to 19 in *K. parri*; developed as fangs in *K. falx*, *K.* in*dica*; *K. kerberti*, and *K. macrodon*).

Description. Moderate-sized species of *Kali*, largest specimen examined 171.2 mm SL. Morphometric data summarized in table 3.9, and meristic in table 3.10. General body pattern as described for genus.

Dentition. Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials; premaxilla and dentary as illustrated in figure 3.1 F and summarized in table 3.2. Tooth crown length 10.6–24.9% in tooth length. Premaxilla elongate, slightly arched in lateral view, with teeth arranged in two series: lateral and mesial. Lateral series in single row; teeth type 4, curved, without flange, moderately and uniformly spaced; increasing in size from anterior to posterior on first half, gradually decreasing in size to posterior end; first tooth at anterior ventral edge of premaxilla, strongly recurved, posterior teeth at lateral edge of premaxilla. Mesial series in single row; teeth with ventral attachment, recurved, with flange, not developed into fangs, largest tooth 10.1–14.2% in premaxillary length. Teeth uniformly and moderately spaced between level of posterior margin of ascending process of premaxilla to posterior margin of eye, decreasing in size from anterior to posterior.

Dentary elongate, moderately arched in lateral view; teeth arranged in two series: lateral and mesial. Lateral series in single row; teeth type 4, curved, without flange, moderately and uniformly spaced; slightly increasing in size from anterior to posterior on first half, gradually decreasing in size to posterior end. Mesial series in single row; teeth with ventral attachment, recurved, with flange, not developed into fangs, largest tooth 8.9–12.5% in dentary length. First tooth at level of gap between first and second teeth in mesial series of premaxilla; other teeth uniformly spaced, opposite to teeth in mesial series of premaxilla, but extending to end of dentigerous area of dentary.

Palatine teeth type 4, needle-like, slightly curved, without flange, in single row. Lower pharyngeal teeth type 4, needle-like, in single row; upper pharyngeal teeth type 4, needle-like, in small patches. Teeth absent on gill arches, basihyal and basibranchials.

Color. Skin covering body very thin, missing in most specimens, description based on NMNZ P. 39323. Epidermis black, thin and fragile, but fairly preserved in several specimens, except for head; dermis gray, with closely spaced melanophores, very thin and closely attached to hypaxial and epaxial muscles. Peritoneum black. Orobranchial chamber pale, with few widely-spaced melanophores in sides of mouth, opercle, membranes between branchiostegal rays and gill arches.

Distribution. Equatorial, tropical, and subtropical regions of the Atlantic, between 30° N and 21° S, Western Pacific and Pacific Plate, between 20° N and 40° S (Fig. 3.2).

Bathymetric distribution. Bathypelagic zone; more frequently recorded at depths between 1300 and 1800 m (mean 1467 m). A single record from above 1000 m (600 m); deepest record at 2270 m.

Etymology. From the Latin *coluber*, snake; *colubrina*, feminine, snake-like. In a reference to the numerous recurved teeth in the upper and lower jaws, resembling the snakes of the family Colubridae.

Kali falx Melo 2008

(Figs. 3.9; Tables 3.1, 3.11, and 3.12)

Kali falx Melo 2008: 28–30, figures 1G, 9 and 10 [original description; type locality, Guinean Province, Atlantic Ocean, 7°32' N, 20°54'W, 0–1300, 14–IV–1971, R/V *Walther Herwig*, holotype USNM 207618, 162.9 mm].

Kali indica Johnson 1969: 587–588 [in part]; Johnson and Cohen 1974: 39–41 [in part]; Mundy 2005: 455 [checklist of Hawaiian species, in part].

Diagnosis. *Kali falx* is diagnosed from its congeners by a unique characteristic:

first tooth in lateral remarkably enlarged, 17.2–20.5% in premaxillary length, sickle-shaped, projecting anteriorly (*vs.* first tooth in lateral series of premaxilla of same size or smaller than adjacent teeth in *K. colubrina*, *K. kerberti*, *K. macrodon*, *K. macrura*, and *K. parri*; fang-like, 15.2–16.4% in premaxillary length, slightly curved, not projecting anteriorly in *K. indica*).

Kali falx can be further distinguished from all species of *Kali*, except *K. indica* by the teeth in lateral series of premaxilla six to nine, very elongated, curved, and widely spaced (*vs.* lateral series of premaxilla with 15 or more teeth; with ventral attachment¸ recurved in *K. parri*; type 4, needle-like, in *K. kerberti* and *K. macrodon* and the anterior third of premaxilla in *K. macrura*; not very elongated in *K. colubrina*); mesial series of premaxilla with three teeth developed as fang (*vs.* mesial series of premaxilla with four or more teeth in all other species, not developed as fangs in *K. colubrina*, *K. macrura*, and *K. parri*); first tooth in lateral series of premaxilla with movement restricted by a tight type 4 ligament, fang-like, positioned at antero-ventral tip (*vs.* first tooth in lateral series of premaxilla not remarkably elongated in any other species). *Kali falx* can be further distinguished from *K. indica* by the smaller eye, orbit width 11.2–16.0% and orbit height 9.7–12.4% in head length (*vs.* eye enlarged, orbit width 15.4–22.7% and orbit height 12.5–18% in head length); basihyal reduced and strongly curved, pointing ventrally (*vs.* basihyal not reduced and curved, pointing forward); first tooth in lateral series of premaxilla anteriorly arched, projecting anteriorly, 17.2–20.5% in premaxillary length (*vs.* first tooth in lateral series of premaxilla slightly curved, not projecting anteriorly, 15.2–16.4 % in premaxillary length); first tooth in mesial series of premaxilla below level of anterior nostril, and beside second tooth of lateral series (*vs.* first tooth in mesial of premaxilla anterior to level of anterior nostril, and to second tooth of lateral series); first tooth in mesial series of dentary between second and third teeth of lateral series (*vs*. first tooth in mesial series of dentary beside second tooth of lateral series).

Description. Moderate-sized species of *Kali*, largest specimen examined 159.5 mm SL. Morphometric data summarized in table 3.11, and meristic in table 3.12. General body pattern as described for genus.

Dentition. Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials; premaxilla and dentary as illustrated in figure 3.1 G and summarized in table 3.1. Tooth crown length 30.6–40.0% in tooth length. Premaxilla elongate, slightly arched in lateral view, with teeth arranged in two series: lateral and mesial. Lateral series in single row; teeth caniniform, with flange, widely spaced. First tooth with tight type 4 attachment, sickle-shaped, with flange, arched anteriorly, remarkably enlarged, 17.2–20.5% in premaxillary length, inserted at antero-ventral tip of premaxilla, tip of tooth pointing slightly caudally, attachment to bone tight, movement restricted. Following teeth in lateral series type 4, curved, with flange, decreasing in size from anterior to posterior, at lateral edge of premaxilla; second tooth halfway between first tooth and anterior nostril; third tooth at level of posterior nostril, fifth below mid-eye, remaining teeth needle-like, at posterior third of premaxilla. Mesial series in single row; teeth with ventral attachment, recurved, with flange, fang-like, largest tooth 23.9–30.0% in premaxillary length. Teeth widely spaced, decreasing in size from anterior to posterior; base of first tooth beside second tooth of lateral series; second tooth below anterior half of eye; and third tooth beside fifth tooth of lateral series.

Dentary elongate, moderately arched in lateral view; teeth arranged in two series:

lateral and mesial. Lateral series in single row; teeth type 4, caniniform, with flange, slightly curved, widely spaced; anterior tooth longest, teeth decreasing in size from anterior to posterior, first and second teeth opposite to first and second teeth in lateral series of premaxilla, respectively; third and fourth slightly posterior to third and fourth teeth in lateral series of premaxilla; remaining teeth at posterior third of dentary. Mesial series in irregular single row; teeth with ventral attachment, recurved, with flange, fang-like, largest tooth 18.8–22.6% in dentary length. Teeth widely spaced, decreasing in size from anterior to posterior; base of first mesial tooth at level of anterior nostril, opposite to gap between first and second teeth in mesial series premaxilla; second, at level of mid-eye, slightly posterior to second mesial tooth of premaxilla; third, slightly posterior to third mesial tooth of premaxilla.

Palatine teeth type 4, needle-like, without flange, in single row. Lower pharyngeal teeth type 4, needle-like, without flange, in single row; upper pharyngeal teeth type 4, needle-like, without flange, in small patches. Tooth-like gill rackers absent in gill arches, basihyal and basibranchials.

Color. Skin covering fragile, body missing in most specimens, description mainly based on holotype. Epidermis black, thin and fragile, completely destroyed or restricted to small patches in all specimens examined; dermis thick and gelatinous, whitish or clear gray, with widely spaced melanophores. Peritoneum transparent, with moderate concentration of melanophores. Orobranchial chamber pale, with few widely-spaced melanophores in roof, sides of mouth, opercle, membranes between branchiostegal rays, basihyal, basibranchials, gill arches and gill filaments.

Distribution. Equatorial and tropical regions of the northern hemisphere: from a single locality in eastern Atlantic at 8° N; two localities in Indian at about 14° N; and Pacific Plate and Eastern Pacific, between 29° N and 10° N (Fig. 3.2).

Bathymetric distribution. Bathypelagic zone; known from few localities between 1300 and 2870 m (mean 2090 m).

Etymology. From the Latin *falx*, sickle; in a reference to the well developed sickle-shaped anterior most tooth, a diagnostic characteristic for the species. A noun in apposition.

Discussion

The dentition pattern of *Kali* is the most distinctive characteristic for the genus, and different patterns provide the best characteristics to diagnose the species. The teeth of the premaxilla and dentary are arranged in two series of single row each: lateral at the lateral edge of bones; and mesial, at the internal edge. In all species, the teeth in the mesial series of both premaxilla and dentary are recurved, with a ventral attachment to the bone, but are variable in number and shape: in *K. parri*, and *K. colubrina* the teeth are not very elongated, the largest tooth on the premaxilla is 10.1–14.9% of premaxillary length, and the largest tooth on the dentary is 8.9–12.5% of dentary length; in *K. macrura* the mesial series has moderately elongate teeth, the largest tooth on the premaxilla is 15.0–18.0% of premaxillary length, and the largest tooth on the dentary is 12.3–15.1% of dentary length; *K. indica*, *K. falx*, *K. kerberti*, *K. macrodon* have very elongated teeth, developed as fangs: the largest tooth on the premaxilla is 20.1–30.0% of premaxillary length, and the largest tooth on the dentary is 14.0–29.3% of dentary length.

The lateral series of teeth is composed exclusively of type 4 teeth extending along the lateral edge of premaxilla and dentary in *Kali colubrina*, *K. falx*, *K. indica*, *K. kerberti*, and *K. macrodon*. In *K. macrura* the type 4 teeth in the lateral series are restricted to the anterior part on both the dentary and premaxilla, and the posterior portion is composed by curved teeth with ventral attachment, similar in shape to the teeth of the mesial series. *Kali parri* has the type 4 teeth completely absent, and the teeth in both mesial and lateral series are recurved with ventral attachment. In *K. kerberti*, *K. macrodon* and *K. macrura* the teeth are closely spaced and needle-like; in *K. falx* and *K. indica* the teeth are caniniform, slightly curved, relatively elongated, and widely spaced; in *K. colubrina,* the teeth are not as elongated and widely spaced as in the previous two species, and are also recurved.

The size of the tooth crown also has intraspecific variation. *Kali colubrina*, *K. indica*, *K. macrodon*, and *K. macrura* have the crown of the largest premaxillary tooth 10.3–20.5% of the tooth length, and the crown of largest dentary tooth 9.5–21.7%. *Kali falx* and *K. kerberti* have teeth with large crown, the crown of largest premaxillary tooth is 30.6–45.4% of tooth length, and the crown of largest dentary tooth, 35.7–46.7%. The teeth of *Kali parri* have small indistinguishable crowns.

Development of replacement teeth is extraosseous (*sensu* Trapani 2001). Replacement teeth are present in very few specimens, and in general when replacement teeth are present, mature teeth are absent. Apparently the replacement of teeth is synchronized and all teeth of premaxilla and dentary are replaced at once. Because of that, a precise identification of few specimens lacking mature teeth was not possible. The holotype of *Kali kerberti* has only soft immature teeth not yet attached to bone; although fragile, the medial and lateral series of both premaxilla and dentary are complete in both sizes. For that reason the dentition was imprecisely reported by Weber (1913), and consequently, erroneously synonymized with *Kali indica* by Johnson (1969) and Johnson and Cohen (1974).

Identification of the gargaropteron (e.g. Johnson & Cohen 1974; Hardy 2005, 2007) is mostly based on meristic data. Although the number of vertebrae is used to diagnose *Kali macrurus* (total vertebrae 33–34 *vs.* 38–40 in other species) and fin-rays counts can distinguish *K. macrurus* and *K. parri* from all other species (second dorsal fin 18–23 *vs.* 21–26; anal fin 19–23 *vs.* 22–28), the other five species of *Kali* can only be diagnosed by dentition pattern, which is not developed in the gargaropteron. Another problem is that juvenile *Kali* are not common and it is rare to have a series of the same species of different sizes.

Biogeographic comments. The species of *Kali* have sympatric distributions and circumglobal patterns of distribution. The absence of a species-specific pattern of distribution within the genus *Kali* is noteworthy: all species of *Kali*, except for *K. falx* are widely distributed in the Atlantic, Indian and Pacific oceans. *Kali indica* is the only species recorded so far in the Southern ocean. *Kali falx* is apparently restricted to the Northern hemisphere, but it will not be surprising if eventually is found in the Southern hemisphere. This prediction is supported by the example of *K. parri*, which for more than 30 years was only known from the records of the original description in the South Atlantic, but was recently discovered in the North Atlantic (Hartel *et al.* in press) and now being reported to have a wider range that includes the Indian and Pacific Oceans.

Regarding the species' vertical distribution, all species of *Kali* are bathypelagic, usually found in depths greater than 1000 m and lower than 3000 m. There is no evidence of dial vertical migration, since very few specimens were collected above 1000 m.

***Kali colubrina,* a senior synonym of *K. caribbea*.** The genus *Kali* is a member of the deep-sea fish family Chiasmodontidae, and it was recently revised by Melo (2008). Melo described two species: *K. colubrina* and *K. falx*. Parallel to that revision, Prokofiev (2008) described *K. caribbea*. Herein, *K. colubrina* is placed as the senior synonym of *K. caribbea*, in accordance to ICZN (1999).

Kali colubrina, was published by Melo (2008) in the New Zealand journal Zootaxa, Volume 1747. The date of publication was specified as April 18, 2008. Prokofiev (2008) published *K. caribbea* in the Russian Journal *Voprosy Ikhtiologii* Volume 48, Number 2. The date of publication of *K. caribbea*, however, is source of confusion.

The Numbers 2 and 3 of the Volume 48 of Voprosy Ikhtiologii were published combined, and the date of publication was not clearly expressed. The tables of contents includes the date of submission (November 9, 2007), and the date which the journal was signed for printing (February 4, 2008). The date of publication was imprecisely specified on the cover as March–April of 2008, but the actual day of publication was not included.

Voprosy Ikhtiologii is published in Russian, and has an English version, which is published simultaneously, the Journal of Ichthyology. Only the Journal of Ichthyology is available online, at the SpringerLink website (http://www.springerlink.com/content/119884/). Online, Volume 48, Numbers 2 and 3 of the Journal of Ichthyology were published separately, and Prokofiev (2008) appeared in Volume 48, Number 3. The date given on the cover of the Journal of Ichthyology is April 2008, and the day is not specified.

Following Article 21.3 of the ICZN (1999), if the date of publication is not specified in a work, the earliest day on which the work is demonstrated to be in existence as a published work is to be adopted as the date of publication. In case only the month and year were specified, Article 21.3.1 determines that the last day of the month should be adopted as the date of publication. Therefore, Voprosy Ikhtiologii Volume 48, Numbers 2–3 and Journal of Ichthyology Volume 48, Number 3, the date that should be adopted is April 31, 2008. Therefore, *Kali colubrina* is the senior synonym of *K. caribbea*, in accordance to the Principle of Priority, Article 2.3.

If the earliest date which *Kali caribbea* was demonstrated to be in existence, is adopted, the day when Journal of Ichthyology Volume 48, Number 3 was posted on-line was April 18, 2008. Then, Melo (2008) and Prokofiev (2008) were published on the same date. Noteworthy, such date fails to fit Article 8.6 of the ICZN (1999), because of the lack of a printed version. Anyway, if that date is considered, the senior synonym should be determined by the first reviser, according to the Article 24.2. In that case, this contribution represents the first time that the names were cited in a published work.

Comparative material

Kali indica, 31 specimens; holotype examined by pictures. Atlantic, Slope Water: MCZ 158887, 1, 132.5 mm, 39°57’ N, 67°30' W, 0–2100 m, 3–XII–2000, R/V *Delaware II*; MCZ 164764, 1, 131.6 mm (female), 39°50’ N, 67°26’ W, 0–1592 m, 18–V–2005, R/V *Delaware II*. South Atlantic Subtropical: MNRJ 26693, 2, 205.8–207.7 mm (both females), 21°07’ S, 39°49’ W, 1633–1665 m, 8–VII–2000, R/V *Thalassa*. Guinean Province: USNM 207986, 1, 131.28 mm, 5°00’ S, 15°00’ W, 1282 m, 23–IV–1965. Atlantic Subantarctic: USNM 207620, 1, 104.27 mm, 39°19’ S, 3°15’ W, 0–2000, R/V *Walther Herwig,* St. 406/71. Pacific, Eastern Pacific: SIO 05–152, 1, 195.2 mm, 32°00’ N, 124°00’ W, 500–3700 m, 1986, R/V *Melville*; SIO 74–41–60, 1, 98.5 mm, 27°43’ N, 115°33’ W, 325 m, R/V *Alexander Agassiz*; SIO 78–190–60, 1, 164.2 mm, 30°57’ N, 120°46’W, 1400 m, 15–VI–1975, R/V *Alexander Agassiz*; LACM 31170, 1, 111.0 mm, 32°42’ N, 118°16’ W, 27–IV–1970, R/V *Velero IV*. Pacific Plate: USNM 367283, 1, 105.4 mm; 21°00’ N 158°00’ W; NMNZ P. 23623, 1, 193.2 mm, 22–IX–1988, 42°57’ S, 174°13’ E, 1112–1180 m, R/V *James Cook*. Western Pacific. SIO 69–19–60, 1, 167.9 mm, 6°00’ N, 122°35 E, 21–IV–1968, J. Pine col.; SIO 70–308–60, 1, 131.7 mm, 29°47’ N, 137°5.9’ E, 0–1350 m, 30–VI–1970, R/V *Melville*; SIO 53–367–60, 2, 111.6–163.95 mm, 34°00’N, 135°00’ E, 24–X–1953, R/V *Spencer Baird*. Indian: ZSI F1054/1, holotype, 170.0 mm, 16°56’ N, 92°33’ E, 2456 m, R/V *Investigator*. Southern Ocean: LACM 10765–11, 1, ca. 100.0 mm, 50°54’ S, 40°15’ W, 2452 m, 5–II–1966, USNS *Eltanin*; LACM 10921–11, 1, 140.3 mm, 60°17’ S, 110°15’ W, 2379 m, 26–X–1964, USNS *Eltanin*; LACM 10958–11, 1, 182.6 mm, 54°56’ S, 149°24’ W, 1601 m, 19–XI–1964, USNS *Eltanin*. Tentative identification. Eastern Pacific: USNM 207987, 1, 164.2 mm, Mexico, 29°19’ N, 121°25’ W, 0–1676 m, 14–IV–1962, R/V *Horizon*.

Kali kerberti: 72 specimens, including holotypes of *Kali kerberti* and *K. normani*. Atlantic, Slope Water: MCZ 60724, 1, 64.9 mm, 38°49' N, 71°40' W, 600–800 m, 30–IV–1982, R/V *Oceanus*. North Sargasso Sea: USNM 207596, 1, 113.2 mm, 32°04’ N, 63°58’ W, 0–1025 m, 22–VIII–1971, Ocean Acre expedition; USNM 207619, 1, 69.8 mm, 33°04’ N, 64°37’ W, 0–1060 m, 4–VII–1967, Ocean Acre expedition. South Sargasso Sea: ZUMC P. 6530, 1, 99.6 mm, 26°58’ N, 56°58’ W, 5–V–1922, R/V *Dana*. Lesser Antillean Province: USNM 207622, 1, 133.1 mm, 11°38’ N, 51°52’ W, 1103 m, 31–V–1965, R/V *Trident*. Amazonian: UW 21249, 1, 148.0 mm (cs), 3°00’ S, 26°16’ W, 0–2000 m, 3–II–1968, R/V *Walther Herwig*. South Atlantic Subtropical: MNRJ 26712, 1, 133.8 mm, 21°07’ S, 39°46’ W, 1686–1699 m, 8–VII–2000 R/V *Thalassa*. Guinean Province: MCZ 61018, 1, 73.2 mm, 0°00’N, 19°45’W, 0–1164 m, 20–IV–1965, R/V *Trident*; UF 220004, 1, 91.2 mm, 0°25’ S, 5°09’ W, 850 m, 23–V–1965, R/V *Pillsbury*; USNM 207614, 3, 131.6–161.8 mm, 7°00’ N, 20°58’ W, 0–1330 m, 14–IV–1971, R/ V *Walther Herwig*. Indian: ZUMC P. 6531, 1, 93.5 mm, 8°24’ S, 42°54’ E, 24–XII–1929, R/V *Dana*. Pacific, Western Pacific: AMS 24859010, 1, 192.68 mm, 33°43’ S, 152°03’ E, 0–1135 m, 16–X–1984, F R/V *Kapala*; AMS 36466019, 1, 93.13 mm, 16°00’ N, 122°59’ E, 4384–4667 m, 28–IX–1995, J. Paxton col.; SIO 76–166–60, 1, 104.2 mm, 14°14' S, 150°54.0' E, 6–III–1975, R/V *Alpha Helix*; SIO 77–171–60, 1, 96.5 mm, 04°40' S, 125°32' E, 0–1500 m, 26–VIII–1976, R/V *Thomas Washington*; ZMA 104006, holotype (ca. 65.0 mm), 5°39’ S, 122°12’ E, 1886 m, Siboga Expedition col. Pacific Plate: AMNH 22566, 1, 147.8 mm, 19°40’ N, 156°20’ W [coordinates inferred], 1975, O. Barton col.; AMS 17853001, 1, 79.6 mm, 1°00’ N, 170°00’ W, 0–1000 m, 16–III–1966, R/V *Coriolis*; FMNH 88149, 1, 152.1 mm, 21°23’ N, 158°18’ W, 20–II–1971, R.E. Young col.; FMNH 88150, 1, 117.1 mm, 21°23’ N, 158°18’ W, 4–IX–1972, R.E. Young col.; HUMZ 144032, 1, 118.3 mm, 20°00’ N, 156°00’ W [coordinates inferred], 5–II–1996, unknown col.; MCZ 56850, 1, 127.6 mm, 21°20’ N, 158°20’ W [coordinates inferred], 2–II–1973, R/V *Teritu*; SIO 60–216–60, 1, 69.1 mm, 10°09’ N, 128°30’ W, 0–1540 m, 24–VI–1960, R/V *Spencer F. Baird*; SIO 60–229–60, 1, 82.0 mm, 01°39’ S, 133°35’ W, 0–2326 m, 29–VI–1960, R/V *Spencer F. Baird*; SIO 69–342–60, 1, 148.9 mm, 17°49’ S, 110°19’ W, 0–1100 m, 29–III–1969, R/V *Thomas Washington*; SIO 73–36–60, 1, 132.1 mm, 9°28’ S, 124°12’ W, 13–XII–1970, R/V *Thomas Washington*; SIO 73–43–60, 1, 128.3 mm, 10°40’ S, 123°38’W, 17–XII–1970, R/V *Thomas Washington*; SIO 73–328–60, 1, 137.6 mm, 27°59’ N, 154°41’W, 20–VI–1973, R/V *Thomas Washington*; SIO 88–154–60, 1, 112.4 mm, 19°18’ N, 168°59' W, +700 m, 5–III–1987, R/V *Atlantis II*; USNM 207600, 1, 196.4 mm, 20°15’ N, 155°31’ W, 823 m, 30–III–

1968, R/V *Townsend Cromwell*; USNM 271063, 1, 144.8 mm (female), 7°00’ N, 150°22’ W, 0–850 m, 17–I–1978, R/V *Kana Keoki*; USMN 272723, 1, 131.3 mm, 11°48’ N, 138°11’ W, 885 m, 01–III–1976, R/V *Oceanographer*; USMN 288994, 1, 64.7 mm, 11°42’ N, 138°12’ W, 0–860 m, Sep 09–IX–1975, R/V *Oceanographer*; USNM 289024, 1, 117.6 mm, 9°02’ N, 150°11’ W, 0–950 m, 7–I–1978, R/V *Kana Keoki*; USNM 289228, 2, 70.8–71.8 mm, 13°30’ N, 150°00’ W, 0–950 m, 7–I–1978, R/V *Kana Keoki*. Eastern Pacific: CAS 61408, 2, 76.8–105.3 mm, 02°26’ S, 88°46’ W, 0–300 m, 27/28–V–1966, R/V *Anton Bruun*; LACM 8736, 1, 104.9 mm, 23°00’ N, 109°40’ W [coordinates inferred], 30–III–1964, R/V *Velero*; LACM 8863–1, 1, 120.8 mm, 24°00’ N, 109°40’ W [coordinates inferred], 18–IV–1964, R/V *Velero*; LACM 9036–6, 1, 136.8 mm, 33°30’ N, 118°00’ W [coordinates inferred], unknown col.; LACM 9651–3, 1, 123.6 mm, 28°30′ N, 118°00′ W [coordinates inferred], 3–VIII–1966, R/V *Velero*; LACM 31104–6, 2, 135.0–61.8 mm, 16°30’ N, 100°00’ W [coordinates inferred], 13–I–1970, R/V *Velero*; LACM 31107–8, 1, 137.2 mm, 20°30’ N, 106°00’ W [coordinates inferred], 15–I–1970, R/V *Velero*; LACM 31110–7, 1, 142.3 mm, 20°30’ N, 106°00’ W [coordinates inferred], 15–I–1970, R/V *Velero*; LACM 31111–7, 2, 54.2–71.0 mm, 21°00’ N, 109°00’ W [coordinates inferred], 17–I–1970, R/V *Velero*; LACM 31112–5, 1, 122.5 mm, 21°00’ N, 109°00’ W [coordinates inferred], 17–I–1970, R/V *Velero*; LACM 31117–9, 1, 131.0 mm, 20°30’ N, 106°00’ W [coordinates inferred], 19–I–1970, R/V *Velero*; LACM 31118, 1, 129.4 mm, 20°30’ N, 106°00’ W [coordinates inferred], 19–I–1970, R/V *Velero*; LACM 31119–6, 1, 149.3 mm, 21°15’ N, 106°15’ W [coordinates inferred], 19–I–1970, R/V *Velero*; LACM 31120–10, 1, 127.1 mm, 21°15’ N, 106°15’ W [coordinates inferred], 19–I–1970, R/V *Velero*; LACM 31130–8, 1, 71.8 mm, 21°00’ N, 109°00’ W [coordinates inferred], 23–I–1970, R/V *Velero*; LACM 31126–12, 1, 130.1 mm, 21°00’ N, 109°00’ W [coordinates inferred], 21–I–1970, R/V *Velero*; SIO 51–90–60, 1, 114.7 mm, 25°48.0' N, 114°46.0' W, 2212 m, 21/22–III–1951, R/V *Paolina*; SIO 56–79–60, 2, 112.9–148.0 mm, 28°58’ N, 118°11’ W, 29–VIII–1956, 1152 m, R/V *Paolina*; SIO 56–83–60, 1, 104.1 mm, 28°55.0' N, 118°11.2' W, 30–VIII–1956, 1152 m, R/V *Paolina*; SIO 57–140–60, 1, 86.9 mm, 22°43’ N, 111°06’ W, 15–VII–1957, R/V *Orca*; SIO 60–203–60, 1, 137.0 mm, 26°52’ N, 120°05’ W, 0–2000 m, 17–VI–1960, R/V *Spencer F. Baird*; SIO 65–236–60, 1, 128.1 mm, 22°35’ N, 110°13’ W, 29–VI–1965, R/V *Horizon*; SIO 65–244–60, 1, 120.7 mm, 23°08’ N, 109°13’ W, 1/2–VII–1965, R/V *Horizon*; SIO 68–52–60, 1, 121.9 mm, 22°40’ N, 109°07’ W, 9–I–1968, R/V *Thomas Washington*; SIO 75–227–60, 1, 139.5 mm, 1°19’ N, 98°01’ W, 0–200 m, 24–VI–1971, R/V *David Starr Jordan*; USNM 207606, 1, 141.4 mm (female), 2°26’ S, 88°46’ W, 0–400 m, 28–V–1966, R/V *Anton Bruun*; YPM 2693, holotype of *Kali normani*, 101.8 mm, 16°14’ N, 99°36’ W, 3291 m, 31–VI–1926, R/V *Pawnee*.

Kali macrodon: 33 specimens, including holotype of *Kali macrodon*; holotype of *K. pterodactylops* examined via pictures and x-rays. Atlantic, Slope Water: MCZ 138040, 1, 145.0 mm, 39°42'N, 71°27'W, 1325–1830 m, 15–IX–1995, F/V *Contender*; MCZ 163317, 1, 238.2 mm, 39°48'N, 67°22'W, 18–V–2003, R/V *Delaware*. North Sargasso Sea: USNM 207651, 1, 190.2 mm (female), 34°26’ N, 75°33’ W, 1925–2200 m, 13–IV–1972, R/V *Eastward*. Straits of Florida: UF 166993, 1, 66.6 mm, 23°30’ N, 75°30’ W [coordinates inferred], 10–II–1976, Staiger *et al.* col. Amazonian: ZMUC P. 6512, 1, 99.2 mm, 12°11’ N, 35°49’ W, 9–XI–1921, R/V *Dana*. South Atlantic Subtropical: SIO 63–542–60, 1, 114.4 mm, 31°9.0’ S, 0°45.5, E, 0–2200 m, 09–VI–1963, R/V *Argo*; SIO 63–

552–60, 1, ca. 50.0 mm, 18°44’ S, 10°14’ W, 25/26–VI–1963, R/V *Argo*; USMN 207598, 2, 67.1–116.0 mm, 15°45’ S, 6°06’ W, 5–IV–1971, R/V *Walther Herwig*; UW 21248, 1, 138.0 mm (cs), 33°00’ S, 7°05’ E, 2000 m, 20–IV–1917, R/V *Walther Herwig*. Azores Britain Province: AMS 25862001, 2, 190.1–194.3 mm, 52°55’ N, 16°15’ W, 2300 m, 9–VII–1986, R/V *Walther Herwig*. North African Subtropical: BMNH 1996.2.14.15, 1, 149.1 mm, 31°15’ N, 16°59’ W, 0–1470 m, 12–X–1995, R.R.S. *Challenger*; ZMH 7123, 1, 263.5 mm, 4°2’ N 15°18’ W, 0–3900, 8–III–1970, R/V *Meteor*. Guinean: MCZ 161015, 1, 71.6 mm, 10° N, 30° W, 24–V–1965, R/V *Trident*. Atlantic Subantarctic: BMNH 1930.1.12.1064, holotype, 129.6 mm, 33°20’ S, 15°18’ E, 2000–2500 m, 4–X–1926, R.R.S. *Discovery*; USMN 207601, 2, 173.2–235.0 mm, 37°08’ S, 5°23’ E, 0–2200 m, 21–III–1971, R/V *Walther Herwig*; USMN 207597, 4, 180.4–239.4 mm, 39°19’ S, 3°15 W, 0–2000 m, 19–III–1971, R/V *Walther Herwig*; ZMUC P. 6513, 1, 166.6 mm, 39°19’ S, 3°15’ W, 19–III–1971, R/V *Walther Herwig*; ZMUC P. 6514, 1, 196.8 mm, collected with ZMUC P. 6513; ZMUC P. 6515, 1, 236.1 mm, collected with ZMUC P. 6513; ZMUC P. 6516, 1, 234.4 mm, collected with ZMUC P. 6513. Indian: SIO 61–31–60, 1, 87.9 mm, 12°05’ S, 115°26’ E, 0–2000 m, 28/29–X–1960, R/V *Argo*; USNM 207610, 1, 225.8 mm, 29°45’ S, 64°58’ E, 1710 m, 28–VI–1964, R/V *Anton Bruun*. Pacific, Western Pacific: NMNZ P. 20019, 1, 217.5 mm, 43º13’ S, 168º50’ E, 932–938 m, 14–XII–1983, R/V *James Cook*; NMNZ P. 30778, 1, 264.1 mm, 41º07’ S, 176º46’ E, 1335–1427 m, 02–IV–1993, R/V *Tangaroa*. Pacific Plate: USMN 207613, 1, 109.1 mm, 8°00’ N, 164°33’ W, 0–1400, 8–VIII–1963, R/V *Te Vega*. Eastern Pacific: SIO 64–16–60, 1, 169.9 mm, 24°37’ N, 113°14’ W, 1–II–1964, R/V *Horizon*; SIO 51–87–60, 1, 189.4 mm, 25°30’ N, 115°16.7’ W, 1900 m, 21–III–1951, R/V *Paolina*; USNM 207599, 1, 180.4 mm, Colombia, 1°51’ N, 81°20’ W, 3300 m, 17–IX–1966, R/V *Anton Bruun*.

Kali macrura: 26 specimens, including holotype. Atlantic, Slope Water: MCZ 165931, 1, 118.03 mm, 39°47’ N, 66°55’ W, 0–2208 m, 18–VI–2006, R/V *Delaware II*. Florida Straits: YMP 2739, holotype, 114.3 mm, 22°31’ N, 74°26’ W, 30–III–1927, R/V *Pawnee*; UF 146164, 1, 112.3 mm, 2450 m, 24–VII–1971, R/V *Pillsbury*. Amazonian Province: MCZ 60723, 1, 72.5 mm, 9°21’ N, 43°09’ W, 2500 m, 27–VII–1983, R/V *Columbus Iselin*. South Atlantic Subtropical: SIO 63–542–60, 1 113.8 mm, 31°09.0’ S, 00°45.5’ E, 0–2200 m, 9–VI–1963, R/V *Argo*; UW 21247, 1, 117.0 mm (cs), 27°14’ S, 2°56’ W, 1900–2000 m, 1–IV–1971, R/V *Walther Herwig*. Guinean Province: USNM 207615, 1, 101.8 mm, 15°45’ S, 6°06’ W, 0–1900 m, 5–VI–1971, R/V *Walther Herwig*. Indian: USMN 207608, 1, 111.3 mm, 24°03’ S, 65°00’ E, 3500 m, 25–VI–1964, R/V *Anton Bruun*; BMNH 1988.2.25.7–8, 2, 125.5–130.4 mm, 31°55’ S, 55°06’ E, 0–930 m, 29–IV–1936, R.R.S. *Discovery II*. Eastern Pacific: LACM 30428, 1, 105.5 mm, 33°00’ N, 119°00’ W [coordinates inferred], 17/18–III–1969, R/V *Velero*; LACM 30040–11, 1, 121.4 mm, 22°00’ N, 107°00’ W [coordinates inferred], 12–XI–1967, R/V *Velero*; Pacific, Pacific Plate: SIO 60–232–60, 1, 108.9 mm, 04°59’ S, 135°19’ W, 0–2750 m, 1–VII–1960, R/V *Spencer Baird*; SIO 60–229–60, 1 100.0 mm, 01°39’S, 133°35.7’ W, 0–2326 m, 29–VII–1960, R/V *Spencer Baird*; SIO 60–239–60, 6, 87.9–115.3 mm, 05°12’ N, 143°07’ W, 0–2500 m, 6–VII–1960, R/V *Spencer Baird*; SIO 60–219–60, 2, 110.6–116.9 mm, 04°42’N, 130°50’ W, 0–2160 m, 26/27–VI–1960, R/V *Spencer Baird*; USNM 207613, 1, 109.3 mm, 8°00’ N, 164°33’ W, 0–1400 m, 8–VIII–1963, R/V *Te Vega*; ZMUC P. 6526, 1, 94.7 mm, 30°08’ S, 176°50’ W, 14–XII–1928, R/V *Dana*; ZMUC P.

6525, 1, 87.6 mm, collected with ZMUC P. 6526.

Kali parri: 11 specimens, including several paratypes. Atlantic, Slope Water: MCZ 162234, 1, 91.9 mm, 39°52’ N, 67°21’ W, 0–1400 m, 26–VII–2002, R/V *Delaware*; MCZ 164284, 1, 56.9 mm, 39°57’ N, 67°30’ W, 0–1428 m, 5–VI–2004, R/V *Delaware*. North Sargasso Sea: MCZ 101643, 1, 55.0 mm, 31°43’ N, 64°10’ W, 1000–1269 m, 13–VI–1992, R/V *Endeavor*. Straits of Florida: UF 131503, 1, 235.5 mm, 23°56’ N, 75°26’ W, 71–2162 m, 5–IX–1975, Staiger *et al.* col. Amazonian Province: ISH 919–1968, 1 (paratype), 109.4 mm, 3°00’ S, 26°16’ W, 0–2000, R/V *Walther Herwig*. South Atlantic Subtropical: USMN 207611, 1 (paratype), 192.0 mm, collected 27°14’ S, 2°56’ E, 0–2000 m, 1–IV–1971, R/V *Walther Herwig*. Guinean Province: ISH 2123b–1971, 1 (paratype), 142.5 mm, 27°14’ S, 2°56’ E, 0–2000 m, 1–IV–1971, R/V *Walther Herwig*; USNM 207604, 1 (paratype, collected with holotype), 18.86 mm, 5°30'S, 16°28'W, 0–1900 m, 9–III–1971, R/V *Walther Herwig*. Indian. AMS 31143012, 1, 90.1 mm, 20°55’ S, 112°51’ E, 1128–1139 m, 23–I–1991, J. Paxton col. Pacific Plate: SIO 56–127–60, 1, 58.8 mm, 13°03’ N, 166°14’ E, 730 m, 23/24–VI–1956, R/V *Horizon*; SIO 72–307–60, 1, 62.7 mm, 25°06’ S, 154°53’ W, 29–VII–1972, R/V *Melville*.

Kali colubrina: 60 specimens, including holotype and several paratypes. Atlantic, Straits of Florida: UF 158087, 1 (paratype), 129.0 mm, Bahamas, 23°46’ S, 76°58’ W, 1307–1317 m, Robins *et al.* col.; UF 149943, 1 (paratype), 151.7 mm, 23°55’ N, 75°26’ W, 2184–2193 m, 11–II–1974, Robins *et al.* col.; UF 149944, 1 (paratype), 95.8 mm, 23°44’ N, 76°49’ W, 1328–1337, 1–XI–1974, Staiger *et al.* col.; UF 148740, 1 (paratype), 100.0 mm, 24° 28’ N, 77°20’ W, 1426–1502 m, 28–II–1976, Staiger *et al.* col.; UF 148742, 1 (paratype), 105.3 mm, 23°52’ N, 77°18’ W, 1387–1390 m, 4–II–1974, Robins *et al.* col. Gulf of Mexico: USNM 186202, 1 (paratype), 84.8 mm, 27°48’ N, 88°45’ W, 1554– 2011 m, 30–VII–1959, R/V *Oregon*. Subtropical South Atlantic: MNRJ 26704, 1 (paratype), 104.9 mm (male), 21°26’ S, 39°49’ W, 1594–1614 m, R/V *Thalassa*; MNRJ 26705, 19 (paratypes), 92.3–140.3 mm, 13°19’ S, 38°19’ W, 1726–1929 m, 20–VI–2000, R/V *Thalassa*; MNRJ 26707, 2 (paratypes), 125.4–155.4 mm, 19°45’S, 39°03’ W, 1183–1318 m, 29–VI–2000, R/V *Thalassa*; MNRJ 26708, 3 (paratypes), 98.2–112.9 mm, 14°36’ S, 38°49’ W, 1055–1173 m, 10–VI–2000, R/V *Thalassa*; MNRJ 26709, 2 (paratype2), 96.3–115.0 mm, 20°08’ S, 38°38’ W, 1614–1680 m, 28–VI–2000, R/V *Thalassa*; MNRJ 26710, 1 (paratype), 107.4 mm (male), 21°26’ S, 39°49’ W, 1594–1614 m, 7–VII–2000, R/V *Thalassa*; MNRJ 26711, 5 (paratypes), 91.6–119.2 mm, collected with holotype; MNRJ 26713, 8 (paratypes), 103.5–144.3 mm, 20°24’ S, 39°46’ W, 1209–1362 m, 2–VII–2000, R/V *Thalassa*; MNRJ 26714, 1 (paratype), 149.4 mm, 20°27’ S, 39°38’ W, 1645–1762 m, 2–VII–2000, R/V *Thalassa*; MRNJ 26715, 1 (paratype), 110.7 mm, 13°21’ S, 38°16’ W, 1981–2271 m, 20–VI–2000, R/V *Thalassa;* MNRJ 31663, 1 (holotype) 123.0 mm, off Brazil, Subtropical South Atlantic, 19°50’ S, 39°10’ W, 1342–1444 m, 29–VI–2000, R/V *Thalassa*. Pacific, Western Pacific: AMS 42761002, 2 (paratypes), 150.0–151.4 mm, 32°36’ S, 167°50’ E, 1303–1313 m; NORFRANZ team col.; NMNZ P. 20216, 2 (paratypes), 143.6–161.6 mm, 39°49’ S, 178°07’ E, 1093 m, 23–VIII–1986, R/V *James Cook*; NMNZ P. 39353, 1 (paratype), 154.3 mm, 32° 38’ S, 167°50’ E, 1303–1313 m, 30–V–2003, R/V *Tangaroa*; NMNZ P. 39323, 1 (paratype), 154.7 mm, 32°37’ S, 167°47’ E, 1021–1052 m, 30–V–2003, R/V *Tangaroa*; USNM 148773, 1 (paratype), ca. 100.0 mm, 1°54’ S, 127°36’ E, 600 m, 2/3–XII–1909; R/V *Albatross*; USNM 207605, 1 (paratype), 93.5 mm, 1°00’ S, 127°50’ E, 1545 m, 2–XII–1909, R/V *Albatross*. Pacific Plate: NMNZ P. 10035, 1 (paratype), 171.2 mm, 30°32’ S, 178°22’ W, 05–XII–1976, 97 m, R/V *James Cook*; SIO 84–43–60, 1 (paratype), 100.0 mm, 19°14’ N, 169°07’ W, 1492 m, R/V *New Horizon*.

Kali falx: 60 specimens, including holotype and several paratypes. Atlantic, Guinean Province: USNM 207618, 1 (holotype) 162.9 mm, 7°32’ N, 20°54’W, 0–1300, 14–IV–1971, R/V *Walther Herwig*. USNM 392645, 2 (paratypes, females), collected with holotype, USNM 392646, 1 (paratype, male), 114.5 mm, collected with holotype. Indian: ISH 5322, 1, 96.3 mm, 15°00’ N, 70°00’ E [coordinates inferred], 18–II–1965; USNM 207617, 1 (paratype), 134.3 mm (female), 13°58’ N, 65° 02 E, 2870 m, 20–V–1964, R/V *Anton Bruun*. Pacific, Pacific Plate. FMNH 88147, 1 (paratype), 126.1 mm, 21°23’ N, 158°18’ W, 20–II–1971, R.E. Young col.; SIO 60–243–60, 1 (paratype), 164.3 mm, 10°22’ N, 147°18’ W, 0–2100 m, 9–VII–1960, R/V *Spencer Baird*; SIO 71–294–60, 1 (paratype), 129.8 mm, 27°28.7’ N, 155°19.6’ W, 29–IX–1971, R/V *Thomas Washington*. Eastern Pacific: SIO 65–198–60, 1 (paratype), 159.5 mm, 28°29’ N, 116°22’ W, 12–VI–1965, R/V *Horizon*

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TABLE 3.1. Dentition and gill rakers of *Kali indica* (n=12), *K. kerberti* (n=19), *K. macrodon* (n=16), and *K. macrura* (n=9). R stands for range and M for mode.

	Kali indica		*Kali kerberti*		*Kali macrodon*		*Kali macrura*	
Character	**R**	**M**	**R**	**M**	**R**	**M**	**R**	**M**
Premaxilla – lateral series								
Type 4	7–11	11	15–31	25	10–33	21	6–10	6
Ventral attachment	0	0	0	0	0	0	7–10	8
Premaxilla – mesial series								
Type 4	0	0	1	1	1	1	0	0
Ventral attachment	3	3	4–5	5	6–9	7	3–4	4
Dentary – lateral series								
Type 4	6–8	6	12–25	19	16–31	21	7–13	12
Ventral attachment	0	0	0	0	0	0	5–11	8
Dentary – mesial series								
Type 4	0	0	0	0	0	0	0	0
Ventral attachment	3–4	3	4–5	5	7–9	8	6–8	8
Palatine								
Type 4	3–7	3	0–6	3	5–10	7	3–9	7
Gill rakers								
First epibranchial	0	0	0–4	3	0–7	4	4–7	5
First ceratobranchial	0	0	2–10	8	1–17	15	11–19	16
First basibranchial	0	0	0	0	0–1	0	0	0

TABLE 3.2. Dentition and gill rakers of *Kali parri* (n=8), *K. colubrina* (n=14), and *K. falx* (n=8). R stands for range and M for mode.

	Kali parri		*Kali colubrina*		*Kali falx*	
Character	**R**	**M**	**R**	**M**	**R**	**M**
Premaxilla – lateral series						
Type 4	0	0	13–22	14	6–9	7
Ventral attachment	21–39	31	0	0	0	0
Premaxilla – mesial series						
Type 4	0	0	0	0	0	0
Ventral attachment	6–15	15	5–9	6	3	3
Dentary – lateral series						
Type 4	0	0	8–18	16	5–7	6
Ventral attachment	18–32	18	0	0	0	0
Dentary – mesial series						
Type 4	0	0	0	0	0	0
Ventral attachment	7–19	18	6–10	7	2–3	3
Palatine						
Type 4	7–17	10	4–15	6	4–7	4
Gill rakers						
First epibranchial	2–11	3	0–2	0	0	0
First ceratobranchial	9–28	14	0–9	7	0	0
First basibranchial	0	0	0	0	0	0

TABLE 3.3. Morphometric data of *Kali indica* (n=12) and *K. kerberti* (n=15). SD means standard deviation.

	Kali indica			*Kali kerberti*		
Character	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length (mm)	105.4–207.7	167.2	32.0	64.9–192.7	124.2	32.4
Head length (mm)	29.0–52.1	41.6	6.3	17.7–41.0	30.5	11.6
Percentage of HL						
Snout	28.5–32.6	30.5	1.4	29.2–35.9	32.4	1.9
Upper jaw	79.0–87.1	83.1	2.8	67.8–83.6	76.1	4.6
Lower jaw	82.0–96.6	87.6	4.1	75.9–91.7	85.5	4.3
Orbit width	15.4–22.7	18.1	2.5	14.2–17.8	16.1	1.1
Orbit height	12.5–18.0	15.6	1.5	10.1–16.3	12.6	1.6
Anterior nostril to eye	6.1–9.5	7.6	1.0	4.9–11.1	7.8	1.5
Posterior nostril to eye	1.3–5.4	2.7	1.3	1.8–3.6	2.5	0.5
Distance between nostrils	3.7–6.6	4.6	0.9	2.2–5.6	3.7	1.1
Interorbital distance	22.8–29.4	25.1	1.7	22.2–29.3	26.1	2.3
Head width	31.2–39.0	33.9	2.0	29.8–37.5	33.1	2.1
Cheek depth	5.0–9.0	6.4	1.3	2.2–6.9	3.8	1.2
Percentage of SL						
Head length	20.9–27.5	25.1	1.9	21.3–27.4	24.3	1.6
Body width	1.8–7.1	4.6	1.3	3.7–7.2	5.3	0.9
Insertion of pectoral fin	24.3–29.7	27.2	1.8	23.9–28.9	26.2	1.5
Insertion of pelvic fin	23.2–29.5	26.9	1.8	23.7–30.5	26.4	1.8
Pectoral-fin length	15.7–21.6	18.3	2.4	6.4–22.5	16.7	5.3
Pelvic-fin length	8.0–12.4	10.4	1.6	5.8–14.7	9.6	2.3
Origin of 1st dorsal fin	25.7–30.7	28.7	1.6	27.3–32.5	29.3	1.3
Base of 1st dorsal fin	21.8–24.6	22.9	1.1	16.8–26.7	23.1	2.2
Origin of 2nd dorsal fin	51.6–56.4	54.7	1.2	51.9–58.8	55.0	1.8
Base of 2nd dorsal fin	33.4–35.3	34.3	0.7	32.4–40.3	35.8	2.1
Origin of anal fin	48.8–59.3	53.0	3.2	49.3–56.5	52.4	2.0
Base of anal fin	28.1–37.8	33.1	3.2	31.2–39.0	36.7	1.9
Peduncle depth	3.2–3.9	3.5	0.2	3.0–4.4	3.6	0.4
Peduncle length	12.0–14.4	13.5	0.8	9.2–13.9	11.2	1.2

TABLE 3.4. Meristic data of *Kali indica* (n=12), and *K. kerberti* (n=19). Asterisk indicates data not available.

	Kali indica		*Kali kerberti*		
Character	**Range**	**Mode**	**Holotype**	**Range**	**Mode**
Fin counts					
First dorsal-fin rays	XI–XIV	XII	XIII	XI–XIII	XII
Second dorsal-fin rays	21–25	24	22	22–26	26
Anal-fin rays	22–26	24	25	24–27	25
Pectoral-fin rays	12–13	12	13	12–14	12
Pelvic-fin rays	I, 5	I, 5	*	I, 5	I, 5
Caudal-fin rays	ii, 6, 7, ii	ii, 6, 7, ii	*	ii, 6, 7, ii	ii, 6, 7, ii
Branchiostegal rays	6	6	*	6	6
Pores of Sensorial System					
Lateral line	*	*	*	39–44 (n=2)	*
Temporal	*	*	*	1 (n=1)	1
Supratemporal	*	*	*	2 (n=1)	2
Otic	*	*	*	2 (n=1)	2
Supraorbital	*	*	*	4 (n=1)	4
Epiphyseal branch	*	*	*	*	*
Infraorbital	8–9 (n=3)	8	*	8–9 (n=2)	*
Preopercular	4	4	*	3	3
Mandibular	5–6	6	*	6–7	7
Osteology					
Total vertebrae	40 (n=1)	40	37	37–38 (n=8)	38
Precaudal vertebrae	*	*	*	*	*

TABLE 3.5. Morphometric data of *Kali macrodon* (n=15). SD means standard deviation.

		Kali macrodon		
Character	**Holotype**	**Range**	**Mean**	**SD**
Standard length (mm)	129.6	108.9–264.1	179.9	54.1
Head length (mm)	32.0	26.4–59.5	42.6	11.4
Percentage of HL				
Snout	33.5	30.4–35.9	33.1	1.6
Upper jaw	62.3	58.2–69.7	64.6	3.4
Lower jaw	74.7	72.4–78.3	75.2	1.5
Orbit width	18.0	14.8–20.2	17.0	1.3
Orbit height	12.8	12.6–16.0	14.0	1.2
Anterior nostril to eye	11.2	7.1–11.2	9.5	1.2
Posterior nostril to eye	3.8	1.7–6.2	3.2	1.3
Distance between nostrils	4.3	1.1–6.6	3.9	1.4
Interorbital distance	*	21.3–24.4	22.8	1.2
Head width	30.5	29.9–33.7	31.9	1.1
Cheek depth	5.4	3.8–6.3	5.3	0.7
Percentage of SL				
Head length	24.7	21.9–25.7	23.9	1.1
Body width	5.1	2.8–6.8	4.5	1.2
Insertion of pectoral fin	26.0	24.8–27.6	26.3	0.9
Insertion of pelvic fin	25.7	25.1–28.2	26.5	0.9
Pectoral-fin length	14.9	9.8–20.0	16.2	3.4
Pelvic-fin length	8.1	8.1–10.6	9.4	1.0
Origin of 1st dorsal fin	31.8	28.0–32.1	29.8	1.4
Base of 1st dorsal fin	22.2	18.1–24.1	21.5	1.7
Origin of 2nd dorsal fin	54.8	51.8–58.3	54.8	1.5
Base of 2nd dorsal fin	31.7	31.7–38.3	34.7	1.6
Origin of anal fin	51.6	50.1–54.5	52.3	1.4
Base of anal fin	35.5	33.8–39.3	36.0	1.5
Peduncle depth	3.3	2.9–3.8	3.3	0.3
Peduncle length	12.2	10.5–13.7	11.7	0.9

TABLE 3.6. Meristic data of *Kali macrodon* (n=16). Asterisk indicates data not available.

	Kali macrodon		
Character	**Holotype**	**Range**	**Mode**
Fin counts			
First dorsal-fin rays	XIII	XI–XIII	XII
Second dorsal-fin rays	22	22–25	22
Anal-fin rays	22	22–25	22
Pectoral-fin rays	11	11	11
Pelvic-fin rays	I, 5	I, 5	I, 5
Caudal-fin rays	ii, 6, 7, ii	ii, 6–7, 7, ii	ii, 6, 7, ii
Branchiostegal rays	6	6–7	6
Pores of Sensorial System			
Lateral line	*	*	*
Temporal	*	*	*
Supratemporal	*	*	*
Otic	*	*	*
Supraorbital	*	*	*
Epiphyseal branch	*	*	*
Infraorbital	*	8–10	8
Preopercular	4	4	4
Mandibular	6	6	6
Osteology			
Total vertebrae	38	37–40 (n=11)	37
Precaudal vertebrae	*	22 (n=1)	22

TABLE 3.7. Morphometric data of *Kali macrura* (n=6) and *K. parri* (n=8). D stands for distance; H, holotype; M, mean; and SD, standard deviation.

	Kali macrura				*Kali parri*		
Character	**H**	**Range**	**M**	**SD**	**Range**	**M**	**SD**
Standard length (mm)	114.3	72.5–121.4	104.7	15.1	56.9–235.5	138.4	61.9
Head length (mm)	24.4	17.3–27.6	24.6	3.9	16.4–56.9	38.0	14.8
Percentage of HL							
Snout	33.0	31.7–35.2	33.2	1.5	30.4–35.8	32.5	2.1
Upper jaw	62.6	56.7–66.2	61.3	3.6	67.9–73.7	70.3	2.2
Lower jaw	71.3	66.3–81.8	73.5	5.2	74.1–83.1	79.0	3.0
Orbit width	14.0	14.0–19.5	16.2	2.2	18.6–27.2	21.4	3.0
Orbit height	14.3	11.7–15.7	13.6	1.5	14.1–18.3	16.0	1.5
Anterior nostril to eye	10.9	10.8–13.5	11.8	1.5	10.2–12.7	11.3	0.9
Posterior nostril to eye	7.9	3.1–7.9	5.8	2.4	3.4–6.0	4.6	0.9
D. between nostrils	2.9	2.9–3.6	3.4	0.4	2.8–5.7	3.9	1.1
Interorbital distance	15.9	15.9–21.8	19.4	2.5	22.4–30.0	26.0	2.7
Head width	33.9	29.2–35.6	32.6	2.2	31.4–36.5	34.9	2.3
Cheek depth	6.6	6.6–8.9	7.4	0.9	2.2–4.9	3.7	1.0
Percentage of SL							
Head length	21.4	21.4–24.3	23.1	1.1	24.2–28.9	26.7	1.7
Body width	5.0	2.3–5.9	4.2	1.3	4.0–6.4	5.3	1.0
Insertion of pectoral fin	25.2	25.2–29.5	26.8	1.5	24.7–29.8	27.8	1.8
Insertion of pelvic fin	25.5	25.5–26.9	26.2	0.6	24.6–28.4	26.8	1.3
Pectoral-fin length	16.4	13.6–19.3	15.8	2.2	16.2–24.5	18.9	3.4
Pelvic-fin length	9.6	8.5–12.0	9.8	1.5	9.1–11.2	10.3	1.1
Origin of 1st dorsal fin	29.5	29.2–33.4	30.8	1.5	29.4–35.9	33.2	2.5
Base of 1st dorsal fin	15.8	15.8–19.2	18.1	1.4	18.6–22.2	20.6	1.7
Origin of 2nd dorsal fin	52.9	52.9–56.0	55.1	1.2	56.0–59.9	57.9	1.5
Base of 2nd dorsal fin	33.2	29.7–34.1	32.3	1.7	27.7–30.7	29.2	1.2

TABLE 3.7 (con.t)

Origin of anal fin	54.5	53.0–57.9	55.5	2.2	55.5–63.7	57.9	2.8
Base of anal fin	32.8	29.1–32.8	31.3	1.7	26.8–30.4	27.9	1.7
Peduncle depth	3.2	2.5–3.7	3.2	0.4	3.0–4.5	3.9	0.5
Peduncle length	13.3	12.7–14.7	13.6	0.8	12.6–13.9	13.3	0.6

TABLE 3.8. Meristic data of *Kali macrura* (n=9) and *K. parri* (n=8). Asterisk indicates data not available.

	Kali macrura			*Kali parri*	
Character	**Holotype**	**Range**	**Mode**	**Range**	**Mode**
Fin counts					
First dorsal-fin rays	IX	IX–XI	IX	X–XII	XI
Second dorsal-fin rays	21	18–21	21	20–23	21
Anal-fin rays	20	19–21	20	20–23	22
Pectoral-fin rays	11	11–12	11	10–11	11
Pelvic-fin rays	I, 5	I, 4–5	I, 5	I, 5	I, 5
Caudal-fin rays	ii, 6, 7, ii	ii, 6, 7, ii	ii, 6, 7, ii	ii, 6, 7, ii	ii, 6, 7, ii
Branchiostegal rays	6	6	6	6	6
Pores of Sensorial System					
Lateral line	38	38 (n=1)	38	41–42 (n=3)	42
Temporal	*	*	*	1	1
Supratemporal	*	*	*	2	2
Otic	*	*	*	open canal	open canal
Supraorbital	*	*	*	3–4 (n=6)	4
Epiphyseal branch	*	*	*	2 (n=6)	2
Infraorbital	8	8–9	8	8–9 (n=6)	8
Preopercular	4	4	4	4	4
Mandibular	6	6	6	6	6
Osteology					
Total vertebrae	*	33–34 (n=5)	34	37–38 (n=4)	38
Precaudal vertebrae	*	*	*	*	*

TABLE 3.9. Morphometric data of *Kali colubrina* (n=13). D stands for distance; H, holotype; M, for mean; and SD, standard deviation.

	Kali colubrina			
Character	**H**	**R**	**M**	**SD**
Standard length (mm)	123.0	95.8–171.2	132.3	33.7
Head length (mm)	31.5	25.8–43.1	25.3	10.4
Percentage of HL				
Snout	30.3	27.4–32.0	30.1	1.5
Upper jaw	80.6	79.3–87.0	81.9	2.7
Lower jaw	84.2	83.6–90.9	86.3	2.1
Orbit width	19.2	17.9–21.6	19.8	1.3
Orbit height	16.6	13.5–19.7	16.1	1.8
Anterior nostril to eye	7.5	7.5–12.8	9.7	1.7
Posterior nostril to eye	2.2	1.8–7.0	3.8	1.5
D. between nostrils	6.2	3.7–6.3	4.9	1.0
Interorbital distance	24.8	23.5–26.7	24.8	1.0
Head width	35.0	31.6–36.5	34.3	1.7
Cheek depth	3.6	3.4–6.2	4.7	0.9
Percentage of SL				
Head length	25.6	24.3–29.1	26.0	1.5
Body width	3.8	3.5–7.1	5.0	1.1
Insertion of pectoral fin	31.3	26.9–32.2	29.2	1.8
Insertion of pelvic fin	32.8	25.6–35.0	29.8	2.4
Pectoral-fin length	23.2	19.0–26.3	22.7	2.0
Pelvic-fin length	11.3	7.8–12.9	10.4	1.6
Origin of 1st dorsal fin	29.3	27.8–32.0	29.6	1.3
Base of 1st dorsal fin	21.3	21.3–25.4	23.2	1.3
Origin of 2nd dorsal fin	53.8	52.1–57.1	55.1	1.7
Base of 2nd dorsal fin	43.4	31.3–38.4	34.6	2.0
Origin of anal fin	54.6	49.8–56.8	54.3	1.9
Base of anal fin	33.2	29.8–36.5	32.6	1.9
Peduncle depth	3.6	2.7–9.6	4.0	1.8
Peduncle length	13.3	11.3–16.4	13.8	1.2

TABLE 3.10. Meristic data of *Kali colubrina* (n=14). Asterisk indicates data not available.

	Kali colubrina		
Character	H	**R**	**M**
Fin counts			
First dorsal-fin rays	XIII	XI–XIV	XIII
Second dorsal-fin rays	23	23–26	23
Anal-fin rays	24	23–25	24
Pectoral-fin rays	11	10–11	11
Pelvic-fin rays	I, 5	I, 5	I, 5
Caudal-fin rays	ii, 6, 7, ii	ii, 6–7, 7, ii	ii, 6, 7, ii
Branchiostegal rays	6	6	6
Pores of Sensorial System			
Lateral line	*	*	*
Temporal	*	*	*
Supratemporal	*	*	*
Otic	*	*	*
Supraorbital	*	*	*
Epiphyseal branch	*	*	*
Infraorbital	*	7–9	8
Preopercular	4	4	4
Mandibular	4	6	6
Osteology			
Total vertebrae	*	39–40 (n=8)	40
Precaudal vertebrae	*	24–26 (n=6)	25

TABLE 3.11. Morphometric data of *Kali falx* (n=4). H stands for holotype; M, for mean; and SD, standard deviation.

	Kali falx			
Character	**H**	**R**	**M**	**SD**
Standard length (mm)	162.9	96.3–162.9	138.7	24.7
Head length (mm)	44.5	38.2–44.7	42.1	22.6
Percentage of HL				
Snout	29.9	29.9–32.3	31.3	1.2
Upper jaw	79.5	77.9–79.5	78.6	0.7
Lower jaw	87.5	87.5–89.4	88.4	0.8
Orbit width	14.7	11.2–16.1	14.2	2.1
Orbit height	9.7	9.7–12.4	11.1	1.3
Anterior nostril to eye	6.9	6.9–9.1	7.7	1.0
Posterior nostril to eye	2.5	1.9–2.5	2.3	0.3
Distance between nostrils	3.4	3.4–5.4	4.4	1.0
Interorbital distance	20.9	20.9–23.3	21.9	1.0
Head width	30.0	28.6–32.6	30.5	1.7
Cheek depth	4.9	3.5–5.1	4.4	0.8
Percentage of SL				
Head length	27.3	25.6–27.5	26.8	0.8
Body width	6.4	5.0–6.9	5.9	0.9
Insertion of pectoral fin	27.2	26.9–28.4	27.6	0.7
Insertion of pelvic fin	27.8	25.6–28.6	27.0	1.4
Pectoral-fin length	12.5	9.8–12.5	11.1	1.9
Pelvic-fin length	12.0	7.7–12.0	9.9	3.1
Origin of 1st dorsal fin	30.2	27.0–31.3	29.0	2.0
Base of 1st dorsal fin	22.3	21.2–24.8	22.6	1.5
Origin of 2nd dorsal fin	54.0	52.1–56.0	53.8	1.6
Base of 2nd dorsal fin	38.7	32.6–38.7	35.3	2.7
Origin of anal fin	53.9	51.6–54.3	53.0	1.3
Base of anal fin	33.7	33.1–35.9	34.5	1.3
Peduncle depth	3.9	3.3–3.9	3.6	0.3
Peduncle length	12.4	11.6–13.9	12.5	1.0

TABLE 3.12. Meristic data of *Kali falx* (n=8). Asterisk indicates data not available.

		Kali falx	
Character	**H**	**R**	**M**
Fin counts			
First dorsal-fin rays	XII	X–XIII	XII
Second dorsal-fin rays	24	22–24	23
Anal-fin rays	26	23–26	25
Pectoral-fin rays	11	11–13	11
Pelvic-fin rays	I, 5	I, 5	I, 5
Caudal-fin rays	ii, 6, 7, ii	ii, 6–7, 7–7, ii	ii, 6, 7, ii
Branchiostegal rays	6	6	6
Pores of Sensorial System			
Lateral line	*	*	*
Temporal	*	*	*
Supratemporal	*	*	*
Otic	*	*	*
Supraorbital	*	*	*
Epiphyseal branch	*	*	*
Infraorbital	*	*	*
Preopercular	4	4	4
Mandibular	6	6	6
Osteology			
Total vertebrae	*	38 (n=1)	38
Precaudal vertebrae	*	*	*

FIGURE 3.1. Schematic of the dentition in species of *Kali*; lower and upper jaws illustrated in lateral view: (A) *K. indica*, SIO 69–19–60; (B) *K. kerberti*, AMNH 225946; (C) *K. macrodon*, USNM 207597; (D) *K. macrura* USNM 207608; (E) *K. parri*, ISH 2123b–1971; (F) *K. colubrina*, UF 149944; (G) *K. falx*, USNM 207618. Teeth with ventral attachment to bone indicated in red, darker in mesial series, lighter in lateral series; type 4 teeth indicated in blue, darker in mesial series, lighter in lateral series; see text for details. Scale bar equals to 1 cm.

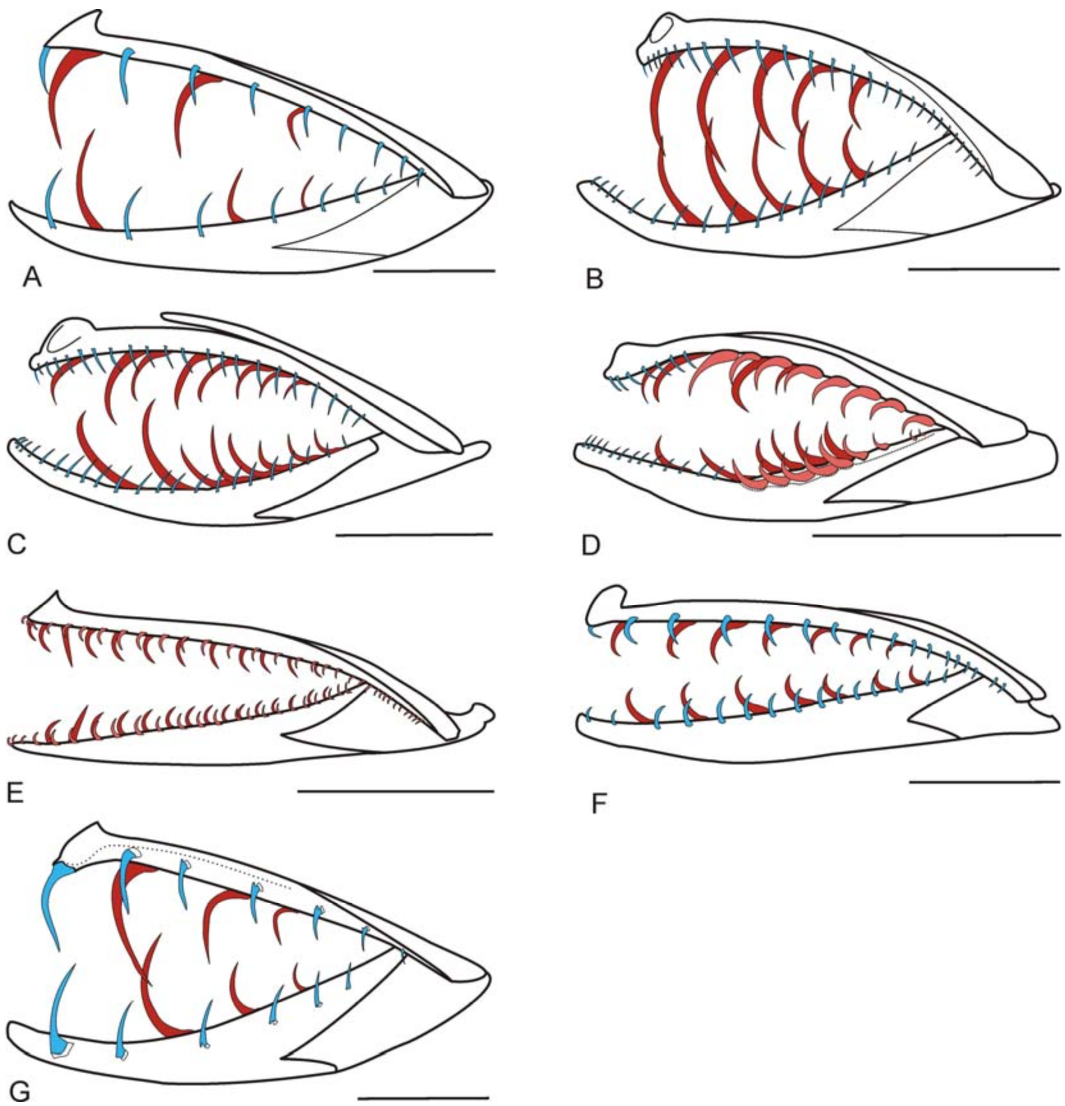
A
B
C
D
E
F
G

FIGURE 3.2. Map of distribution of *Kali*: (A) *K. indica* (squares) and *K. kerberti* (triangles); (B) *K. macrodon* (diamonds) and *K. macrura* (circles); and (C) *K. parri* (asterisks), *K. colubrina* (crosses) and *K. falx* (pentagons). Solid symbols stand for type localities; each symbol may represent more than one sampling locality or lot of specimens.

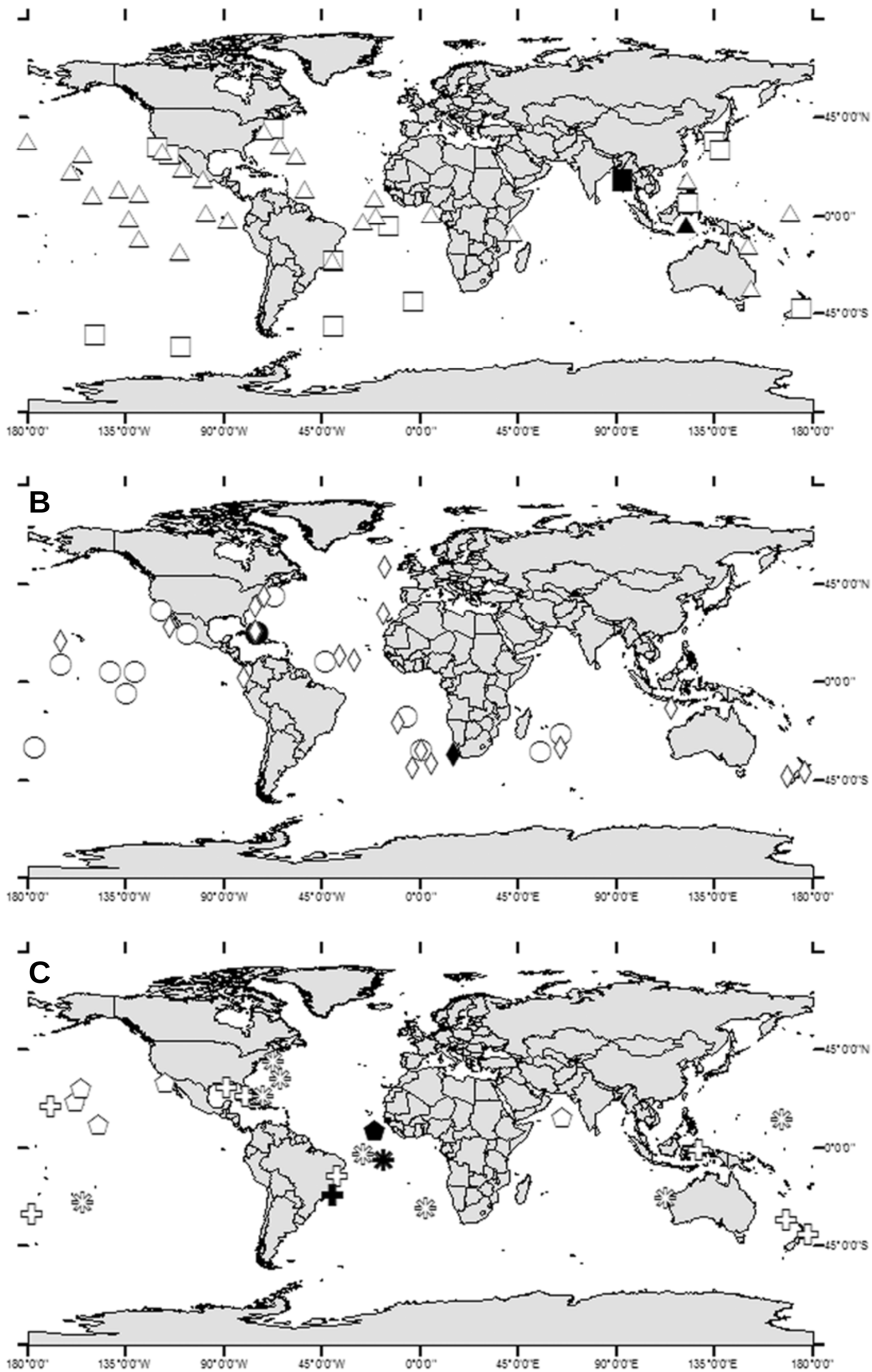
45°0'0"N
0°0'0"
45°0'0"S
180°0'0"
135°0'0"W
90°0'0"W
45°0'0"W
0°0'0"
45°0'0"E
90°0'0"E
135°0'0"E
180°0'0"
B
45°0'0"N
0°0'0"
45°0'0"S
180°0'0"
135°0'0"W
90°0'0"W
45°0'0"W
0°0'0"
45°0'0"E
90°0'0"E
135°0'0"E
180°0'0"
C
45°0'0"N
0°0'0"
45°0'0"S
180°0'0"
135°0'0"W
90°0'0"W
45°0'0"W
0°0'0"
45°0'0"E
90°0'0"E
135°0'0"E
180°0'0"

FIGURE 3.3. *Kali indica* in lateral view: preserved specimen, SIO 05–152, 195.2 mm, Eastern Pacific, 32°00’ N, 124°00’ W, 500–3700 m.

FIGURE 3.4. *Kali kerberti* in lateral view: in (A) preserved specimen, ZMA 104006, ca. 65.0 mm, holotype, western Pacific, 5°39’ S, 122°12’ E, 1886 m; in (B) preserved specimen, AMNH 225663, 147.8 mm, Pacific Plate, 19°40’ N, 156°20’ W; in (C) fresh specimen, not preserved, collected at the Loihi Seamount, Southeast off Hawaii Island – picture by S. Constable and K. Key (Scripps Institute of Marine Sciences, University of California in San Diego).

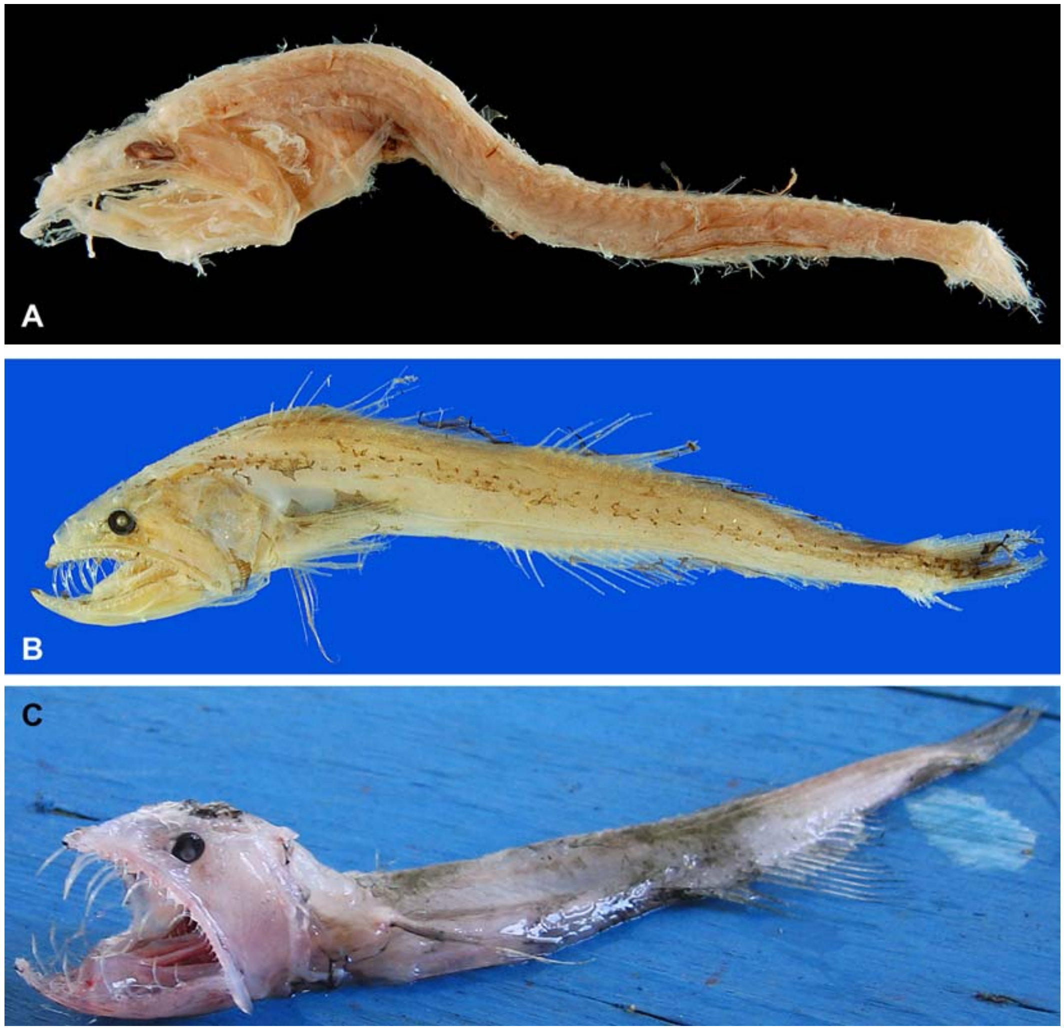
A
B
C

FIGURE 3.5. *Kali macrodon* in lateral view: in (A) preserved specimen, BMNH 1930.1.12.1064, 129.6 mm, holotype, West of Cape Town, South Africa, 33°20' S, 15°18' E, 2000–2500 m; in (B) preserved specimen, BMNH 1996.2.14.15, 149.1 mm, North African Subtropical, 31°15' N, 16°59' W, 0–1470 m.

FIGURE 3.6. *Kali macrura* in lateral view: in (A) preserved specimen, YPM 2739, 114.3 mm, holotype, off Acklins Islands, Bahamas, 22°31' N, 74°26' W; in (B) preserved specimen, USNM 207608, 111.3 mm, Indian Ocean, 24°03' S, 65°00' E, 3500 m.

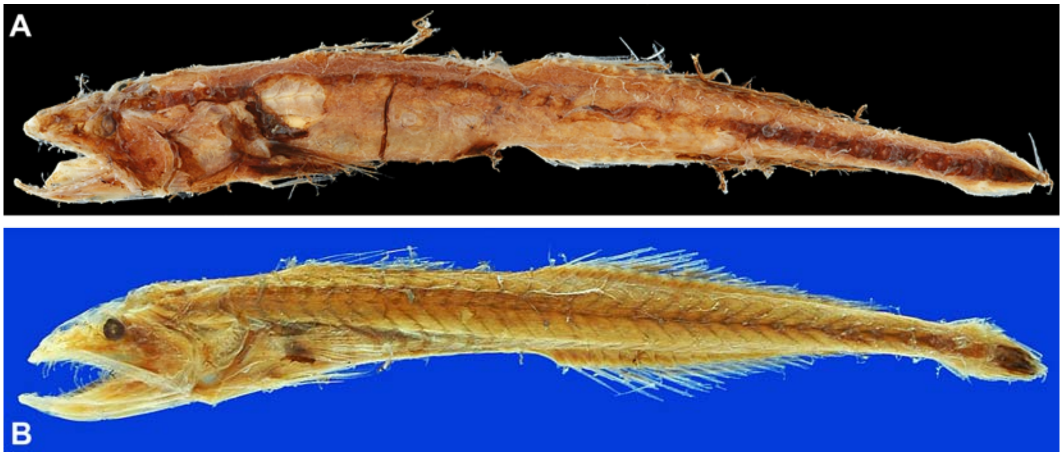
A
B

FIGURE 3.7. *Kali parri* in lateral view: preserved specimen, ISH 2123b–1971, 142.5 mm, paratype, Guinean Province, 27°14’ S, 2°56’ E, 0–2000 m.

FIGURE 3.8. *Kali colubrina* in lateral view: in (A) preserved specimen, AMS 42761002, 151.4 mm, paratype, Western Pacific, 32°36’ S, 167°50’ E, 1303–1313 m; in (B) fresh specimen, NMNZ P. 39353, 154.3 mm, paratype, 32° 38’ S, 167°50’ E, 1303–1313 m – picture by R. McPhee/K. Parkinson (NORFANZ Founding Parties).


A
B

FIGURE 3.9. *Kali falx* in lateral view: preserved specimen, USNM 207618, 162.9 mm, holotype, Guinean Province, 7°32’ N, 20°54’W, 0–1300.

CHAPTER 4 – REVISION OF THE GENUS PSEUDOSCOPELUS LÜTKEN

Publications:

Melo, M. R. S., Walker, H. J. & Klepadlo, C. (2007) Two new species of *Pseudoscopelus* (Teleostei: Chiasmodontidae), with a new diagnosis for the genus, *Zootaxa* 1605: 33–46

Melo, M. R. S. (submitted) Revision of the swallowers genus *Pseudoscopelus* Lütken with description of three new species (Perciformes: Chiasmodontidae). *Zootaxa*, 111 pages MS

Abstract

Pseudoscopelus Lütken are mesopelagic fishes with a worldwide distribution. The genus is the most diversified within the family Chiasmodontidae, containing 16 valid species, three of which are described herein as new: *Pseudoscopelus scriptus* Lütken, from the western Central and North Atlantic; *P. sagamianus* Tanaka from the Eastern Pacific and Indian Oceans; *P. altipinnis* Parr, widely distributed in the Atlantic and Pacific Oceans; *P. cephalus* Fowler, only known from its type locality in the Indo-Pacific; *P. obtusifrons* Fowler, from the Atlantic, Indian and Pacific Oceans; *P. scutatus* Krefft, widely distributed in the Atlantic, Indian and Pacific Oceans; *P. aphos* Prokofiev and Kukuev, from the western North Atlantic; *P. parini* Prokofiev and Kukuev, from the western Central Pacific to Hawaiian islands; *P. astronesthidens* Prokofiev and Kukuev, from the North Atlantic; *P. australis* Prokofiev and Kukuev, widely distribution in the southern Indian and Pacific, and the Southern Oceans; *P. pierbartus* Spitz et al., from eastern North Atlantic, western South and North Atlantic; *P. bothrorrhinos* Melo et al., from the western Pacific and Indian Oceans; *P. lavenbergi* Melo et al., from the western North, Central and South Atlantic, *P. paxtoni*, n. sp. from western South Pacific; *P. cordilluminatus*, n. sp. from Indian and South Altantic; and *P. odontoglossum* n. sp, from Central Pacific. Herein, *Pseudoscopelus stellatus* is placed in synonymy of *P. scriptus*; *P. albeolus*, in synonymy of *P. australis*; and *P. vityazi*, in synonymy of *P. parini*. *Pseudoscopelus microps* is confirmed as a junior synonym of *P. altipinnis*. The type of *P. sagamianus*, considered to be lost, was found at the Field Museum of Natural History. Diagnosis to each species of *Pseudoscopelus* is given, with an updated key to the species of and maps of distribution.

Introduction

The genus *Pseudoscopelus* has 16 valid species of meso- and bathypelagic fishes with a world-wide distribution (Melo et al. 2007; this publication). The type species, *Pseudoscopelus scriptus* Lütken 1892, was described based on a single specimen collected in the Old Bahamas channel, Straits of Florida. Lütken (1892:65) diagnosed both genus and species by the presence of lines consisting of rows of closely spaced pores [sic] beginning on isthmus to pelvic fin, and then to anal opening; along and around pelvic fin; in front of caudal fin; and along the inner pelvic fin ray [translation by P. Møller, 2007]. Curiously, Lütken (1982) did not recognize the presence of luminescent organs along the body confunsing them with pores and named the genus as a "false lanternfish"–the Greek *Pseude*, means false, and *Scopelus* [now valid as *Myctophum*].

Tanaka (1908) described *Pseudoscopelus sagamianus* as a subspecies of *P. scriptus*, based on two specimens collected by Allan Owston in the Sagami Bay, Japan. The specimens used for description had no catalog numbers and types were not established; and they were considered to be lost by Eschmeyer (1998). Because Tanaka was not able to clearly distinguish *P. sagamianus* from *P. scriptus*, Norman (1929) considered it to be a junior synonym of *P. scriptus* (based on a misidentified specimen of *P. altipinnis*), and Parr (1933), as a subspecies of *P. scriptus*. Prokofiev and Kukuev (2005, 2006c) considered the species valid, but provided an erroneous diagnosis and species range.

Beebe (1932:7) described *Pseudoscopelus stellatus* based on five larval specimens between 6.5 mm and 20.3 mm SL, collected off the Bahamas. Beebe was also the first author to recognize the presence of light organs in *Pseudoscopelus*; nevertheless, the holotype of *P. stellatus* is the only specimen within the type series to have light organs within the type series. Other authors (Parr 1933; Prokofiev and Kukuev 2006a, 2008; Sptiz et al. 2007) considered the species valid without type examination. Melo *et al*. (2007) considered it to be *species inquirenda*, due to lack of data on ontogenetic larval development. Herein, after examination of type series, juveniles of other species, photophore pattern and a number of specimens collected around the type locality, the species is formally assigned as a junior synonym of *P. scriptus*.

Parr (1933) described *Pseudoscopelus altipinnis* and Fowler (1934) described three species and a new genus, *P. microps*, *P. cephalus*, and *Myersiscus obtusifrons*. *Pseudoscopelus microps* is a junior synonym of *P. altipinnis* (Melo et al., 2007). *Pseudoscopelus cephalus* was considered valid by several authors (e.g. de Beaufort & Chapman 1951; Prokofiev and Kukuev 2005 2006a; Melo et al. 2007), and a junior synonym of *P. scriptus* by Spitz et al. (2007); herein it is confirmed as valid, but it is known only from the poorly preserved holotype collected in the Philippines. The genus *Myersiscus* is a junior synonym of *Pseudoscopelus* (de Beaufort & Chapman 1951), but *P. obtusifrons* is a valid species. Krefft (1971) described the very distinct species *P. scutatus* based on the material collected by the German R/V *Walter Herwig* throughout the Atlantic Ocean.

Lavenberg (1974) provided the first comprehensive review of the genus for his dissertation, based on the examination of the types of all species described until that time and an extensive amount of material. His results included the identified six undescribed species, which were never formally described according to the ICZN (1999); therefore, the names are not available. Prokofiev and Kukuev (2005, 2006a) reviewed the species from the Atlantic Ocean, but included several misidentifications. Over the recent years, nine species were described increasing considerably the knowledge regarding the taxonomy of the group: *Pseudoscopelus aphos* Prokofiev and Kukuev 2005; *P. parini* Prokofiev and Kukuev 2006b; *P. astronesthidens* Prokofiev and Kukuev 2006c; *P. australis* Prokofiev and Kukuev 2006c; *P. bothrorrhinos* Melo et al. (2007); *P. lavenbergi* Melo et al. (2007); *P. pierbartus* Spitz et al. (2007).

Prokofiev and Kukuev (2008) provided another revision for the genus, but did not included the species described by Melo et al. (2008). Two species were described in that work: *Pseudoscopelus albeolous* and *P. vitiazi*. That work is dated of 2007, but only appeared in May 2008 [Sergei Golovatch, pers. comm., 18–VIII–2008]. Herein, *P. albeolus* is placed in synonymy of *P. australis*, and *P. vitiazi* in synonymy of *P. parini*.

A revision of the genus *Pseudoscopelus* is presented herein based on examination of types where possible and extensive material from 26 different institutions allover the world. Three species are being described as new: *P. cordilluminatus*, from the Indian and eastern South Atlantic Oceans; *P. paxtoni*, from the western South Pacific Ocean; and *P. odontoglossum*, from Central Pacific Ocean. *Pseudoscopelus scriptus*, the type species of the genus is redescribed. The type of *P. sagamianus* was considered to be lost (Eschmeyer, 2007) was found at the Field Museum of Natural History fish collection and is formally described. Comparative diagnoses for each species of *Pseudoscopelus* are given, with a key the species and updated maps of distribution.

Material and Methods

Morphometric and meristic data follows Melo et al. (2007). Measurements were recorded to the nearest 0.1 mm using digital calipers. Vertebral counts were made from cleared-and-stained or x-rayed specimens. Terminology for light organs follows Melo et al. (2007) with modification proposed by Melo (submitted) and is summarized in figure 4.1. Classification of tooth attachment follows Fink (1981).

A regression analysis was performed using the computer program JMP 5.0.1 (SAS Institute Inc. 2002) between the standard length and the ratio between standard length and pectoral fin length to determine if allometric growth of pectoral fin is statistically significant. Results are only presented for those species with statistically significant results.

Atlantic material is organized following the classification provided by Backus et al. (1977); Pacific material follows Springer (1982). Institutional abbreviations follow Leviton et al. (1985) with the following addition changes: NMNZ now refers to the Museum of New Zealand Te Papa Tongerewa; Atlantic Research Institute of Marine Fisheries and Oceanography of the State Fisheries Committee of the Russian Federation (AtlantNIRO); the Zoological Institute, Russian Academy of Sciences (ZIN); Zoological Museum, Moscow State University (ZMMU, ZM MGU); the Museum of the World Ocean (MMO); and P.P. Shirshov Institute of Oceanology (IORAN).

List of abbreviations.

Photophores on head:

amf – anteromaxillary photophores

apf – anteropreopercular photophores

dnf – dorsonasal photophores

inof 1, 2 – interorbital photophores

lpf – longitudinal preopercular photophores

lvf – lateral pelvic-fin photophores

mxf – maxillary photophores

opf – opercular photophores

pmf – posteromandibular photophores

pof – postorbital photophores

ppf – posteropreopercular photophores

vf – ventral-fin photophores

vnf – ventronasal photophores

Photophores on body:

if – isthmus photophores

paf – pectoral-fin axillary photophores

pf – pectoral-fin photophores

prcf – precaudal-fin photophores

prvf – preventral-fin photophores

ptvf – postventral-fin photophores

rtf – random trunk photophores

saf – anal-fin photophores

scf – supracaudal-fin photophores

spf – suprapectoral-fin photophores

svf – supraventral-fin photophores

trf – transverse ventral-fin photophores

vaf – ventral-fin axillary photophores

Results

Key to the species of *Pseudoscopelus*

(valid for specimens larger than 45 mm SL)

1a Photophores as discrete organs completely absent, or replaced by white lines; supranasal pore of supraorbital canal with four openings .... 2 (*P. aphos* group)

1b Photophores present as discrete organs on body, fins and head; supranasal pore of supraorbital canal with one to three openings.. 3

2a. White lines with few chromatophores present, in place of *if*, *prvf*, *ptvf*, *pf*, *paf*, *saf*, and *vf*.. *P. parini*

2b.White lines absent.. *P. aphos*

3a. Tip of snout concave; distal radials of first dorsal fin developed into bony, plate-like structures; *mxf*, *trf*, *ppf*, *pf*, *paf*, *vf*, *vaf* absent, *svf* present, *prvf* and *ptvf* fused, with single row of photophores, *amf* restricted to space between pores three and four of mandibular canal; supranasal pore of supraorbital canal with three openings ...... 4 (*P. scutatus* group)

3b. Tip of snout convex; distal radials of first dorsal fin not developed into bony, plate-like structures; *mxf* and *trf* present or not, *ppf*, *pf*, *paf*, *vf*, *vaf* always present, *svf* absent, *prvf* and *ptvf* separated, *amf* extending posteriorly to the gap between pores four and five of mandibular canal; supranasal pore of supraorbital canal with one to two opening........ 5

4a. *lpf* present .... *P. bothrorrhinos*

4b. *lpf* absent .... *P. scutatus*

5a. Teeth on basihyal and second basibranchial present, canine, type 4; palatine teeth type 4; *mxf* interrupted short, not connected to *apf*.................................. 6 (*P. australis* group)

5b. Teeth on basihyal absent, teeth on second basibranchial conical, type 1; palatine teeth type 1; *mxf* absent or if present connected posteriorly to *apf* 8

6a. Teeth on ceratobranchial of first gill arch usually absent, or only a single small tooth present; palatine teeth in a single row, total teeth 10–16; three to four photophores on caudal margin of posterior nostril (*dnf*) present; *ppf* absent; *prcf* oval with three small prongs, medial prong extending slightly over lower procurrent rays .... *P. australis*

6b. Teeth on ceratobranchial of first gill arch present, two to16; palatine teeth in two rows, total teeth 15–38, *dnf* absent; *ppf* present, *prcf* two pronged, *U*-shaped, extending around, but not over, lower procurrent caudal-fin rays 7

7a. Teeth on basihyal and second basibranchial in two rows, basihyal teeth 10–16 ....
....*P. astronesthidens* (western North Atlantic)

7b. Teeth on basihyal and second basibranchial in three rows, basihyal teeth 20–26 ....
.... *P. odontoglossum*

8a. *trf* in a broad band of three to six rows, total photophores in *trf* more than 20; *prvf* short, not reaching anterior tip of pelvic griddle; *ptvf* short, not reaching anus, and extending anteriorly only halfway to pelvic-fin origin; *mxf* absent......................................
.... *P. lavenbergi*

8b. *trf* in a single row, total photophores less than 15; *prvf* elongated, extending to anterior tip of pelvic girdle; *ptvf* elongate, extending close to anus, and extending anteriorly to very close to pelvic-fin origin; *mxf* present... 9

9a. *trf* in single row of widely spaced organs, medial cluster of organs absent; *mxf* in single irregular row, photophores widely spaced; *apf* present; supraorbital pores six ....
....10 (*P. altipinnis* group)

9b. *trf* in single row, photophores closely spaced, with a circular cluster in midline; *mxf* in single regular row of closely spaced photophores; *apf* absent; supraorbital pores five
.... 11 (*P. scriptus* group)

10a. Teeth of first arch few and elongated, attached to bone individually, total teeth on ceratobranchial seven to 11 (mode nine); teeth on premaxilla and dentary moderately developed, but not long enough to reach other side of mouth; only last tooth of lateral series of premaxilla type 1; *ppf* present with few photophores .... *P. altipinnis*

10b Teeth of first arch short and numerous, attached to bone in groups of three to five, total teeth on ceratobranchial 7–22 (mode 15); teeth on premaxilla and dentary very enlarged, reaching other side of mouth; last four to six teeth of external series of premaxilla type 1; *ppf* absent .... *P. paxtoni*

11a. Total vertebrae 31, precaudal 14 .... *P. cephalus*

11b. Total vertebrae 35–36, precaudal 18–19 12

12a Mesial premaxillary teeth in a single row, three to five; premaxilla narrow, widest point 10–14% of premaxillary length, *lvf* present... 13

12b. Mesial premaxillary teeth in three to four rows, nine to 13; premaxilla narrow or wide, widest point 10–17 % of premaxillary length, *lvf* absent....................................... 14

13a Hooked teeth present on lateral series of dentary and premaxilla absent, teeth not visible from dorsal and ventral views .... *P. pierbartus*

13b. Hooked teeth present on lateral series of dentary and premaxilla present, teeth visible from dorsal and ventral views .... *P. obtusifrons*

14a. Teeth on lateral, medial and mesial series of premaxilla, and lateral and mesial series of dentary less than half the size of those from internalmost row; premaxilla narrow, widest point 10–14% of premaxillary length ....*P. cordilluminatus*

14b. Premaxillary teeth of lateral, medial and mesial rows, and dentary teeth increasing in size gradually; premaxilla wide, widest point 15–17 % of premaxillary length 15

15a. *saf* not extending anterior to level of anus; internal part of mouth mostly clear, except for few dusk areas... *P. scriptus*

15b. *saf* extending anteriorly beyond the level of anus; mouth cavity entirely dark, including gill arches... *P. sagamianus*

Pseudoscopelus Lütken 1892

Pseudoscopelus scriptus Lütken 1892: 284–286, plate 1, figures 4–5 [Type by monotypy *Pseudoscopelus scriptus* Lütken].

Myersiscus Fowler 1934:362, figures 112–3 [type by monotypy *Myersiscus obtusifrons* Fowler].

Diagnosis. The genus *Pseudoscopelus* is diagnosed from other chiasmodontid genera by two unique characteristics present in all species: the dorsal margin of orbit is formed by the infraorbital 6 (*vs*. infraorbital 6 on the posterior dorsolateral border of eye); and the position of the last infraorbital pore located anterior to middle of the pupil (*vs*. last infraorbital pore posterior to pupil).

Pseudoscopelus is further distinguished from *Chiasmodon* by premaxillary teeth in three series with variable number of rows, lateral, middle, and mesial(*vs.* premaxillary teeth in two series); dentary teeth in two series, lateral and mesial, with mesial series in two or more rows (*vs.* dentary teeth in two series, mesial in a single row); anteriormost premaxillary tooth not very well developed (*vs.* anteriormost premaxillary tooth very a well developed fang); total vertebra 31–38, precaudal 16–19 (*vs.* total vertebra 43–48, precaudal 19–23).

Pseudoscopelus is further distinguished from *Kali* and *Dysalotus* by having the bones that form the cranium well calcified and compact (*vs.* bones forming cranium poorly calcified with trabeculae easily distinguishable with the naked eye); nasal strongly calcified, spoon-shaped, located anterolaterally, and covered by thin transparent skin (*vs.* nasal weakly calcified, circular but not spoon-shaped, located dorsally, and covered by pigmented skin); parietals well developed, of same length or little smaller than supraoccipital (*vs.* parietals poorly developed, less than half the length of supraoccipital); crest on frontal weakly developed (*vs.* well developed longitudinal crest on frontal); pre- and postzygapophyses present on vertebrae (*vs.* pre- and postzygapophyses absent); presence of enlarged, elongated neuromasts exposed on surface of head, over supraoccipital, parietals, frontals and pterotic cranial bones, face, snout, lower jaw, and on body as two parallel rows anterior to first dorsal fin (*vs.* exposed neuromasts on head and body circular and small, present only on lateral side of head, anterior to preopercle, or as two rows anterior to first dorsal fin; no elongated neuromasts present); the last pored scale of lateral line well separated from the penultimate scale and positioned over the lower lobe of the caudal fin (*vs.* last pored lateral line scale contiguous with penultimate scale). From *Kali,* it can be also be distinguished by having the teeth of the premaxilla and dentary in several rows (*vs.* two rows), and from, and from *Dysalotus* by lacking prickles on body (vs. prickles present on flank, from mid-body to caudal peduncle).

Distribution. *Pseudoscopelus* are recorded from the Atlantic, Indian, Pacific, and Southern Oceans, including polar zones from 60º N to 60º S, but are absent from the Baltic, Mediterranean, Black, and Red Seas and some almost enclosed gulfs, such as the Persian Gulf and Gulf of Oman (Figs. 4.2 and 4.3)

Remarks. Among the chiasmodontids photophores are exclusive to the genus *Pseudoscopelus*, present as small discrete organs in 14 of the 16 valid species. *Pseudoscopelus parini* has white lines on ventral part of body in the same place as some ventral photophore groups (see species account for more details), and *P. aphos* completely lack photophores. For the remaining species, the arrangement of photophores groups is diagnostic to the species group level and even for some species. It is not clear so far whether the lack of photophores in certain species is plesiomorphic or a reversal.

Pseudoscopelus scriptus group

Composition. The *Pseudoscopelus scriptus* group comprises six species: *P. cephalus*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus*, and *P. scriptus*.

Diagnosis. The *Pseudoscopelus scriptus* group is diagnosed from its congeners by its unique supraorbital canal configuration and photophore pattern: supraorbital canal modally five, a small pore of supraorbital canal, medial to supranasal pore usually absent, with the exception of the holotype of *P. cephalus* and a few specimens of *P. cordilluminatus* (*vs.* supraorbital canal six, the small pore of supraorbital medial to supranasal pore always present in all other species of *Pseudoscopelus*); luminescent tissue present as discrete photophores (*vs.* completely absent in *P. aphos* and ventral white lines in *P. parini*); *mxf* arranged in an elongate continuous row that extends from level of posterior margin of eye to the angle between preopercle and dentary, and *apf* absent (*vs.* both *mxf* and *apf* absent in the species of the *P. scutatus* group, *lpf* present instead; *mxf* absent and *apf* present in *P. lavenbergi*; *mxf* short, not connected posteriorly with *apf* present in the *P. astronesthidens* group; and *mxf* irregular, with widely spaced photophores anteriorly, and connected with *apf* posteriorly in the *P. altipinnis* group); *if* and *prvf* continuous (*vs. if* and *prvf* disconnected at level of cleithrum in all other species of *Pseudoscopelus*); *trf* in a single row of closely spaced organs, with a medial, circular cluster of organs (*vs. trf* absent in the *P. astronesthidens* and *P. scutatus* groups; *trf* arranged in a broad band of three or four organs in *P. lavenbergi*; and in a single row of widely spaced organs without the medial cluster of organs in the *P. altipinnis* group).

Description. Dentition, photophore pattern, and color detailed in species' account. Body elongate, fusiform, not greatly compressed anteriorly, but progressively more compressed in caudal region. Greatest body depth at origin of first dorsal fin. Scales absent, except for embedded lateral-line scales.

Anterior profile of head elongated in lateral view in *Pseudoscopelus scriptus*, *P. sagamianus*, *P. pierbartus* and *P. cordilluminatus*; tip of snout protruding, with gentle curve at level of anterior naris. Anterior profiled of head curved in lateral view in

Pseudoscopelus obtusifrons; tip of snout rounded. Mouth terminal, oblique and enlarged, reaching ventral edge of preopercle. Orbit circular. Nares distinctly separated, anterior naris circular, close to third supraorbital pore; posterior naris crescent shaped, closer to anterodorsal margin of eye than to anterior naris.

Pectoral fin of *Pseudoscopelus scriptus*, *P. sagamianus*, *P. pierbartus*, and *P. cordilluminatus* very elongate, reaching posterior half of body in specimens larger than 80.0 mm; not reaching level of last ray of first dorsal-fin in *P. obtusifrons*; condition unknown in *P. cephalus*. Pelvic-fin origin slightly posterior to pectoral-fin base; dorsal fins two, first dorsal-fin insertion slightly posterior to level of pelvic-fin insertion, second dorsal-fin origin at level of anal-fin origin. Caudal fin forked. Lateral line complete, with pores opening between scales; last scale of lateral line separated from anterior part, on lower lobe of caudal fin, with two pores. True spines (*sensu* Johnson & Patterson 1993) present in entire first dorsal fin, and first ray of pelvic fin.

Gill arches four; pseudobranchia present. Epibranchial of first arch attached to opercle to midline; hypobranchial and ceratobranchial of first arch free. Epibranchials of second, third and fourth arches connected anteriorly to each other and to pharyngobranchials. Ceratobranchial of second arch free. Hypobranchial of second, third and four arches connected medially. Ceratobranchial of second arch free. Ceratobranchial of third and fourth arches connected distally. Ceratobranchial of fourth arch connected to body wall at proximal half. Basihyal, elongated, free anteriorly, with posterior and ventral connection to first basibranchial; first basibranchial small, triangular, connected to basihyal and second basibranchial; second basibranchial elongated; third basibranchial extremely elongated, extending posteriorly beyond fourth basibranchial, posterior half cartilaginous and ventrally curved; four basibranchial small, diamond-shaped, cartilaginous. Hypohyals with dorsal and ventral elements, attached to first basibranchial; first hypobranchial attached immediately posterior to basihyal, between joint of first and second basibranchials; second hypobranchial connected to joint between second and third basibranchials; third hypobranchial proximally connected to anterior edge of fourth basibranchial, distal tip of fourth hypobranchial ventrally pointed; fourth hypobranchial absent or fused to ceratobranchial, fourth ceratobranchial connected to posterior edge of fourth basibranchial; ventral pharyngobranchials connected posteriorly to fourth ceratobranchial.

Ontogenetic changes and the identification of Juveniles. Tooth morphology is important in diagnosing the *Pseudoscopelus scriptus* group; however, they are not completely developed in specimens less than 45.0 mm – with the exception of *P. obtusifrons*. Ontogenetic changes across dentition are best understood in *P. scriptus*, because it is very well represented in scientific collections in a wide range of sizes.

Juveniles of *Pseudoscopelus scriptus* have teeth arranged similar to *P. pierbartus*, the premaxilla is not very wide (10–12% of its length) and dentition arranged in three series of a single row of teeth, with the mesial series having few teeth. Because the distribution of *P. scriptus* and *P. pierbartus* overlaps, juveniles can not be separated easily, but in *P. pierbartus* the *saf* extends a little forward, reaching the level of anus; allowing tentative identifications. The number of rows of teeth in the mesial series of the premaxilla increases with size, starting in specimens of about 31.0–32.0 mm SL and reaching full development by 45.0 mm. Teeth of the mesial row in a specimen of 31.0 mm SL (MCZ 68463) are externally developed, but are not attached to the bone; in a 31.8

mm specimen (UF 19987), the teeth of the left side of the premaxilla has the adult arrangement and are completely attached to bone, but in the left side it is as juvenile. A 44.5 mm specimen (MCZ 101790) is the smallest specimen examined with fully developed dentition on the premaxilla and dentary. *Pseudoscopelus cephalus*, *P. cordilluminatus*, and *P. sagamianus* are not common in scientific collections and a good series of juveniles was not available, nevertheless, because they belong to the same species group, it is very likely that they also undergo the same ontogenetic changes. A 24.4 mm specimen (USNM 200533) was tentatively identified as *P. cordilluminatus* based largely on capture locality, and has some growing teeth below the skin. In *P. obtusifrons* the diagnostic dention of hooked teeth flared outwards is already developed in specimens as small as 16.8 mm (USNM 200535).

Allometric growth of pectoral fin was observed in *Pseudoscopelus scriptus* and *P. obtusifrons* (Fig. 4.11 A and B). *Pseudoscopelus scriptus* has a positive statistically significant allometric growth of pectoral fin (p=0.001), and this explains the large standard deviation found for this characteristic (SD=5.3). *Pseudoscopelus obtusifrons* has a negative statistically significant allometric growth of pectoral fin (p=0.042) and this also explains the large standard deviation variation found for this species characteristic (SD=3.2).

Pseudoscopelus scriptus Lütken 1892

Figures 4.4 A, 4.9 A, 4.12 A–J; Tables 4.1 and 4.2

Pseudoscopelus scriptus Lütken 1892: 284–286, plate 1, figures 4–5 [type locality western Central Atlantic, Mouth of "Gamle Bahama Kanalen" (Old Bahamas Channel), holotype ZMUC P. 65171, 70.0 mm]; Goode and Bean 1895: 292–3, plates 76, figure 286 [western North Atlantic]; Parr 1933: 40–41, figure 17 [western North Atlantic]; Norman 1966: 366–367 [key to genus and species list]; Uyeno et al. 1983: 404 [western Central Atlantic, off Suriname; questionable]; Bañón et al. 1999 [western North Atlantic, questionable]; Moore et al. 2003: 227 [western North Atlantic]; Prokofiev and Kukuev 2006c [key to species, questionable]; Sptiz et al. 2007: 2–3 [western North Atlantic].

Pseudoscopelus sagamianus Prokofiev and Kukuev 2006a: 221–225 [in part, western North Atlantic]; Prokofiev 2009 [in part, western North Atlantic].

Pseudoscopelus stellatus Beebe 1932: 76–79, figure 18 [type locality Bermuda]; Prokofiev and Kukuev 2005 [questionable]; Sptiz et al. 2007 [mentioned]. **NEW SYNONYMY.**

Diagnosis. A species of the *Pseudoscopelus scriptus* group distinguished within the group by a single characteristic: *saf* not extending anterior to the level of anus (*vs*. *saf* extending anteriorly to level of or beyond anus). It can be further diagnosed from the other species by a combination of characteristics: mesial series of premaxillary teeth in three-four rows (*vs*. mesial series of premaxilla in single row *P. obtusifrons* and *P. pierbartus*); mesial series of teeth arranged in rows of three to four teeth gradually increasing of size from lateral to mesial (*vs*. mesial series arranged in rows of two to three teeth, with internal row much larger than other teeth in *P. cordilluminatus*); total vertebrae 35–36, precaudal 18–19 (*vs*. 31, 14 in *P. cephalus*); and pigmentation in mouth confined to the skin covering areas around teeth on premaxilla and dentary (*vs*. internal surface of mouth and gill arches darkly pigmented *P. sagamianus*).

Description. Medium-sized species, largest specimen examined 203.0 mm SL. Meristic data summarized in table 1, morphometric in table 2. General body shape similar as of species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary (Fig. 4.7 A). Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 15–17% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, and curved caudally in body and caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of two to three straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in six to eight transverse rows of three to four straight, needle-like, type 4 teeth, gradually increasing in size from medial to mesial.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, slightly curved, type 4 teeth, usually recovered by skin. Mesial in six to eight transverse rows of one to four teeth straight, needle-like, type 4 teeth, increasing in size from lateral to mesial. Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, small, conical, type 1; absent on third and fourth arches. Conical, type 1 teeth also present on ventral and dorsal pharyngeals and in *V*-shaped row on second basibranchial; absent on basihyal and other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.4 A. Photophores on head: *apf*, *dnf*, *inof* 1–2, *lpf*, *opf*, and *pof* absent; *mxf* elongated, in single row anteriorly and two posteriorly, parallel to maxilla, from level of posterior edge of eye to angle between preopercle and dentary; *vnf* usually absent, but present in some specimens; *ppf* in small patch on ventral edge of interopercle; *amf* in two to three rows, medial to third pore of mandibular canal, from posterior of second pore to halfway between third and fourth pores; *pmf* in one to three rows lateral to fifth pore of mandibular canal, from halfway between fourth and fifth pores to halfway between fifth and sixth pores of mandibular canal.

Photophores on body: *lvf, rtf*, *scf*, *spf*, and *svf* absent; *pf* in single row extending to half pectoral fin, on ventral ray; *paf* continuous with *pf*, at pectoral-fin axil; *vf* in single row, along mesial pelvic-fin ray; *vaf* continuous with *vf* and *trf*, extending over base of pelvic rays three to five; *if* and *prvf* continuous, in irregular two to three rows, from isthmus to anterior part of pelvic girdle; *ptvf* in two rows, from posterior half of pelvic fin to close to anus; *trf* laterally in single row, with medial circular group of photophores; *saf* in two rows, with smaller photophores closely spaced and ventral, and larger photophores widely spaced and dorsal, heart-shaped, from far anterior to anus, to almost halfway between pelvic and anal fins, and connected posteriorly; *prcf* in posterior half of peduncle, oval-shaped or three-pronged, medial prong extending over anteriormost lower procurrent rays.

Color. Recently collected specimens with uniformly black or dark brown body, except for triangular area on top of head over epiphyseal branch; most specimens examined bleached clear brown or white, including holotype. Pectoral and pelvic fins hyaline; anal, first and second dorsal fins with melanophores uniformly distributed over rays, more concentrated on fin base; and caudal fin pigmented at base. Mouth and gill arches mostly clear, except for skin covering toothed area of premaxilla and dentary, and delicate membrane between anterior portion of premaxillae and dentaries.

Distribution. Western Atlantic from the United States to Brazil, 69º N to 22º S; from the continental shelf and Islands of the Caribbean in the west to Central Atlantic, 39º W to 23º W (Fig. 4.2 A). A possible juvenile specimen was tentatively identified from off Nigeria (UF 19987), possibly extending the species range to the Eastern Atlantic.

Bathymetric distribution. From 250 to 1370 m (mean 786 m), juveniles to about 30 mm are known from 95 to 590 m.

Identification of juveniles. Specimens nominally identified as juveniles of *Pseudoscopelus scriptus* are not distinguishable from those of *P. pierbartus* by dentition pattern, but were tentatively identified by the shape of *saf*, not extending to level of anus.

Remarks. Lavenberg (1974) tentatively distinguished *Pseudoscopelus scriptus* from *P. sagamianus* based on three characteristics: anterior organs of *mxf* below ventral margin of orbit (*vs.* anterior organs below middle of eye); presence of *vnf* (*vs. vnf* absent);

and single aperture in supranasal pore (*vs.* two in *P. sagamianus*). None of Lavenberg' S characters, are useful to separate the two species because of individual variation, even comparing specimens from the same locality: in *P. sagamianus*, anterior organs of *mxf* can also extend anteriorly to below mid-eye; *vnf* is variable, it is absent in most specimens of *P. scriptus*, including the holotype, but present in a few specimens (e.g., MCZ 101790; the same is true for *P. sagamianus*, see species account); in addition, most specimens of *P. scriptus*, including the holotype, have two supranasal pores.

The diagnosis of *Pseudoscopelus scriptus* provided by Prokofiev and Kukuev (2006a: 218–221) is imprecise and erroneous, despite their statement that "the identity of the aforementioned fish [*P. scriptus*] is not in doubt" (p.221). Characteristics of dentition as described by those authors as "manifestations of individual variation" (p. 221), actually reflects the pattern of two different species: *P. pierbartus* and *P. cordilluminatus*. *Pseudoscopelus scriptus* and *P. sagamianus* are very similar species, and pigmentation of the internal area of the mouth and shape of *saf* are the only useful characteristics to distinguished them. Unfortunately the former can only be used reliably in fresh specimens.

The status of *Pseudoscopelus stellatus*. *Pseudoscopelus stellatus* was described based on five larval specimens between 6.5 mm and 20.3 mm, from Bermuda, western North Atlantic – a brief description of the specimens is given by Melo et al. (2007). Eschmeyer (1998) considered the types to be lost, but in Eschmeyer (2007) a lot from the USNM and three others from CAS were listed as holotype and paratypes, respectively (Fig. 4.12 D-J). Prokofiev and Kukuev (2005, 2006c, 2008) considered this species valid. Melo et al. (2007) were not able to determine its correct identification at that time, and preferred to refer to it as *species inquirenda*.

Beebe (1932) was the first author to identify the existence of photophores in *Pseudoscopelus*, and illustrated and described the photophore groups in the holotype of *P. stellatus*, but did not mention that the other specimens examined do not have photophores. The specimen, however, is a juvenile and after the examination of more specimens it becomes clear that not all photophore groups are developed in that specimen. Adults of seven species were identified from the Bermuda (*P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. scutatus*, *P. pierbartus*, *P. scriptus*, and *P. obtusifrons*) and none of them have the photophore pattern as described.

The holotype is in bad condition, but the examination of it revealed some details not described by Beebe (1932), and are useful to establish the correct identity of *Pseudoscopelus stellatus*: photophores are present as discrete photophores (*vs.* absent in *P. aphos*); *saf* (=circum-anal of Beebe 1932) not interrupted anteriorly (*vs.* interrupted anteriorly in *P. astronesthidens*); *if* and *prvf* are continuous and separate from *ptvf* (*vs. if* and *prvf* separate in *P. altipinnis* and *P. scutatus*, and *prvf* and *ptvf* continuous in the latter). The photophores in the angle between maxilla and dentary (=preopercular) are in a small group, but different from what was illustrated, this group is not oval; instead, it is arranged in a straight line, a condition that is only found in the *P. scriptus* group.

The most remarkable characteristic of the holotype is the shape of *saf*, which does not extend anteriorly to the level of anus, and is connected posteriorly behind the last anal-fin ray (*vs. saf* extending to the level of, or slightly beyond anus and not connected posteriorly in *Pseudoscopelus obtusifrons* and *P. pierbartus*). That only fits with *P. scriptus*. Although some of the diagnostic photophores for that species are not present yet (*trf*, *ppf*, *prcf*, *pf*, *vf*, and *vaf*), this is because the specimen a juvenile with some of the groups undeveloped. On the basis of this, *P. stellatus* is placed in synonymy of *P. scriptus*.

Pseudoscopelus sagamianus Tanaka 1908

Figures 4.4 B, 4.13 A and B; Tables 4.1 and 4.2.

Pseudoscopelus scriptus sagamianus Tanaka 1908:13–17, plate 1, figure 2 [type locality: Sagami Sea, Japan, holotype, FMNH 55551]; Parr 1933: 29 [key to subspecies].

Pseudoscopelus sagamianus Matsuda et al. 1984: 221, plate 217, figure D [western North Pacific, off Japan]; Nakabo 2002: 1073 [key to species]; Prokofiev and Kukuev 2006a: 221–225 [questionable, one lot from eastern Indian]; 2006c [key to species, questionable]; Prokofiev 2009, in part.

Diagnosis. A species of the *Pseudoscopelus scriptus* group distinguished within the group by a single characteristic: internal part of mouth, including roof of mouth and gill arches, intensely darkly pigmented, including the roof of mouth and gill arches. Bleached specimens can be further distinguished from *P. scriptus* by *saf* extending anteriorly beyond and the level of anus (*vs. saf* not extending anteriorly to anus); from *P. pierbartus* and *P. obtusifrons* by mesial series of premaxillary teeth in three to four rows (*vs.* mesial series in a single row); from *P. cordilluminatus* by mesial series of teeth arranged in rows of three to four teeth gradually increasing in size from lateral to mesial (*vs.* mesial series arranged in rows of two to three teeth, with internal row much larger than other teeth); from *P. cephalus* by vertebral count (total vertebrae 35–36, precaudal 18–19 *vs.* 31, 14 in *P. cephalus*).

Description. Medium-sized species, largest specimen examined 143.0 mm SL. Meristic data summarized in table 4.1, morphometric in table 4.2. General body shape similar as of species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary same as illustrated for *Pseudoscopelus scriptus*. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 15–17% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, and curved caudally in body and caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of two to three straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in six to eight transverse rows of three to four straight, needle-like, type 4 teeth, gradually increasing in size from medial to mesial.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, slightly curved, type 4 teeth, usually recovered by skin. Mesial series in six to eight transverse rows of two to four straight, needle-like, type 4 teeth, increasing in size from lateral to mesial. Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, small, conical, type 1; absent on third and fourth arches. Conical, type 1 teeth also present on ventral and dorsal pharyngeals and in *V*-shaped row on second basibranchial; absent on basihyal and other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.4 B . Photophores on head: *apf*, *dnf*, *inof* 1–2, *lpf*, *opf*, and *pof* absent; *mxf* elongated, in single row anteriorly, and two posteriorly, parallel to maxilla, from posterior edge of eye to angle between preopercle and dentary; *vnf* variable, absent from most specimens or, if present, as small patch posterior to anteriormost supraorbital pore; *ppf* as small patch in ventral edge of interopercle; *amf* in two to three rows, medial to third pore of mandibular canal, from posterior of second pore to halfway between third and fourth pores; *pmf* in rows of one to three photophores, lateral to fifth pore of mandibular canal, from halfway between fourth and fifth pores to halfway between fifth and sixth pores.

Photophores on body: *lvf, rtf*, *scf*, *spf*, and *svf* absent; *pf* in single row extending to half pectoral fin, on ventral ray; *paf* continuous with *pf,* at pectoral-fin axil; *vf* in single row, along mesial pelvic-fin ray; *vaf* continuous with *vf* and *trf*, extending over base of pelvic rays 3–5; *if* and *prvf* continuous, in two irregular rows, from isthmus to anterior part of pelvic girdle; *ptvf* in rows of two organs, from posterior half of pelvic fin to close to anus; *trf* laterally in single row, with medial circular group of photophores; *saf* in two rows, with smaller photophores closely spaced and ventral, and larger photophores widely spaced and dorsal, heart-shaped, extending far anterior to anus, to almost halfway between pelvic and anal fins, and connected posteriorly; *prcf* in posterior half of peduncle, oval or three-pronged, medial prong extending over anteriormost lower procurrent rays.

Color. Two specimens collected off Japan (CAS–SU 64331 and FMNH 55551) severely bleached white, and one (CAS–SU 25626) with coloration poorly preserved in few areas. Color description based on specimens with preserved colors (BMNH 1984.1.1.83, 1984.1.1.84, and NMNZ P. 26211), collected in the Indo-Pacific and Western South Pacific. Body uniformly black or dark brown, except for a triangular area on top of head, over epiphyseal branch. Pectoral fin mostly hyaline; pelvic, dorsal, anal, and caudal fins with few melanophores over rays and fin bases. Internal part of mouth and gill arches entirely black, including skin on toothed area of premaxilla and dentary, over basihyal and basibranchials, roof, floor and lateral wall of mouth, internal part of opercle, membrane between dentaries and premaxillae, and gill arches; gill filaments pale. Clear pigmentation is present in ventral part of body and internal part of opercle of CAS 25626.

Distribution. Western Pacific from Japan to New Zealand, 35º N to 40º S; from western Indian Ocean, off Indonesia to the Pacific Plate, 114º E to 132º W (Fig. 4.2 A).

Bathymetric distribution. A single lot (NMNZ. P. 26211) had the depth of capture recorded, of 1060 to 1200 m.

Remarks. *Pseudoscopelus sagamianus* has been misidentified frequently with other species of the *Pseudoscopelus scriptus* group scientific collections and recent publications. Prokofiev and Kukuev (2005) listed specimens from the western North Atlantic and eastern South Atlantic Oceans; Prokofiev and Kukuev (2006a) recorded the species in the western Indian Ocean; and Prokofiev (2009) listed specimens from Indian and Atlantic Oceans as possible subspecies of *P. sagamianus*. *Pseudoscopelus cordilluminatus* is probably the species that occurs in the Indian and eastern South Atlantic, and *P. scriptus*, the type species of the genus, is the species from the North Atlantic.

Spitz et al. (2007) did not examine any specimen of *P. sagamianus* and based their diagnosis on the illustration provided by Tanaka (1908). Their diagnosis, based on the distance between anus and anal fin, is incorrect as none of the specimens examined showed any difference in the distance between the anus and anal fin, when compared to other species of *Pseudoscopelus*.

The type specimens of Pseudoscopelus sagamianus. *Pseudoscopelus sagamianus* was described by Tanaka 1908 as a subspecies of *P. scriptus* based on two specimens of 120 and 150 mm, collected in the Sagami Sea by Allan Owston. Those specimens were obtained at the collector collection, and no catalog number was provided. Allan Owston sold parts of his collection to David S. Jordan, and they were incorporated into the Stanford University and Carnegie Museum fish collections (*e.g.*, Jordan and Snyder 1904). Later, those collections were transferred to the California Academy of Sciences and Field Museum of Natural History, respectively (D. Catania and M.A. Rogers, pers. comm. 2007).

As search of the collections at the CAS and FMNH found three specimens of *P. sagamianus* collected on the Sagami Bay by A. Owston and D. Jordan. The specimen FMNH 55551 was collected at the type locality and measurements fit perfectly for the specimen used by Tanaka (1908). In addition, it also agrees with the illustration. The information contained on the label (not original) records D. Jordan as the collector, probably because he was responsible for the transfer of the specimen to the FMNH. A similar conclusion concerning the collector was made by Barbour (1941) for the type of *Paraceratias mitsukurii*, which was re-discovered at the MCZ.

Prokofiev (2009) designated a neotype for *Pseudoscopelus sagamianus* (NSMT-P 35337) from the western North Pacific Ocean, more than 5,000 Km west of the type locality. As the previously lost holotype was rediscovered, the original type specimen automatically displace the neotype and become the name-bearing type, according to the ICZN (1999).

Pseudoscopelus cephalus Fowler 1934

Figures 4.4 C, 4.13 C; Table 4.3.

Pseudoscopelus cephalus Fowler 1934:361, figure 111 [type locality western Central Pacific, Philippines Islands, 9º38’ N, 121º11’ E]; de Beaufort in de Beaufort and Chapman 1951: 7–8, figure 4 [western Central Pacific]; Prokofiev and Kukuev 2005: 231; 2006c [key to species].

Diagnosis. *Pseudoscopelus cephalus* is diagnosed by an unique characteristic: a low number of vertebrae, total vertebrae 31; precaudal vertebrae 14 (*vs.* 35–38, 16–18 in all other species of *Pseudoscopelus*).

Description. Medium-sized species, only known specimen 74.0 mm. Meristic data summarized in table 4.3, morphometric not available (see remarks). General body shape as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary same as illustrated for *Pseudoscopelus scriptus*. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, anteriorly narrowing in posterior third, widest point 15–17% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, and curved caudally in body and caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of two to three straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in six to eight transverse rows of three to four straight, needle-like, type 4 teeth, gradually increasing in size from medial to mesial.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, slightly curved, type 4 teeth, usually recovered by skin. Mesial series in six to eight transverse rows of two to four straight, needle-like, type 4 teeth, increasing in size from lateral to mesial. Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, small, conical, type 1; absent on third and fourth arches. Conical, type 1 teeth also present on ventral and dorsal pharyngeals and in *V*-shaped row on second basibranchial; absent on basihyal and other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.4 C. Most of photophores partially destroyed by loss of skin or washed out, see remarks for details. Organs on head: Photophores on head: *apf*, *dnf*, *inof* 1–2, *lpf*, *opf*, *pof*, and *vnf* absent or not preserved. *mxf* elongated, in single row, parallel to maxilla, from level of posterior margin of eye to posterior third of maxilla; *ppf* poorly preserved on left side, completely destroyed on right; *amf* not preserved or absent; *pmf* partially preserved, in one to two rows, lateral to fifth pore of mandibular canal, elongate, from halfway between fourth and fifth pores to halfway between fifth and sixth pores of mandibular canal.

Photophores on body: Most of photophores partially destroyed by loss of skin or bleached out; see remarks. *Lvf, rtf*, *spf*, and *svf* absent or lost; *scf* present as three organs in posterior part of peduncle; *pf* in single row along ventral-most pectoral-fin ray, continuous with *paf*; *vf* in single row, along mesial pelvic-fin ray; *vaf* continuous with *vf* and *trf*, extending over base of pelvic rays 3-5; *if* and *prvf* continuous, in irregular two rows, from isthmus to anterior part of pelvic girdle; *ptvf* in two rows, from posterior half of pelvic fin to close to anus; *trf* laterally in single row, with medial circular group of photophores; *saf* in two rows, with smaller photophores closely spaced and ventral, and larger photophores widely spaced and dorsal, heart-shaped, extending anteriorly beyond anus, not preserved posteriorly; *prcf* in posterior half of peduncle, elongated, three-pronged, medial prong extending over anteriormost lower procurrent rays.

Color. Unknown; single specimen bleached out, entirely white.

Distribution. Known from holotype, collected from the Jolo Sea in Philippines, 9º38.5’ N, 121º11’ E (Fig. 4.2. A).

Bathymetric distribution. Known from a single specimen collected at 508 fathoms (927 m).

Remarks. *Pseudoscopelus cephalus* is only known from the poorly preserved holotype, with severe damages: the head is almost disconnected from body; the opercle is destroyed on both sides; the pectoral, pelvic, second dorsal and anal fins have their tips broken. The skin is partially destroyed on both sides of the cheeks, the area between head and first dorsal fin, opercles, and dorsal peduncle. The groups of photophores *amf,* left and part of right side *pmf*, *vnf,* posterior part of *mxf*, *ppf*, left side and anterior part of *saf* are not preserved. Despite the damages, the vertebral column is complete, allowing the specimen to be confidently distinguished as a valid species.

Pseudoscopelus obtusifrons (Fowler 1934)

Figures 4.5 A, 4.9 B, 4.14; Tables 4.3, 4.4, and 4.5

Myersiscus obtusifrons Fowler 1934:362, figures 112–3 [type locality: western Central Pacific, Sulawesi, Indonesia, 3º32’ S, 120º31’ E].

Pseudoscopelus obtusifrons de Beaufort in de Beaufort and Chapman 1951: 6–7 [western Central Pacific]; Moore et al. 2003: 227 [western North Atlantic]; Prokofiev and Kukuev 2006a: 225–228, figure 4 [western North Pacific, off Japan]; 2006c [key to species].

Pseudoscopelus obtusirostris Krefft 1971: 165 [misspelled in introduction].

Diagnosis. *Pseudoscopelus obtusifrons* is diagnosed from its congeners by two unique characteristics: *spf* present (*vs. spf* absent); and anterior teeth of lateral series in dentary and premaxillary hook-like curved, inserting on the lateral edge of bone and positioned outside of mouth so that teeth are visible in ventral and dorsal views (*vs.* lateral series of dentary and premaxillary teeth straight, or if curved, not hook-like, and inserted at oral edge of bone, not allowing them to be seen in dorsal or ventral views).

Description. Medium-sized species, largest specimen examined 144.0 mm SL. Meristic data summarized in tables 4.3 and 4.4, and morphometric in table 4.5. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine, as illustrated in figure 4.9 B. Premaxilla elongated, dentigerous area divided into four processes: head, anterior mesially curved; neck, narrow region at angle of head; body, wide anteriorly, narrowing in posterior third, widest point 10–14% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk not very enlarged, on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process; teeth on head, five to six, hook-like, attached to external edge of premaxilla, flared outwards; remaining curved caudally. Middle and mesial series restricted to body of premaxilla; middle series in single of slightly curved, type 4 teeth; mesial series in single row of three to five slightly curved, type 4 teeth.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series along lateral edge of dentary in single series of type 4 teeth; anteriormost four to six teeth hook-like, attached to external edge of bone, flared outwards; posterior teeth curved orally. Mesial series in single row of slightly recurved, type 4. Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, small, conical, type 1; absent on third and fourth arches. Conical, type 1 teeth also present on ventral and dorsal pharyngeals and in *V*-shaped row on second basibranchial; absent on basihyal and other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.5 A. Photophores on head: *apf*, *dnf*, *inof* 1–2, *lpf*, *opf*, and *pof* absent; *mxf* elongated, in single row, parallel to maxilla, from level of posterior margin of eye to angle between preopercle and dentary; *vnf* in triangular patch, or straight line of few photophores; *ppf* in small patch on ventral edge of interopercle; *amf* in one to three rows, medial to third pore of mandibular canal, from between first and second pores to halfway between third and fourth; *pmf* in one to three rows, lateral to fifth pore of mandibular canal, from halfway between fourth and fifth pores to halfway between fifth and sixth pores.

Photophores on body: *scf* and *svf* absent; *rtf* on single specimen (USNM 268429, Fig. 4.13 C), with single photophores widespread over body; *spf* present in at least in one side of all specimens larger than 100.0 mm, from two to 16 small photophores; *pf* in single row along ventral-most pectoral-fin ray; *paf* in row of up to three organs at pectoral-fin axil; *vf* in single row, along mesial pelvic-fin ray; *lvf* at base of first pectoral fin; *vaf* continuous with *vf* and *trf*, extending over base of pelvic rays 4–5, and first pelvic-fin ray; *if* and *prvf* continuous, in irregular two rows, from isthmus to anterior part of pelvic girdle; *ptvf* in two rows, from posterior half of pelvic fin to close to anus; *trf* laterally in single row, with medial circular group of photophores; *saf* in two rows, with smaller photophores closely spaced and ventral, and larger photophores widely spaced and dorsal, heart-shaped, extending to level of or slightly anterior to anus, and connected posteriorly; *prcf* in posterior half of peduncle, elongated, three-pronged, medial prong extending over anteriormost lower procurrent rays.

Color. Most specimens examined were faded brown; holotype bleached white; color description based on BMNH 2003.6.10.7. Preserved color uniformly black, except for triangular area in the top of head, over epiphyseal branch; most specimens examined bleached clear brown or white, including holotype. Pectoral, pelvic and first dorsal fins mostly hyaline, with few melanophores over fin-rays; second dorsal, anal and caudal fins with melanophores distributed over rays, more concentrated at fins base. Mouth and gill arches mostly clear, except for skin on toothed area of premaxilla and dentary, and delicate membrane between anterior portion of premaxillae and dentaries.

Distribution. In the Atlantic, from the United States to Suriname in the East, 32º N to 20º S, Canary Islands to off Liberia in the East 93º W to 14º W; a single record in the Indian Ocean; and in the Pacific from Hawaii to east of Northfolk Islands, 24º N to 26º S, Indonesia to Middle Pacific, 120º E to 153º W (Fig. 4.2 B).

Bathymetric distribution. From 124 to 2250 m (mean 718 m). The records below 2000 m are questionable as specimens may have been be taken during gear transition.

Ontogenetic changes. *Pseudoscopelus obtusifrons* has a negative statistically significant allometric growth of pectoral fin ($p=0.042$, Fig. 4.11 B). Such variation explains the large standard deviation variation found for this characteristic (SD=3.2). Juveniles of at least 20.0 mm (*e.g.*, USNM 200535) could readily identified by their distinctive hooked teeth.

Remarks. The number of lateral-line pores in *Pseudoscopelus* is generally very stable. In *P. obtusifrons*, however, the total number of pores varies from 52 to 74, with a single pore between two scales of the lateral line, two pores between each scale, or one pore every two scales. Two specimens (LACM 31528 and HUMZ 310746) have the lateral line incomplete on one side. The number of pores in the lateral line forms a gradient without a clear mean between populations (Table 4). Because of that wide range in counts Lavenberg (1974) decided to split it into two species. The specimens cited by Lavenberg were re-examined and some x-rayed, including the lot listed as a manuscript holotype, but no further differences were found.

The *rtf* was found on a single specimen of *P. obtusifrons* (USNM 268429). No other specimen examined had such group, even from adjacent regions (*e.g.*, MCZ 68446, USNM 2406975). The body of those specimens also have a relatively large variation, but measurements were biased as the specimen HUMZ 310746 had a large prey item in its stomach.

Pseudoscopelus pierbartus Sptiz et al. (2007)

Figures 4.5 B, 4.9 C, 4.15 A–C; Tables 4.3 and 4.5.

Pseudoscopelus pierbartus Spitz Quéro & Vayne 2007: 333–339, figure 2 [type locality western North Atlantic, Golfe de Gascogne, France, holotype MHNLR 2005171, 138.0 mm].

Diagnosis. A species of the *Pseudoscopelus scriptus* group distinguished within the group by a combination of characteristics: mesial series of premaxillary teeth in a single row, with two to four teeth (*vs.* medial series in three to four rows, with 20 or more teeth in *P. scriptus*, *P. cephalus*, *P. sagamianus*, and *P. cordilluminatus*), dentary teeth in two series, lateral and medial, of single row each(*vs.* dentary teeth with two series, lateral in single row and mesial with three or more rows); teeth at the anterior edge of premaxilla recurved and dentary inserted on the ventral edge of the bone and pointing mesially or caudally (*vs.* teeth of lateral series extremely curved with anterior teeth inserted in the lateral edge of bone, turned to the externally).

Description. Medium-sized species, the largest specimen examined has 179.8 mm SL. Meristic data summarized in table 4.3, morphometric in table 4.5. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine, as illustrated in figure 4.9 C. Premaxilla elongated, dentigerous area divided into four processes: head, anterior mesially curved; neck, narrow region at angle of head; body, wide anteriorly, narrowing in posterior third, widest point 10–13% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk moderately developed, on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process; teeth on head strongly recurved, remaining curved caudally. Middle and mesial series restricted to body of premaxilla; middle series in single row of conical, orally curved, type 4 teeth; middle series in single of slightly curved, type 4 teeth; mesial series in single row of three to five slightly curved, type 4 teeth.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series along lateral edge of dentary in single series of type 4 teeth, four to six anterior most teeth recurved, the remaining slightly curved orally. Mesial series in single row of slightly recurved, type 4. Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, small, conical, type 1; absent on third and fourth arches. Conical, type 1 teeth also present on ventral and dorsal pharyngeals and in *V*-shaped row on second basibranchial; absent on basihyal and other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.5 B. Photophores on head: *apf*, *dnf*, *inof* 1–2, *lpf*, *opf*, *pof* and *vnf* absent; *mxf* elongated, in single row, parallel to maxilla, from level of posterior margin of eye to angle between preopercle and dentary; *ppf* in small patch on ventral edge of interopercle; *amf* in one to two rows, medial to third pore of mandibular canal, from immediately posterior to second pore to immediately anterior to fourth pore; *pmf* in one to two rows, lateral to fifth pore of mandibular canal, from halfway between fourth and fifth pores to halfway between fifth and sixth pores.

Photophores on body: *rtf*, *scf*, and *svf* absent; *spf* in single row, with four to five photophores; *pf* in single row along ventral-most pectoral-fin ray; *paf* continuous with *pf*, at pectoral-fin axil; *vf* in single row, along mesial pelvic-fin ray; *lvf* at base of first pectoral fin; *vaf* continuous with *vf* and *trf*, extending over base of pelvic rays three to five; *if* and *prvf* continuous, in irregular two rows, from isthmus to anterior edge of pelvic girdle; *ptvf* in two rows, from posterior half of pelvic fin to close to anus; *trf* in single row, with medial circular group of photophores; *saf* in two rows, with smaller photophores closely spaced and ventral, and larger photophores widely spaced and dorsal, heart-shaped, extending to level of, or slightly anterior anus, not connected posteriorly; *prcf* in posterior half of peduncle, oval-shaped, three-pronged, extending over anteriormost lower procurrent rays.

Color. Recently collected specimens uniformly black or dark brown, except for triangular area in the top of head, over epiphyseal branch. Most preserved specimens examined pale brown. Pectoral and pelvic fins mostly hyaline, with few chromatophores on rays; anal, first and second dorsal fins with melanophores uniformly distributed over rays, more concentrated on fin base; and caudal fin entirely black. Mouth and gill arches mostly clear, except for skin covering toothed area of premaxilla and dentary, and delicate membrane between anterior portion of premaxillae and dentaries.

Distribution. Atlantic, from off the Untied States to Brazil in the west, to off France in the East, 48º N to 20º S, 67º W to 4º W (Fig. 4.2 B).

Bathymetric distribution. From 829 to 1770 m (mean 1069 m), and juveniles from 50 to 1025 m. Some of those deepest records, especially for the juveniles, are questionable, as specimens may have been taken during gear transition.

Remarks. Spitz et al. (2007) diagnosed the species based on the *prcf* shaped as three double lines forming an arrow pointing forward, length of pectoral fin, extending to sixth ray of second dorsal fin, and teeth recurved at anterior end of premaxilla. As noticed previously by Prokofiev and Kukuev (2008), the description is incomplete and of little value to distinguish *P. pierbartus* from its congeners. The *prcf* in variable *Pseudoscopelus* and different shapes are present in the same species, from oval to three-pronged (see Figs. 4.2, 4.3, 4.4, 4.5, 4.6). The elongate pectoral fin is also not exclusive to *P. pierbartus* within the group, being also found in *P. scriptus*, *P. sagamianus* and *P. cordilluminatus*. Finally, the anterior teeth of premaxilla are recurved, but not hook-like as in *P. obtusifrons*.

Prokofiev and Kukuev (2008), however, was not able to diagnose the species and referred to it as *species inquirenda* and *nomen dubium*. According to the ICZN (1999) those terms should only apply if the types are not available, which is not the case. Prokofiev (2009) erroneously referred to *P. pierbartus* as a possible synonym or subspecies of *P. sagamianus*.

Pseudoscopelus pierbartus is a very similar species to *P. scriptus* and can only be separated by having fewer teeth in the middle series of premaxilla, organized in a single row. It can be tentatively separated from *P. scriptus* by the shape of *saf*, which extends anteriorly to the level of anus, but this characteristic varies in some specimens. That can be used to tentatively identify the juveniles, before dentition is completely formed.

Pseudoscopelus cordilluminatus, new species

Figures 4.5 C, 4.9 D, 4.15 D, E, Tables 4.6 and 4.7

Holotype. MCZ 161017, 77.0 mm, Eastern Atlantic, Guinean, 0º00’, 19º45’ W, 0–1164 m, 0–1164 m, 20–IV–1965, R/V *Trident*.

Paratypes. Atlantic, Guinean Province: CAS 223102, 1, 88.7 mm, 8°35’ S, 12°51’ E, 548–526 m, 11–IV–2005, R/V *Dr. Fridtjof Nansen*. **Indian:** BMNH 2003.4.23.51, 1, 87.3 mm, 10º16’ N, 57º56’ E, 14–III–1964, R.R.S. *Discovery*. **Pacific, West Pacific:** SIO 77–171, 1, 97.3 mm, 4°40.2’ S, 125°32.8’ E, 0–1500 m, 26–VIII–1976, R/V *Thomas Washington*.

Non-type (juvenile, tentative identification). Indian: USNM 200533, 1, 24.4 mm, 4º01’ S, 65º00’ E, 615 m, 30–V–1964, R/V *Anton Bruun*.

Diagnosis. A species of the *Pseudoscopelus scriptus* group diagnosed by a unique dentition pattern of the premaxilla: mesial series in rows of two to three teeth, with first and second teeth much smaller than innermost tooth (*vs.* single row in *P. pierbartus* and *P. obtusifrons*; and teeth gradually increasing in size in *P. cephalus*, *P. sagamianus*, and *P. scriptus*). It can be further distinguished from *P. scriptus* by *saf* extending anteriorly beyond and around anus (*vs. saf* not extending anteriorly to anus), from *P. cephalus* by vertebral count (total vertebrae 35–36, precaudal 18–19 *vs.* 31, 14 in *P. cephalus*), and from *P. sagamianus* by melanophores inside mouth restricted to tooth insertion region (*vs.* internal area of mouth and gill arches completely black).

Description. Middle-sized species of *Pseudoscopelus*, largest specimen examined 97.3 mm SL. Meristic data summarized in table 4.6, morphometric in table 4.7. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine, not as enlarged as in *Pseudoscopelus cephalus*, *P. sagamianus*, and *P. scriptus*, and illustrated in figure 4.9 D. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 10–14% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, and slightly curved orally in body and caudal process. Middle and mesial series restricted to body of premaxilla; middle series in single row of small conical, type 4 teeth; mesial series in transverse rows of two to three needle-like, type 4 teeth, internal row with teeth greater than twice length of other teeth.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, slightly curved, type 4 teeth, usually recovered by skin. Mesial in 10–15 transverse rows of one to three needle-like, type 4 teeth, with internal-most teeth more than double sized of other teeth. Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, small, conical, type 1; absent on third and fourth arches. Conical, type 1 teeth also present on ventral and dorsal pharyngeals and in *V*-shaped row on second basibranchial; absent on basihyal, and other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.5 C. Photophores on head: *apf*, *dnf*, *inof* 1–2, *lpf*, *opf*, and *pof* absent; *mxf* elongated, in single row, parallel to maxilla, from level of posterior margin of eye to angle between preopercle and dentary; *vnf* in small group just posterior to anteriormost supraorbital pore; *ppf* as small patch in ventral edge of interopercle; *amf* in one to three rows, medial to third pore of mandibular canal, from between first and second mandibular pores to halfway between third and fourth mandibular pores; *pmf* in one to three rows, lateral to fifth pore of mandibular canal, from just posterior to fourth pore to halfway between fifth and sixth pores.

Photophores on body: *lvf*, *rtf*, *scf*, *spf*, and *svf* absent; *pf* in single row along ventral-most pectoral-fin ray; *paf* continuous with *pf* at pectoral-fin axil; *vf* in single row, along mesial pelvic-fin ray; *vaf* continuous with *vf* and *trf*, extending over base of pelvic rays three to five; *if* and *prvf* continuous or separated by distance of less than two organs wide, in irregular rows of two organs, from isthmus to anterior edge of pelvic girdle; *ptvf* in one to three rows, from posterior half of pelvic fin to close to anus; *trf* laterally in single row, with medial circular group of photophores; *saf* in two rows, with smaller photophores closely spaced and ventral, and larger photophores widely spaced and dorsal, heart-shaped, extending to level of or anterior to anus, and connected posteriorly; *prcf* in posterior half of peduncle, oval-shaped, three-pronged, medial prong extending over anteriormost lower procurrent rays.

Color. Single preserved specimen (CAS 223102) retained color, remaining specimens faded. Body uniformly black, except for a triangular area in the top of head, over epiphyseal branch. Pectoral, pelvic, and first dorsal fins slightly pigmented on fin-rays; second dorsal and anal with chromatophores extending to fin membranes, especially at fin bases; caudal fin uniformly black, except at tip of rays. Mouth and gill arches mostly clear, except for dusky skin over toothed area of premaxilla and dentary, and thin membrane between anterior portion of premaxillae and dentaries.

Distribution. Eastern South Atlantic, from Middle Atlantic to off Angola, 20º W to 12º W, 0º to 9º S; Indian to west Pacific from off Oman to Indonesia , and eastern Central Atlantic, 57º E to 125º E, 10º N to 5º S (Fig. 4.2 A).

Bathymetric distribution. From 537 to 1164 m (mean 954 m).

Identification of Juveniles. A small specimen of 24.4 mm (USNM 200533) was tentatively identified based on the shape of *saf*, anteriorly passing level of anus and connected posteriorly.

Etymology. From the Latin *cordis*, means heart, and *luminosus*, full of light, in a reference to the *saf* row of photophores heart shaped.

Pseudoscopelus altipinnis group

Composition. The *Pseudoscopelus altipinnis* group is composed of two species: *P. altipinnis* and *P. paxtoni*.

Diagnosis. The *Pseudoscopelus altipinnis* group is diagnosed from its congeners by a combination of characteristics: luminescent tissue present as discrete photophores (*vs.* absent or in white lines in *P. aphos* group); *trf* in a single series of widely spaced organs, without a medial circular cluster or organs (*vs. trf* on a single row of closely spaced organs, with a medial, circular cluster of organs in the *P. scriptus* group; absent in the *P. astronesthidens* and *P. scutatus* groups; *trf* arranged in a broad band of three or four organs in *P. lavenbergi* group); *mxf* in an irregular elongated single row with widely spaced organs anteriorly, extending from below mid-eye anteriorly and connected to *apf* posteriorly (*vs.* both *mxf* and *apf* absent in the species of the *P. scutatus* group; *mxf* absent and *apf* present in *P. lavenbergi*; *mxf* short, not connected posteriorly with *apf* present in the species of the *P. astronesthidens* group; *mxf* on single elongate continuous row from level of posterior margin of eye anteriorly to angle between preopercle and dentary, and *apf* absent in the species of the *P. scriptus* group).

Description. Dentition, photophore pattern, and color detailed in species' account. Body elongate, fusiform, not greatly compressed anteriorly, but progressively more compressed in caudal region. Greatest body depth at origin of first dorsal fin. Scales absent, except for lateral line, embedded in skin.

Anterior profile of head elongated in lateral view. Tip of snout convex, with gentle curve at level of anterior naris. Mouth terminal and large, reaching ventral edge of preopercle. Orbit circular. Nares distinctly separated, anterior naris circular, close to third supraorbital pore; posterior naris crescent shaped, close to anterodorsal edge of eye. Pectoral fin very not very elongate, reaching just beyond anus in adult specimens; pelvic-fin origin slightly posterior to pectoral-fin base; dorsal fins two, first dorsal-fin insertion slightly posterior to level of pelvic-fin insertion, second dorsal-fin origin slightly anterior to level of anal-fin origin. Lateral line complete, with pores opening between scales; last scale of lateral line separate, in lower lobe of caudal fin, with two pores.

Gill arches four; pseudobranchia present. Epibranchial of first arch attached to opercle to midline; hypobranchial and ceratobranchial of first arch free. Epibranchials of second, third and fourth arches connected anteriorly to each other and to pharyngobranchials. Ceratobranchial of second arch free. Hypobranchial and basibranchial of second, third and four arches connected medially. Ceratobranchial of second arch free. Ceratobranchial of third and fourth arches connected distally. Ceratobranchial of fourth arch connected to body wall at proximal half. Basihyal, elongated, free anteriorly, with posterior and ventral connection to first basibranchial; first basibranchial small, triangular, connected to basihyal and second basibranchial; second basibranchial elongated; third basibranchial extremely elongated, extending posteriorly beyond fourth basibranchial, posterior half cartilaginous and ventrally curved; four basibranchial small, diamond-shaped, cartilaginous. Hypohyals with dorsal and ventral elements, attached to first basibranchial; first hypobranchial attached immediately posterior to basihyal, between joint of first and second basibranchials; second hypobranchial connected to joint between second and third basibranchials; third hypobranchial proximally connected to anterior edge of fourth basibranchial, distal tip of fourth hypobranchial ventrally pointed; fourth hypobranchial absent or fused to ceratobranchial, fourth ceratobranchial connected to posterior edge of fourth basibranchial; ventral pharyngobranchials connected posteriorly to fourth ceratobranchial.

Pseudoscopelus altipinnis Parr 1933

Figures 4.6 A, 4.10 A, 4.16 A, B; Tables 4.8 and 4.9

Pseudoscopelus altipinnis Parr 1933:41–42, figure 18 [type locality western Central Atlantic, off Cat Island, Bahamas, 24º51’ N, 76º28’ W, holotype YPM 2798, 185.8 mm]; Uyeno et al. 1983: 403 [western Central Atlantic, off Suriname, with brief description and picture, questionable]; Figueiredo et al. 2003:94 [literature compilation]; Prokofiev and Kukuev 2006a [key to species, questionable]; 2006c [in key].

Pseudoscopelus scriptus Norman 1929: 543–544 [specimen misidentified].

Pseudoscopelus microps Fowler 1933:359, figure 110 [type locality Gulf of Boni, Sulawesi, Indonesia, holotype USNM 93139, 122.7 mm]; de Beaufort in de Beaufort and Chapman 1951: 8–9 [western Central Pacific]; Prokofiev and Kukuev 2006a: 212–116, figure 1 [questionable].

Diagnosis. A species of the *Pseudoscopelus altipinnis* group distinguished from *P. paxtoni* by dentition and photophore pattern: innermost teeth of mesial row of premaxilla not extremely elongated, when mouth is closed and premaxilla is retracted teeth reach the medial border of the contralateral premaxilla (*vs.* innermost teeth of mesial rows of premaxilla and dentary elongate, reaching the medial border of the contralateral premaxilla when mouth is closed); teeth of mesial row of premaxilla and internalmost row of dentary slightly curved (*vs.* teeth of mesial rows of premaxilla and internalmost row of dentary straight); mesial series of premaxillary teeth arranged in transverse rows of one to five rows of teeth (*vs.* mesial series of premaxillary teeth arranged in transverse rows of one to three rows of teeth); *ppf* present with one to five organs (*vs. ppf* absent).

Description. Large-sized species of *Pseudoscopelus*, the largest specimen examined is 188.3 mm SL. Meristic data summarized in table 4.8, morphometric in table 4.9. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary, as illustrated in figure 10 A. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 15–20% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, and curved orally in body and caudally in caudal process; last one or two teeth straight, with restrict or no movement. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of two to three straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in seven to 10 transverse rows of three to five slightly curved, needle-like, type 4 teeth, gradually increasing in size from medial to mesial; teeth not long enough to reach contralateral premaxilla.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, slightly curved, type 4 teeth, usually recovered by skin. Mesial series in 10–14 transverse rows of one to four straight, needle-like teeth, gradually increasing in size from lateral to mesial. Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, elongated, conical, type 1; absent on third and fourth arches. Elongated conical teeth also present on ventral and dorsal pharyngeals and in *Y*-shaped row on second basibranchial; absent on basihyal, and other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.6 A. Photophores on head: *dnf*, *inof* 1–2, *lpf*, *opf*, and *pof* absent; *mxf* elongated, on single irregular row with widely spaced photophores, parallel to maxilla, from below mid-eye and connected to *apf* posteriorly; *apf* at angle between dentary and preopercle; *vnf* as triangular patch posterior to anteriormost supraorbital pore; *ppf* usually present as small patch of one to four photophores in ventral edge of interopercle (in BMNH 1961.1.30.7, and ZMUC P. 6542 present as single organ on one side); *amf* in two to three rows, medial to and around third pore of mandibular canal; *pmf* in one to three rows, lateral to fifth pore of mandibular canal, from immediately posterior of fourth to halfway between fifth and sixth pores.

Photophores on body: *lvf, rtf*, *spf*, *svf* and *vf* absent; *pf* extending to halfway of pectoral-fin length, in ventral ray; *paf* continuous with *pf*, at pectoral-fin axil; *vaf* triangular, continuous with *trf*, not extending over base of pelvic rays three to five; *if* in one irregular to two rows, from isthmus to ventral edge of cleithrum, *prvf* in irregular one to two rows, in anterior part of pelvic girdle; *ptvf* in two rows, from posterior half of pelvic fin to close to anus; *trf* in single irregular row with widely spaced photophores; *saf* in single row, heart-shaped, extending anteriorly to level of anus, and connected posteriorly immediately after last anal-fin ray; *prcf* in posterior half of peduncle, tri-pronged, medial prong extending over lower procurrent rays, and lateral prongs extending lateral to lower procurrent rays; *scf* usually absent, but present in few specimens from single photophore to linear irregular row of four photophores.

Color. Recently collected specimens with body uniformly black or dark brown, except for triangular area in the top of head, over epiphyseal branch. Most specimens examined faded brown or bleached white; holotype partially bleached, with brown belly and pale yellow in the head, dorsum, caudal peduncle, and fins. Pectoral, pelvic, first and second dorsal fins, and anal fin slightly pigmented; caudal fin pigmented. Internal part of mouth and gill arches entirely black, including skin on toothed area of premaxilla and dentary, over basihyal and basibranchials, roof, floor and lateral wall of mouth, internal part of opercle, membrane between dentaries and premaxillae, and gill arches; gill filaments pale.

Distribution. Widespread in the Atlantic and Pacific Oceans; in the Atlantic from 46º N to 36º S, 7º W to 88º W, in the Pacific from 33º N to 27º S, 99º W to 121º E (Fig. 4.2 A).

Bathymetric distribution. From 50 to 4631 m; however the deepest record for this species is questionable, probably taken during gear transit. Removing those extreme capture depths, the deepest record for this species is 2000 m (mean 828 m).

Identification of juveniles. The smallest specimen recognized has 23.6 mm (USNM 288992); the identification was tentatively made based on the photophore pattern and pigmentation of mouth. The smallest specimen with complete photophore pattern and dentition has 38.5 mm (USNM 288991); with the exception that *trf* and *mxf* are closely spaced.

Remarks. The *scf* was found exclusively, and in almost every specimen of *Pseudoscopelus altipinnis* from the western North and South Atlantic (*e.g.* BMNH 1961.1.30.7, MCZ 96843, ZMUC P. 6540); however, it was not present in all specimens within that range (*e.g.* BMNH 1930.1.12.1065; ZMUC P. 6546). This may be an indication of isolation of the western Atlantic populations, but because no other characteristic was found to diagnose them as a separate species, this characteristic is being interpreted as a geographical variation.

Prokofiev and Kukuev (2005, 2006a) confused the identification of *Pseudoscopelus altipinnis*, *P. microps*, *P. astronesthidens* and *P. australis*. Prokofiev and Kukuev (2006c, 2008) rectified this fixed the mistake, describing the latter two species.

Pseudoscopelus paxtoni, new species

Figures 4.6 B, 4.10 B, 4.16 C, D; Tables 4.8 and 4.9

Holotype. NMNZ P. 28657, 205.1 mm, West Pacific, New Zealand, off the Chatham Islands, at East Chatham Rise, 42º39’ S, 176º57’ W, 1409 m, 13–VII–1992, R/V *Tangaroa*;

Paratypes. Pacific, West Pacific. NMNZ P. 18068, 1, 157.5 mm, 44º44’ S, 172º50’ E, 979–1010 m, 22–VIII–1984, R/V *James Cook*; NMNZ P. 20235, 1, 145.0 mm, 39º28’ S, 178º25’ E, 17–VIII–1986, R/V *James Cook*; NMNZ P. 20236, 1, 147.4 mm, 39º21’ S, 178º27’ E, 836–836 m, 17–VIII–1986, R/V *James Cook*; NMNZ P. 21272, 1, 82.8 mm, 39º59’ S, 167º54’ E, 954–957 m, 18–VI–1987, F/V *Explorer*; NMNZ P. 24155, 1, 227.9 mm, 44º47’ S, 175º29’ E, 979–1063, 06–XI–1986, F/V *Arrow*; NMNZ P. 24161, 1, 126.8 mm, collected with NMNZ P. 24155; NMNZ P. 24255, 1, 129.2 mm, 40º15’ S, 168º23’ E, 925 m, 16–VII–1989, F/V *Explorer*; NMNZ P. 25805, 1, 158.5 mm, 40º02’ S, 167º58’ E, 893–964 m, 09–VII–1990, F/V *Will Watch*; NMNZ P. 25806, 1, 203.0 mm, collected with NMNZ P. 25805; NMNZ P. 36790, 1, 196.9 mm, 42º35’ S, 173º23’ W, 1223 m, col. unknown; NMNZ P. 37858, 1, 200.4 mm, 48º18’ S, 170º06’ E, 896 m, 15–X–2000, R/V *Tangaroa*; NMNZ P. 38679, 1, 234.2 mm, 42°48’ S, 179°47.33’ E, 1031 m, 27–VI–2002, R/V *Tangaroa*; SIO 07-164 (former NMNZ P. 28793), 1, 213.2 mm, 44º40’ S, 177º33’ W, 1183 m, 03–XI–1991, R/V *Tangaroa*; USNM 391143 (former NMNZ P. 28700), 1, 227.2 mm, 42º41’ S, 179º43’ W, 1288 m, 19–VII–1992, R/V *Tangaroa*.

Non-type (tentative identification). Pacific, West Pacific. NMV A. 6008, 1, 52.2 mm, 38º01’ S, 150º14’ E, 20–XI–1981, R/V *Soela*.

Diagnosis. A species of the *Pseudoscopelus altipinnis* group distinguished from *P. altipinnis* by dentition and photophore pattern: innermost teeth of mesial rows of premaxilla and dentary elongate, elongated, when mouth is closed and premaxilla is retracted reach the medial border of the contralateral premaxilla (*vs.* innermost teeth of mesial rows of premaxilla not extremely elongated, when mouth is closed and premaxilla is retracted teeth do not reach the medial border of premaxilla of the other side); teeth of mesial row of premaxilla and internalmost row of dentary straight (*vs.* teeth of mesial row of premaxilla and internalmost row of dentary slightly curved); mesial series of premaxillary teeth arranged in transverse rows of one to three rows of teeth (vs. mesial series of premaxillary teeth arranged in transverse rows of one to five rows of teeth); *ppf* absent (*vs. ppf* present with one to five organs).

Description. Large-sized species of *Pseudoscopelus*, largest specimen examined 234.0 mm SL. Meristic data summarized in table 4.8, and morphometric in table 4.9. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary, as illustrated in figure 4.10 B. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 15–20% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, and curved orally in body and caudally in caudal process, last four to five teeth firmly attached to bone, with restrict or no movement. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of two to three straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in eight to 10 transverse rows of one to three straight, needle-like, type 4 teeth, gradually increasing in size from medial to mesial; teeth of internalmost row long enough to reach contralateral premaxilla.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, slightly curved, type 4 teeth, usually recovered by skin. Mesial series in 10–14 transverse rows of one to four straight, needle-like teeth, gradually increasing in size from lateral to mesial. Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, small, conical, type 1, in patches of two to four; absent on third and fourth arches. Small, conical teeth also present on ventral and dorsal pharyngeals and in *Y*-shaped row on second basibranchial; absent on basihyal and other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.6 B. Photophores on head: *dnf*, *inof* 1–2, *lpf*, *opf*, *ppf* and *pof* absent; *mxf* elongated, on single irregular row with widely spaced organs, parallel to maxilla, from below mid-eye, connected to *apf* posteriorly; *apf* in angle between dentary and preopercle; *vnf* in triangular patch posterior to anteriormost supraorbital pore; *amf* in two to three rows medial to and around third pore of mandibular canal; *pmf* in one to three rows, lateral to fifth pore of mandibular canal, from posterior to fourth pore to halfway between fifth and sixth pores.

Photophores on body: *lvf, rtf*, *scf*, *spf*, *svf*, and *vf* absent; *pf* in single row along ventral-most pectoral-fin ray; *paf* continuous with *pf*, at pectoral-fin axil; *vaf* triangular, continuous *trf*, not extending over base of pelvic rays three to five; *if* in one irregular to two rows, from isthmus to ventral edge of cleithrum, *prvf* in one irregular to two rows, at anterior portion of pelvic girdle; *ptvf* in two rows, from posterior half of pelvic fin to close to anus; *trf* in single irregular row with widely spaced photophores; *saf* in single row, heart-shaped, extending anteriorly to level of anus, and not connected posteriorly, not extending further to next to last anal fin ray; *prcf* in posterior half of peduncle, tri-pronged, medial prong extending over lower procurrent rays, and lateral prongs extending lateral to lower procurrent rays.

Color. Recently collected specimens with body uniformly black or dark brown, except for area on the top of head, over epiphyseal branch; bleached clear brown or white in many older specimens. Pectorals, pelvics, first and second dorsal fins, anal and caudal fins pigmented. Internal part of mouth and gill arches entirely black, including skin on toothed area of premaxilla and dentary, over basihyal and basibranchials, roof, floor and lateral wall of mouth, internal part of opercle, membrane between dentaries and premaxillae, and gill arches; gill filaments pale.

Distribution. Southern portion of west Pacific Ocean, from Chatham Islands to west of New Zealand, 173° W to 167° E, 39° to 48° S (Fig. 4.2 A).

Bathymetric distribution. From 893 to 1223 m (mean 1027 m).

Etymology. The species is named after the North American/Australian ichthyologist John Paxton (Senior Fellow, AMH), in recognition of his lifetime contribution to the knowledge of deep-sea ichthyofauna, and his support for this project.

Pseudoscopelus scutatus group

Composition. The *Pseudoscopelus scutatus* group is composed of two species: *P. scutatus* and *P. bothrorrhinos*.

Diagnosis. The *Pseudoscopelus scutatus* group is diagnosed from its congeners by characteristics of external morphology, osteology, and photophore pattern: snout concave, with nasals and anterior naris positioned anteriorly at tip of snout (*vs.* snout convex, elongate or rounded, with nasals and anterior naris positioned in the dorsolateral part of snout); distal radials of first dorsal fin modified into plate-like structures (*vs.* distal radials of first dorsal fin normal, not modified into a plate-like structure); *svf* present (*vs.* *svf* absent); *pf*, *paf*, *vf*, and *vaf* absent (*vs.* *pf*, *paf*, *vf*, and *vaf* present); *prvf* and *ptvf* continuous (*vs.* *prvf* and *ptvf* disconnected).

Description. Dentition, photophore pattern, and color detailed in species' account. Body elongate, fusiform, not greatly compressed anteriorly, but progressively more compressed in caudal region. Greatest body depth at origin of first dorsal fin. Scales absent, except for lateral-line scales, embedded in skin.

Head elongated, anterior profile of head elongated concave in lateral and anterior views, anterior nostril anteriorly positioned. Mouth terminal and large, reaching edge of preopercle. Orbit circular. Nares distinctly separated, anterior naris circular, close to third supraorbital pore; posterior naris crescent shaped, close to anterodorsal edge of eye.

Pectoral fin sort, not reaching level of last ray of first dorsal fin; dorsal fins two, first dorsal-fin insertion slightly posterior to level of pelvic-fin insertion; distal radials of first dorsal-fin plate-like (total nine to ten); second dorsal-fin origin at level of anal-fin origin. Caudal fin forked. Lateral line complete, with pores opening between scales; last scale of lateral line separate from anterior, in lower lobe of caudal fin, with two pores.

Gill arches four; pseudobranchia present. Epibranchial of first arch attached to opercle to midline; hypobranchial and ceratobranchial of first arch free. Epibranchials of second, third and fourth arches connected anteriorly to each other and to pharyngobranchials. Ceratobranchial of second arch free. Hypobranchial and basibranchial of second, third and four arches connected medially. Ceratobranchial of second arch free. Ceratobranchial of third and fourth arches connected distally. Ceratobranchial of fourth arch connected to body wall at proximal half. Basihyal, elongated, free anteriorly, with posterior and ventral connection to first basibranchial; first basibranchial small, triangular, connected to basihyal and second basibranchial; second basibranchial elongated; third basibranchial extremely elongated, extending posteriorly beyond fourth basibranchial, posterior half cartilaginous and ventrally curved;

four basibranchial small, diamond-shaped, cartilaginous. Hypohyals with dorsal and ventral elements, attached to first basibranchial; first hypobranchial attached immediately posterior to basihyal, between joint of first and second basibranchials; second hypobranchial connected to joint between second and third basibranchials; third hypobranchial proximally connected to anterior edge of fourth basibranchial, distal tip of fourth hypobranchial ventrally pointed; fourth hypobranchial absent or fused to ceratobranchial, fourth ceratobranchial connected to posterior edge of fourth basibranchial; ventral pharyngobranchials connected posteriorly to fourth ceratobranchial.

Pseudoscopelus scutatus Krefft 1971

Figures 4.7 A, 4.17 A, B; Tables 4.10 and 4.11

Pseudoscopelus scutatus Krefft 1971:165–174, Figs. 1–8 [type locality: eastern North Atlantic, 2°44’ N, 25°12’ W, holotype ZMH 25241 (former ISH 567-1966 a), 84.7 mm].

Pseudoscopelus scutatus Nakabo et al. 1992 [western North Pacific]; Nakabo 2002 [key to species]; Moore et al. 2003: 227 [western North Atlantic]; Figueiredo et al. 2003:94 [literature compilation]; Prokofiev and Kukuev 2006a: 228–229, figure 5 [western North Atlantic, eastern Central Atlantic]; 2006c [key to species].

Diagnosis. A species of the *Pseudoscopelus scutatus* group, which is diagnosed from *P. bothrorrhinos* by a single characteristic: *lpf* absent (*vs. lpf* present).

Description. Small-sized species of *Pseudoscopelus*, largest specimen examined 91.0 mm SL. Meristic data summarized in table 4.10, and morphometric in table 4.11. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary similar to *P. bothrorrhinos* (Melo et al. 2007). Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 12–14% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, and curved orally in body and caudally in caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of one to two straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial in single row of 7–9 posteriorly curved, needle-like teeth.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, elongated, curved, type 4 teeth; not recovered by skin. Mesial series in single series of 14–17 slightly curved needle-like teeth; four to five anteriormost teeth distinctly more enlarged than remaining. Palatine teeth conical, type 1, in single row.

Gill rakers short, conical, similar to type 1 tooth; present on first and second gill arches present, elongated, conical, type 1; absent on third and fourth arches. Elongated, conical teeth also present on ventral and dorsal pharyngeals and in *Y*-shaped row on second basibranchial; absent on basihyal and other basibranchials.

Photophores. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.5 A. Photophores on head: *dnf*, *inof* 1–2, *lpf*, *mxf*, *opf*, and *pof* absent; *apf* in angle between dentary and preopercle; *vnf* absent from most specimens, and if present as small patch posterior to anteriormost pore of supraorbital canal; *ppf* in small patch on ventral edge of interopercle; *amf* in two to three rows, medial to third pore of mandibular canal, from immediately posterior to second pore of mandibular canal, to halfway between third and fourth pores; *pmf* in rows of one to three photophores, lateral to fifth pore of mandibular canal, from halfway between fourth and fifth pores, to halfway between fifth and sixth pores.

Photophores on body: *lvf*, *pf, paf*, *vaf*, *vf*, *trf*, *rtf*, *spf*, and *svf* absent; *scf* usually absent, present as three organs in a single specimen (USNM 240671); *if* and *prvf* continuous, in irregular one to two rows, from isthmus to anterior edge of pelvic girdle; *ptvf* in two rows, from posterior half of pelvic fin to close to anus; *saf* in two rows, with smaller photophores closely spaced and ventral, and larger photophores widely spaced and dorsal, heart-shaped, not extending anteriorly to anus, and connected posteriorly; *prcf* in posterior half of peduncle, oval-shaped, three-pronged, medial prong extending over anteriormost lower procurrent rays.

Color. No freshly collected specimen known, most specimens are dark brown with hyaline fins, including membranes, except for caudal fin. Oral and branchial cavities pale.

Identification of Juveniles. The smallest specimen recognized has 28.4 mm (SIO

68–537); the identification was concave shape of snout and the complete development of photophore groups.

Distribution. Widely distributed in the Atlantic from 40° N to 30° S, 22° to 83° W; from a single record in the Arabian Sea, Indian Ocean; and in the Pacific Plate 22° N to 25° S, 100° W to 157° W (Fig. 4.3 A).

Bathymetric distribution. From 85 to 1716 m (mean 578 m). The majority of specimens were collected to 600 m. Records below 1000 m are questionable because specimens may have been takes during gear transition. Mean depth excluding those lots equals to 432 m.

Remarks. Prokofiev and Kukuev (2008: 134) listed and illustrated the lot IORAN uncat. (1, 27.0) as *P. scutatus*, however, the photophores as illustrated shows *P. bothrorrhinos*.

Pseudoscopelus bothrorrhinos Melo, Walker and Klepadlo 2007

Figures 4.7 B, 4.10 D, 4.17 C, D; Tables 4.10, 4.11

Pseudoscopelus bothrorrhinos Melo, Walker and Keplado 2007: 41–44, figures 7, 8, and 9 [type locality: western Central Pacific, 2°51' S, 169°55' E, holotype LACM 31502–2, 45.9 mm].

Pseudoscopelus scutatus (non Kreft) Prokofiev and Kukuev, 2008: (in part), figures 184–186.

Diagnosis. A species of the *Pseudoscopelus scutatus* group which is diagnosed from its congeners by the presence of *lpf*, extending dorsally to the middle of the preopercle (vs. *lpf* absent).

Description. Small sized species of *Pseudoscopelus*, largest specimen examined 55.1 mm SL. Meristic data summarized in table 4.10, and morphometric data in table 4.11. General shape of body as for the species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary as illustrated in Fig. 4.10 C. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 12–14% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, and curved orally in body and caudally in caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of one to two straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial in single row of 7–9 posteriorly curved, needle-like teeth.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, elongated, curved, type 4 teeth; not recovered by skin. Mesial series in single series of 14–17 slightly curved needle-like teeth; four to five anteriormost teeth distinctly more enlarged than remaining. Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, elongated, conical, type 1; absent on third and fourth arches. Elongated, conical teeth also present on ventral and dorsal pharyngeals and in *Y*-shaped row on second basibranchial; absent on basihyal and other basibranchials.

Gill rakers short, conical, similar to type 1 tooth; present on first basibranchial, first and second gill arches and pharyngeals; absent on basihyal, other basibranchials, third and fourth gill arches; rakers of first basibranchial in two rows.

Photophores. Luminescent organs present as discrete photophores on head and body; pattern illustrated on figure 7 B. Photophores on head: *apf*, *dnf*, *inof* 1-2, *mxf*, *vnf*, *opf*, *pof*, and *ppf* absent; *lpf* at anterior edge of preopercle, extending dorsally to middle of preopercle; *amf* medial on dentary, short, with few organs, restricted to gap between second and third mandibular pores; *pmf* in a single row, originating immediately posterior to fourth mandibular pore, extending to midpoint between fifth and sixth pores.

Photophores on body: *lvf*, *paf*, *pf*, *rtf*, *spf*, *spt*, *vaf*, *scf*, and *vf* absent; *svf* anterodorsally to insertion of pelvic-fin origin, free organs halfway between *svf* and pectoral fin present or absent; *if* in two rows; *prvf* in single row, extending from posterior to cleithrum, passing trough pelvic fins and continuous with *ptvf*; *ptvf* in two rows, extending to close to anus; *saf* oval, in single row, continuous anteriorly, but not connecting posteriorly, not extending anteriorly beyond anus, and connected to anal fin by single row of photophores; *prcf* two-pronged, extending laterally to lower procurrent caudal-fin rays.

Color. No freshly collected specimen known, most specimens slightly bleached brown; all fin rays hyaline, including membranes. Oral and branchial cavities hyaline. Like all other described species of *Pseudoscopelus*, body probably entirely black or dark brown in life.

Distribution. Equatorial western Central Pacific from 1° to 4° S, 169° to 129° E, and a single locality in the western Indian, West of Madagascar, 12° S, 44° E (Fig. 4.3 A).

Bathymetric distribution. From 146 to 1200 m (mean 719 m).

Pseudoscopelus aphos group

Composition. The *Pseudoscopelus aphos* group is composed of two species: *P. aphos* and *P. parini*.

Diagnosis. The *Pseudoscopelus aphos* group is diagnosed from all other groups of *Pseudoscopelus* by the absence of small discrete photophores on head and body (*vs.* small discrete photophores present in groups on head and body).

Description. Dentition, photophore pattern, and color detailed in species' account. Body elongate, fusiform, not greatly compressed anteriorly, but progressively more compressed in caudal region. Greatest body depth at origin of first dorsal fin. Scales absent, except for lateral-line scales, embedded in skin.

Anterior profile of head slightly curved in lateral view, with gentle curve at level of anterior naris. Mouth terminal and large, reaching edge of preopercle. Orbit circular. Nares distinctly separated, anterior naris circular, close to third supraorbital pore; posterior naris crescent shaped, close to anterodorsal edge of eye.

Pectoral fin very elongate, not reaching posterior half of body; pelvic-fin origin slightly posterior to pectoral-fin base; dorsal fins two, first dorsal-fin insertion slightly posterior to level of pelvic-fin insertion, second dorsal-fin origin at level of anal-fin origin. Caudal fin forked. Lateral line complete, with pores opening between scales; last scale of lateral line separate from anterior, in lower lobe of caudal fin, with two pores.

Gill arches four; pseudobranchia present. Epibranchial of first arch attached to opercle to midline; hypobranchial and ceratobranchial of first arch free. Epibranchials of second, third and fourth arches connected anteriorly to each other and to pharyngobranchials. Ceratobranchial of second arch free. Hypobranchial and basibranchial of second, third and four arches connected medially. Ceratobranchial of second arch free. Ceratobranchial of third and fourth arches connected distally. Ceratobranchial of fourth arch connected to body wall at proximal half. Basihyal, elongated, free anteriorly, with posterior and ventral connection to first basibranchial; first basibranchial small, triangular, connected to basihyal and second basibranchial; second basibranchial elongated; third basibranchial extremely elongated, extending posteriorly beyond fourth basibranchial, posterior half cartilaginous and ventrally curved; four basibranchial small, diamond-shaped, cartilaginous. Hypohyals with dorsal and ventral elements, attached to first basibranchial; first hypobranchial attached immediately posterior to basihyal, between joint of first and second basibranchials; second hypobranchial connected to joint between second and third basibranchials; third hypobranchial proximally connected to anterior edge of fourth basibranchial, distal tip of fourth hypobranchial ventrally pointed; fourth hypobranchial absent or fused to ceratobranchial, fourth ceratobranchial connected to posterior edge of fourth basibranchial; ventral pharyngobranchials connected posteriorly to fourth ceratobranchial.

Pseudoscopelus aphos Prokofiev and Kukuev 2006

Figure 4.18 A, B; Tables 4.12 and 4.13.

Pseudoscopelus aphos Prokofiev and Kukuev 2006a: 572–727 [type locality: western North Atlantic, 34º N, 50º W, holotype ZMMU 16468, 145.0 mm].

Pseudoscopelus stellatus Beebe 1932: 76–79 [in part; western North Atlantic].

Diagnosis. A species of the *Pseudoscopelus aphos* group, diagnosed from *P. parini* by the complete absence photophores or clear lines on body (*vs.* clear lines in place of photophores in ventral part of body in *P. parini*, and photophores present in all other species).

Description. Small-sized species of *Pseudoscopelus*, largest specimen examined 60.7 mm SL. Meristic data summarized in table 4.12, morphometric in table 4.13. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 10–14% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, and curved caudally in body and caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of one to two straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in eight to ten transverse rows of one to four slightly curved, needle-like, type 4 teeth.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, slightly curved, type 4 teeth, usually recovered by skin. Mesial series in 10 to 15 transverse rows of one to five straight or slightly curved, needle-like, type 4 teeth, increasing in size from lateral to mesial. Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, conical, type 1, in patches of one or two; absent on third and fourth arches. Conical, type 1 teeth also present on ventral and dorsal pharyngeals and in *Y*-shaped row on second basibranchial; absent on basihyal and other basibranchials.

Luminescent organs. Photophores completely absent.

Color. Body uniformly dark brown, including skin over epiphyseal branch. Pectoral, pelvic, first and second dorsal fins, and anal fin slightly pigmented at their bases; caudal fin pigmented. Internal area of mouth with few widely-spaced melanophores in membrane of anterior part of dentary and premaxilla, and skin over hyoid arch pale.

Distribution. Western North Atlantic, from 24º N to 40º N, 50º W to 76º W (Fig. 4.3 A).

Bathymetric distribution. From 220 to 1634 m (mean 667).

Remarks. Beebe (1932) referred to the lot CAS–SU 66497 in his description of

Pseudoscopelus stellatus, and Eschmeyer (2007) considered it them be paratypes of *P. stellatus*. The lot contains two specimens, and both lack photophores. In other species, such as *P. scriptus*, juveniles of the same size have some groups of photophores present on ventral part of body and head. Those two specimens are identified herein as *P. aphos*.

The color description given differs from that presented by Prokofiev and Kukuev (2005). Their description was based on a single, apparently faded specimen. A reasonable number of specimens from the type locality and adjacent areas have been examined, some of which have fairly well-preserved pigmentation allowing a more accurate description of coloration.

Pseudoscopelus parini Prokofiev and Kukuev 2006

Figures 4.18 C, D; Tables 4.12 and 4.13

Pseudoscopelus parini Prokofiev and Kukuev 2006b: 481–484 [type locality: western North Pacific, Marcus-Nekker Ridge, 24°07’ N, 150º00’ W, holotype ZMMU 21250, 168.0 mm].

Pseudoscopelus sp. Prokofiev and Kukuev 2008: 135-136 [species diagnosis].

Pseudoscopelus vityazi Prokofiev and Kukuev 2008: 158–161 [type locality: Indian Ocean, 15°07’ N, 150º00’ W, 3400–3473 m, holotype ZM MGU nr. 21254, 46.0 mm]. **NEW SYNONYM.**

Diagnosis. A species of the *Pseudoscopelus aphos* group distinguished from *P. aphos* by the presence of white lines in the ventral part of body (*vs.* photophores completely absent in *P. aphos*, and small discrete circular photophores present on body and head in other species).

Description. Medium-sized species of *Pseudoscopelus*, largest specimen examined 82.9 mm SL. Meristic data summarized in table 4.12, morphometric in table 4.13. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 15–20% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, and curved caudally in body and caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of two to three straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in 11 transverse rows of one to five slightly curved, needle-like, type 4 teeth, gradually increasing in size from medial to mesial.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, slightly curved, type 4 teeth, usually recovered by skin. Mesial series in 13 transverse rows of one to four straight or slightly curved, needle-like, type 4 teeth, increasing in size from lateral to mesial.

Palatine teeth conical, type 1, in single row.

Teeth on first and second gill arches present, small, conical, type 1; absent on third and fourth arches. Conical, type 1 teeth also present on ventral and dorsal pharyngeals and in *V*-shaped row on second basibranchial; absent on basihyal and other basibranchials.

Luminescent organs. Photophores on head absent. White longitudinal lines present in place of *if*, *prvf*, *prcf*, *ptvf*, *pf*, *paf*, *saf*, *vf* photophore groups (Fig. 4.18 D).

Color. Most specimens examined faded or bleached white; description based on LACM 44392–1 and 56622–1. Body dark brown, except for triangular area on the top of head, over epiphyseal branch; ventral part of body darker than dorsal. Pectoral, pelvic, first and second dorsal fins, and anal fin slightly pigmented at their bases; caudal fin pigmented. Internal part of mouth and gill dark including skin on toothed area of premaxilla and dentary, over basihyal, roof, floor and lateral walls of mouth, internal part of opercle, membrane between dentaries and premaxillae; basibranchials, gill arches and filaments not pigmented.

Distribution. In the Pacific Plate and West Pacific, from 19° N to 19° S, 150° E to 150° W (Fig. 4.3 A). Prokofiev and Kukuev (2008) recorded the species from the western Indian.

Bathymetric distribution. From 50 to 4631 m (mean 892 m).

Remarks. Most specimens examined were completely or partially faded, including internal parts of mouth. Prokofiev and Kukuev (2006b:483) based their description on a single poorly preserved, faded specimen; according to them, the general color of specimen was “brownish to light yellow”, and “buccobranchial [sic] cavity (…)

yellowish white”. This uniform color pattern is found in most specimens preserved in collections for many years, and is an artifact of time. Because of the lack of specimens with well preserved color, the true coloration of this species is not currently known.

The status of *P. vityazi*. Prokofiev and Kukuev (2006b:484) recognized the presence of areas with “whitish tissue “in the place of the *prcf* series, and in other areas it is present only at the anal and paired fins, pronounced weakly, and is not well discernible at the background of the skin”. Later, Prokofiev and Kukuev (2006c) recognized that *P. parini* is distinguished by Lavenberg (1974) by the presence of the white lines in place of discrete photophores. Prokofiev and Kukuev (2008) first referred to that species (p. 135–136) as *Pseudoscopelus* sp., but listed no specimen. In that same work they described *P. vityazi* as an addendum (p. 158–161). The species was diagnosed by the presence of trough-like bands of luminescent tissues in place of photophores, a new diagnosis for *P. parini* was given as photophores absent. Based on pictures of the holotype of *P. parini* provided by the authors, there is no question about the presence of white lines. Therefore, *P. vityazi* is placed in synonymy of *P. parini.*

Pseudoscopelus astronesthidens group

Composition. The *Pseudoscopelus astronesthidens* group is composed of three species: *P. astronesthidens*, *P. australis*, and *P. odontoglossum*.

Diagnosis. The *Pseudoscopelus astronesthidens* group is diagnosed from all other species groups of *Pseudoscopelus* by its unique photophore and dentition patterns: luminescent tissue present as discrete photophores (*vs.* absent or in white lines in *P.*

aphos group); *mxf* short, restricted to area below orbit, not connected to *apf* posteriorly (*vs. mxf* absent or if present connected to *apf* posteriorly); elongate canine teeth present on basihyal and second basibranchial (*vs.* teeth absent on basihyal; small conical teeth present on second basibranchial); palatine teeth type 4, with considerable ability to bend caudally (*vs.* palatine teeth of type 1, firmly attached to bone).

Description. Dentition, photophore pattern, and color detailed in species' account. Body elongate, fusiform, not greatly compressed anteriorly, but progressively more compressed in caudal region. Greatest body depth at origin of first dorsal fin. Scales absent, except for lateral line, embedded in skin.

Anterior profile of head elongated in lateral view. Tip of snout protruding, with gentle curve at level of anterior naris. Mouth terminal and large, reaching edge of preopercle. Orbit circular. Nares distinctly separated, anterior naris circular, close to third supraorbital pore; posterior naris crescent shaped, close to anterodorsal edge of eye.

Pectoral fin very elongate reaching the level of anus; pelvic-fin origin slightly posterior to pectoral-fin base; dorsal fins two, first dorsal-fin insertion slightly posterior to level of pelvic-fin insertion, second dorsal-fin origin at level of anal-fin origin. Lateral line complete, with pores opening between scales; last scale of lateral line separate, on the lower lobe of caudal fin, with two pores.

Gill arches four; pseudobranchia present. Epibranchial of first arch attached to opercle to midline; hypobranchial and ceratobranchial of first arch free. Epibranchials of second, third and fourth arches connected anteriorly to each other and to pharyngobranchials. Ceratobranchial of second arch free. Hypobranchial and basibranchial of second, third and four arches connected medially. Ceratobranchial of second arch free. Ceratobranchial of third and fourth arches connected distally. Ceratobranchial of fourth arch connected to body wall at proximal half. Basihyal, elongated, free anteriorly, with posterior and ventral connection to first basibranchial; first basibranchial small, triangular, connected to basihyal and second basibranchial; second basibranchial elongated; third basibranchial extremely elongated, extending posteriorly beyond fourth basibranchial, posterior half cartilaginous and ventrally curved; four basibranchial small, diamond-shaped, cartilaginous. Hypohyals with dorsal and ventral elements, attached to first basibranchial; first hypobranchial attached immediately posterior to basihyal, between joint of first and second basibranchials; second hypobranchial connected to joint between second and third basibranchials; third hypobranchial proximally connected to anterior edge of fourth basibranchial, distal tip of fourth hypobranchial ventrally pointed; fourth hypobranchial absent or fused to ceratobranchial, fourth ceratobranchial connected to posterior edge of fourth basibranchial; ventral pharyngobranchials connected posteriorly to fourth ceratobranchial.

Ontogenetic changes. The pectoral fin of *Pseudoscopelus australis* has a statistically significant negative ontogenetic growth ($P<0.05$); because of limited samples available, it could not be determined if this is also true in *P. astronesthidens* and *P. odontoglossum* (Fig. 11 C). Dentition pattern of specimens was formed in specimens as small as 32.0 mm (CAS–SU).

Pseudoscopelus astronesthidens Prokofiev and Kukuev 2006

Figures 4.8 A, 4.19 A; Tables 4.14 and 4.15

Pseudoscopelus astronesthidens Prokofiev and Kukuev 2006c: S27–S32, figures. 2d, 2g–2j, 3c, 4, 5 [type locality western North Atlantic, 37°34’ N, 59°56’ W, holotype ZM MGU 16455, 150.0 mm].

Pseudoscopelus altipinnis Prokofiev and Kukuev 2005: 752, figure 2 [missidentified].

Diagnosis. A species of the *Pseudoscopelus astronesthidens* group, diagnosed within the group by a combination of characteristics: teeth present on ceratobranchial of *P. australis* and *P. odontoglossum*); basihyal and second basibranchial teeth in two rows (*vs.* basihyal and second basibranchial teeth in three rows in *Pseudoscopelus odontoglossum*); teeth on first ceratobranchial well developed, total teeth two to nine (*vs.* teeth on first ceratobranchial often absent or, if present, only a single small tooth in *P. australis*); palatine teeth in two rows (*vs.* palatine teeth in a single row); *dnf* absent (*vs.* *dnf* present); *ppf* present (*vs.* *ppf* absent).

Description. Medium-sized species of *Pseudoscopelus*, largest specimen examined 143.0 mm SL. Meristic data summarized in table 4.14, morphometric in table 4.15. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary same as illustrated for *Pseudoscopelus odontoglossum*. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 15–20% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, curved caudally in body, and straight, caniniform, type 4 in caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of two to four straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in six to eight transverse rows of one to four straight or slightly curved, needle-like, type 4 teeth, gradually increasing in size from medial to mesial.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, straight, type 4 teeth, recovered by skin. Mesial in six to eight transverse rows of one to four teeth straight or slightly curved, needle-like, type 4 teeth, increasing in size from lateral to mesial. Palatine teeth conical, type 1, in single row. Palatine teeth anteriorly in two rows of straight, needle-like, type 4 teeth; posterior three to four teeth in single row of caniniform type 1 teeth, similar to teeth on caudal process of premaxilla.

Tooth on first and second gill arches present, small, conical, type 1; absent on third and fourth arches. Teeth on basihyal and second basibranchial in two rows of caniniform, type 4; absent on other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.8 A. Photophores on head: *dnf*, *inof* 1–2, *lpf*, *opf*, *pof*, and absent; *mxf* short, in single row, parallel to maxilla, from level of mid-eye to posterior third of maxilla, not connected to *apf* posteriorly; *apf* in angle between preopercle and maxilla; *vnf* in small group of few organs; *ppf* in ventral edge of interopercle; *amf* in one to three rows, medial to third pore of mandibular canal, from slightly anterior to third pore to fourth pore; *pmf* in one to three rows, lateral to fifth pore of mandibular canal, from halfway between fourth and fifth pores to almost sixth pore.

Photophores on body: *lvf, rtf*, *scf*, *spf*, *svf* and *trf* absent; *pf* in single row, in ventral ray along pectoral fin; *paf* continuous with *pf*, at pectoral-fin axil; *vf* in single row, along mesial pelvic-fin ray to first third of pelvic fin; *vaf* continuous with *vf*; *if* short, in two rows, from isthmus to cleithrum; *prvf* short, in two rows, from cleithrum to anterior part of pelvic bone; *ptvf* in two rows, from posterior third of pelvic fin to close to anus; *saf* in single row, not connected anteriorly at anterior angle, neither posteriorly; *prcf* in posterior half of peduncle, *U*-shaped, surrounding lower procurrent rays.

Color. Uniformly black, excluding triangular area over epiphyseal branch. Pectoral, pelvic, first and second dorsal fins, and anal fin mostly hyaline, pigmented at their bases; caudal fin dusk. Internal part of mouth pigmented including area of teeth insertion of dentary and premaxilla, roof, lateral sides and floor of mouth, skin over basihyal, basibranchials, and gill arches; gill filaments not pigmented.

Identification of Juveniles. The smallest specimen recognized has 31.9 mm (CAS–SU 66492); the identification was based on the presence of teeth on basihyal, second basibranchial, first ceratobranchial and palatine, and the presence of *ppf*.

Distribution. Western North Atlantic, from 15° to 65° W, 60° to 30° N (Fig. 4.3 C).

Bathymetric distribution. From 154 to 1482 m (mean 858 m).

Pseudoscopelus australis Prokofiev and Kukuev 2006

Figures 4.8 B, 4.19 B; tables 4.14 and 4.15.

Pseudoscopelus australis Prokofiev and Kukuev 2006: S32–S36, figure 6 a–g [type locality: not precisely known, Subantarctic part of the Atlantic Ocean, holotype ZM MGU (former IORAN) 21251, 150 mm].

Pseudoscopelus altipinnis Prokofiev and Kukuev 2005: 752, figure 2 [missidentified].

Pseudoscopelus sp. A Prokofiev and Kukuev 2005: 727–729, figure 7 [Antarctic Ocean].

Pseudoscopelus albeolus Prokofiev and Kukuev 2008: 69–76, figures 118–124 [type locality: not precisely known, Antarctic, holotype ZIN 43959, 115.0 mm]. **NEW SYNONYM.**

Diagnosis. A species of the *Pseudoscopelus astronesthidens* group diagnosed within the group by a unique combination of characteristics: teeth on ceratobranchial of first gill arch usually absent, or if present only as a single small tooth, total teeth zero to one, mode zero (*vs.* teeth on ceratobranchial of first gill arch present, one to 16); teeth absent on second gill arch (*vs.* teeth present on second ceratobranchial of *P. astronesthidens*); palatine teeth in a single row, total teeth 10–16 (*vs.* palatine teeth in two rows, total teeth 15–38); basihyal and second basibranchial teeth in two rows (*vs.* basihyal and second basibranchial teeth in three rows in *P. odontoglossum*); *dnf* present (*vs. dnf* absent), *ppf* absent (vs. *ppf* present).

Description. Large-sized species of *Pseudoscopelus*, largest specimen examined 196.4 mm SL. Meristic data summarized in table 4.14, morphometric in table 4.15. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary same as illustrated for *Pseudoscopelus odontoglossum*. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 15–20% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, curved caudally in body, and straight, caniniform, type 4 in caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of two to four straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in six to eight transverse rows of one to four straight or slightly curved, needle-like, type 4 teeth, gradually increasing in size from medial to mesial.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, straight, type 4 teeth, recovered by skin. Mesial in six to eight transverse rows of one to four teeth straight or slightly curved, needle-like, type 4 teeth, increasing in size from lateral to mesial. Palatine teeth conical, type 1, in single row. Palatine teeth anteriorly in two rows of straight, needle-like, type 4 teeth; posterior three to four teeth in single row of caniniform type 1 teeth, similar to teeth on caudal process of premaxilla.

Teeth on first hypobranchial present, small conical, type 1 teeth; few specimens with one small tooth on first ceratobranchial; absent on other gill arches. Teeth on basihyal and second basibranchial in one to two rows of caniniform, type 4; absent on other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated on figure 4.8 B. Photophores on head: *lpf*, *opf*, *pof*, and *ppf* absent; *dnf* with few organs, posterior to posterior nostril; *inof* one to two photophores present in one specimen (CAS 91022), *mxf* short, in single row, parallel to maxilla, from level of mid-eye to posterior third of maxilla, not connected to *apf* posteriorly; *apf* in angle between preopercle and maxilla; *vnf* in small group of few organs; *amf* in one to two rows, medial to third pore of mandibular canal, from second to fourth pore; *pmf* in one to two rows, lateral to fifth pore of mandibular canal, from halfway between fourth and fifth pores to halfway between fifth sixth pores.

Photophores on body: *lvf, rtf*, *scf*, *spf*, *svf* and *trf* absent; *pf* in single row, in ventral ray along pectoral fin; *paf* continuous with *pf*, at pectoral-fin axil; *vf* in single row, along mesial pelvic-fin ray to first third of pelvic fin; *vaf* continuous with *vf*; *if* short, in two rows, from isthmus to cleithrum; *prvf* short, in two rows, from cleithrum to anterior part of pelvic bone; *ptvf* in two rows, from posterior third of pelvic fin to close to anus; *saf* in single row, not connected anteriorly at anterior angle, neither posteriorly; *prcf* in posterior half of peduncle, oval, three-pronged, with medial prong enlarged and extending over lower procurrent rays.

Color. Uniformly black, excluding triangular area over epiphyseal branch. Pectoral, pelvic, first and second dorsal fins, anal and caudal fins dusk. Internal part of mouth pigmented including area of teeth insertion of dentary and premaxilla, roof, lateral sides and floor of mouth, skin over basihyal, basibranchials, and gill arches; gill filaments not pigmented.

Ontogenetic changes. *Pseudoscopelus australis* has a negative statistically significant allometric growth of the pectoral fin ($P<0.001$, Fig. 11). The variation explains the large standard length variation found for this characteristic ($SD=5.6$).

Distribution. Circumglobal in the cold waters of the **s**outhern hemisphere; occurs in the southern ocean, eastern and western South Pacific, southern part of Indian, and eastern and western South Atlantic, from 31° S to 60° S (Fig. 4.3 C).

Bathymetric distribution. From 410 to 4667 m; however the deepest records for this species (4667 and 2776 m) are questionable. The deepest record for this species probably is 1196 (mean 796 m).

Remarks. The type locality for *Pseudoscopelus australis* and *P. albeolus* are not precisely defined.

The status of *Pseudoscopelus albeolus*. It was first referred by Prokofiev and Kukuev (2005) as *Pseudoscopelus* sp. A, and described by Prokofiev and Kukuev (2008) as *P. albeolus*. The description is based on a single, poorly preserved, disfigured specimen, obtained from the Southern Ocean, off Antarctic in 26–I–1972. The precise locality and coordinates is unknown. The species was (p. 75). Prokofiev and Kukuev (2008: 75) diagnose *P. albeolus* based on the color pattern, and few morphometric differences. Many specimens of *Pseudoscopelus* examined during this work were severely faded, some of them completely white bleached (e.g. figures 4.10, 4.12, 4.13, 4.14, 4.15, 4.17, 4.18). Fading and bleaching are natural processes in collection specimens especially after a few decades, therefore, should not be considered as representative of life coloration. This process can be accelerated by poor preservation, exposition to light or chemicals (pers. obs.). A remarkable example of color loss of a preserved specimen was illustrated by Pietsch et al. (2009), in which the preserved specimens of *Histiophryne psychedelica* do not resemble that species' amazing coloration in life. The morphometric differences proposed between those two species proposed by Prokofiev and Kukuev (2008) are clearly caused by the poor conditions of the holotype of *P. albeolus*. Although the authors mention, but do not list, differences in the photophore pattern, the illustrations (figs. 123–124) and description provided are extremely similar to the pattern as *P. australis*. Moreover, photophores groups can also be difficult or impossible to discern in poorly preserved specimen (e.g. the type of *P. cephalus*). Until fresh specimens of a white pigmented species *Pseudoscopelus* become available, this author is very skeptical about the diagnostic value of the color pattern for *P. albeolus*. *Pseudoscopelus albeolus* is therefore placed in synonymy of *P. australis*.

Pseudoscopelus odontoglossum, new species

Figures 4.8 C, 4.10 D, 4.19 C; Tables 4.16 and 4.17

Holotype. SIO 61–48, 70.2 mm, Pacific Plate, 10°24' S, 161°01' W, 2700 m, 29–V–1967, R/V *Argo*.

Paratypes. Pacific, Pacific Plate: SIO 70–311, 1, 48.7 mm, 26°33' N, 139°10' E, 0–2500 m, 1–IX–1970, R/V *Melville*; SIO 71–290, 1, 44.2 mm, 24°18' S, 154°37' W, 0–1000 m, 11–III–1971, R/V *Thomas Washington*; USNM 391142 (former SIO 68–486), 1, 43.3 mm, 27°32’ N, 177°46’ W, 21–IX–1968, R/V *Alexander Agassiz*.

Non-type specimen (juvenile). Pacific, Pacific Plate: LACM 44397–1, 1, 35.4 mm, 21°20’ N, 158°10’ W, 0–325 m, 3–VII–1978, R/V *Kana Keoki*.

Diagnosis. A species of the *Pseudoscopelus astronesthidens* group diagnosed within the group by a unique characteristic: teeth on basihyal and second basibranchial in three rows (*vs.* teeth on basihyal and second basibranchial in two rows in *P. astronesthidens* and *P. australis*). It can be further distinguished from *P. australis* by the presence of teeth on first ceratobranchial (*vs.* teeth usually absent, if present, only a single small tooth), palatine teeth in two rows, total teeth 16–26 (*vs.* palatine teeth in two rows, 10–16), and *dnf* present (*vs. ppf* absent); and from *P. astronesthidens* by teeth absent on second gill arch (*vs.* teeth present on second ceratobranchial of *P. astronesthidens*);

Description. Small-sized species of *Pseudoscopelus*, largest specimen examined 70.2 mm SL. Meristic data summarized in table 4.16, morphometric in table 4.17. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary, as illustrated in figure 4.10 C. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 15–20% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, curved caudally in body, and straight, caniniform, type 4 in caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of two to four straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in six to eight transverse rows of one to four straight or slightly curved, needle-like, type 4 teeth, gradually increasing in size from medial to mesial.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along lateral edge of dentary, with conical, straight, type 4 teeth, recovered by skin. Mesial in six to eight transverse rows of one to four teeth straight or slightly curved, needle-like, type 4 teeth, increasing in size from lateral to mesial. Palatine teeth conical, type 1, in single row. Palatine teeth anteriorly in two rows of straight, needle-like, type 4 teeth; posterior three to four teeth in single row of caniniform type 1 teeth, similar to teeth on caudal process of premaxilla

Teeth on first and second gill arches present, small, conical, type 1; absent on second and third arches. Teeth on basihyal and second basibranchial in two rows of caniniform, type 4; absent on other basibranchials.

Luminescent organs. Luminescent organs present as discrete photophores on head and body, pattern illustrated in figure 4.8 C. Photophores on head: *dnf*, *inof* 1–2, *lpf*, *opf*, and *pof* absent; *mxf* in single row, parallel to maxilla, from level of mid-eye to posterior third of maxilla, not connected posteriorly with *apf*; *apf* in angle between preopercle and maxilla; *vnf* in small group of few organs; *ppf* in interopercle; *amf* in one to three rows, medial to third pore of mandibular canal, from slightly anterior to third pore to fourth pore; *pmf* in one to three rows, lateral to fifth pore of mandibular canal, from halfway between fourth and fifth pores, to halfway between fifth and sixth pores.

Photophores on body: *lvf, rtf*, *scf*, *spf*, *svf* and *trf* absent; *pf* in single row extending to half pectoral fin, on ventral ray; *paf* continuous with *pf*, at pectoral-fin axil; *vf* in single row, to half halfway of pelvic fin, on mesial ray; *vaf* continuous with *vf*; *if* short, in two rows, from isthmus to cleithrum; *prvf* short, in two rows, from cleithrum to anterior part of pelvic bone; *ptvf* in two rows, from posterior half of pelvic fin to close to anus; *saf* in single row, not connected anteriorly at anterior angle, connected posteriorly; *prcf* in posterior half of peduncle, *Y*-shaped, prongs extending lateral to lower procurrent rays.

Color. No recently collected specimens known; preserved specimens bleached brown, with body uniformly pigmented except for area over epiphyseal branch. Pectoral, pelvic, anal, first and second dorsal fins pigmented in their bases; caudal fin entirely pigmented. Mouth and gill apparently pigmented, except for gill filaments.

Identification of Juveniles. The smallest specimen recognized has 35.4 mm (LACM 44397–1); the identification was based on the presence of three rows of teeth on second basibranchial, palatine teeth in two rows, teeth present on first ceratobranchial, and *dnf* present.

Distribution. Pacific Plate from 154° W to 139° E, 28° N to 24° S (Fig. 4.3 B).

Bathymetric distribution. From 325 to 2700 m (mean 1631 m).

Etymology. From the Greek *odont-*, meaning tooth, and *glosso*, means tongue; in reference to the presence of well developed teeth on the bones of the tongue, basihyal and first ceratobranchial.

Pseudoscopelus lavenbergi group

Composition. The *Pseudoscopelus lavenbergi* group is composed of a single species: *P. lavenbergi*.

Diagnosis. The *Pseudoscopelus lavenbergi* group is diagnosed from its congeners by it three unique characteristics: *trf* in a broad band of three or more rows (*vs. trf* absent in *P. scutatus* and *P. astronesthidens* groups; in a single row with widely spaced organs in *P. altipinnis* group, and in a single row of closely spaced photophores, with a medial cluster in *P. scriptus* group); *ptvf* short, not reaching anus, and extending anteriorly only halfway to pelvic-fin origin (*vs. ptvf* elongate, extending close to anus, and extending anteriorly to very close to pelvic-fin origin in all the other species); *mxf* completely absent and *apf* present (*vs.* both *mxf* and *apf* absent on *P. scutatus* group; both *apf* and *mxf* present in the remaining species).

Description. Body elongate, fusiform, not greatly compressed anteriorly, but progressively more compressed in caudal region. Greatest body depth at origin of first dorsal fin. Scales absent, except for lateral line.

Anterior profile of head round in lateral view. Tip of snout protruding, with abrupt curve dorsally at level of anterior naris. Mouth terminal and large, reaching edge of preopercle. Orbit circular. Nares distinctly separated, anterior naris circular, close to third supraorbital pore; posterior naris C-shaped, close to anterodorsal edge of eye. Pectoral fin elongate, reaching origin of second dorsal and anal fins; pelvic-fin origin slightly posterior to pectoral-fin base; dorsal fins two, first dorsal-fin origin slightly posterior to pelvic-fin insertion, second dorsal-fin origin at level of anal-fin origin. Lateral line complete, with pores opening between scales; last scale of lateral line separate, on the lower lobe of caudal fin, with two pores.

Gill arches four; pseudobranchia present. Epibranchial of first arch attached to opercle to midline; ceratobranchial, hypobranchial and basibranchial of first arch free. Epibranchials of second, third and fourth arches connected anteriorly to each other and pharyngobranchials; ceratobranchial of second arch free. Hypobranchial and basibranchial of second, third and four arches connected medially. Ceratobranchial of fourth arch connected to body wall at proximal half. Basihyal, elongated, free anteriorly, with posterior and ventral connection to first basibranchial; first basibranchial small, triangular, connected to basihyal and second basibranchial; second basibranchial elongated; third basibranchial extremely elongated, extending posteriorly beyond fourth basibranchial, posterior half cartilaginous and ventrally curved; four basibranchial small, diamond-shaped, cartilaginous. Hypohyals with dorsal and ventral elements, attached to first basibranchial; first hypobranchial attached immediately posterior to basihyal, between joint of first and second basibranchials; second hypobranchial connected to joint between second and third basibranchials; third hypobranchial proximally connected to anterior edge of fourth basibranchial, distal tip of fourth hypobranchial ventrally pointed; fourth hypobranchial absent or fused to ceratobranchial, fourth ceratobranchial connected to posterior edge of fourth basibranchial; ventral pharyngobranchials connected posteriorly to fourth ceratobranchial.

Pseudoscopelus lavenbergi Melo, Walker and Klepadlo 2007

Figures 4.6 C, 4.21 C; Tables 4.18, 4.19

Pseudoscopelus lavenbergi Melo, Walker and Keplado 2007: 36–41, figures 4, 5, 6. [type locality: eastern Central Pacific, off Ecuador, 01°21' N, 086°36' W, holotype SIO 71–358, 73.0 mm].

Diagnosis. Same as for the group.

Description. Middle-sized species of Pseudoscopelus, largest specimen 181.0 mm SL. Meristic data summarized in table 4.16, and morphometric data in table 4.17. General shape of body as for species group.

Dentition. Teeth present on premaxilla, dentary, and palatine. Premaxillary and dentary dentition of *P. lavenbergi* illustrated in figure 4.5. Premaxilla elongated, dentigerous area divided into four processes: head, anterior, mesially curved; neck, narrow region at angle of head; body wide, wide, anteriorly narrowing in posterior third, widest point 15–20% of upper jaw length; and caudal, elongated posteriormost process. Premaxillary teeth arranged in anterior tusk, fang of head, and three series: lateral, middle and mesial. Tusk on head of premaxilla, anteriormost, recurved, type 1; fang of head posterior to tusk, straight, caniniform, type 4. Lateral series along edge of premaxilla, in single row of type 4 teeth, extending from head, trough neck and body to caudal process, recurved in head and neck, curved caudally in body, and straight, caniniform, type 4 in caudal process. Middle and mesial series restricted to body of premaxilla; middle series in irregular transverse rows of two to four straight, needle-like, type 4 teeth, gradually increasing in size from lateral to medial; mesial series in six to eight transverse rows of one to four straight or slightly curved, needle-like, type 4 teeth, gradually increasing in size from medial to mesial.

Dentary elongated, with two series of teeth: lateral and mesial. Lateral series in single row along edge of dentary, with conical, straight, curved, type 4 teeth, recovered by skin. Mesial in one to two rows, teeth needle-like, type 4, increasing in size from lateral to mesial. Palatine teeth conical, type 1, arranged in single row.

Gill rakers on first and second gill arches present small, conical, as type 1 teeth. Teeth on basibranchial, first and second gill arches, and pharyngeals; absent on basihyal, other basibranchials, third and fourth gill arches. Rakers of first basibranchial arranged in V-shaped row.

Luminescent organs. Luminescent organs present as discrete photophores on head and body; pattern of *P. lavenbergi* illustrated in Fig. 4.6. Photophores on head: *dnf, info 1-2, mxf, opf, pof* absent; *vnf* as small triangular patch of few organs, slightly posterior to first supraorbital pore; *apf* triangular, short, restricted to angle between premaxilla and preopercle; *amf* medial on dentary, elongate, beginning halfway between second and third mandibular pores, extending to midpoint between third and fourth pores; *pmf* lateral on dentary, elongate, originating slightly posterior to fourth mandibular pore, extending halfway between fifth and sixth pores, in one to two irregular rows.

Photophores on body: *rtf*, *spf*, *svf*, and *scf* absent; *pf* in single row along ventralmost pectoral-fin ray; *paf* in triangular patch at pectoral-fin axil; *vf* short, in single row, restricted to first third of mesial pelvic-fin ray; *vaf* extending over base of pelvic rays 4-5; if elongate, in two to four rows of photophores; *prvf* short, 1/3 of *if*, in one to four rows; *ptvf* short, from halfway between anus and pelvic fin, to close to anus, in one to three rows; *trf* in broad band of three or four rows; *saf* reaching anus, but not extending further anteriorly, in single row except for anterior part, posterior ends not connected;

prcf in two rows anteriorly and three to four rows posteriorly, short, extending from posterior part of peduncle and extending over anterior lower procurrent caudal-fin rays.

Color. No freshly collected specimens known, most specimens bleached; two well preserved specimens completely dark brown, including fins. Oral and branchial cavities dark, including gill arches; gill filaments not pigmented.

Distribution. Eastern Pacific, from California to Chile, 32^{o} N to 23^{o} S; extending west to near the Hawaiian Islands, 158^{o} W (Fig. 4.3 A)

Bathymetric distribution. From 50 to 4631 m, being the lowest record questionable (mean 1113 m).

Discussion

The species of *Pseudoscopelus* are organized herein in groups based on the photophore pattern, dentition and external morphology. Although some of the characters used to diagnose the groups may have some phylogenetic importance, the arrangement is merely didactic, as no cladistic analysis was performed to test validity of them as monophyletic clades. One example is the status of the *P. aphos* group, which includes *P. aphos* and *P. parini* and is diagnosed by the absence of discrete photophores. Prior to any phylogenetic analysis, those conditions can be interpreted in two ways: absence of photophores is plesiomorphic and therefore not useful to diagnose a group; or the discrete photophores were secondarily lost. Moreover the condition found in those two species is not the same, since *P. aphos* completely lacks photophore, and *P. parini* has the white lines on the body.

The *Pseudoscopelus scriptus* group is the largest, including six species, and is likely to be monophyletic. The species share the same photophore groups, with little interspecific variation in shape – specially *saf*; diagnostic features are based on vertebral counts, dention and pigmentation of orobranchial chamber and gill arches. Other groups also may also be monophyletic, such as the *Pseudoscopelus scutatus* group, composed of two very distinctive species with concave snout, *svf* present, and the unique configuration of other photophore groups. The *P. astronesthidens* group is also defined by unique characteristics, especially the dention, with type 4 teeth on the palatine, basihyal and second basibranchial, and the caniniform teeth on the caudal portion of premaxilla. The *P. altipinnis* group is composed of two very similar species that can only be distinguished by number of teeth rows in premaxilla, and therefore may also represent a monophyletic group.

Prokofiev and Kukuev (2006c) proposed that the dark pigmentation of the internal areas of orobranchial chamber and gill arches diagnosis a group of species that includes *Pseudoscopelus altipinnis*, *P. astronesthidens* and *P. australis*. This characteristic misevaluated by them for other species within *Pseudoscopelus*, such as *P. aphos*, *P. sagamianus* and *P. parini*, and was not compared with other chiasmodontids. For example, *Kali parri* also has a dark orobranchial chamber and gill arches. The pigmentation of the mouth may be a synapomorphy for higher level groups than those presented herein, but it is important to note that within the *P. scriptus* group this character is variable, with *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, and *P. scriptus* possessing light pigmentation restricted to certain areas of the mouth, and *P. sagamianus* with the mouth completely pigmented. Oral pigmentation of *P. cephalus* was not possible to determine owing to the condition of available material.

The presence of photophores in *Pseudoscopelus* had been used to diagnose the genus even after the description of *P. aphos* (*e.g.*, Prokofiev and Kukuev 2006c, Smith *in press*; Spitz et al. 2007). Spitz et al.(2007) suggested that *P. aphos* should not be included in *Pseudoscopelus*, but also gave no clue of where it should be placed (apparently their work was submitted before the publication of *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. lavenbergi*, and *P. parini* because they also made no mention of those species in the work). Melo et al. (2007) included *P. aphos* in *Pseudoscopelus* and listed two possible synapomorphies to support the monophyly of the genus, both present in *P. aphos* and *P. parini*: the dorsal margin of the orbit is formed by infraorbital 6; the position of the last infraorbital pore in the dorsal edge of the orbit is anterior to the middle of the pupil. Spitz et al. (2007) also proposed that a new family should be created to include exclusively the photogenetic species of *Pseudoscopelus*. This hypothesis would require further phylogenetic analysis before adoption in order to avoid the creation of more taxonomic problems within the family by leaving a possible paraphyletic Chiasmodontidae with *Chiasmodon*, *Kali*, and *Dysalotus*.

Biogeographic aspects. The genus *Pseudoscopelus* has a wide distribution through the Atlantic, Pacific, Indian and Southern Oceans, from equatorial to subpolar zones between 60º N and 60º S. They have not being recorded from enclosed seas, such as the Mediterranean, and the Baltic, Red and Black Seas, and Baja California. The species of *Pseudoscopelus* also have well defined ranges of disjunct distribution, which are likely to be a result of surface or sub-surface water temperatures.

Four species have circumglobal distribution: *Pseudoscopelus australis*, *Pseudoscopelus altipinnis*, *P. scutatus*, and *P. obtusifrons. Pseudoscopelus australis* is circumglobal in the cold waters of the Southern Ocean, and occurs marginally in the cool temperate zones of the Atlantic, Indian and Pacific Oceans. The latter three species are found in the equatorial to the temperate zones the Atlantic and Pacific Oceans, except for the east Pacific; *P. scutatus* and *P. obtusifrons* are wide spread in the Atlantic Ocean, but from a single locality each in the Indian Ocean. Because of their relatively small size, deep habitat and apparently low densities, *Pseudoscopelus* are infrequently caught. Some of these restricted species may be found to have a much wider distribution with increasing fishing effort and awareness.

The Atlantic Ocean has four endemic species: *Pseudoscopelus scriptus*, *P. pierbartus*, and *P. aphos*, and *P. astronesthidens*. *Pseudoscopelus scriptus* and *P. aphos* have a western distribution, and *P. pierbartus* also occurs in the east North Atlantic. *Pseudoscopelus aphos* is endemic to western North Atlantic from Slope Water to the Straits of Florida, and *P. astronesthidens*, to the cold waters northern North Atlantic. Regarding the Atlantic fauna, it is interesting to note that only *P. obtusifrons* and *P. altipinnis* occurs in the west part of Gulf of Mexico and Caribbean, but other species are found marginally of those provinces, off the West Indies: *P. scutatus*, *P. scriptus*, and *P. aphos*. *Pseudoscopelus cordilluminatus* occurs in the eastern South Atlantic and extends its range to the Indian Ocean.

Six species are endemic to the Pacific Ocean: *P. cephalus*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, and *P. sagamianus*. *Pseudoscopelus cephalus* is apparently endemic to the Indo West-Pacific off the Philippines; *P. odontoglossum* and *P. parini* are distributed along the Pacific Plate, with the latter being found marginally in border of the west Pacific; *P. lavenbergi* is associated with low oxygen waters of the East

Pacific (Brinton 1979); and *P. paxtoni* endemic to the cold waters around New Zealand in the west Pacific. *Pseudoscopelus sagamianus* occurs in the Pacific Plate and West-Pacific, and marginally in the Indian Ocean. A single species, *Pseudoscopelus bothrorrhinos*, is mostly restricted to the Indian Ocean, but was also recorded marginally in the West-Pacific.

Bathymetric distribution. There are depth records for 178 lots of *Pseudoscopelus*; this makes possible to estimate the depth range of the genus with reasonable confidence. As stated before, shallower depths are more reliable, as of the deepest records may be the result of capture during net transition. Very few lots come from depths greater than 200 meters, and juveniles were collected close to the surface. Excluding those records, *Pseudoscopelus* occurs on average of 832 m deep (SD = 521). The four species with deepest averages are *P. odontoglossum* (1631 m), *P. sagamianus* (1130 m), *P. paxtoni* (1031 m), and *P. pierbartus* (1069 m). The species that occur in shallower waters are *P. scutatus* (578 m), *P. aphos* (678 m), *P. obtusifrons* (718 m), *P. bothrorrhinos* (719 m).

There are no records in literature regarding dial vertical migration in *Pseudoscopelus*, and unfortunately only very few lots examined had their collection time recorded. Nevertheless, there is evidence that they undergo vertical migration, since number of lots, 20 of 178 (>10%), were collected around 200 m, and a wide bathymetric range was recorded for all species of *Pseudoscopelus*.

Comparative material

Pseudoscopelus altipinnis: 96 specimens, including holotype and paratypes. Atlantic, North Sargasso Sea: MCZ 68419, 1, 143.1 mm, 31°30’ N, 76°33’ W, 400–1000 m, 30–VII–1978, R/V *Oceanus*; USNM 240669, 1, 44.4 mm, 32º07’ N, 64º13’ W, 928 m, 20–VIII–1971, R/V *Delaware*; USNM 240670, 1, 30.5 mm, 33º05’ N, 64º40’ W, 0–700 m, 5–VII–1968, R/V *Delaware*. Gulf of Mexico Province: MCZ 41116, 2, 53.8–86.4 mm, 29°05’ N, 88°09’ W, 820 m, 20–V–1960, M/V *Oregon*; UF 166865, 1, 117.8 mm, 28°36’ N, 87°07’ W, 1073 m, 21–VI–1969, M/V *Oregon II*; USNM 202255, 3, 66.3–74.1 mm, 29º06’ N, 88º02’ W, 910 m, 9–II–1961, R/V *Oregon*; USNM 202257, 1, 62.1 mm, 29º04’ N, 87º37’ W, 1456 m, 28–IV–1961, R/V *Oregon*; USNM 202259, 1, 103.6 mm, 29º10’ N, 87º55’ W, 738–928 m, 4–II–1959, R/V *Oregon*; USNM 202260, 3, 67.27–68.3 mm, 29º06’ N, 88º02’ W, 928 m, 9–II–1961, R/V *Oregon*. Straits of Florida: YPM 2798, 1 (holotype), 185.8 mm, 24º51’ N, 76º28’ W, 17–III–1927, R/V *Pawnee*; YPM 2800, 1 (paratype), 39.1 mm, 21º44’ N, 72º43’ W, 6–IV–1927, R/V *Pawnee*. South Atlantic subtropical: MCZ 96677, 1, 79.7 mm, 35°20’ S, 7°22’ E, 500–540 m, 26–VI–1971, R/V *Atlantis II*; MNRJ 26700, 1, 182.5 mm, 21°25’ S, 39°43’ W, 1721 m, 7–VII–2000, R/V *Thalassa*; MNRJ 26871, 1, 156.0 mm, 21°50’ S, 39°48’ W, 1360 m, 21–VIII–2003, R/V *Astro Garoupa*; MZUSP 78216, 2, 54.1–63.9 mm, 34°07’ S, 51°22’ W, 940 m, 23–IV–1997, R/V *Atlântico Sul*. Amazonian Province: MCZ 49084, 1, 79.4 mm, 1°35’ N, 27°03’ W, 290 m, 25–II–1963, R/V *Chain*; MCZ 49085, 1, 85.6 mm, 13°55’ N, 57°00’ W, 300 m, 29–IV–1966, R/V *Atlantis II*; MCZ 68391, 1, ca. 70.0 mm, 9°03’ N, 49°16’ W, 0–490 m, 22–IX–1973, R/V *Atlantis II*; MCZ 68460, 1, 88.0 mm, 3°58’ N, 31°33’ W, 175–190 m, 17–III–1977, R/V *Oceanus*; MCZ 60727, 1, 113.8 mm, 2°59’ N, 33°46’ W, 2000 m, 20–VII–1983, R/V *Columbus Iselin*; MCZ 60728, 1, 85.9 mm, 9°02’ N, 43°48’ W, 0–495 m, 20–IX–1973, R/V *Atlantis II*; ZMUC P. 6539, 1, 89.6 mm, 5°35’ N, 51°08’ W, 16–XI–1921, R/V *Dana*. Azores–Britain Province: MCZ 49086, 1, 96.8 mm, 40°47’ N, 28°41’ W, 20–IX–1964, 450 m, R/V *Atlantis II*; ZMUB 16373, 2, 116.4–164.7 mm, 42º48’ N, 27º52’ W, 829–1770 m, 27–VI–2004; R/V *G.O. Sars*; ZMUB 16374, 1, 155.1 mm, 42º56’ N 29º18’ W, 604–1500 m, 28–VI–2004; R/V *G.O. Sars*; ZMUB 16375, 1, 92.8 mm, 42º46’ N, 29º28’ W, 810–1870 m, 28–VI–2004; R/V *G.O. Sars*; ZMUB 16376, 3, 133.1–148.5 mm, 41º31’ N, 29º54’ W, 800–1800 m, 30–VI–2004; R/V *G.O. Sars*; ZMUB 16377, 2, 87.9–127.1 mm, 41º28’ N, 29º53’ W, 0–800 m, 30–VI–2004; R/V *G.O. Sars;* ZMUC P. 6540, 1, 80.6 mm, 37°23’ N, 26°02’ W, 14–VI–1922, R/V *Dana*. Mediterranean outflow: BMNH 1961.1.30.7, 1, 139.4 mm, 44°19’ N, 4°30’ W, 220 m, 11–7–1985, G. Brown col.; ZMUC P. 6538, 1, 98.7 mm, 45°37' N, 7°03' W, 9–III–1909, R/V *Thor*. North Mauritanian upwelling: MCZ 96853, 1, 72.2 mm, 20°19' N, 17°59' W, 6–XI–1978, R/V *Oceanus*. South Mauritanian upwelling: MCZ 96690, 1, 112.4 mm, 14°26' N, 18°50' W, 620–690 m, 22–XI–1970, R/V *Atlantis II*. Guinean Province: BMNH 1930.1.12.1065, 1, 88.6 mm, 0°56' S, 14°08' W, 21–VIII–1927, R/V *Discovery*; LACM 56621–1, 1, 99.6 mm, 4º26' S, 23º05' W, 0–1560 m, 14–I–1972, R/V *Akademik Kurchatov*; MCZ 41376, 1, 112.0 mm, 11°17' N, 30°00' W, 230 m, 2–V–1961, R/V *Chain*; MCZ 41375, 1, 87.4 mm, 3°00' N, 21°15' W, 275 m, 27–IV–1961, R/V *Chain*; UF 148739, 1, 59.3 mm, 3°39' N, 19°48' W, 4631 m, 20–VIII–1973, R/V *Gilliss*; UF 166992, 1, 98.2 mm, 12°00' N, 28°57' W, 260 m, 15–VIII–1966, R/V *Gilliss*; ZMUC P. 6546, 1, 111.8 mm, 11°00' S, 7°36' W, 27–II–1930, R/V *Dana*. Pacific, West Pacific: LACM 36062–34, 1, 95.4 mm, 0º13.5' S, 128º23.7' E, 350–390 m, R/V *Alpha Helix*; USNM 93139, 1 (holotype of *P. microps*), 122.7 mm, 4°43' S, 121°23' E, 1280 m, 17–XII–1909, R/V *Albatross*; ZMUC P. 6542, 1, 122.5 mm, 27°00' S, 177°41' W, 13–12–1928, R/V *Dana*; ZMUC P. 6543, 1, 93.2 mm, 1°42' N, 124°29' E, 29–III–1929, R/V *Dana*; ZMUC P. 6544, 1, 137.8 mm, 7°22' N, 121°16' E, 5–IV–1929, R/V *Dana*; ZMUC P. 6545, 1, 97.8 mm, 9°17' N, 123°58' E, 28–VI–1929, R/V *Dana*. Pacific Plate: LACM 31436, 1, 101.1 mm, 0°03' N, 136°38' W, 22–IX–1968, R/V *Caride I*; LACM 31437–1, 1, 89.3 mm, 0°02' N, 136°51' W, 23–IX–1968, R/V *Caride I*; LACM 31447–1, 2, 38.1–73.1 mm, 0°00' N, 145°30' W, 29–IX–1968, R/V *Caride I*; LACM 31453–2, 1, 86.0 mm, 0°09' S, 147°45' W, 1–X–1968, R/V *Caride I*; LACM 31462–1, 1, 76.1 mm, 0°03' N, 138°30' W, 17–II–1967, R/V *Caride III*; LACM 31465–2, 1, 107.0 mm, 0°09' S, 139°32' W, 18–II–1969, R/V *Caride III*; LACM 31471–1, 1, 80.2 mm, 0°00' N, 143°47' W, 22–II–1969, R/V *Caride III*; LACM 31480–1, 1, 82.0 mm, 0°03' N, 147°23' W, 25–II–1970, R/V *Caride III*; LACM 31481–1, 1, 67.7 mm, 0°02' N, 148°24' W, 26–II–1969, R/V *Caride III*; LACM 31482–1, 1, 42.6 mm, 0°01' N, 148°33' W, 26–II–1969, R/V *Caride III*; LACM 31486–1, 1, 82.0 mm, 0°00' N, 150°06' W, 27–II–1969, R/V *Caride III*; LACM 31487–1, 1, 40.6 mm, 0°00' N, 150°17' W, 860–m, 27–II–1970, R/V *Caride III*; LACM 31488–1, 1, 69.0 mm, 0°05' N, 153°36' W, 2–III–1969, R/V *Caride III*; LACM 31489–1, 1, 106.5 mm, 0°05' N, 153°36' W, 2–III–1969, R/V *Caride III*; LACM 31529–1, 1, 98.7 mm, 0°14' S, 148°07' W, 19–II–1965, R/V *Alize*; LACM 33375–1, 1, 73.1 mm, 3°03’ N, 145°00 W, 0–100 m, 7–II–1970, col. unknown; LACM 46069–21, 1, 23.3 mm, 19°35’ N, 156°09’ W, 22–VIII–1964, R/V *Townsend Cromwell*; LACM 56620–1, 1, 84.4 mm, 11º21’ S, 133º28’ W, 5–IV–1978, R/V *Dimitri Mendeleev*; taken from USNM 288999, 1, 38.5 mm, 0º52’ N, 153º02’ W, 0–655 m, 23–V–1979, R/V *Gyre*; SIO 52–328–60A, 1, 93.9 mm, 6°49’ S, 115°00’ W, 1620 m, 4–VI–1952, R/V *Horizon*; SIO 60–235–60, 1, 112.0 mm, 0°05’ S, 139°08’ W, 4–VII–1960, R/V *Spencer F Baird*; SIO 60–225–60, 1, 74.7 mm, 1°28’ N, 132°30’ W, 0–2750 m, 28–VI–1960, R/V *Spencer F Baird*; SIO 68–534–60, 1, 91.4 mm, 0°01’ N, 165°44’ W, 11–12–VIII–1968, R/V *Alexander Agassiz*; SIO 73–164–60, 1, 77.1 mm, 0°08’ S, 155°00’ W, 14–VII–1972, R/V *Melville*; SIO 73–165–60, 2, 77.5–87.0 mm, 0°10’ S, 155°00’ W, 15–VII–1972, R/V *Melville*; SIO 73–166–60, 1, 104.4 mm, 0°07’ N, 155°02’ W, 15–VII–1972, R/V *Melville*; SIO 73–167–60, 1, 88.7 mm, 0°06’ S, 155°02’ W, 900 m, 16–VII–1972, R/V *Melville*; SIO 73–336–60, 1, 118.7 mm, 28°28’ N, 155°23’ W, 10–11–VII–1973, R/V *Thomas Washington*; SIO 75–303–60, 1, 56.9 mm, 1°59.0’ N, 118°23’ W, 24–I–1973, R/V *David Starr Jordan*; SIO 77–134–60, 1, 74.9 mm, 11°14’ N, 150°33’ W, 6–IX–1976, R/V *Alexander Agassiz*; SIO 91–15–60, 1, 93.9 mm, 33°36’ N, 133°01’ W, 50 m, 15–IX–1980, T. Bailey col.; SIO 93–7–60, 1, 64.6 mm, 1°30’ S, 111°53’ W, 28–VIII–1967, R/V *Thomas Washington*; USNM 271995, 1, 92.2 mm, 0º09’ S, 158º08’ W, 0–310 m, 18–IX–1979, R/V *Wecoma*; USNM 288974, 1, 31.0 mm, 10°28’ N, 150°06’ W, 0–1040 m, 23–IX–1975, R/V *Oceanographer*; USNM 288984, 1, 37.8 mm, 7°30’ N, 158°00’ W, 0–1000 m, 29–I–1980, R/V *Wecoma*; USNM 288989, 1, 37.6 mm, 3°01’ N, 158°00’ W, 0–340 m, 17–V–1979, R/V *Gyre*; USNM 288991, 1, 38.5 mm, 0°53’ N, 157°58’ W, 0–290 m, 07–VIII–1979, R/V *Gyre*; USNM 288992, 1, 23.6 mm, 3°44’ S, 155°51’ W, 0–310 m, 16–XII–1979, R/V *Wecoma*; ZMUC P. 6541, 1, 71.2 mm, 0°18’ S, 99°07’ W, 18–IX–1928, R/V *Dana*.

Pseudoscopelus obtusifrons: 18 specimens, including holotype. Atlantic, North Sargasso Sea: USNM 240675, 1, 64.2 mm, 32º14’ N, 64º20’ W, 0–800 m, 24–VIII–1971, R/V *Delaware*. Gulf of Mexico Province: MCZ 49073, 1, 72.3 mm, 29°5’ N, 88°9’ W, 822 m, 20–V–196, R/V *Oregon*; MCZ 49076, 1, 21.1 mm, 23°13’ N, 94°50’ W, 18–VI–1960, 124–128 m, R/V *Chain*; USNM 194495, 4, 39.5–56.8 mm, 20º55’ N, 93º00’ W, 275–2250 m, 28–V–1964, R/V *Anton Bruun*. Caribbean Sea: MCZ 68446, 1, 37.5 mm, 16°56’ N, 76°56’ W, 10–X–1966, R/V *Anton Bruun*. Amazonian Province: USNM 268429, 1, 115.2 mm, 7º15’ N, 54º15’ W, 680–740 m, 15–XI–1969, R/V *Oregon II*. North African Subtropical Sea: BMNH 2003.5.13.113, 1, 69.5 mm, 28º00’ N, 14º09’ W, 225 m, R.R.S. *Discovery*. Guinean Province: BMNH 2003.6.10.7, 1, 70.5 mm, 17º12’ N, 23º23’ W, 175 m, R.R.S. *Discovery*; MCZ 71612, 1, 144.9 mm, 2°30’ N, 19°22’ W, 15–XI–1978, R/V *Oceanus*. Indian: USNM 200535, 2, 16.8–17.7 mm, 0º21’ S, 65º05’ E, 275–2250 m, 28–V–1964, R/V *Anton Bruun*. Pacific, West Pacific: AMNH 49715, 1, 40.5 mm, 26º21’ S, 177º39’ E, 1024 m, 13–XII–1967, R/V *Eltanin*; LACM 31523, 1, 25.1 mm, 0°53’ S, 169°52’ E, R/V *Cyclone IV*; USNM 93141, 1 (holotype), 93.3 mm, 3º32’ S, 120º31’ E, 532 m, 19–XII–1909, R/V *Albatross*. Pacific Plate: LACM 31528–2, 1, 127.5 mm, 16°17’ S, 166°40’ E, 1395 m, 20–VII–1968, R/V *Santo 68*; LACM 33379, 1, 21.3 mm, 12°29’ N, 162°10’ E, 16–VI–1956, unknown col.; NMNZ P. 20074, 1, 100.7 mm, 25º21’ S, 175º0 8’ W, 591–613 m, 13–XI–1976, R/V *James Cook.*; HUMZ 86851, 1, 33.0 mm, area between Hawaii and New Caledonia, unknown col.; HUMZ 130746, 1, 118.6 mm, 23º58’ N, 166º04’ W, 400 m, II–1994, unknown col.

Pseudoscopelus aphos: nine specimens. Atlantic, Slope Water: MCZ 68461, 1, 60.7 mm, 38°53’ N, 70°48’ W, 340 m, 17–VIII–1977, R/V *Endeavor*. North Sargasso Sea: CAS–SU 66497, 2, 16.7–20.3 mm, 32°12’ N; 64°36’ W, 15–VII–1932, W. Beebe and J. Tee–Van col.; USNM 296957, 1, 71.9 mm, 32º08’ N, 64º09’ W, 0–450 m, 23–VIII–1971, R/V *Delaware*; USNM 296948, 1, 58.6 mm, 32º25’ N, 64º14’ W, 0–760 m, 23–VIII–1971, R/V *Delaware*; USNM 296955, 1, 35.3 mm, 31º48’ N, 64º10’ W, 0–220 m, 23–IX–1969, R/V *Delaware*; USNM 297022, 1, 76.6 mm, 32º08’ N, 63º55’ W, 0–660 m, 21–VIII–1971, R/V *Delaware*. Straits of Florida: MCZ 160792, 1, 26.9 mm, 25°56’ N, 77°28’ W, 23–X–1984, R/V *Cape Florida*; UF 148741, 1, 73.5 mm, 24°38’ N, 76°26’ W, 1632–1637 m, 7–IX–1974, Staiger et al. col.

Pseudoscopelus astronesthidens: 11 specimens. Atlantic, Slope Water: MCZ 41443, 2, 44.8–74.7 mm, 41°38’ N, 65°41’ W, 154 m, 14–X–1961, R/V *Delaware II*; MCZ 68420, 1, 33.9 mm, 37°40’ N, 66°50’ W, 100–105 m, 25–VIII–1967, R/V *Chain*; MCZ 163443, 1, 71.8 mm, 40°00’ N, 67°23’ W, 15–V–2005, R/V *Delaware*; MCZ 164169, 1, 79.2 mm, 39°54’ N, 67°30’ W, 0–1482 m, 6–VI–2004, R/V *Delaware II*; MCZ 164170, 1, 75.3 mm, 39°55’ N, 67°18’ W, 0–1082 m, 5–VI–2004, R/V *Delaware*

II; MCZ 164171, 1, 119.4 mm, 39°55’ N, 67°24’ W, 0–870 m, 5–VI–2004, R/V *Delaware II*. North Sargasso Sea: CAS–SU 66492, 1, 31.9 mm, Bermuda, 32°00’ N, 65°00’ W [coordinates inferred], 5–VIII–1931, W. Beebe & J. Tee-Van col.; LACM 56732–1, 1, 152.0 mm, 35°57’ N, 48°45’ W, 0–1400 m, no date, R/V *AtlantNIRO*; MCZ 49077, 1, 34.9 mm, 35°39’ N, 67°17’ W, 155–165 m, 26–VIII–1967, R/V *Chain*; MCZ 148307, 1, 170.2 mm, 32°13’ N, 63°53’ W, XII–1970, R/V *Trident*.

Pseudoscopelus australis: 29 specimens. South Atlantic Subtropical Sea: MZUSP 81802, 1, 38.0 mm, 31°11’ S, 51°17’ W, 1246 m, 23–IV–1997, R/V Atlântico Sul; MZUSP 92964, 9, 28.1–39.4 mm, 34°07’ S, 51°22’ W, 940 m, 23–IV–1997, R/V Atlântico Sul. Indian: LACM 11578, 1, 103.6 mm, 47°28’ S, 116°53’ E, 430 m, 18–IX–1968, R/V *Eltanin*; MCZ 60731, 1, 92.6 mm, 36°03’ S, 17°07’ E, 380–410 m, 30–IV–1971, R/V *Atlantis II*; NMV A 23564, 1, 154.3 mm, 35°25’ S, 118°21’ E, 932–953 m, 22–VII–2001, L. Brown col. Pacific, West Pacific: AMNH 215820, 1, 159.8 mm, 26°21’ S, 177°39’ E, 1020 m, 13–XII–1967, R/V *Eltanin*; CAS 91022, 1, 161.2 mm, 25°42’ S, 167°15’ E; 14–XI–1996,1068–1170 m, R/V *Tangaroa*; NMV A 4927, 1, 152.7 mm, 48°26’ S, 148°18’ E, 3–IV–1986, R/V *Soela*; NMV A 4928, 1, 136.9 mm, 47°53’ S, 148°24’ E, 22–III–1986, R/V *Soela*; NMV A 7093, 1, 105.2 mm, 47°42’ S, 148°10’ E, 22–III–1986, R/V *Soela*; NMNZ P. 4307, 1, 157.0 mm, 33º09’ S, 176º06’ E, 549–823 m, 23–VII–1962, RNZFA *Tui*. East Pacific: LACM 10665–6, 1, 108.8 mm, 59°25’ S, 78°27’ W, 2776 m, 23–XI–1963, R/V *Eltanin*; LACM 10621–4, 1, 99.5 mm, 59°52’ S, 82°50’ W, 549 m, 20–X–1963, R/V *Eltanin*; LACM 10837–4, 1, 113.7 mm, 59°37’ S, 89°06’ W, 476 m, 27–V–1964, R/V *Eltanin*; Pacific Plate: LACM 10862–3, 1, 142.9 mm, 51°50’ S, 159°50’ W, 4667 m, 3–VIII–1964,R/V *Eltanin*; LACM 10875–9, 1, 115.1 mm, 55°57’ S, 159°23’ W, 1080 m, 10–VIII–1964, R/V *Eltanin*; LACM 11579, 1, 88.8 mm, 49°44’ S, 100°19’ W, 530 m, 17–X–1966, R/V *Eltanin*; LACM 11221–15, 1, 100.8 mm, 47°08’ S, 167°37’ W, 775 m, 19–V–1966, R/V *Eltanin*; NMNZ P. 17574, 1, 77.4 mm, 42º50’ S, 175º37’ W, 1058 m, 20–VII–1985, F/V *Otago Buccaneer*; NMNZ P. 33792, 1, 165.4 mm, 43°07’ S, 174°16’ W, 844–938 m, 8–VIII–1996, R/V *Tangaroa*; NMNZ P. 40787, 1, 197.4 mm,43º03’ S, 174º04’ W, 1196 m, 17–VII–2004, R/V *Tangaroa*.

Pseudoscopelus bothrorrhinos: 13 specimens, including holotype and paratypes: Western Central Pacific: LACM 31495-1, 1 (paratype), 40.0 mm, 0°36’ S, 169°32’ E, 146 m, 26–XI–1966, R/V *Coriolis*; LACM 31502-1, 1 (paratype), 31.4 mm, collected with holotype; LACM 31502-2, 1 (holotype), 45.9 mm, 2°51' S, 169°55' E, 1000 m, 3–V–1967, R/V *Coriolis*; LACM 31507-1, 1 (paratype), 28.4 mm, 0°26' S, 169°45' E, 1200 m, 13–VI–1967, R/V *Coriolis*; LACM 31521-1, 2 (paratypes), 29.8–32.8 mm, 0°18' S, 169°57' E, 1200 m, 02–IX–1967, R/V *Coriolis*; LACM 31522-1, 1 (paratype), 31.7 mm, 0°35' S, 169°54' E, 1200, 02–IX–1967, R/V *Coriolis*; LACM 31524-1, 1 (paratype), 55.1 mm, 1°14' S, 169°49' E, 1200 m, 02–IX–1967, R/V *Coriolis*; LACM 36054-1, 1 (paratype), 38.3 mm, 4°49.5' S, 129°55' E, 650 m, 27–IV–1975, R/V *Alpha Helix*; LACM 36059-6, 1 (paratype), 27.9 mm, 4°49' S, 129°31' E, 550 m, 07–V–1975, R/V *Alpha Helix*; SIO 07-6 (former LACM 31494–1), 2 (paratypes), 36.6–39.6 mm, 0°36' S, 169°32' E, 146 m, 23–XI–1966, R/V *Coriolis*; LACM 56616-1, 1 (paratype), 38.1 mm, 1°42' S, 143°02' E, 0–200 m, 6–IV–1975, R/V *Vityaz*. Western Indian: LACM 33346-1, 1 (paratype), 48.7 mm, 12°06' S, 44°22' E, 900 m, 20–VIII–1964, *Te Vega 4*.

Pseudoscopelus lavenbergi: 30 specimens, including holotype and paratypes. Eastern Pacific: CAS 61407, 1 (paratype), 63.0 mm, 2°26' S, 88°46' W, 0–300 m, 27/28–V–1966, R/V *Anton Bruun*; LACM 30205-29, 1, 133.1 mm, 32°33.45' N, 118°10.08' W, 1812–1464m, 26–VII–1968, R/V *Velero IV*; LACM 30530-1, 1 (paratype), 166.6 mm, 32°19.75' N, 117°49.11' W, 27–I–1968, R/V *Velero IV*; LACM 30074-8, 1 (paratype), 102.7 mm, 28°48' N, 114°28.48' W, 11–IV–1968, R/V *Velero IV*; LACM 30379-2, 1 (paratype), 91.4 mm, 26°00.66' N, 114°10' W, 24–VI–1968, R/V *Velero IV*; LACM 30573-1, 2 (paratypes), 86.3–97.6 mm, 22°30' N, 110°00' W [inferred], 1324–1624 m, 23–VI–1968, R/V *Velero IV*; LACM 31793-1, 1 (paratype), 143.9mm, 32°40' N, 118°20' W [inferred], 29–VII–1969, R/V *Velero IV*; LACM 33334–1, 1, 39.9 mm, probably off Southern California or Baja California, 13–V–1966; LACM 33335-1, 1 (paratype), 82.2 mm, 1°48' S, 90°19' W, 400 m, 26–V–1966; LACM 33336-1, 1 (paratype), 76.5 mm, 24°55' N, 114°12' W, 29/30–III–1962; LACM 33337-1, 1, 60.4 mm, Gulf of California; LACM 33339–1, 1, 181.8 mm, California, 0.3 miles 183°T from West End Light, Santa Catalina Island, 27–VIII–1970, R/V *Velero*; LACM 33340-1, 1 (paratype), 45.3mm, 2°59' S, 88°11' W, 2300–3000 m, *Te Vega* Expedition, 25–IX–1968; SIO 56-109-60A, 1 (paratype), 30.2 mm, 1°57.5' N, 110°39.0' W, M/V *N.B. Scofield*; LACM 56617-1, 1, 84.8 mm, 23°52' S, 71°08' W, 0–200 m, 23–IX–1968, R/V *Akademik Kurchatov*; LACM

56618-1, 1, 173.6 mm, 0°00', 85°00' W, 0–1500 m, 29–VII–1968, R/V *Akademik Kurchatov*; SIO 71-358, 1 (holotype), 73.0 mm, 1°21.0' N, 086°36.0' W, 21–III–1967, R/V *Alaminos*; SIO 75-316, 1 (paratype), 73.0, 6°03.1' N, 117°46.0' W, 30–I–1973, R/V *David Starr Jordan*; SIO 92-9, 1 (paratype), 54.9 mm, 8°05.0' N, 95°02.0' W, 21–IX–1967, R/V *Rockaway*; SIO 93-22, 1 (paratype), 67.7 mm, 19°2.5' N, 105°40.5' W, 14–IX–1967, R/V *Thomas Washington*; SIO 63-165, 1, 159.9 mm, 28°53.0' N, 118°08.4' W, 21–IV–1963, 0–750 m, R/V *Horizon*; SIO 95-83, 1 (paratype), 70.4 mm, 8°36' N, 111°32' W, 5–I–1968, R/V *David Starr Jordan*; SIO 95-131, 1, 36.4 mm, 3°11.5' N, 119°21.0' W, 26–X–1967, R/V *David Starr Jordan*; SIO 97-203, 1 (paratype), 81.6 mm, 20°00' N, 129°00' W, 27–V–1973, R/V *David Starr Jordan*; SIO 69-330, 1, 34.2 mm, 14°46.0' S, 93°32.5' W, 18–III–1969. Central Pacific: LACM 30042-10, 1, ca. 80.0 mm, 21°20.5' N, 158°20.5' W, 600–650 m, 9–X–1970, R/V *El Pescadero II*; USNM 289000, 1 (paratype), 47.4 mm, 10°58' N, 150°00' W, 950 m, 14–I–1978, R/V *Kana Keori*; USNM 289002, 1 (paratype), 44.5 mm, 10°10' N, 150°00' W, 710 m, 30–V–1979, R/V *Gyre*; UW 116439 (former SIO 60-243), 1 (paratype), 44.7 mm, 10°22.3' N, 147°18.8' W, 0–2100 m, 8/9–VII–1960, *Tethys* Expedition.

Pseudoscopelus cephalus: one specimen, including holotype. Pacific, Indo-West Pacific: USNM 93142, 1 (holotype) 74.5 mm, 9°38' N, 121°11' E, 0–508 fathoms (0–924 m), 31–III–1909, R/V *Albatross* col.

Pseudoscopelus parini: 10 specimens, holotype examined via pictures. Pacific, West Pacific: LACM 56622–1, 1, 69.1 mm, 7°38' S, 150°20' E, 0–1000 m, 12–I–1977, R/V *Dmitry Mendeleev*; USNM 288990, 1, 37.7 mm, 8°16' S, 150°00' E, 0–1000 m, 16–VII–1987, R/V *Gyre*. Pacific Plate: LACM 44401–1, 1, 57.8 mm, 21°20' N, 158°10' W, 0–310 m, 26–X–1978, R/V *Kana Keoki*; LACM 44392–1, 1, 82.9 mm, 21°20' N, 158°10' W, 0–310 m, 10–VIII–1977, R/V *Kana Keoki*; LACM 44394–1, 1, 33.1 mm, 21°20' N, 158°10' W, 2–III–1978, 2146–2347 m, R/V *Kana Keoki*; LACM 44399–1, 1, 80.4 mm, 21°20' N, 158°10' W, 0–310 m, 28–IX–1978, R/V *Kana Keoki*; USNM 288990, 1, 37.7, 8°16' S, 150°02' W, 0–1000 m, 6–VI–1979, R/V *Gyre*; SIO 68–442, 1, 42.0 mm, 19°48' N, 168°46' W, 0–1250 m, 27–VIII–1968, R/V *Alexander Agassiz*; SIO 72–321, 1, 92.4 mm, 19°10' S, 150°10' W, 0–1215 m, 8–VIII–1972, R/V *Melville*; NMNZ P. 24463, 1, 100.8 mm, 25°21' S, 175°08' W, 591–613 m, 13–X–1976, R/V

James Coock.

Pseudoscopelus pierbartus: 27 specimens, holotype examined via pictures. Atlantic, Slope Water: MCZ 164762, 1, 94.1 mm, 39º50' N, 67º19' E, 0–1360 m, 17–IV–2005, R/V *Delaware II*. North Sargasso Sea: LACM 56615–1, 1, 133.4 mm, 35º29' N, 54º54W, 5–V–1977, R/V *AtlantNIRO*; LACM 56619–1, 2, 69.9–82.4 mm, 34º47' N, 50º25' W, VI–1977, R/V *AtlantNIRO*; MCZ 164590, 1, 77.5 mm, 27°57' N, 65°34' W, 0–1077 m, 6–XI–1965, R/V *Trident*; USNM 240687, 1, 87.1 mm, 32º13' N, 64º60' W, 0–950 m, R/V *Delaware*, 24–VIII–1971; USNM 240676, 1, 47.1 mm, 32º08' N, 063º55' W, 0–660 m, 21–VIII–1971, R/V *Delaware*. South Atlantic Subtropical Sea: MNRJ 26698, 1, 86.8 mm, 19º43' S, 38º39' W, 895–1004 m, 27–VI–2000, R/V *Thalassa*. Azores – Britain Province: ZMUB 16378, 1, 179.8 mm, 42º48' N, 27º52' W, 829–1770 m, 27–VI–2004; R/V *G.O.* Juveniles, tentative identification. Atlantic, North Sargasso Sea: USNM 240674, 3, 32.7–35.4 mm, 32º11' N, 064º10' W, 0–150 m, R/V *Delaware*; USNM 240677, 2, 28.2–30.4 mm, 32º13' N, 064º22' W, 0–1025 m, 24–VIII–1971, R/V *Delaware*; USNM 240678, 1, 25.1 mm, 32º10' N, 063º47' W, 0–150 m, 21–VIII–1971, R/V *Delaware*; USNM 240679, 1, 26.8 mm, 32º00' N, 063º58' W, 0–50 m, 23–VIII–1971, R/V *Delaware*; USNM 240682, 3, 36.2–37.3 mm, 32º10' N, 063º53' W, 0–760 m, 21–VIII–1971, R/V *Delaware*; USNM 240683, 3, 22.5–39.8 mm, 32º25' N, 064º14' W, 0–760 m, 23–VIII–1971, R/V *Delaware*; USNM 240684, 1, 35.9 mm, 32º26' N, 064º07' W, 0–760 m, 23–VIII–1971, R/V *Delaware*; USNM 240685, 2, 22.9–32.4 mm, 32º14' N, 064º14' W, 0–150 m, 24–VIII–1971, R/V *Delaware*; USNM 240686, 2, 33.1–34.1 mm, 32º11' N, 064º00' W, 0–780 m, 24–VIII–1971, R/V *Delaware*.

Pseudoscopelus sagamianus: 23 specimens, including holotype. Indian: BMNH 1984.1.1.93, 3, 97.8–111.5 mm, 8º43' S, 114º15' E, R/V *Jurong*; BMNH 1984.1.1.94, 1, 111.5 mm, 8º33' S, 114º37' E, R/V *Jurong*. Pacific, West Pacific: CAS–SU 25626, 1, 120.4 mm, 34º00' N, 135º00' E [coordinates inferred], Alan Owston col., 26–XI–1906; CAS–SU 64331, 1, 119.1 mm, 35º00' N, 139º30' E, [coordinates inferred], 18–IV–1925, A. Owston col.; FMNH 55551, 1 (holotype), 143.5 mm, 35º00' N, 139º30' E, [coordinates inferred], no date, D.S. Jordan col. [sic]; NMNZ P. 26211, 1, 138.5 mm, 39º49' S, 178º23' E, 1060–1200 m, 6–X–1990, R/V *Cordella*. Pacific Plate: CAS 224350, 1, 57.5 mm, 21º10' N, 157º45' W [coordinates inferred], 14–XI–1972, R.K.

Johnson col.; LACM 31452-1, 1, 34.7 mm, 1–I–1968, 0º05' S, 147º28' W, R/V Caride I; LACM 32747-4, 1, 60.8 mm, 21º20' N 158º20' W, 950–1000, 16–X–1970, R/V El Pescadero II; LACM 32776-3, 1, 57.7 mm, 6–VII1970, 21º20' N, 158º20' W, 0–925m, col. unknown; LACM 32782-3, 1, 61.9 mm, 15–IX–1970, 21º20' N, 158º20' W, 0–1000 m, R/V El Pescadero I; LACM 32787-2, 1, 63.1 mm, 16–IX–1970, 21º20' N 158º20' W, 0–190, R/V El Pescadero I; LACM 32794-2, 1, 37.5 mm, 23–IX–1970, 21º20' N, 158º20' W, 0–775, R/V El Pescadero; LACM 32799-2, 1, 43.3 mm, 14–X–1970, 21º20' N, 158º20' W, 790–810 m, R/V El Pescadero II; LACM 33324-2, 1, 27.7 mm, 10–VI–1971, 21º00' N, 158º20' W, R/V El Pescadero IV; LACM 33341-1, 1, 51.4 mm, 9–VII–1970, 21º20' N, 158º20' W, col. unknown; LACM 33342-1, 1, 43.2 mm, 9–X–1970, 21º20' N, 158º20' W, R/V El Pescadero II; LACM 33343-1, 1, 47.6 mm, 15–IX–1970, 21º20' N, 158º20' W, 0–1000 m, R/V El Pescadero I; LACM 44400-1, 1, 35.8 mm, 25–X–1978, 21º20' N, 158º10' W, 0–310 m, R/V Kana Keoki; SIO 73-42, 1, 89.4 mm, 16°06' S, 132°16' W, 0–2000 m, R/V Thomas Washington; USNM 289005, 1, 39.6, 1º00' N, 153º00' W, 0–330 m, 3–VII–1979, R/V *Gyre*.

Pseudoscopelus scriptus: 20 specimens, including holotype: Atlantic, Slope Water: MCZ 68449, 1, 55.0 mm, 37º32' N, 69º32' W, R/V *Delaware*; MCZ 138069, 1, 51.9 mm, 39º05' N, 72º27' W, 992–1098 m, 16–IX–1995, R/V *Contender 08*; MCZ 162235, 1, 44.4 mm, 40°4' N, 68°5' W, 0–930 m, 19–VII–2002, R/V *Delaware*. North Sargasso Sea: LACM 56625–1, 1, 203.5 mm, 35º N, 50º W, AtlantNIRO col.; LACM 56626–1, 1, 166.9 mm, 35º29' N, 51º54' W, 900 m, 8–VIII–1978, AtlantNIRO col.; LACM 56627–1, 1, 137.8 mm, 35º29' N, 51º50' W, 10–IX–1977, AtlantNIRO col.; LACM 56628–1, 2, 104.9–151.8 mm, 34º47' N, 51º25' W, 12–VI–1977, AtlantNIRO col.; LACM 56629–1, 1, 159.27 mm, 34º47' N, 51º25' W, 10–VI–1977, AtlantNIRO col.; UF 216555, 1, 31.1 mm; 28º50' N, 73º20' W, 550 m, 7–VIII–1964; R/V *Phillsbury*; UF 228876, 1, 76.1 mm, 28º13' N, 76º31' W, 15–X–1969, Charbonneaux col.; USNM 240671, 1, 104.4 mm, 32º09' N, 63º45' W, 0–250 m, 07–IX–1969, R/V *Delaware*; USNM 240688, 1, 115.2 mm, 32º09' N, 64º11' W, 0–750 m, 24–VIII–1971, R/V *Delaware*; MCZ 43252, 4, 69.0–85.1 mm, from stomach of *Thunnus albacores*, 29º42' N, 77º12' W, 19–X–1957, R/V *Delaware*; South Sargasso Sea: MCZ 101790, 1, 44.8 mm, 10º46' N, 49º01' W, 29–VII–1983, R/V *Columbus Iselin*; Straits of Florida: MCZ

68450, 2, 72.4–83.2 mm, from stomach of blue marlin, 23º00' N, 74º39' W; YPM 2740, 1, 56.3 mm, 21º44' N, 72º43' W, R/V *Pawnee*; ZMUC P. 65171, 1 (holotype), 70.0 mm, Mouth of Old Bahamas Channel, 23º30' N 77º45' W [coordinates inferred], ?–1966. Caribbean Sea: MCZ 45060, 2, 69.7–100.8 mm, Puerto Rico, off La Parguera, 17º30' N, 67º00' W [coordinates inferred], 8–VI–1958, D.S. Erdman col.; MCZ 47850, 1, 86.6 mm, 17º N, 71º W, II–1960, R/V *Chain*. Lesser Antilles Province: MCZ 68385, 1, 63.1 mm, 16º30' N, 49º04' W, 0–650 m, 11–X–1973, R/V *Atlantis*. Amazonian Province: MCZ 160938, 1, 36.5 mm, 3º58' N, 31º33' W, 175–190 m, 17–III–1977, R/V *Oceanus*. South Atlantic Subtropical Sea: MNRJ 26697, 1, 73.0 mm, 21º46' S, 39º53' W, 1081–1141 m, 6–VII–2000, R/V *Thalassa*; MNRJ 26699, 1, 73.2 mm, 21º26' S, 39º49' W, 1594–1614 m, 7–VII–2000, R/V *Thalassa*. Guinean Province: MCZ 161016, 1, 95.1 mm, 10º00' N, 30º00' W, 0–1370 m, 24–V–1965, R/V *trident*. Juvenile (tentative identification). Atlantic, North Sargasso Sea: USNM 240681, 1, 39.2 mm, 32º08' N, 63º59' W, 22–VI–1971, R/V *Delaware*. Amazonian: MCZ 68463, 1, 31.0 mm, 0º13' N, 35º44' W, 90–100 m, 15–III–1977, R/V *Oceanus*; MCZ 101790, 1, 44.8 mm, 10º46' N, 49º01' W, 29–VII–1983, R/V *Columbus Iselin*. Guinean Province: UF 19987, 1, 31.8 mm, 5º56' N, 4º03' E, 590 m, 11–V–1965, R/V *Pillsbury*.

Pseudoscopelus scutatus: 49 specimens, including several paratypes.: Atlantic, Slope Water: MCZ 45180, 1, 52.8 mm, 40°25' N, 66°45' W, 9–VII–1978, R/V *Delaware*. North Sargasso Sea: MCZ 68418, 1, 76.8 mm, 32°25' N, 60°0' W, 0–400 m, 16–3–1974, R/V *Knorr;* UF 216154, 1, 41.8 mm, 32°41' N, 64°38' W, 900–1300 m, 4–VIII–1964, R/V *Pillsbury*; USNM 236773, 1, 82.9 mm, 32°09' N, 64°11' W, 0–750 m, 24–VIII–1971, R/V *Delaware*; USNM 236774, 1, 54.6 mm, 32°26' N, 64°07' W, 0–760 m, 23–VIII–1971, R/V *Delaware*; USNM 236775, 1, 70.0 mm, 32°10' N, 63°53' W, 0–760 m, 21–VIII–1978, R/V *Delaware*; USNM 236776, 1, 70.0 mm, 32°10' N, 63°53' W, 0–760 m, 21–VIII–1978, R/V *Delaware*. South Sargasso Sea: MCZ 73014, 1, 30.5 mm, 23°24' N, 67°30' W, 130–0140, 23°24' N, 67°30' W, R/V *Chain*. Straits of Florida: MCZ 60851, 1, ca. 55.0 mm, 26°42' N, 79°35' W, 150–200 m, 18–2–1979, R/V *Oceanus*; MCZ 68439, 1, 59.1 mm, 26°42' N, 79°35' W, 0–680 m, 18–2–1979, R/V *Oceanus*; MCZ 49089, 1, 67.1 mm, 23°55' N, 83°12' W, 130– 145 m, 25–6–1966, R/V *Chain*; Caribbean Sea: LACM 56624–1, 1, 52.8 mm, 19º53' N, 65º14' W, 0–1500 m, 30–I–1973, R/V *Akademik Kurchatov*; MCZ 42288, 1, 71.0 mm, 15°59’ S, 110°19’ W, 400–600 m, 3–V–1962, R/V *Chain*; MCZ 49088, 1, 71.2 mm, 15°59’ N, 64°58’ W, 400–600 m, 3–5–1962, R/V *Chain*. Lesser Antillean Province: MCZ 68416, 1, 39.5 mm, 13°29’ N, 52°57’ W, 0–450 m, 8–10–1973, R/V *Atlantis II*. Amazonian: ZMH 25242 (fomer ISH 567b–c/1966), 2 (paratypes), 80.4–57.0 mm, 2°44’ N, 25°12’ W, 175–380 m, 18–V–1966, R/V *Walter Herwig*; ZMH 25243 (former ISH 647a–d/1966), 4 (paratypes), 65.6–85.8 mm, 5°34’ N, 26°58’ W, 160–320 m, 20–V–1966, R/V *Walter Herwig*; MCZ 68462, 4, 29.98–75.8 mm, 0°53’ N, 38°59’ W, 120–130 m, 14–3–1977, R/V *Oceanus*; MCZ 73015, 3, 29.6–31.5 mm, 0°53’ N, 38°59’ W, 120–130 m, 14–3–1977, R/V *Oceanus*. South Atlantic Subtropical Province: MNRJ 26700, 1, 91.0 mm, 21º25’ S, 39º43’ W, 1712–1721 m, 7–VII–2000, R/V *Thalassa*. North Mauritanian Upwelling: MCZ 96854, 2, 48.6–53.1 mm, 20°19’ N, 17°58’ W, 6–IX–1978, R/V *Oceanus*. Guinean Province: ZMH 25244 (former ISH 687a–b/1966), 2, 86.5–86.7 mm, 9°41’ N, 27°39’ W, 160–400 m, 21–V–1966, R/V *Walter Herwig*; MCZ 41380, 1, 31.7 mm, 0°15’ S, 18°40’ W, 85 m, 26–4–1961, R/V *Chain*. Indian: ZMH 5322 (former ISH 5322), 1, North of Seychellen, 2°00’ N, 55°00’ W [coordinates inferred]. Pacific, Pacific Plate: LACM 31445–1, 1, 45.8 mm, 0°05’ N, 144°22’ W, 28–Sep–1968, R/V *Caride I*; LACM 31468–1, 1, 44.7 mm, 0°03’ S, 140°18’ W, 19–Feb–1969, R/V *Caride III*; LACM 31474–1, 1, 38.3 mm, 22°00’ N, 158°00’ W, 600–625 m, 13–Nov–1969, R/V *Vanilla Fudge*; LACM 32801–2, 1, 42.1 mm, 21°20’ N, 158°20’ W, 0–690 m, 15–Dec–1970, R/V *El Pescadero II*; LACM 33376–1, 1, 63.0 mm, 3°03’ N, 145°00’ W, 0–500 m, 7–Feb–1970, col. unknown; LACM 33377–1, 1, 41.2 mm, 21°20’ N, 158°20’ W, 0–175 m, 1–Mar–1971, R/V *Townsend Cromwell*; LACM 33382–1, 1, 55.0 mm, 21°20’ N, 158°20’ W, 16–17–IX–1970, R/V *El Pescadero I*; LACM 33383–1, 1, 35.7 mm, 21°20’ N, 158°20’ W, 18–Sep–1971, R/V *Luna I*; SIO 68–537, 1, 28.4 mm, 14°59’ N, 160°19’ W, 16–VIII–1968, R/V *Alexander Agassiz*; SIO 69–342, 1, 84.7 mm, 17°49’ S, 110°19’ W, 0–1100 m, 15–III–1969, R/V *Thomas Washington*; SIO 70–308, 1, 90.6 mm, 29°47’ N, 137°15’ E, 0–1350 m, 30–VIII–1970, R/V *Melville*; USNM 272499, 1, 75.6 mm, 6°08’ N, 153°06’ W, 0–300 m, 26–V–1979, R/V Gyre; USNM 272504, 1, 65.1 mm, 6°07’ N, 153°05’ W, 0–320 m, 30–VIII–1979, R/V *Wecoma*; USNM 296645, 1, 39.5 mm, 4°28’ S, 150°10’ W, 0–555 m, 7–XII–1977, R/V *Kana Keoki*.

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TABLE 4.1. Meristic data for *Pseudoscopelus scriptus* (n=11) and *P. sagamianus* (n=9). H stands for holotype.

Character	*P. scriptus*			*P. sagamianus*		
	H	**Range**	**Mode**	**H**	**Range**	**Mode**
First dorsal-fin rays	VIII	VIII–IX	VIII	VIII	VII–IX	VIII
Second dorsal-fin rays	ii, 21	ii, 19–21	ii, 21	ii, 19	ii–iii, 19–21	ii, 20
Anal-fin rays	iii, 20	iii, 19–21	iii, 20	iii, 19	iii, 19–21	iii, 19
Pectoral-fin rays	13	12–14	13	14	13–14	14
Pelvic-fin rays	I, 5	I, 5	I, 5	I, 5	I, 5	I, 5
Caudal-fin rays	i, 7, 8, i	i, 7–8, 8, i	i, 7, 8, i	i, 7, 8, i	i, 7–8, 8, i	i, 7, 8, i
Branchiostegal rays	7	7	7	7	7	7
Sensorial Pores						
Lateral line	75	74–78	77	74	73–77	76
Temporal	2	2	2	2	2	2
Supratemporal	3	3	3	3	2–3	3
Otic	2	2	2	2	2	2
Supraorbital	5	5	5	5	5	5
Supranasal pore	2	1–2	2	2	2	2
Epiphyseal branch	2	2–3	3	3	2–3	2
Infraorbital	11	11–12	11	11	11–12	11
Preopercular	5	5	5	5	5	5
Mandibular	6	6	6	6	6	6
Fifth mandibular pore	2	2	2	2	2	2
Gill Rakers and Dentition						
Epibranchial	0	0	0	0	0	0
Ceratobranchial	11	7–11	11	11	11–18	12
Hypobranchial	7	2–7	4	8	4–18	7
Basihyal	0	0	0	0	0	0
First basibranchial	11	5–11	10	9	5–10	9
Teeth on palatine	7	3–7	7	5	5–8	5
Osteology						
Total vertebrae	–	35–36 (n=8)	36	–	36 (n=6)	36
Pre-caudal vertebrae	–	18–19 (n=8)	18	–	18 (n=6)	18

TABLE 4.2. Morphometric data for *Pseudoscopelus scriptus* (n=11) and *P. sagamianus* (n=9). H stands for holotype and SD, standard deviation.

Character	*P. scriptus*				*P. sagamianus*			
	H	**Range**	**Mean**	**SD**	**H**	**Range**	**Mean**	**SD**
Standard length (mm)	70.0	36.0–115.2	73.3	23.3	143.2	57.6–143.3	109.2	26.4
Head length (mm)	21.4	15.7–36.2	6.7	7.2	45.6	18.2–45.6	35.1	8.4
Proportions of HL								
Snout	23.4	22.6–27.3	25.0	1.6	25.7	22.0–26.6	25.1	1.3
Upper jaw	72.9	70.9–77.5	74.0	2.4	74.0	73.6–79.8	75.4	2.2
Lower jaw	76.8	76.8–83.6	79.8	2.4	79.1	78.4–84.0	80.6	1.9
Orbit width	18.1	16.2–23.6	19.5	1.8	17.6	15.6–20.5	18.2	1.6
Orbit height	17.3	14.5–19.8	16.7	1.7	16.6	15.0–17.9	16.5	0.9
Anterior nostril to eye	10.7	10.7–13.7	11.8	0.9	13.4	10.6–14.0	12.5	1.0
Posterior nostril to eye	4.9	4.4–7.4	5.8	0.9	6.0	5.6–7.8	6.4	0.7
Distance between nostrils	5.5	5.3–8.3	6.1	1.0	7.1	4.1–7.1	5.5	1.0
Interorbital distance	21.6	21.6–30.3	24.8	2.3	21.9	19.2–23.0	21.2	1.3
Head width	34.1	33.0–37.5	35.4	1.3	32.8	31.3–35.7	33.2	1.4
Cheek depth	8.0	6.5–9.0	7.7	1.0	9.0	5.4–9.0	7.5	1.2
Proportions of SL								
Head length	30.6	28.6–32.7	31.0	1.2	31.8	31.5–33.4	32.1	0.7
Body width	12.7	6.8–12.7	9.4	1.6	8.4	5.1–11.9	8.5	1.9
Insertion of pectoral fin	30.7	30.2–36.1	32.5	1.7	33.1	32.0–36.4	33.9	1.3
Insertion of pelvic fin	32.8	29.0–38.6	33.7	2.7	34.6	32.7–37.3	34.9	1.5
Pectoral-fin length	21.9	20.3–34.7	27.7	5.3	31.2	17.4–33.4	29.0	4.7
Pelvic-fin length	7.3	7.3–11.9	10.7	1.2	11.6	7.7–13.0	11.2	1.5
Origin of first dorsal fin	38.5	36.4–40.3	38.1	1.2	39.2	36.6–39.2	37.7	1.0
Base of first dorsal fin	12.7	11.7–14.6	13.1	0.9	52.6	11.9–14.4	13.2	1.1
First dorsal-fin depth	11.2	7.8–11.9	10.7	1.4	14.4	11.3–15.2	13.0	4.8
Origin of second dorsal fin	54.0	52.4–56.8	54.3	1.6	14.2	53.6–55.4	54.7	0.5
Base of second dorsal fin	36.7	35.6–38.3	37.0	0.9	54.9	36.0–40.1	37.7	1.3
Second dorsal-fin depth	15.0	15.0–19.9	17.0	2.0	89.3	15.7–22.7	19.8	2.4
Origin of anal fin	51.8	49.8–56.4	53.5	2.1	37.5	51.4–57.5	55.3	2.0
Base of anal fin	34.4	34.4–37.8	35.5	1.2	19.2	32.9–37.5	35.0	1.4

TABLE 4.2. (cont.)

Anal-fin depth	17.2	15.9–19.6	17.8	1.2	55.9	13.0–20.5	17.6	2.8
Peduncle depth	6.7	5.6–6.9	6.4	0.4	88.6	4.4–7.1	6.1	0.9
Peduncle length	13.2	10.4–13.2	11.8	0.9	34.6	9.3–13.3	11.3	1.3

TABLE 4.3. Meristic data for *Pseudoscopelus cephalus* (n=1), *P. obtusifrons* (n=12), and *P. pierbartus* (n=7). H stands for holotype; asterisk for destroyed parts.

Character	*P. cephalus*	*P. obtusifrons*			*P. pierbartus*	
	H	**H**	**Range**	**Mode**	**Range**	**Mode**
First dorsal-fin rays	VIII	VII	II–IX	VIII	VII–IX	VII
Second dorsal-fin rays	ii, 20	iii, 19	ii–iii, 17–21	ii, 21	ii, 18–22	ii, 19
Anal-fin rays	iii, 19	iii, 18	ii–iv, 17–20	iii, 20	ii–iii, 17–20	iii, 19
Pectoral-fin rays	14	13	12–13	13	13–14	13
Pelvic-fin rays	I, 5	I, 5	I, 5	I, 5	I, 5	I, 5
Caudal-fin rays	i, 7, 8, i	i, 7, 7, i	i, 7, 8–7, i	i, 7, 8, i	i, 7, 8, i	i, 7, 8, i
Branchiostegal rays	7	7	7	7	7	7
Sensorial Pores						
Lateral line	*	ca. 70	57–74	69	72–77	74
Temporal	*	2	2	2	2	2
Supratemporal	3	3	3	3	3	3
Otic	2	2	2	2	2	2
Supraorbital	6	5	5	5	5	5
Supranasal pore	2	1	1	1	1–2	2
Epiphyseal branch	3	2	2	2	2–3	2
Infraorbital	11*	11	11	11	11–13	11
Preopercular	5	5	5	5	5	5
Mandibular	6	6	6	6	6	6
Fifth mandibular pore	2	1	1–2	1	2	2
Gill Rakers and Dentition						
Epibranchial	0	0	0	0	0	0
Ceratobranchial	13	6	3–15	11	8–15	11
Hypobranchial	8	3	3–9	5	2–13	6
Basihyal	0	0	0	0	0	0
First basibranchial	6	*	0–9	6	8–16	9
Teeth on palatine	7	5	3–8	5, 6	7–10	7

TABLE 4.3. (cont.)

Osteology						
Total vertebrae	31 (n=1)	36	35–37 (n=13)	36	35–36 (n=8)	36
Pre-caudal vertebrae	14 (n=1)	17	16–18	17	18–19 (n=7)	18

TABLE 4.4. Frequency of lateral line pores of *Pseudoscopelus obtusifrons*, specimens as listed in Table 3. Asterisk (*) indicates data for Holotype. Specimens as listed in Table 3.

# pores	52	57	60	62	63	65	67	69	70*	74
Frequency	1	1	1	1	1	1	1	2	1	2

TABLE 4.5. Morphometric data for *Pseudoscopelus obtusifrons* (n=12) and *P. pierbartus* (n=7). H stands for holotype and SD, standard deviation.

Character	*P. obtusifrons*				*P. pierbartus*		
	H	Range	Mean	SD	Range	Mean	SD
Standard length (mm)	93.2	33.0–144.9	84.6	37.6	47.0–179.9	93.4	41.1
Head length (mm)	26.9	10.3–39.5	24.6	10.2	13.8–51.7	27.9	11.6
Proportions of HL							
Snout	23.4	21.2–27.4	24.3	1.9	22.2–25.8	24.1	1.5
Upper jaw	67.5	65.0–76.1	70.6	3.2	73.0–79.6	77.0	2.6
Lower jaw	72.3	69.2–91.0	75.0	3.3	79.3–83.8	81.7	2.0
Orbit width	19.0	15.8–25.1	20.2	3.2	14.2–20.0	17.7	2.0
Orbit height	15.2	12.2–20.3	17.3	2.5	13.6–18.5	15.7	1.7
Anterior nostril to eye	14.3	10.2–15.8	13.1	1.6	10.7–14.0	12.3	1.0
Posterior nostril to eye	6.5	4.4–8.5	6.4	1.3	5.4–7.4	6.6	0.7
Distance between nostrils	9.4	5.2–9.4	7.2	1.2	5.3–6.8	5.9	0.5
Interorbital distance	28.1	28.1–34.1	30.6	2.2	21.5–27.6	25.2	2.1
Head width	40.7	37.5–43.1	40.6	2.0	34.7–38.3	37.0	1.2
Cheek depth	6.7	6.2–13.0	8.6	2.0	6.6–10.7	8.8	1.5
Proportions of SL							
Head length	28.9	25.9–32.8	29.6	1.8	28.8–30.9	29.9	0.8
Body width	7.8	6.8–16.3	10.8	2.7	37.4–41.1	38.4	1.3
Insertion of pectoral fin	27.7	26.1–33.5	30.4	2.2	15.2–20.4	18.0	2.2
Insertion of pelvic fin	27.0	27.0–36.7	32.8	2.7	48.8–57.1	53.4	3.0
Pectoral-fin length	20.3	19.0–27.4	23.5	3.2	19.5–34.0	29.3	4.9
Pelvic-fin length	9.1	8.7–11.8	10.1	0.9	9.7–12.5	11.4	1.0
Origin of first dorsal fin	37.2	34.4–41.7	37.7	2.1	35.9–40.2	38.2	1.7
Base of first dorsal fin	13.2	2.4–15.8	11.6	3.3	9.6–15.2	12.6	1.8
First dorsal-fin depth	*	8.9–14.3	11.1	1.9	8.9–13.5	11.9	1.8
Origin of second dorsal fin	52.5	49.7–57.1	53.1	2.1	51.8–56.9	53.7	1.7
Base of second dorsal fin	37.6	36.0–39.8	37.7	1.2	37.4–41.1	38.4	1.3
Second dorsal-fin depth	16.3	15.0–20.5	17.6	1.7	15.2–20.4	18.0	2.2
Origin of anal fin	52.8	49.3–61.0	53.6	3.4	48.8–57.1	53.4	3.0
Base of anal fin	37.4	32.3–37.7	35.9	1.7	32.8–38.3	35.6	1.9

TABLE 4.5. (cont.)

Anal-fin depth	15.7	15.7–19.7	17.3	1.3	14.8–18.9	16.9	1.9
Peduncle depth	6.1	5.1–7.6	6.2	0.7	5.8–6.8	6.2	0.4
Peduncle length	13.7	11.8–15.0	13.2	1.0	11.3–12.6	12.0	0.5

TABLE 4.6. Meristic data for *Pseudoscopelus cordilluminatus* (n=5). H stands for holotype.

Character	***P. cordilluminatus***		
	H	**Range**	**Mode**
First dorsal-fin rays	VIII	VII–VIII	VIII
Second dorsal-fin rays	ii, 20	ii, 20–21	ii, 20
Anal-fin rays	iii, 20	ii–iii, 18–20	iii, 20
Pectoral-fin rays	12	12–13	12
Pelvic-fin rays	I, 5	I, 5	I, 5
Caudal-fin rays	i, 8, 7, i	i, 7–8, 7–8, i	i, 7, 8, i
Branchiostegal rays	7	6–7	7
Sensorial Pores			
Lateral line	75	75–76	75
Temporal	2	2	2
Supratemporal	3	3	3
Otic	2	2	2
Supraorbital	5	5–6	5
Supranasal pore	2	2	2
Epiphyseal branch	2	2–3	2
Infraorbital	11	11	11
Preopercular	5	5	5
Mandibular	6	6	6
Fifth mandibular pore	2	1–2	2
Gill Rakers and Dentition			
Epibranchial	0	0	0
Ceratobranchial	8	6–9	8
Hypobranchial	7	3–8	3, 5, 6, 7, 8
Basihyal	0	0	0
First basibranchial	9	5–10	5, 6, 7, 9, 10
Teeth on palatine	16	8–16	9
Osteology			
Total vertebra e	36	36 (n=3)	36
Pre-caudal vertebrae	17	17–18 (n=3)	18

TABLE 4.7. Morphometric data for *Pseudoscopelus cordilluminatus* (n=5). H stands for holotype and SD, standard deviation.

Character	*P. cordilluminatus*			
	H	**Range**	**Mean**	**SD**
Standard length (mm)	77.0	44.8–97.3	79.0	20.4
Head length (mm)	24.1	13.6–30.4	24.1	6.3
Proportions of HL				
Snout	26.1	25.1–27.4	25.8	1.0
Upper jaw	77.9	70.2–80.4	74.3	4.3
Lower jaw	78.4	73.1–81.6	76.9	3.4
Orbit width	23.6	19.2–23.6	21.6	1.7
Orbit height	20.1	15.3–21.2	18.2	2.4
Anterior nostril to eye	13.1	12.0–14.5	13.1	1.1
Posterior nostril to eye	6.1	5.4–8.3	6.8	1.1
Distance between nostrils	6.3	5.9–8.1	6.8	0.9
Interorbital distance	24.5	23.3–24.6	24.0	0.6
Head width	35.1	34.6–38.4	36.9	1.9
Cheek depth	5.8	5.8–8.5	7.9	1.2
Proportions of SL				
Head length	31.3	28.7–31.3	30.5	1.1
Body width	8.5	7.9–14.0	10.3	2.4
Insertion of pectoral fin	31.8	31.1–33.0	32.1	0.7
Insertion of pelvic fin	33.2	33.2–36.4	34.2	1.3
Pectoral-fin length	27.4	22.5–29.5	26.4	2.9
Pelvic-fin length	11.8	10.5–11.8	11.2	0.6
Origin of first dorsal fin	39.0	36.0–39.0	37.2	1.5
Base of first dorsal fin	12.4	12.4–15.3	13.7	1.1
First dorsal-fin depth	11.5	11.2–14.1	12.3	1.3
Origin of second dorsal fin	54.4	52.4–56.6	54.3	1.5
Base of second dorsal fin	37.1	35.1–37.5	36.7	0.9
Second dorsal-fin depth	19.5	14.3–19.5	17.1	2.3
Origin of anal fin	55.0	54.1–59.0	56.4	2.0
Base of anal fin	34.3	34.5–37.5	35.3	1.4

TABLE 4.7. (cont.)

Anal-fin depth	15.2	15.2–17.4	15.9	1.0
Peduncle depth	5.5	5.5–7.5	6.1	0.8
Peduncle length	12.0	12.0–14.3	12.9	1.0

TABLE 4.8. Meristic data for *Pseudoscopelus altipinnis* (n=25) and *P. paxtoni* (n=11). H stands for holotype.

Character	*P. altipinnis*			*P. paxtoni*		
	H	Range	Mode	H	Range	Mode
First dorsal-fin rays	IX	VII–IX	VIII	IX	VII–X	IX
Second dorsal-fin rays	iv, 21	ii–iv, 21–23	ii, 22	ii, 23	i–ii, 22–24	ii, 22
Anal-fin rays	iv, 21	ii–iv, 21–24	iii, 22	iii, 23	iii, 21–23	iii, 23
Pectoral-fin rays	12	12–14	13	12	11–13	13
Pelvic-fin rays	I, 6	I, 5–6	I, 5	I, 5	I, 5	I, 5
Caudal-fin rays	i, 7, 8, i	i, 7–8, 8, i	i, 7, 8, i	i, 8, 7, i	i, 7–8, 7–8, i	i, 7, 8, i
Branchiostegal rays	7	7–8	7	7	7–8	7
Sensorial Pores						
Lateral line	80	75–81	78	81	77–82	81
Temporal	2	2	2	2	2	2
Supratemporal	3	3	3	3	3	3
Otic	2	2	2	2	2	2
Supraorbital	6	6	6	6	5–6	6
Supranasal pore	2	1–3	2	2	1–2	1
Epiphyseal branch	2	3	3	3	2–3	2
Infraorbital	12	12	12	11	11–12	11
Preopercular	5	5	5	5	5	5
Mandibular	6	6	6	6	6	6
Fifth mandibular pore	1	1–2	1	1	1–2	2
Gill Rakers and Dentition						
Epibranchial	0	0–1	0	0	0	0
Ceratobranchial	10	7–11	9	14	7–22	15
Hypobranchial	7	3–8	6	8	1–12	12
Basihyal	0	0	0	0	0	0
First basibranchial	13	7–13	5	9	9–18	9
Teeth on palatine	3	3–10	8	5	4–8	5
Osteology						
Total vertebrae	–	36–38 (n=17)	37	–	36–38 (n=5)	37, 38
Pre-caudal vertebrae	–	16–18 (n=15)	17	–	17–18 (n=5)	18

TABLE 4.9. Morphometric data for *Pseudoscopelus altipinnis* (n=25) and *P. paxtoni* (n=11). D stands for distance; H, holotype; M, mean; and SD, standard deviation.

Character	*P. altipinnis*				*P. paxtoni*			
	H	**Range**	**M**	**SD**	**H**	**Range**	**M**	**SD**
Standard length (mm)	188.3	38.5–188.9	100.7	37.9	205.1	51.6–234.2	168.9	60.3
Head length (mm)	51.8	12.6–51.8	29.6	10.16	56.0	16.2–67.2	47.4	16.7
Proportions of HL								
Snout	25.8	24.4–31.4	27.0	1.8	29.8	26.9–32.7	30.1	1.6
Upper jaw	73.6	67.4–76.8	71.6	2.2	73.5	70.1–82.5	74.5	3.3
Lower jaw	76.2	75.1–84.9	78.1	2.4	80.3	76.4–85.8	80.6	2.9
Orbit width	16.3	15.2–22.1	17.6	1.7	15.6	15.1–18.8	16.3	1.2
Orbit height	12.5	11.7–17.4	14.0	1.6	14.4	12.6–15.6	14.0	1.0
Anterior nostril to eye	14.1	11.0–15.8	14.0	1.3	16.5	14.1–16.5	16.1	0.7
Posterior nostril to eye	7.1	4.6–8.6	6.3	1.0	8.9	6.1–9.9	8.7	0.7
D. between nostrils	6.3	5.8–8.9	6.8	0.8	7.1	4.9–7.6	6.3	0.9
Interorbital distance	23.2	22.4–27.0	24.7	1.3	22.0	20.3–24.8	22.3	1.4
Head width	43.1	32.7–39.3	36.2	1.6	33.2	32.4–37.8	34.4	1.7
Cheek depth	8.7	5.8–10.5	8.3	1.2	10.2	8.3–10.7	9.5	0.7
Proportions of SL								
Head length	27.6	26.2–32.8	29.7	1.5	27.3	26.2–29.0	28.0	0.9
Body width	9.4	6.3–11.0	8.2	1.1	8.9	6.0–9.6	7.9	1.0
Insertion of pectoral fin	27.6	27.6–33.0	31.0	1.3	28.3	27.3–30.5	29.1	1.0
Insertion of pelvic fin	30.1	29.2–35.4	33.1	1.5	30.1	30.0–32.4	31.0	0.9
Pectoral-fin length	18.2	14.5–22.7	18.7	2.0	15.5	15.0–18.3	16.2	1.3
Pelvic-fin length	11.9	8.0–12.9	11.4	1.1	8.8	8.5–14.4	10.7	1.8
Origin of first dorsal fin	32.1	30.6–36.2	34.1	1.4	33.1	31.6–35.3	33.5	1.1
Base of first dorsal fin	11.2	10.9–15.5	13.3	1.2	13.1	9.9–16.9	13.8	2.0
First dorsal-fin depth	10.7	8.4–13.6	11.1	1.6	9.4	8.2–9.4	8.8	0.5
Origin of second dorsal fin	49.5	48.1–53.5	51.5	1.3	50.7	50.5–52.4	51.3	0.7
Base of second dorsal fin	38.7	36.3–41.1	39.0	1.2	41.0	37.3–41.0	39.5	1.2
Second dorsal-fin depth	20.0	14.6–25.0	21.2	2.7	19.9	16.7–21.3	19.5	1.3

TABLE 4.9. (cont.)

Origin of anal fin	52.4	47.5–54.0	51.4	1.5	48.4	48.4–54.4	51.4	2.0
Base of anal fin	39.7	36.4–42.8	38.6	1.6	36.8	36.0–40.3	38.3	1.4
Anal-fin depth	21.4	15.6–25.1	20.7	2.1	19.5	19.5–23.5	21.1	1.4
Peduncle depth	5.7	4.8–6.8	5.4	0.5	6.1	5.3–7.2	6.2	0.7
Peduncle length	13.4	9.5–13.4	11.0	1.2	13.1	9.7–13.6	12.0	1.5

TABLE 4.10. Meristic data of *Pseudoscopelus scutatus* (n=12) and *P. bothrorrhinos* (n=11).

Character	*P. scutatus*		*P. bothrorrhinos*		
	Range	**Mode**	**Holotype**	**Range**	**Mode**
First dorsal-fin rays	VI–VIII	VIII	VII	VII	VII
Second dorsal-fin rays	ii, 20–22	ii, 21	ii, 21	ii, 20-22	ii, 21
Anal-fin rays	ii–iii, 20–22	iii, 20	iii, 21	ii-iii, 20-22	iii, 21
Pectoral-fin rays	13–15	14	14	12-14	14
Pelvic-fin rays	I, 5	I, 5	i, 5	i, 5	i, 5
Caudal-fin rays	i, 7, 8, i	i, 7, 8, i	i, 7, 7, i	i, 7, 7-8, i	i, 7, 8, i
Branchiostegal rays	7	7	7	7	7
Sensorial Pores					
Lateral line	74–80	77	76	73-77	76
Temporal	2	2	2	2	2
Supratemporal	3	3	3	3	3
Otic	2	2	2	2	2
Supraorbital	6	6	6	6	6
Supranasal pore	3	3	3	3	3
Epiphyseal branch	3	3	3	2-3	3
Infraorbital	12	12	12	12-13	12
Preopercular	5	5	5	5	5
Mandibular	6	6	6	6	6
Fifth mandibular pore	1	1	1	1	1
Gill Rakers and Dentition					
Epibranchial	0	0	0	0	0
Ceratobranchial	5–8	7	6	6-9	7
Hypobranchial	1–3	2	2	1-4	2
Basihyal	0	0	8	5-11	6
First basibranchial	6–12	9	5	4-8	5
Teeth on palatine	3–5	4	6	6-9	7
Osteology					
Total vertebrae	35–37 (n=14)	36	–	33–35 (n=13)	35
Pre-caudal vertebrae	17–18 (n=14)	18	–	17–18 (n=10)	18

TABLE 4.11. Morphometric data for *Pseudoscopelus scutatus* (n=12). H stands for holotype and SD for standard deviation.

Character	*P. scutatus*			*P. bothrorrhinos*			
	Range	Mean	SD	H	Range	Mean	SD
Standard length (mm)	39.5–91.0	71.9	15.0	45.9	29.61–55.1	39.8	7.7
Head length (mm)	10.0–23.6	18.3	3.8	12.5	8.15–14.8	10.7	2.0
Proportions of HL							
Snout	22.7–26.6	24.7	1.2	23.5	23.5–27.6	25.5	1.4
Upper jaw	64.5–70.5	67.7	2.0	67.8	63.8–70.8	67.1	2.2
Lower jaw	73.2–77.7	74.9	1.4	76.1	71.7–78.8	74.8	2.2
Orbit width	13.3–17.2	15.4	1.4	15.8	14.7–18.3	16.7	1.2
Orbit height	11.4–15.3	13.6	1.3	14.6	13.7–16.6	15.0	1.0
Anterior nostril to eye	16.2–18.7	17.7	0.8	17.6	15.9 –18.6	17.6	0.7
Posterior nostril to eye	4.7–6.9	6.2	0.7	6.6	5.3–7.8	6.4	0.7
Distance between nostrils	10.1–12.2	11.0	0.7	11.1	9.1–12.1	10.8	1.0
Interorbital distance	27.1–30.7	29.0	1.5	28.6	28.6–32.1	30.7	1.0
Head width	37.1–41.0	39.0	1.1	41.1	38.2 –43.3	41.3	1.5
Cheek depth	7.4–11.1	9.6	1.1	9.7	7.4–10.6	8.9	1.0
Proportions of SL							
Head length	24.2–26.6	24.4	0.8	27.2	25.2–29.2	26.9	1.2
Body width	6.1–9.4	8.0	1.0	8.4	7.0–11.6	8.6	1.4
Insertion of pectoral fin	24.1–28.1	27.0	1.1	26.6	26.6–29.1	27.3	0.9
Insertion of pelvic fin	26.3–30.8	29.0	1.4	27.9	27.9–33.7	30.2	1.9
Pectoral-fin length	12.1–15.7	14.0	1.1	32.8	31.5–35.5	33.5	1.1
Pelvic-fin length	8.2–11.0	9.7	0.7	11.9	9.3–12.8	11.6	1.2
Origin of first dorsal fin	30.4–33.5	32.0	1.2	52.4	51.6–57.9	53.7	1.8
Base of first dorsal fin	8.2–13.1	11.1	1.3	39.6	33.9–40.5	37.3	2.0
First dorsal-fin depth	10.2–12.2	10.8	0.8	50.5	47.4–55.6	50.9	2.5
Origin of second dorsal fin	49.6–54.2	51.8	1.4	38.1	34.2–41.5	37.0	2.1
Base of second dorsal fin	35.8–39.0	37.3	1.0	16.0	13.2–19.2	16.0	1.5
Second dorsal-fin depth	18.3–21.1	19.9	1.1	10.1	8.6–11.5	9.8	1.0
Origin of anal fin	46.4–52.6	50.1	1.7	9.3	7.4–12.2	8.9	1.3
Base of anal fin	35.8–40.3	37.8	1.3	19.3	17.6–21.7	19.3	1.2

TABLE 4.11. (cont.)

Anal-fin depth	17.4–24.3	20.5	2.7	18.1	14.2–20.5	18.6	1.8
Peduncle depth	4.4–6.0	5.5	0.4	6.8	5.2–8.0	6.3	0.8
Peduncle length	10.9–13.7	13.0	1.2	12.5	11.1–15.5	12.7	1.5

TABLE 4.12. Meristic data of *Pseudoscopelus aphos* (n=5), and *P. parini* (n=7).

Character	*P. aphos*		*P. parini*	
	Range	Mode	Range	Mode
First dorsal-fin rays	VII–IX	VIII–IX	VI–IX	IX
Second dorsal-fin rays	ii–iii, 20–25	ii. 21	ii, 23–24	ii. 24
Anal-fin rays	iii, 20–23	iii, 20; 21	iii, 21–24	iii, 22
Pectoral-fin rays	12–15	15	13–16	13–14
Pelvic-fin rays	I, 5	I, 5	I, 5	I, 5
Caudal-fin rays	i, 7–8, 7–8, i	i, 7, 8, i	i, 7, 8, i	i, 7, 8, i
Branchiostegal rays	7	7	7	7
Sensorial Pores				
Lateral line	74–77	77	77–78	77
Temporal	2	2	2	2
Supratemporal	3	3	3	3
Otic	2	2	2	2
Supraorbital	5–6	5	5–6	6
Supranasal pore	4	4	3–4	4
Epiphyseal branch	3	3	3	3
Infraorbital	12	12	12	12
Preopercular	5–6	6	5	5
Mandibular	6	6	6	6
Fifth mandibular pore	1	1	1–2	2
Gill Rakers and Dentition				
Epibranchial	0	0	0	0
Ceratobranchial	8–14	8	8–16	13
Hypobranchial	4–9	6	4–18	9
Basihyal	0	0	0	0
First basibranchial	9–12	10	15–21	15, 19
Teeth on palatine	3–5	3	3–5	5
Osteology				
Total vertebrae	36 (n=2)	36	36 (n=7)	36
Pre-caudal vertebrae	18 (n=2)	18	17–19 (n=7)	18

TABLE 4.13. Morphometric data for *Pseudoscopelus aphos* (n=5), and *P. parini* (n=7). SD stands for standard deviation.

Character	*P. aphos*			*P. parini*		
	Range	Mean	SD	Range	Mean	SD
Standard length (mm)	58.6–76.6	68.3	8.1	34.8–100.8	74.0	22.4
Head length (mm)	16.7–22.7	19.9	2.6	10.1–27.7	21.7	6.4
Proportions of HL						
Snout	25.9–30.0	27.6	1.5	26.1–28.8	27.4	1.1
Upper jaw	68.9–72.2	70.2	1.4	67.7–74.8	70.3	2.6
Lower jaw	73.6–80.0	77.4	2.8	75.0–82.1	78.3	2.7
Orbit width	15.1–17.6	16.3	1.1	15.6–21.8	17.6	2.1
Orbit height	12.0–14.7	12.8	1.3	12.0–18.2	14.3	2.1
Anterior nostril to eye	13.4–14.9	13.9	0.6	13.1–15.9	14.1	1.0
Posterior nostril to eye	6.2–7.3	6.7	0.5	5.9–8.4	7.2	0.9
Distance between nostrils	5.0–7.4	6.4	0.9	5.5–7.4	6.7	0.6
Interorbital distance	23.9–27.0	26.1	1.3	23.3–26.0	24.5	0.9
Head width	35.9–40.2	38.1	1.9	33.5–36.8	35.2	1.3
Cheek depth	6.8–10.4	8.6	1.5	6.8–9.6	7.9	1.2
Proportions of SL						
Head length	27.5–29.9	29.1	1.0	27.6–30.4	29.4	0.9
Body width	7.0–10.2	8.1	1.2	7.1–8.5	7.9	0.5
Insertion of pectoral fin	27.8–33.1	30.4	2.0	28.9–30.9	30.1	0.8
Insertion of pelvic fin	32.2–35.9	33.7	1.6	29.1–34.7	32.5	2.1
Pectoral-fin length	20.3–23.0	22.0	1.2	18.6–29.4	21.6	3.6
Pelvic-fin length	10.5–13.2	12.1	1.2	8.5–10.5	9.4	0.8
Origin of first dorsal fin	32.6–35.5	33.7	1.1	30.8–36.7	33.8	2.2
Base of first dorsal fin	50.6–52.5	51.8	0.7	13.0–15.8	14.7	0.9
First dorsal-fin depth	87.0–92.2	89.3	1.9	9.1–13.9	11.4	1.6
Origin of second dorsal fin	50.6–52.5	51.8	0.7	48.1–56.0	53.4	2.6
Base of second dorsal fin	36.0–40.6	38.5	1.7	36.5–38.7	37.4	0.8
Second dorsal-fin depth	19.8–23.5	22.1	2.0	17.3–20.3	19.1	1.1
Origin of anal fin	48.8–54.6	52.0	2.6	49.8–54.6	51.9	1.9
Base of anal fin	34.1–38.7	37.5	1.9	36.2–40.2	37.9	1.4

TABLE 4.13. (cont.)

Anal-fin depth	20.6–25.2	23.6	2.6	15.3–21.4	18.9	2.1
Peduncle depth	5.2–8.5	6.0	1.4	4.9–5.6	5.2	0.3
Peduncle length	11.7–14.4	13.3	1.4	9.2–11.2	10.7	0.7

TABLE 4.14. Meristic data for *Pseudoscopelus astronesthidens* (n=9) and *P. australis* (n=12).

Character	*P. astronesthidens* Range	*P. astronesthidens* Mode	*P. australis* Range	*P. australis* Mode
First dorsal-fin rays	VI–IX	VIII	VII–VIII	VIII
Second dorsal-fin rays	ii, 21–23	ii, 22	ii, 20–23	ii, 22–23
Anal-fin rays	iii–iv, 20–23	iii, 21–23	iii, 20–22	iii, 21
Pectoral-fin rays	11–13	12	11–13	12
Pelvic-fin rays	I, 5	I, 5	I, 5	I, 5
Caudal-fin rays	i, 7–8, 8, i	i, 7, 8, i	i, 7–8, 7–8, i	i, 7, 8, i
Branchiostegal rays	7	7	6–7	7
Sensorial Pores				
Lateral line	75–78	78	74–80	75
Temporal	2	2	2	2
Supratemporal	3	3	3	3
Otic	2	2	2	2
Supraorbital	6	6	6	6
Supranasal pore	3–4	3	4	4
Epiphyseal branch	1–4	3	3–5	3
Infraorbital	12	12	11–12	12
Preopercular	5	5	5	5
Mandibular	6	6	6	6
Fifth mandibular pore	2	2	1–2	2
Gill Rakers and Dentition				
Epibranchial	0	0	0	0
Ceratobranchial	2–9	2	0–1	0
Hypobranchial	5–12	6	0–12	6
Basihyal	10–16	15	9–15	9
First basibranchial	8–10	8	5–13	8
Teeth on palatine	15–38	15, 16, 21, 29, 33, 38	10–16	12
Osteology				
Total vertebrae	36–37 (n=9)	37	36 (n=9)	36
Pre-caudal vertebrae	17–19 (n=9)	18	18–19 (n=9)	18

TABLE 4.15. Morphometric data for *Pseudoscopelus astronesthidens* (n=9) and *P. australis* (n=12). SD stands for standard deviation.

Character	*P. astronesthidens*			*P. australis*		
	Range	Mean	SD	Range	Mean	SD
Standard length (mm)	71.8–170.2	111.5	42.8	77.4–197.4	130.3	37.4
Head length (mm)	22.42–52.4	35.3	13.8	23.4–57.3	39.4	11.0
Proportions of HL						
Snout	26.0–28.6	27.1	1.0	25.6–29.8	27.6	1.4
Upper jaw	65.2–67.8	66.4	0.9	61.5–69.4	66.1	2.3
Lower jaw	71.0–74.1	73.0	1.4	70.3–78.0	73.0	2.3
Orbit width	14.7–17.4	15.8	1.2	13.4–17.7	14.9	1.2
Orbit height	11.8–15.4	13.4	1.3	11.2–13.6	12.5	0.9
Anterior nostril to eye	12.7–14.0	13.2	0.5	12.5–15.5	14.3	1.0
Posterior nostril to eye	5.3–8.0	6.7	1.1	6.2–8.7	7.4	0.8
Distance between nostrils	5.6–7.5	6.3	0.9	5.2–8.0	6.8	0.8
Interorbital distance	16.3–18.7	16.5	0.3	17.7–20.4	19.0	0.9
Head width	28.9–31.9	30.3	1.1	29.3–33.3	31.5	1.1
Cheek depth	9.2–10.9	10.1	0.6	8.4–11.6	10.1	1.1
Proportions of SL						
Head length	30.4–33.0	31.6	1.0	29.0–31.2	30.3	0.7
Body width	7.6–9.3	8.1	0.7	6.8–9.2	8.0	0.7
Insertion of pectoral fin	31.4–33.0	32.3	0.7	28.9–32.3	30.5	1.0
Insertion of pelvic fin	31.4–33.0	34.1	1.2	29.4–35.0	32.5	1.4
Pectoral-fin length	17.5–32.0	11.7	5.6	11.8–19.8	16.3	2.9
Pelvic-fin length	9.4–11.7	10.0	1.0	8.9–11.3	9.9	0.6
Origin of first dorsal fin	33.3–36.3	34.6	1.2	32.3–36.8	35.1	1.2
Base of first dorsal fin	10.7–15.2	13.2	1.6	10.3–17.7	14.0	2.1
First dorsal-fin depth	9.5–10.7	10.1	0.8	7.5–12.2	9.9	1.7
Origin of second dorsal fin	50.8–53.9	52.0	1.0	51.2–53.9	52.6	0.9
Base of second dorsal fin	38.5–39.9	39.3	0.6	37.5–40.2	38.6	0.8
Second dorsal-fin depth	19.0–19.4	19.2	0.3	16.9–22.2	19.2	1.9
Origin of anal fin	51.8–54.8	52.8	0.6	50.7–54.1	52.5	1.2
Base of anal fin	36.8–40.2	38.3	1.2	33.1–40.7	37.9	1.9

TABLE 4.15. (cont.)

Anal-fin depth	20.0–21.1	20.5	0.8	18.0–22.3	19.9	1.1
Peduncle depth	4.3–5.3	4.6	0.4	4.9–6.0	5.5	0.4
Peduncle length	9.5–10.2	9.8	0.5	9.8–13.5	11.1	1.1

TABLE 4.16. Meristic data for *Pseudoscopelus odontoglossum* (n=3) and *P. lavenbergi* (n=11). H stands for holotype.

Character	*P. odontoglossum*		
	H	**Range**	**Mode**
First dorsal-fin rays	IX	VII–IX	VII, VII, IX
Second dorsal-fin rays	ii, 24	ii, 21–24	ii, 21–23–24
Anal-fin rays	iii, 24	iii, 21–24	iii, 24
Pectoral-fin rays	12	12–13	13
Pelvic-fin rays	I, 5	I, 5	I, 5
Caudal-fin rays	i, 7, 8, i	i, 7, 8, i	i, 7, 8, i
Branchiostegal rays	7	7	7
Sensorial Pores			
Lateral line	79	78–79	79
Temporal	2	2	2
Supratemporal	3	3	3
Otic	2	2	2
Supraorbital	6	6	6
Supranasal pore	3	3, 4	3
Epiphyseal branch	3	3	3
Infraorbital	12	12	12
Preopercular	5	5	5
Mandibular	6	6	6
Fifth mandibular pore	2	2	2
Gill Rakers and Dentition			
Epibranchial	1	1	1
Ceratobranchial	5	5–16	5, 8, 16
Hypobranchial	8	7–8	8
Basihyal	26	20–26	20, 25,26
First basibranchial	13	6–13	6, 8, 13
Teeth on palatine	24	16–26	16, 26, 26
Osteology			
Total vertebrae	37	37 (n=2)	37
Pre-caudal vertebrae	18	18 (n=1)	18

TABLE 4.17. Morphometric data for *Pseudoscopelus odontoglossum* (n=3) and *P. lavenbergi* (n=11). H stands for holotype and SD, standard deviation.

Character	*P. odontoglossum*			
	H	Range	M	SD
Standard length (mm)	70.5	44.0–70.3	54.8	13.9
Head length (mm)	23.16	14.2–23.2	18.4	5.6
Proportions of HL				
Snout	26.8	25.6–26.8	26.0	0.7
Upper jaw	63.6	63.3–68.0	65.0	2.6
Lower jaw	71.0	68.2–72.8	70.7	2.3
Orbit width	14.9	14.9–17.7	16.1	1.4
Orbit height	12.0	12.0–15.2	13.9	1.7
Anterior nostril to eye	12.7	12.7–13.2	13.0	0.3
Posterior nostril to eye	5.7	5.5–6.8	6.0	0.7
D. between nostrils	7.0	6.8–7.0	6.9	0.1
Interorbital distance	17.7	16.9–18.6	17.7	0.8
Head width	31.0	31.0–32.1	31.4	0.6
Cheek depth	11.0	9.2–11.0	10.1	0.9
Proportions of SL				
Head length	32.8	32.3–34.1	33.1	0.9
Body width	8.1	6.2–8.1	7.0	1.0
Insertion of pectoral fin	33.4	32.8–33.4	33.2	0.4
Insertion of pelvic fin	35.3	31.1–35.3	32.9	2.2
Pectoral-fin length	20.4	17.2–20.4	19.3	1.8
Pelvic-fin length	10.0	8.9–10.8	9.9	1.0
Origin of first dorsal fin	36.7	34.8–36.7	36.0	1.0
Base of first dorsal fin	11.8	11.8–12.4	12.2	0.4
First dorsal-fin depth	9.6	9.6–10.4	10.1	0.4
Origin of second dorsal fin	53.3	53.3–53.9	53.6	0.3
Base of second dorsal fin	39.6	37.7–42.4	39.9	2.4
Second dorsal-fin depth	22.5	18.2–22.5	20.9	2.4
Origin of anal fin	54.8	49.1–54.8	52.6	3.1
Base of anal fin	39.3	34.5–39.3	37.6	2.7

TABLE 4.17. (cont.)

Anal-fin depth	20.9	18.7–21.2	20.3	1.4
Peduncle depth	4.7	3.8–4.7	4.3	0.4
Peduncle length	9.2	8.7–12.4	10.1	2.0

TABLE 4.18. Meristic data for *Pseudoscopelus lavenbergi* (n=11). H stands for holotype.

Character	*P. lavenbergi*		
	H	**Range**	**Mode**
First dorsal-fin rays	VIII	VIII	VIII
Second dorsal-fin rays	ii, 21	ii, 21-23	ii, 21
Anal-fin rays	iii, 20	iii–iv, 20–22	iii, 21
Pectoral-fin rays	12	12–15	13
Pelvic-fin rays	i, 5	i, 5	i, 5
Caudal-fin rays	i, 7, 8, i	i, 7–8, 7–8, i	i, 7, 8, i
Branchiostegal rays	7	7	7
Sensorial Pores			
Lateral line	78	77–81	80
Temporal	2	2	2
Supratemporal	3	3	3
Otic	2	2	2
Supraorbital	6	6	6
Supranasal pore	2	2–3	2
Epiphyseal branch	3	2–3	3
Infraorbital	12	12	12
Preopercular	5	5	5
Mandibular	6	6	6
Fifth mandibular pore	2	1–2	2
Gill Rakers and Dentition			
Epibranchial	0	0-2	0
Ceratobranchial	9	9-23	12
Hypobranchial	6	6-16	9
Basihyal	13	9-19	14
First basibranchial	7	4-8	5
Teeth on palatine	13	9-19	14
Osteology			
Total vertebrae	13	9-19	14
Pre-caudal vertebrae	7	4-8	5

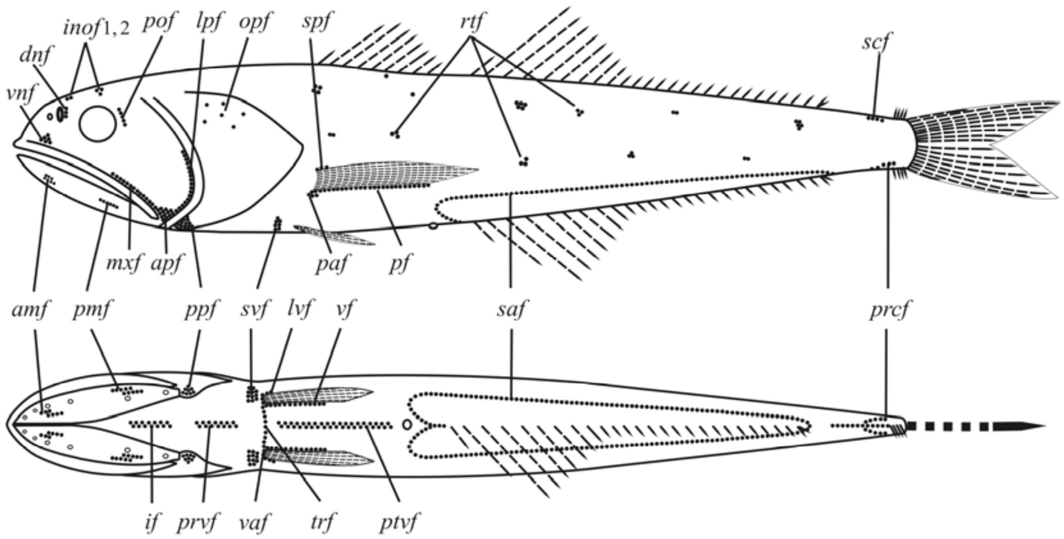
TABLE 4.19. Morphometric data for *Pseudoscopelus lavenbergi* (n=11). H stands for holotype and SD, standard deviation.

Character	*P. lavenbergi*			
	H	**Range**	**M**	**SD**
Standard length (mm)	73.0	44.9-166.6	90.9	37.3
Head length (mm)	24.8	14.8-55.2	29.6	12.4
Proportions of HL				
Snout	25.6	23.7-28.4	25.8	1.2
Upper jaw	63.2	60.4-68.5	63.8	2.4
Lower jaw	71.3	67.7-76.3	71.4	2.4
Orbit width	14.9	12.6-18.1	15.4	1.8
Orbit height	12.5	10.6-15.0	12.7	1.3
Anterior nostril to eye	14.4	11.9-14.6	13.5	1.3
Posterior nostril to eye	7.8	5.1-8.7	6.6	1.0
D. between nostrils	7.9	5.5-7.9	6.8	0.8
Interorbital distance	24.9	22.4-25.5	23.8	1.1
Head width	34.2	30.9-35.8	33.8	1.9
Cheek depth	8.3	7.8-10.1	9.0	0.8
Proportions of SL				
Head length	33.9	30.5-33.9	32.5	0.9
Body width	9.1	7.7-11.7	8.9	1.2
Insertion of pectoral fin	32.4	32.1-34.7	33.4	0.9
Insertion of pelvic fin	33.0	32.3-34.7	33.5	0.9
Pectoral-fin length	35.5	32.8-37.6	35.2	1.2
Pelvic-fin length	14.0	11.2-16.1	13.8	1.6
Origin of first dorsal fin	52.7	49.7-54.2	52.6	1.2
Base of first dorsal fin	37.4	36.1-40.3	37.6	1.2
First dorsal-fin depth	52.7	50.2-54.6	52.2	1.5
Origin of second dorsal fin	36.1	34.8-39.1	36.9	1.4
Base of second dorsal fin	21.3	14.1-24.0	18.6	2.9
Second dorsal-fin depth	13.1	9.5-14.4	11.9	1.5
Origin of anal fin	12.4	11.2-12.5	12.2	0.5
Base of anal fin	18.5	12.5-22.4	18.8	3.7

TABLE 4.19. (cont.)

Anal-fin depth	19.3	15.5-20.7	18.7	2.0
Peduncle depth	6.1	4.7-6.1	5.6	0.4
Peduncle length	11.5	9.7-12.1	11.3	0.8

FIGURE 4.1. Schematic of photophore groups in the genus *Pseudoscopelus*.



inof1,2
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lpf
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scf
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vnf
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vaf
trf
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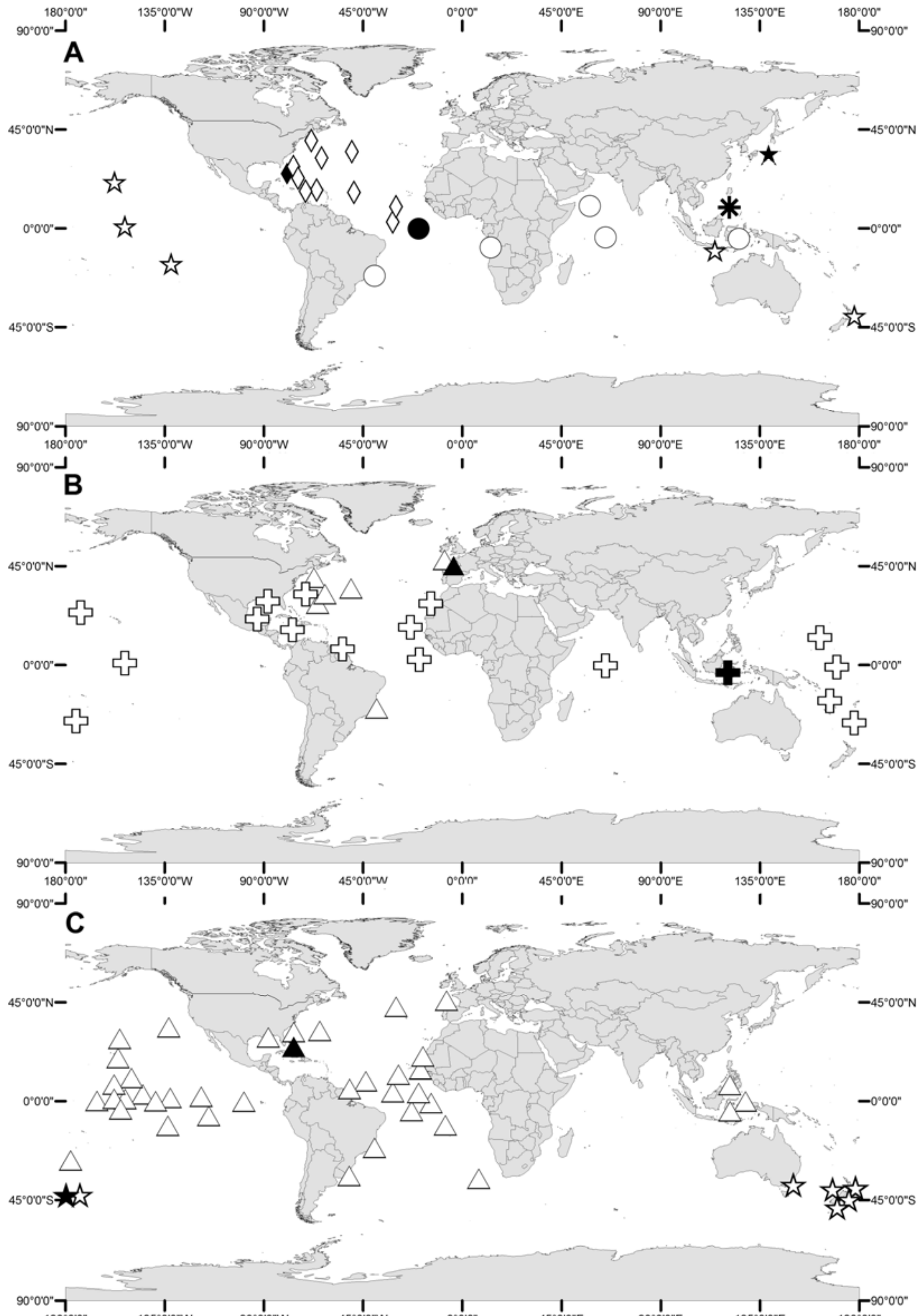
FIGURE 1

FIGURE 4.2. Maps of distribution of (A) Map of distribution of *Pseudoscopelus scriptus* (diamond), *P. sagamianus* (star), *P. cephalus* (asterisk), and *P. cordilluminatus* (circle); (B) *P. obtusifrons* (cross), and *P. pierbartus* (triangle); (C) *P. altipinnis* (triangle) and *P. paxtoni* (star). Each symbol may represent more than one locality; solid symbols represent type localities.


A
B
C
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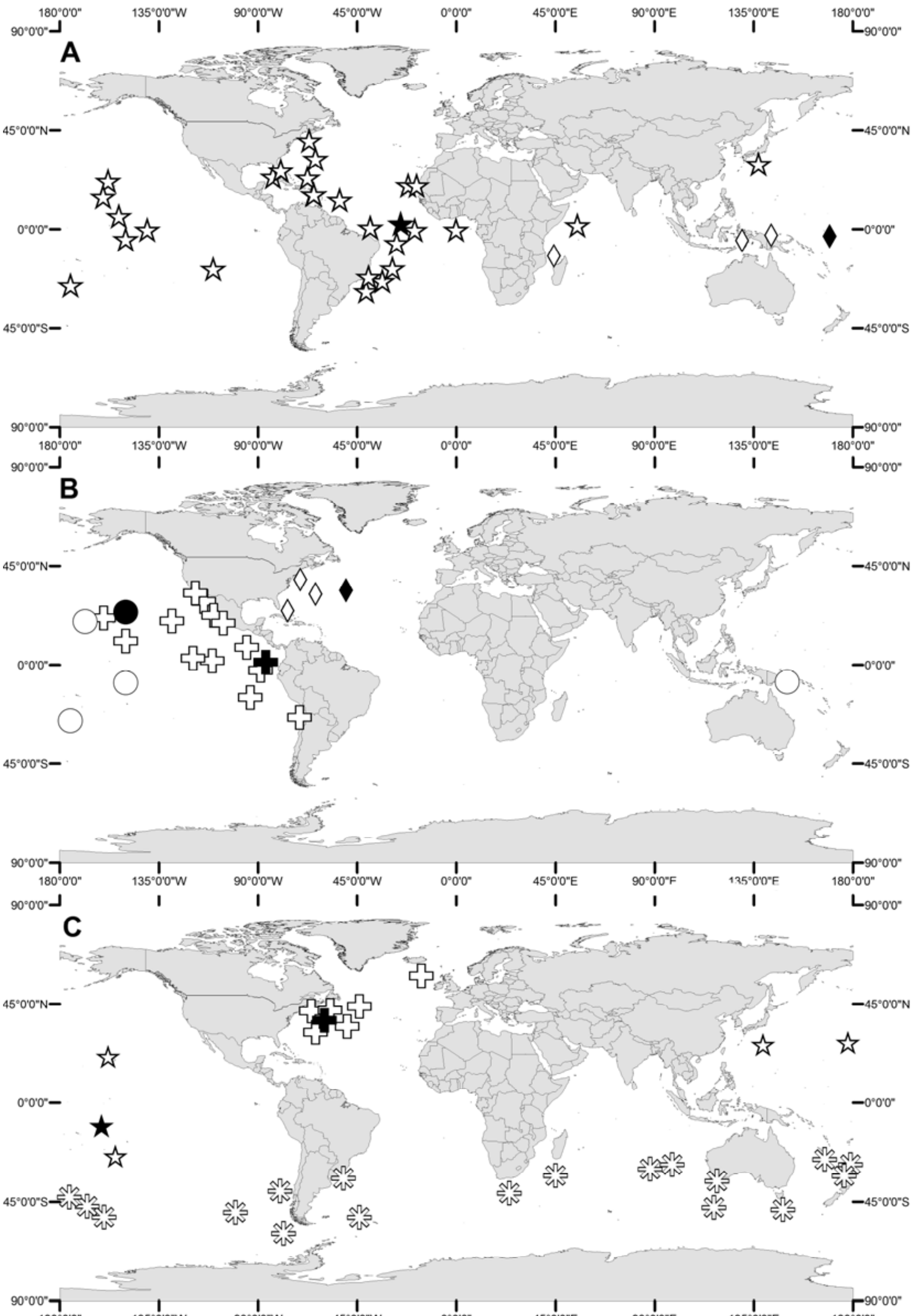
135°0'0"W
90°0'0"W
45°0'0"W
0°0'0"
45°0'0"E
90°0'0"E
135°0'0"E
180°0'0"
90°0'0"
45°0'0"N
0°0'0"
45°0'0"S
90°0'0"

FIGURE 4.3. Maps of distribution of (A) *Pseudoscopelus scutatus* (star) and *P. bothrorrhinos* (diamond), (B) *P. aphos* (diamond), *P. lavenbergi* (cross), and *P. parini* (circle); (C) *P. astronesthidens* (cross), *P. australis* (asterisk), and *P. odontoglossum* (star). Each symbol may represent more than one locality; solid symbols represent type localities.


A
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180°0'0"
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45°0'0"E
90°0'0"E
135°0'0"E
90°0'0"
45°0'0"N
0°0'0"
45°0'0"S

FIGURE 4.4. Schematic of the photophore pattern in lateral and ventral views of (A) *Pseudoscopelus scriptus*, based on ZMUC P. 65171 (70.0 mm, holotype); (B) *P. sagamianus*, based on BMNH 1984.1.1.93 (97.8 mm); (C) *P. cephalus*, USNM 93142 (74.5 mm, holotype). Dashed line indicates level of anus; gray area represents area of damage in holotype (see text for details).

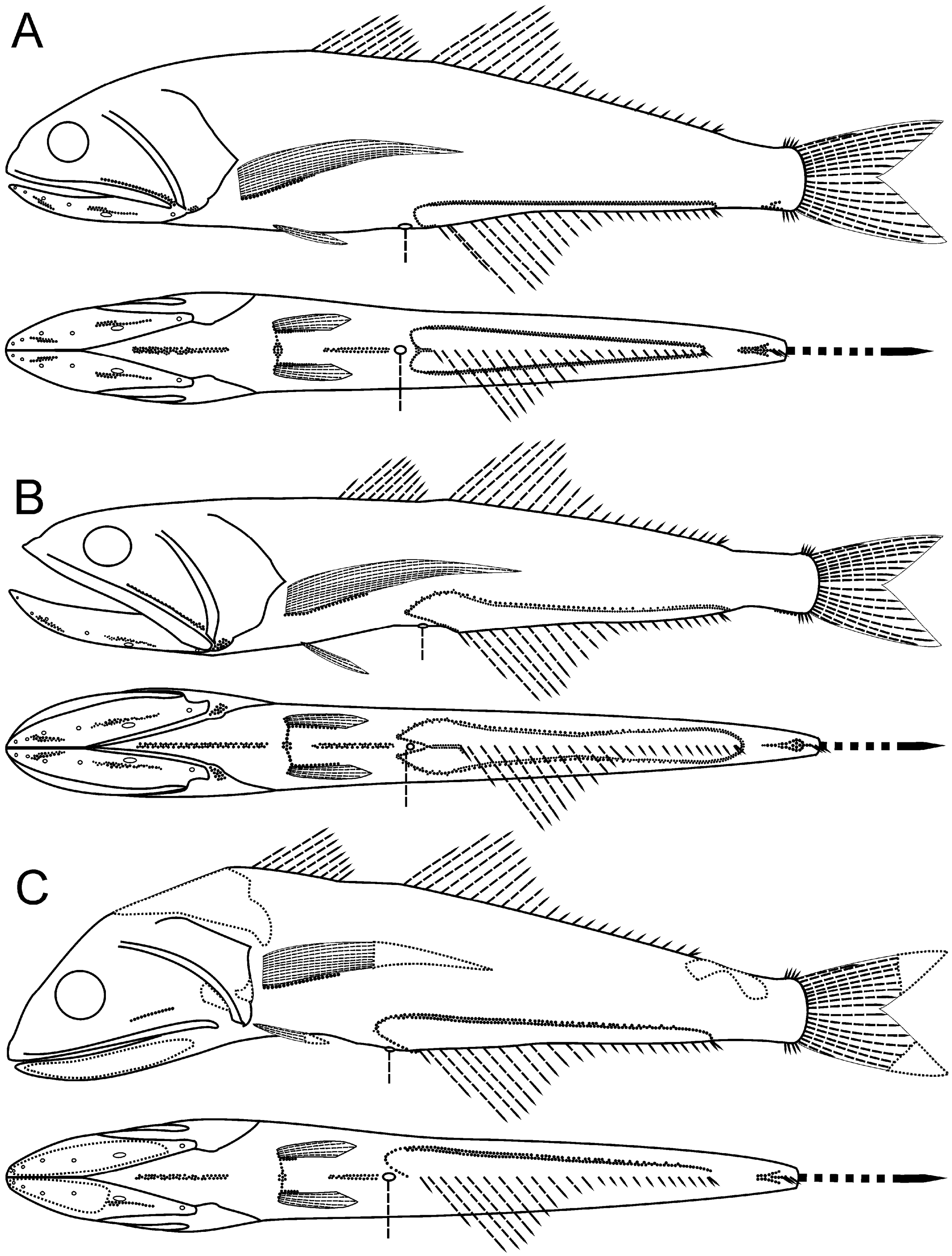

A
B
C

FIGURE 4.5. Schematic of the photophore pattern in lateral and ventral views of A) *Pseudoscopelus obtusifrons* based on USNM 268429 (115.2 mm); B) *P. pierbartus*, USNM 240687 (87.1 mm); C) *P. cordilluminatus*, BMNH 2003.4.23.51 (87.3 mm, paratype). Dashed line indicates level of anus.

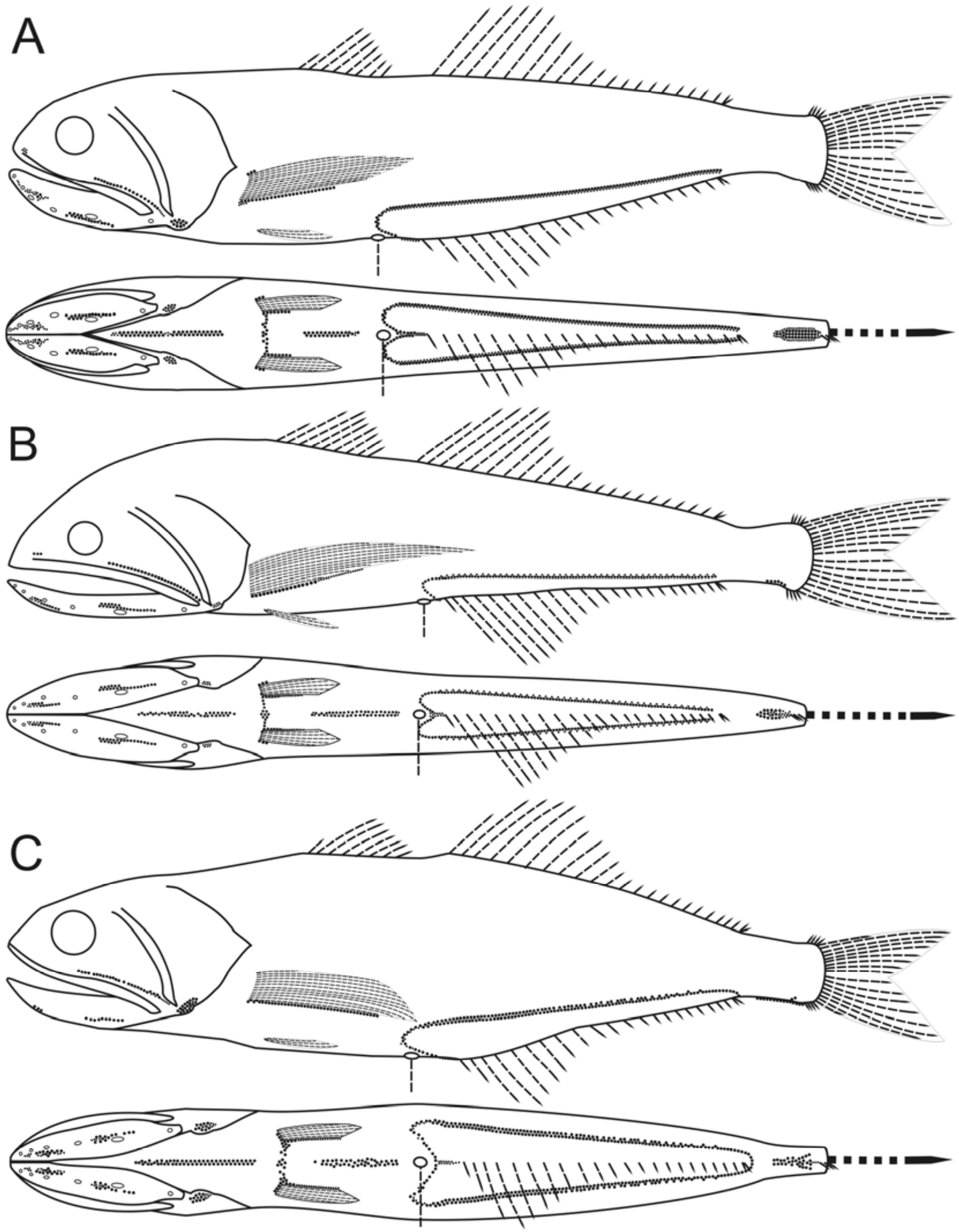

A
B
C

FIGURE 4.6. Schematic of the photophore pattern in lateral and ventral views of (A) *Pseudoscopelus altipinnis*, YPM 2798 (185.8 mm, holotype); (B) *P. paxtoni*, MNMZ P. 37858 (200.4 mm, paratype); (C) *P. lavenbergi*, CAS 61407 (63.0 mm).

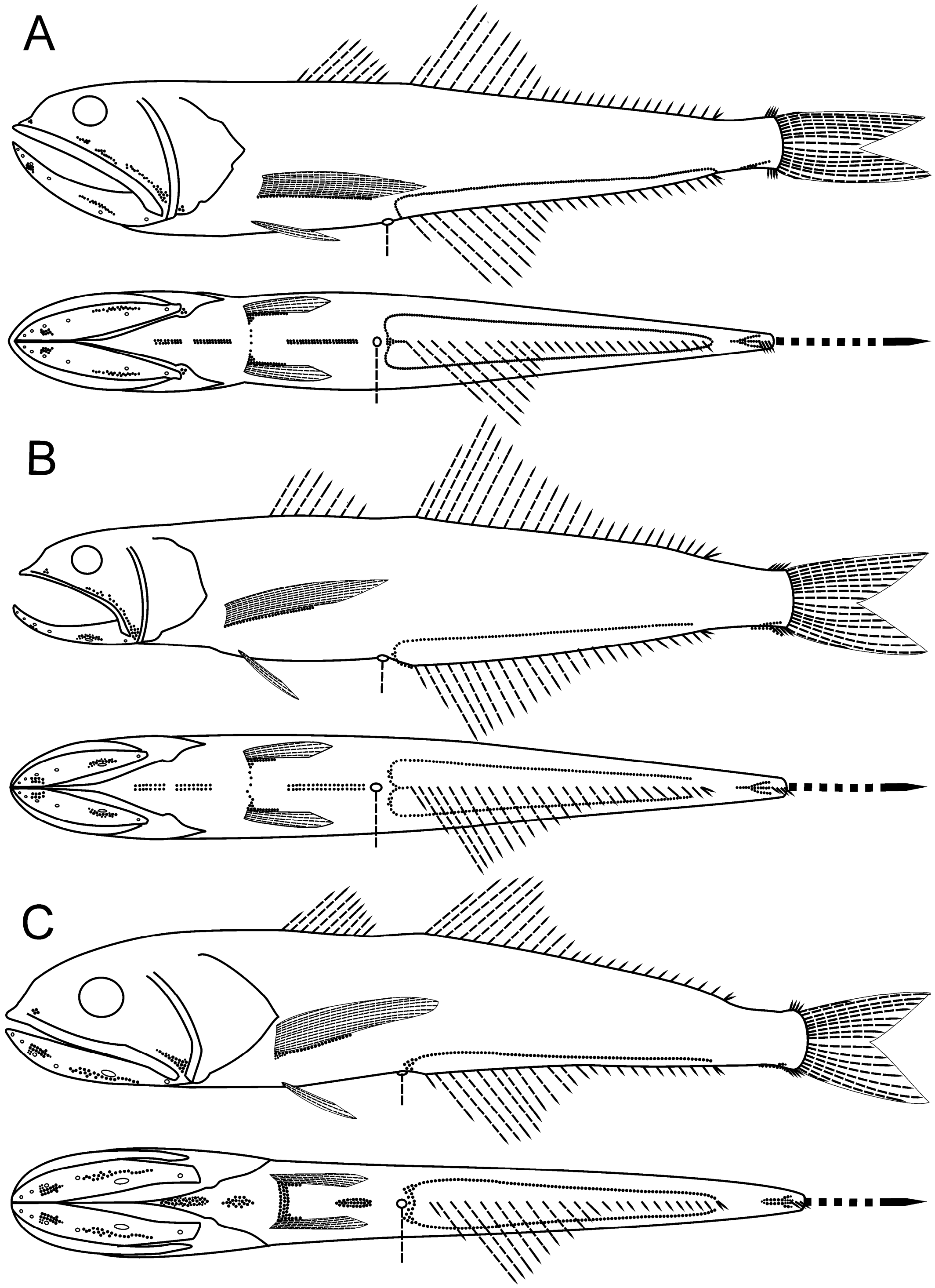

A
B
C

FIGURE 4.7. Schematic of the photophore pattern in lateral and ventral vies of (A) *Pseudoscopelus scutatus*, based on ZMH 25242 (80.4 mm, paratype); (B) *P. bothrorrhinos*, LACM 31494–1 (39.6 mm, paratype).

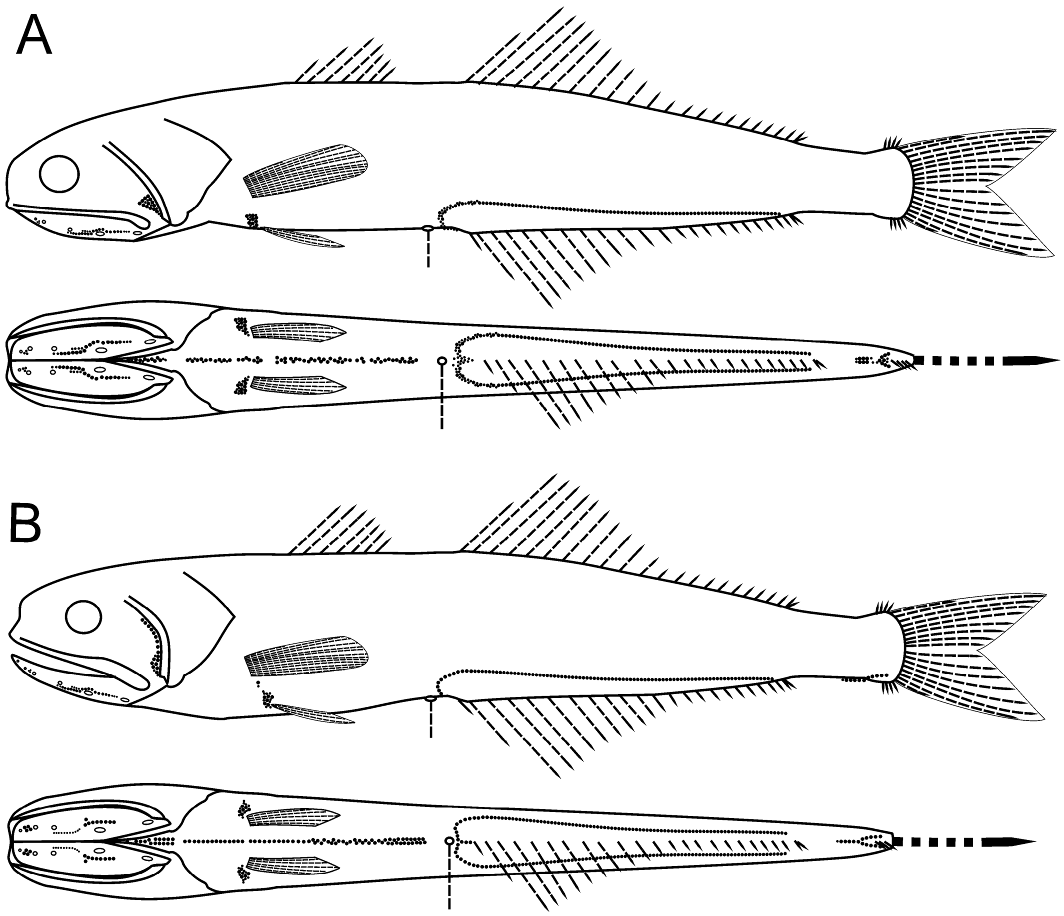

A
B

FIGURE 4.8. Schematic of the photophore pattern in lateral and ventral views of (A) *Pseudoscopelus astronesthidens*, based on MCZ 163443 (71.8 mm); (B) *P. australis*, NMNZ P. 40787, 197.4 mm; (C) *P. odontoglossum*, SIO 61–48, 70.2 mm, holotype.

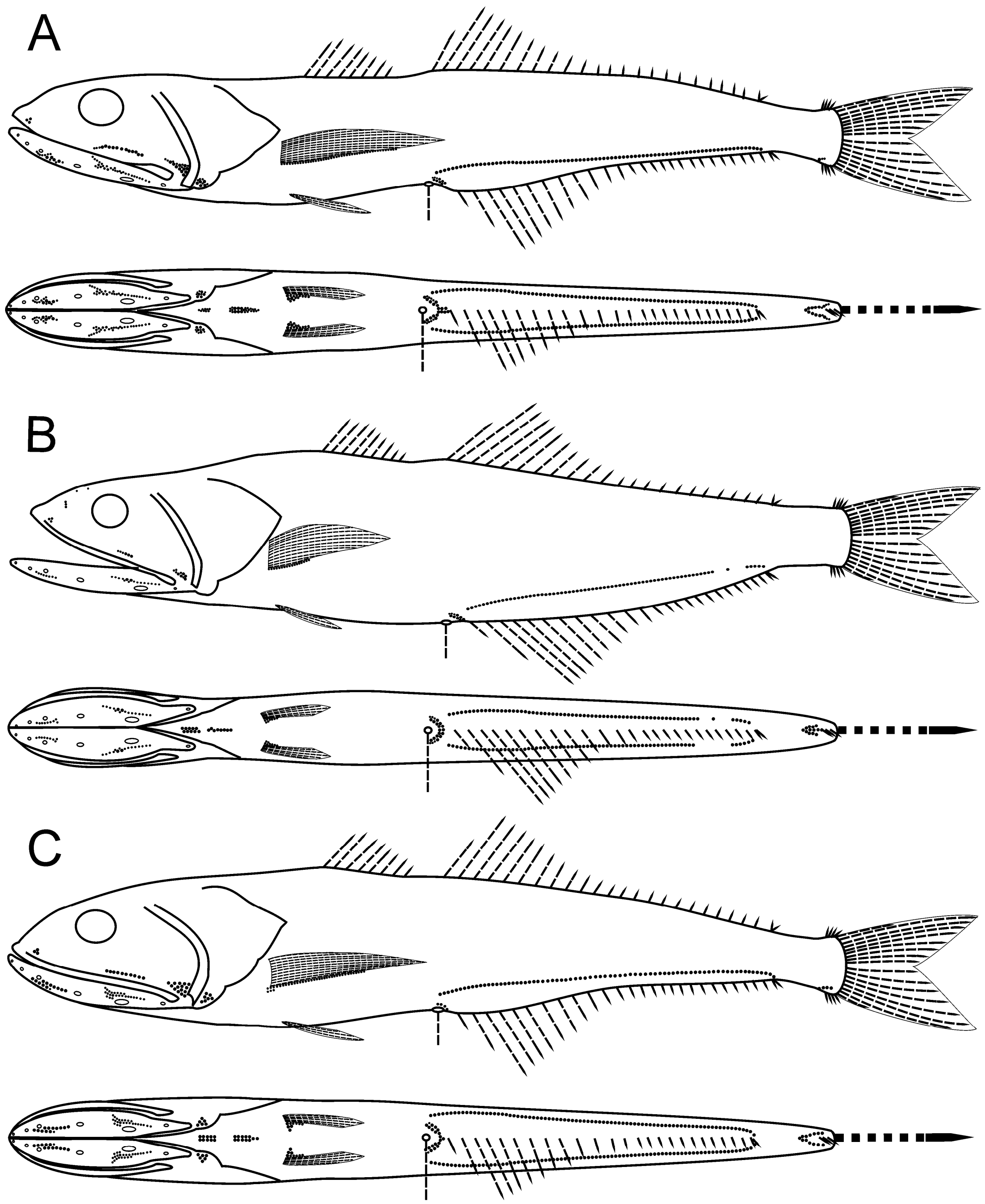

A
B
C

FIGURE 4.9. Schematic of dentition pattern in the species of *Pseudoscopelus*: premaxilla (above) and dentary (below); teeth arrangement is represented in the top, and tooth insertion sites bottom bone, with proportional circles to the tooth-base diameter. (A) *P. scriptus* based on ZMUC P 65171 (holotype); (B) *P. pierbartus*, LACM 56615; (C) *P. obtusifrons*, LACM 20074; (D) *P. cordilluminatus*, SIO 77–171. Scale bar equals 10 mm.

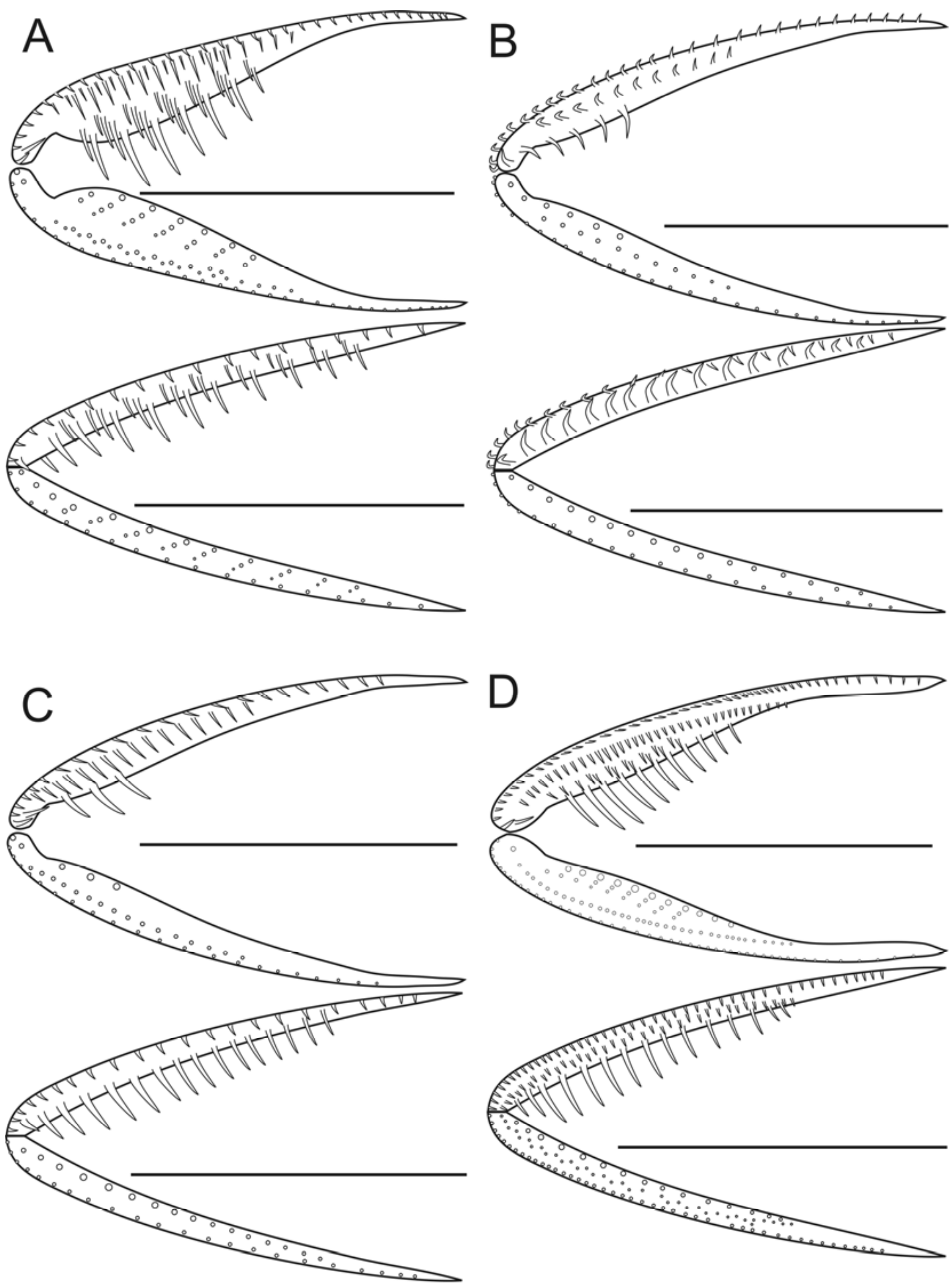

A
B
C
D

FIGURE 4.10. Schematic of dentition pattern in the species of *Pseudoscopelus*: premaxilla (above) and dentary (below); teeth arrangement is represented in the top, and tooth insertion sites bottom bone, with proportional circles to the tooth-base diameter. (A) *P. altipinnis* based on ZMUC P. 6546; (B) *P. paxtoni*, NMNZ P. 38679; (C) *P. scutatus*, based on ZMH 25243; (D) *P. odontoglossum*, SIO 61–48. Scale bar equals 10 mm.

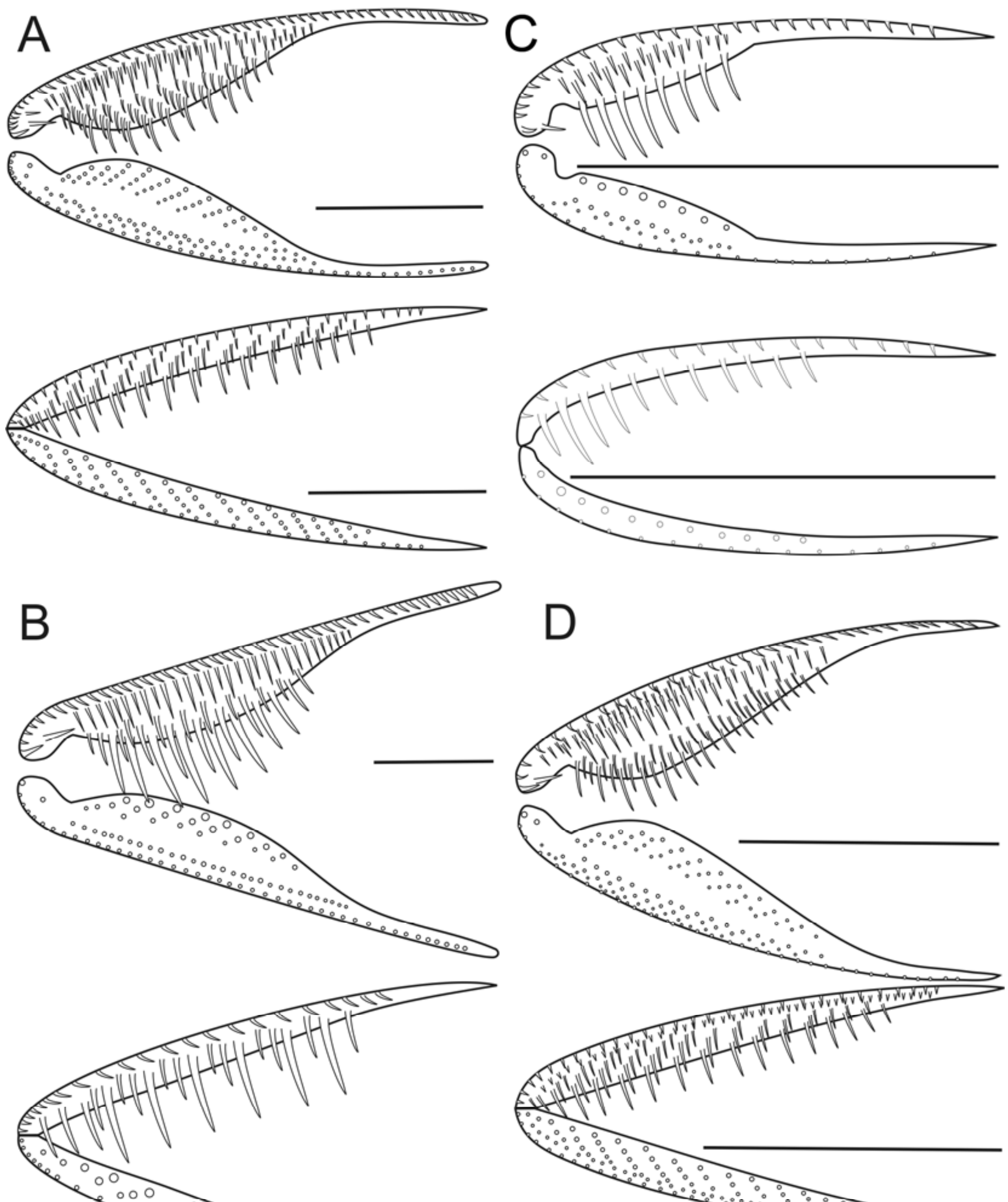
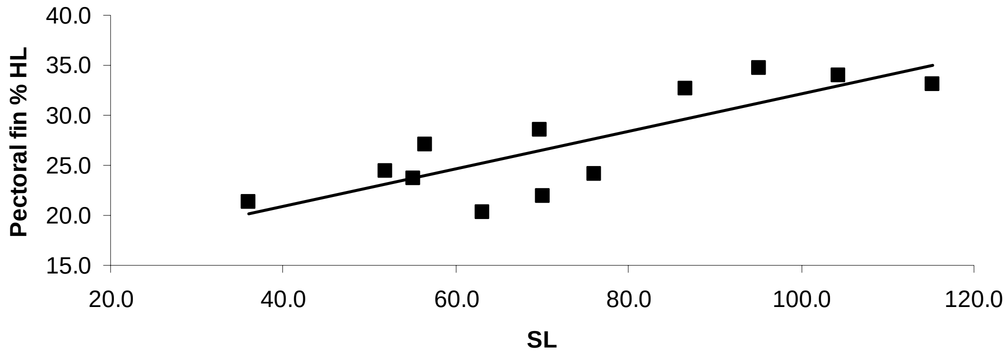
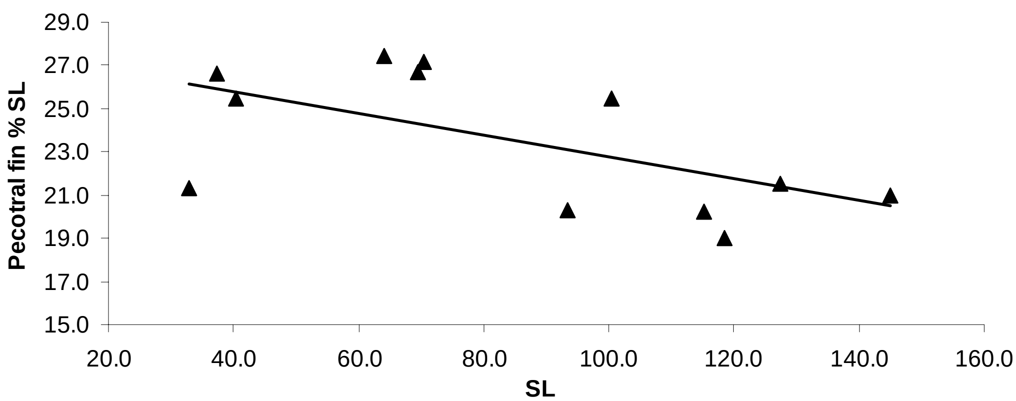

A
B
C
D

FIGURE 4.11. (A) Graphic of the statistically significant positive allometric growth of the pectoral fin in relation to standard length in *Pseudoscopelus scriptus* ($P=0.001$); (B) significant negative allometric growth of the pectoral fin in relation to standard length in *P. obtusifrons* ($P=0.042$); and (C) significant negative allometric growth of the pectoral fin in relation to standard length in *P. australis* ($P<0.001$).

A


Pectoral fin % HL
40.0
35.0
30.0
25.0
20.0
15.0
20.0
40.0
60.0
80.0
100.0
120.0
SL

B


Pecotral fin % SL
29.0
27.0
25.0
23.0
21.0
19.0
17.0
15.0
20.0
40.0
60.0
80.0
100.0
120.0
140.0
160.0
SL

C

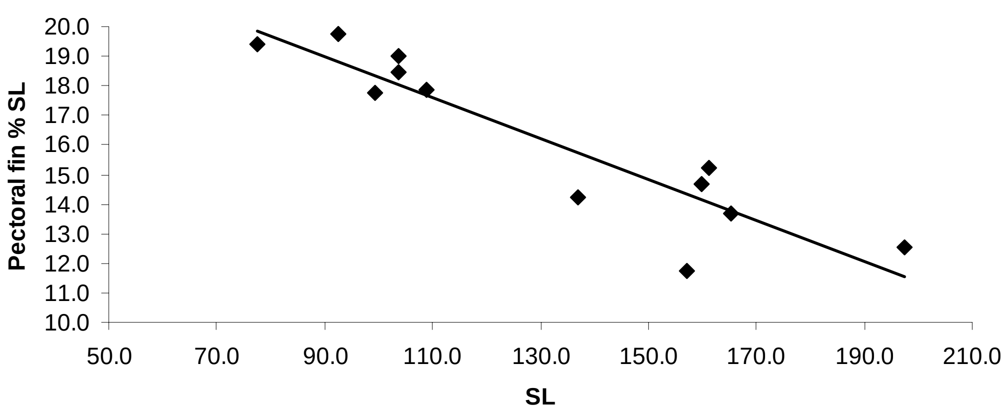

Pectoral fin % SL
20.0
19.0
18.0
17.0
16.0
15.0
14.0
13.0
12.0
11.0
10.0
50.0
70.0
90.0
110.0
130.0
150.0
170.0
190.0
210.0
SL

FIGURE 4.12. (A) *Pseudoscopelus scriptus*, ZMUC P. 65171, 70.0 mm, holotype; (B) *P. scriptus* USNM 240671, 104.4 mm; (C) MCZ 68449, 55.0 mm. (D–J) type series of *P. stellatus*, (D) USNM 170941, 18.7 mm, holotype; (E) CAS–SU 66496, 6.5 mm, paratype; (F) CAS–SU 66494, 10.7 mm, paratype; (G) CAS–SU 66497, 16.7–20.3 mm, paratypes ; (H) ventral view of holotype; (I) head of holotype, left side in lateral view; (J) detail of *mxf* photophores in head of holotype.

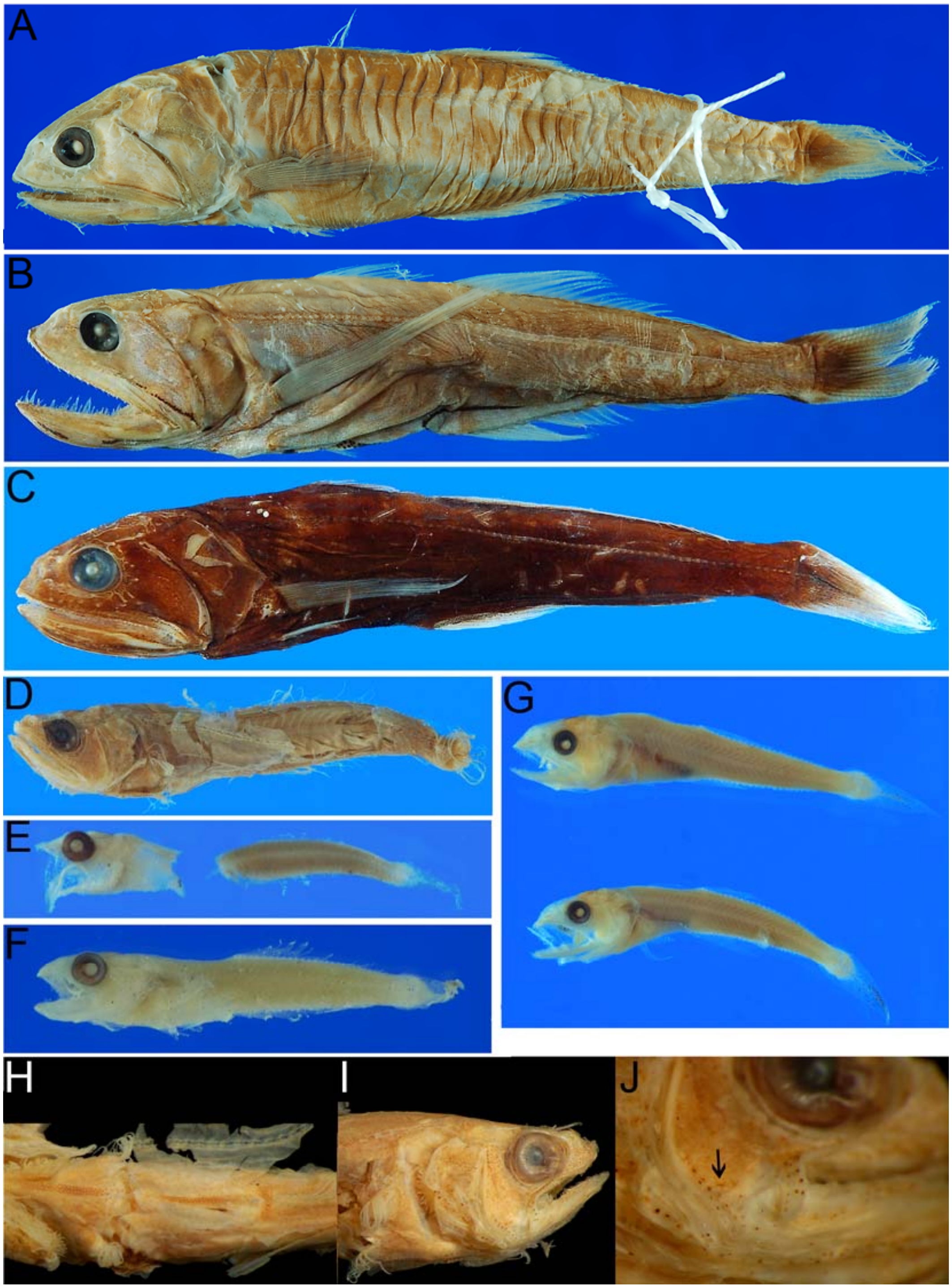

A
B
C
D
E
F
G
H
I
J

FIGURE 4.13. (A) *Pseudoscopelus sagamianus*, FMNH 55551, 143.5 mm, holotype; (B) *P. sagamianus*, BMNH 1984.1.1.93, 97.8 mm; (C) *P. cephalus*, USNM 93142, 74.5 mm, holotype.


A
B
C

FIGURE 4.14. (A) *Pseudoscopelus obtusifrons*, USNM 93141, 93.3 mm, holotype; (B) *P. obtusifrons*, HUMZ 130764, 118.6 mm; (C) *P. obtusifrons,* USNM 268429, 115.2 mm (notice *rtf* photophores along body); (D) *P. obtusifrons,* NMNZ P. 20074, 100.7 mm, lateral view of head with anterior teeth of premaxilla and dentary evident; and (E) *P. obtusifrons,* NMNZ P. 20074, 100.7 mm, ventral view of body, with *lvf* indicated by arrows.

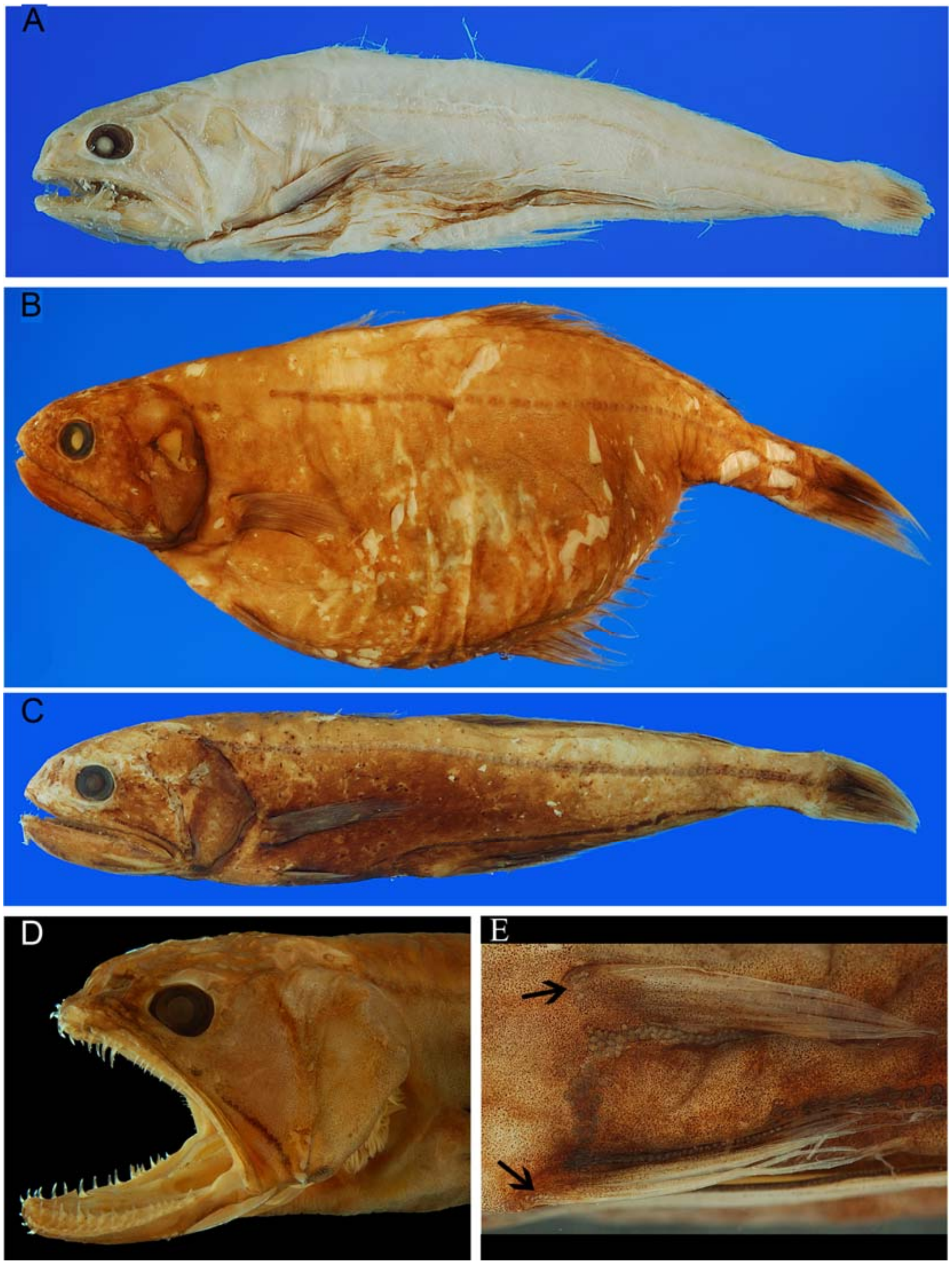

A
B
C
D
E

FIGURE 4.15. (A) *Pseudoscopelus pierbartus*, USNM 240687, 87.1 mm; (B) *P*. *pierbartus*, ZMUB 16378, 1, 179.8 mm; (C) *P*. *pierbartus*, MCZ 164762, 96.0 mm, lateral view of head; (D) *P*. *cordilluminatus*, MCZ 161017, 77.0 mm, holotype; E) *P*. *cordilluminatus*, CAS 223102, 88.7 mm, paratype.

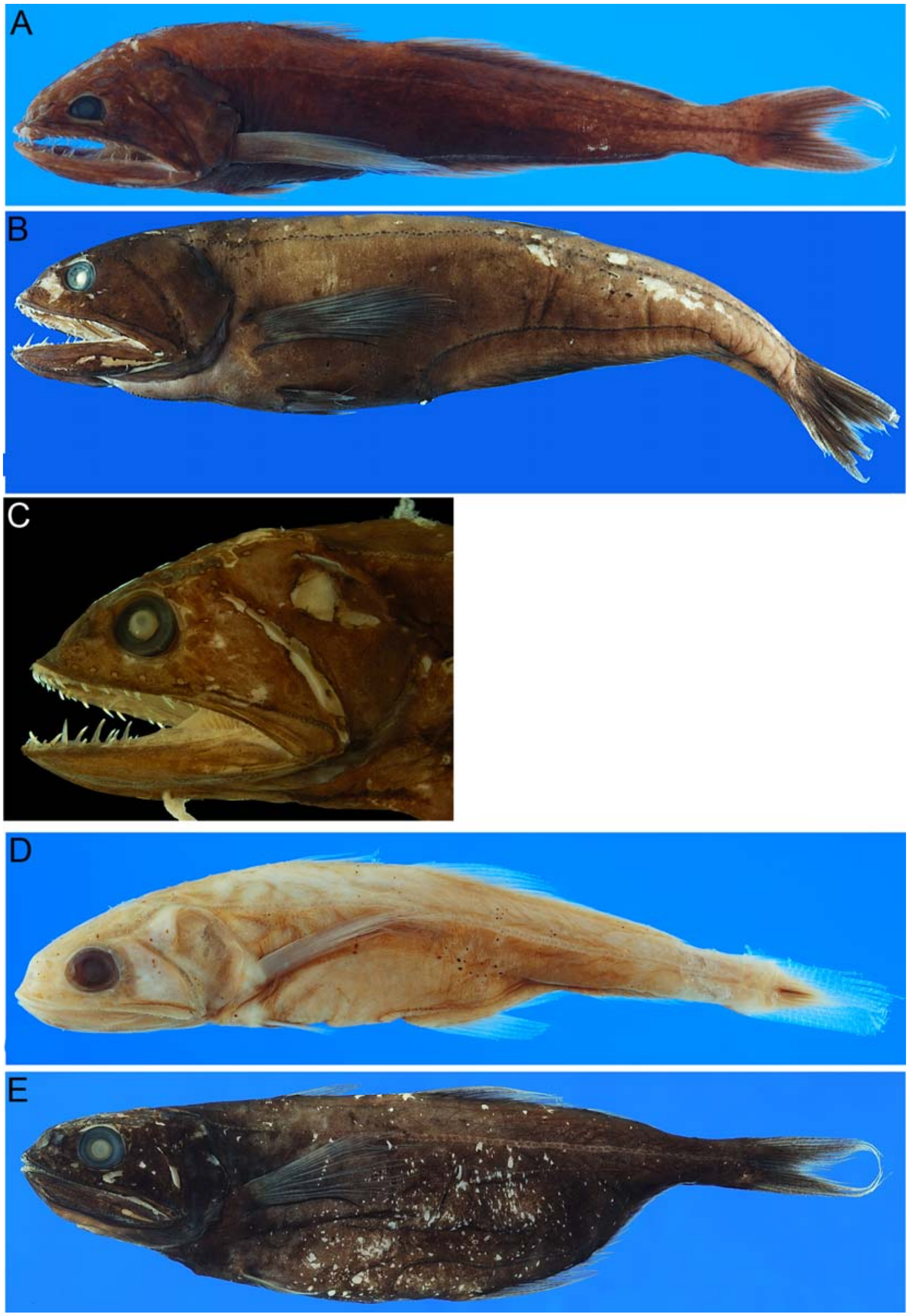

A
B
C
D
E

FIGURE 4.16. (A) *Pseudoscopelus altipinnis*, YPM 2798, 185.8 mm, holotype; (B) holotype of *P. microps*, USNM 93139, 122.7 mm; (C) *P. paxtoni*, NMNZ P. 28657, 205.1 mm, holotype; (D) *P. paxtoni*, MNMZ P. 37858, 200.4 mm, paratype.


A
B
C
D

FIGURE 4.17. (A) *Pseudoscopelus scutatus*, USNM 236776, 70.0 mm; (B) *P. scutatus*, lateral view of head of ZMH, 25243, 80.4 mm, paratype; (C) *P. bothrorrhinos*, LACM 31502–2, 45.9 mm, holotype; (D) *P. bothrorrhinos*, LACM 56616-1, dorsal view of a cleared stained specimen, arrows indicate the plate-like distal radials of first dorsal fin. Scale bar equals 5.0 mm.

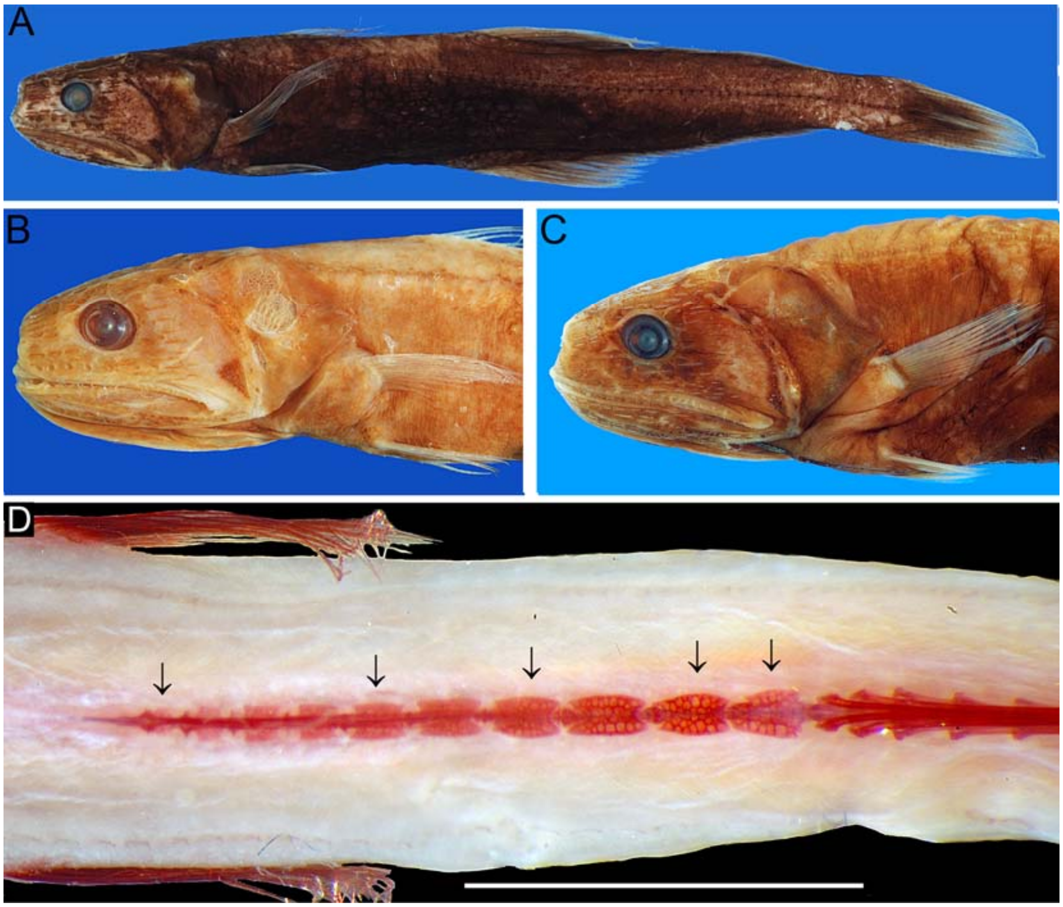

A
B
C
D

FIGURE 4.18. (A) *Pseudoscopelus aphos*, USNM 296957, 71.9 mm, (B) *P. aphos* USNM 296948, 58.6 mm, detail of internal pigmentation of mouth; (C and D) *P. parini*, NMNZ P. 24463, 100.8 mm, in lateral and ventral views.


A
B
C
D

FIGURE 4.19. (A) *Pseudoscopelus astronesthidens*, MCZ 163443, 71.8 mm; (B) *P. australis*, NMNZ P. 40787, 197.4 mm; (C) *P. odontoglossum*, SIO 68–48, 43.3 mm, holotype; (D) *P. lavenbergi*, LACM 30573–1, 86.3 mm, holotype.


A
B
C
D

CHAPTER 5 – A NEW SPECIES OF *DYSALOTUS* MACGILCHRIST

Publication:

Melo, M. R. S. (to be submitted) A new chiasmodontid of the genus *Dysalotus* MacGilchrist (Acanthomorpha: Chiasmodontidae)

Abstract

A new chiasmodontid is described: *Dysalotus acanthobrychos*. It is diagnosed from the other two species in this genus, *D. alcocki* and *D. oligoscolus*, by the teeth on premaxilla and dentary extremely numerous, 198 and 199, respectively (vs. premaxillary teeth 75–138; dentary teeth 67–132). *Dysalotus acanthobrychos* is only known from a single sites in the North Pacific, north of Hawaii. Updated maps of distribution with new records and a key for the species of *Dysalotus* are provided.

Introduction

Dysalotus MacGilchrist is a rare genus of the family Chiasmodontidae; it is very distinctive because of the enlarged prickles along the flank, fragile bones of the head, and numerous needle-like teeth on the premaxilla and dentary. It is a typical representative of the bathypelagic zone and has a tropical and subtropical distribution in the Atlantic, Indian and Pacific Oceans. Three species are currently recognized as valid, one of which is described herein. *Dysalotus alcocki* MacGilchrist 1905 was described based on a single specimen obtained from off the Bengal Bay, India, in the Indian Ocean; *D. oligoscolus* Johnson and Cohen 1974, from the Pacific and several localities in the Atlantic and Indian Oceans; and *D. acanthobrychos* n. sp. from the north Pacific.

Along with the description of *Dysalotus oligoscolus*, Johnson and Cohen (1974) provided a very detailed osteological description of it and *Kali parri*, as well as morphometric and meristic comparisons between all species of *Dysalotus* and *Kali* known up to date. Herein *Dysalotus acanthobrychos*, a new species is described, and an updated map of distribution of all species is given with additional material available.

Material and Methods

Morphometric and meristic data were taken according to the protocol described by Melo (2007), with modifications proposed by Melo (2008). Measurements were recorded to the nearest 0.1 mm using digital calipers. Counts of dorsal-, anal-, caudal-, and pelvic-fin rays are indicated as follows: true spines (*sensu* Johnson and Patterson, 1993) in uppercase Roman numerals, soft unbranched rays in lowercase Roman numerals, and soft branched rays in Arabic numerals. Pectoral-fin rays are listed as the total number of rays, rather than branched/unbranched, because rays were frequently broken. Counts of the caudal-fin rays were made ventral to dorsal, with the first principal caudal-fin ray as the most anteroventral ray, and the last as the most dorsal ray Vertebral counts were made from cleared and stained or x-rayed specimens. Terminology for tooth attachment follows Fink (1981). Morphometric data for the previously described species are given in Table 5.1, meristic in Table 5.2, and dentition in Table 5.3.

Major ocean terminology follows Tomczack and Godfrey (2003); biogeographic zones for the Atlantic follow Backus *et al.* (1977) with the addition of Atlantic Subantarctic to the region between the South Atlantic Subtropical and Guinean Provinces, and Southern Ocean; classification for Indian and Pacific Oceans follows Springer (1982). Institutional abbreviations are as listed at http://www.asih.org/codons.pdf; cs stands for cleared and stained.

Results

Key to the species of *Dysalotus*

1a Prickles of body arranged in one row above and parallel to lateral line, and one row below and parallel to lateral line (Fig. 1 A). .... *Dysalotus oligoscolus*

1b Prickles of body in several rows, above and below lateral line (Fig. 1). 2

2a Premaxilla very long, 64–74% in head length; teeth relatively fewer, 100 or less, in 3–4 rows, pectoral-fin rays 12. ....*Dysalotus alcocki*

2b Premaxilla is short, 55% in head length; teeth numerous, 200 or more in both premaxilla and dentary, arranged in 6–7 rows, pectoral-fin rays 13……………….
.... *Dysalotus acanthobrychos*

Dysalotus acanthobrychos, new species

Figure 5.2, Tables 5.1 and 5.2

Holotype. FMNH 88135, 1, 160.7 mm SL, Off Leeward Oahu, Hawaiian Islands, North Atlantic, 21º23’ N, 158º18’ W, 1500 m, 20–II–1971, R. E. Young col.

Diagnosis. *Dysalotus acanthobrychos* is diagnosed from its congeners by the larger number of teeth in premaxilla and dentary and the shorter premaxilla: premaxillary teeth 198, in five to seven rows (*vs*. premaxillary teeth 75–117 in *D. alcocki* and 60–138 in *D. oligoscolus*, in three rows) and dentary teeth 199, in five to seven rows (vs. dentary teeth 76–126 in *D. alcocki*, 67–132 in *D. oligoscolus*, in three rows); premaxilla 54.9 %

in head length (vs. 62.4–68.3 % in *D. alcocki*, 64.4–74.4 % in *D. oligoscolus*). *Dysalotus acanthobrychos* further differs from *D. oligoscolus* by the presence of several rows of prickles on body, above and below lateral line (vs. prickles on body in a single row above and below lateral line); and vomerine teeth absent (vs. 1-3 vomerine teeth present).

Description. Morphometric data summarized in table 5.1, and meristic in table 5.2. Body elongated, laterally compressed. Greatest body depth at origin of first dorsal fin. Scales absent, except for lateral-line scales, embedded in skin. Well developed and pungent prickles in three to four rows above and below lateral line, from posterior half of body to caudal peduncle.

Anterior profile of head elongated, triangular in lateral view, slightly concave dorsally. Snout pointed. Bones of head fragile, with bone trabeculae visible by naked eye. Head with cavernous appearance, with dorsal concavity at level of braincase medially and well developed crests in frontals, extending laterally to concavity in posterior part of cranium, and converging at level of posterior naris; foramina of sensorial system of head wide. Lower jaw projecting anterior to upper jaw; medial ventral knob at symphysis of dentaries, projecting anteriorly. Orbit circular, nares oval and distinctly separated.

Pectoral-fin rays 13, rays of fins fragile and often broken, pectoral fin insertion lateral on body, posterior to angle of opercle. Pelvic-fin rays I+5, insertion ventral, below and slightly anterior to insertion of pectoral fin. Dorsal fin two, first-dorsal fin rays X; second dorsal-fin rays 26. Anal-fin rays 26, opposite to second dorsal fin, lacking true spines. Caudal-fin rays ii+6+6+ii, forked, lacking true spines. Lateral line complete, pores 41, wide. Sensory system of head mostly destroyed. Pores in infraorbital canal 10; preopercular canal six; mandibular canal five. Branchiostegal rays 7.

Gill arches four; pseudobranchia present. Epibranchial of first gill arch attached to opercle until midline; ceratobranchial of second, third and fourth arches linked; fourth gill arch mostly attached to body wall, except for oval slit in ceratobranchial. Gill rakers teeth-like, needle-shaped, pungent; rakers on epinbranchial 13; rakers on ceratobranchial 17; rakers on hypobranchial absent.

Teeth present on premaxilla, dentary, palatine, upper and lower pharyngobranchials. Premaxillary teeth 198; dentary teeth 199. Premaxilla elongated, slightly arched in lateral view; premaxillary teeth 198, arranged in two to seven transverse rows; increasing in size in first half and decreasing in size posteriorly, and from lateral to medial; needle-like, type 4. Dentary elongated, slightly curved in lateral view; dentary teeth199, in two to seven transverse rows; increasing in size in first half and decreasing in size posteriorly, and from lateral to medial; needle-like, type 4. Palatine teeth 19, anteriorly in two rows and posteriorly in single row; needle-like, type 4. Lower pharyngeal teeth type 4, needle-like, in single row; upper pharyngeal teeth type 4, needle-like, in one to two rows.

Color in alcohol. Specimen severely faded. Epidermis thin and fragile, light brown. Mouth and branchial chamber pale; gill arches and filaments pale.

Distribution. Known only from holotype, collected in the North Pacific.

Etymology. From the Greek *akantha*, means thorn, prickle, and the suffix *-ychos*, meaning from the depth of the sea. In allusion to the many prickles on the sides of body, and to the great depths from where it was collected.

Discussion

The genus *Dysalotus* is diagnosed from the other chiasmodontid genera by three unique characteristics: a ventral knob projecting ventrally at the dentary symphysis (vs. knob absent); and enlarged and pungent prickles on the posterior portion of the flank (vs. prickles absent, or, if present, small and not pungent); total vertebrae 39 to 40, precaudal vertebrae 15 to 16 (vs. total vertebrae 42 to 48, precaudal vertebrae 19 to 25 in *Chiasmodon*; 33 to 40 and 20 to 26 in *Kali*; and 31 to 38 and 14 to 19 in *Pseudoscopelus*).

Dysalotus further differs from *Chiasmodon* and *Pseudoscopelus* by the bones forming cranium, with trabeculae easily distinguishable with the naked eye (vs. bones forming the cranium compact); nasal weakly calcified, circular but not spoon-shaped, located dorsally, and covered by pigmented skin (vs. nasal strongly calcified, spoon-shaped, located anterolaterally, and covered by thin transparent skin); parietals poorly developed, less than half the length of supraoccipital (*vs.* parietals well-developed, of same length or a little smaller than supraoccipital); pre- and postzygapophyses absent (vs. pre- and postzygapophyses present on vertebrae) large elongated neuromasts absent; small circular neuromasts present or absent on cheek and in two rows between supraoccipital and dorsal fin (*vs.* large, elongated neuromasts present on surface of head, over supraoccipital, parietals, frontals and pterotic cranial bones, cheek, snout, lower jaw, and in body as two parallel rows anterior to first dorsal fin); last pored lateral line scale contiguous with penultimate scale (vs. last pored scale of lateral line well separated from the penultimate scale and positioned over the lower lobe of the caudal fin); and caudal fin with two unbranched rays, six to seven branched rays in the ventral lobe and two unbranched rays, six to seven branched rays in the upper lobe (vs. caudal fin with one unbranched ray and seven branched in the lower lobe, and one unbranched ray and eight branched in the upper lobe).

Dysalotus is further diagnosed from *Kali* by dentition in three to seven rows (vs. two rows), teeth needle-like, straight, type 4 (vs. strikingly recurved teeth with ventral attachment to bone absent in mesial row teeth), and branchiostegal rays seven (*vs.* six).

The species of *Dysalotus* are externally very similar; *D. acanthobrychos* shares the pattern of prickes on body with *D. alcocki*. *Dysalotus oligoscolus* differs from both species by having a reduced number of prickles, restricted to a single row above and another below lateral line. Both *D. oligoscolus* and *D. alcocki* differ from *D. acanthobrychos* by the lower number of teeth in premaxilla and dentary and the longer premaxilla.

Comparative material

Dysalotus alcocki: 25 specimens; holotype examined via pictures. Atlantic, Slope Water: MCZ 60722, 1, 34.3 mm, 39°28’ N, 64°36’ W, 800–1000 m, 2–X–1984, R/V *Knorr*; MCZ 65494, 1, 29.8 mm, 36°04’ N, 71°29’ W, 746–1001 m, 19–VIII–1982, R/V *Oceanus*; MCZ 163223, 1, 42.4 mm, 39°54’ N, 67°33’ W, 16–V–2003, R/V *Delaware*. North Sargasso Sea: CAS 27550, 1, 49.4 mm, 32°12’ N; 64°36’ W, 6–II–1930, 1280 m, W. Beebe col. South Sargasso Sea: UF 158785, 1, 69.8 mm, 22°38’00” N; 75°18’24” W, 2250 m, 24–VII–1971, R/V Phillsbury; MCZ 60760, 1, 37.0 mm, 26°21’N, 78°46’ W, 12–X–1983; R/V *Iselin*. Caribbean Sea: UF 106427, 1, 105.6 mm, 9°24’48” N; 78°12’42” W, 51 m, 19–VII–1966, R/V Phillsbury. Lesser Antillean Province: ZMUC P.

658, 1, 176.1 mm, 13°47’ N, 61°26’ W, 24–11–1921, R/V *Dana*. South Atlantic Subtropical: MNRJ 26733, 1, ca. 190.0 mm, 21°26’19” S, 39°49’07” W, 1598 m, 7–VII–2000, R/V *Thalassa*. Guinean Province: USNM 207603, 1 of 2, 207.1, 7°32’ N, 20°54’ W, 0–1300 m, 14–IV–1971, R/V Walter Herwig; ZMUC P. 6584, 1, 160.7 mm, 10°57’ S, 11°20’ W, 7–IV–1971, R/V *Walter Herwig*; ZMUC P. 6585, 1, 161.6 mm, collected with USNM 207603; ZMUC P. 6586, 1, 210.8 mm, collected with USNM 207603. Pacific, Pacific Plate: FMNH 88134, 1, 118.2 mm, 21°23’ N; 158°18’ W, 1–VIII–1971, R. E. Young col.; SIO 60-234-60, 1, 186.6 mm, 2°21’ S, 137°16’ W, 0–2500 m, 2–VII–1960, R/V *Spencer F Baird*; SIO 61-31-60, 1, 78.4 mm, 12°05’ S, 115°26’ E, 0–2000 m, R/V *Argo*; SIO 73-170, 1, ca. 92.0 mm, 0°02’ N, 154°55°’ W, 1280 m, R/V *Melville*; SIO 88-179, 1, 48.4 mm, 7°05’ N, 176°48” W, 20–III–1987, R/V *Atlantis II*. Western Pacific: MCZ 60806, 1, 107.3 mm, 3°11’ S, 149°51’ E, 0–2075 m, 9–II–1982, R/V *Lady Basten*; MCZ 60807, 1, 86.6 mm, 4°49’ S, 153° 18’ E, 2–II–1982, R/V *Lady Basten*; MCZ 60808, 1, ca. 163.0 mm, 11°46’ S, 145°00’ E, 0–1130 m, 30–XI–1981, R/V *Lady Basten*; MCZ 60809, 1, 44.9 mm, 6°43’ S, 152°14’ E, 1180 m, 23–V–1981, R/V *Lady Basten*; SIO 60-130-60, 1, 142.3 mm, 0°07’ N, 169°00’ E, 0–2000 m, 1–XII–1952, R/V *Horizon*; SIO 76-164-60, 1, 137.0 mm, 9°25’ S, 159°06’ E, 3–III–1975, R/V *Alpha Helix*; SIO 70-346-60, 1, 147.9 mm, 14°34’ N, 119°33’ E, 0–1500 m, 19–IX–1970, R/V *Melville*; ZMUC P. 6511, 1, 62.8 mm, 5°36’ S, 131°05’ E, 22–IX–1951, R/V *Galathea*.

Dysalotus oligoscolus: Atlantic, Azores-Britain Province: BMNH 2002.3.2.86, 1, 55.9 mm, 48°53’52” S, 16°45’52” E, 4835 m, 7–X–2000, R.R.S. *Discovery*. South Atlantic Subtropical: USMN 207607, 1, 207.0 mm (paratype); 15°45’ S, 6°06’ W, 0–1900, 5–IV–1971, R/V *Walther Herwig*; ISH 1459/71, 1, 117.0 mm (paratype), 33°00’ S, 7°50’ E, 0–2000 m, R/V *Walter Herwig*. Atlantic Subantarctic: BMNH 1930.1.12.1063, 1, 123.4 mm, 38°20’ S, 22°18’ W, 1800 m, 10–VI–1927, R.R.S. *Discovery*; ISH 878/71, 2, 147.2–220.3 mm (paratypes), 39°55’ S, 26°02 W, 0–2000 m, R/V *Walter Herwig*; ISH 960/71, 1, 135.7 mm, (paratype), 39°45’ S, 17°40’ W, 0–2000 m, R/V *Walter Herwig*. Pacific Plate: LACM 9708, 1, 127.5 mm (paratype), 27°31’ N, 115°51’ W, 25–I–1967, R/V *Velero IV*; SIO 60-239-60, 1, 66.3 mm (paratype). 5°12.3, N, 143°07’ W, 0–2500 m, 6–VII–1960, R/V *Spencer F Baird*; SIO 60-247-60, 1, 241.2 mm (paratype), 14°52’ N, 151°31’ W, 0–2100 m, 11–VII–1960, R/V *Spencer F Baird*; USNM 288987, 1, 49.6 mm, 9°50’ N, 150°00’ W, 0–1500, 8–II–1979, R/V *Gyre*;

Eastern Pacific: SIO 59-200-60, 1, 115.9 mm (paratype), 25°15’ N, 109°50’ W, 1261 m, 14–III–1959, R/V *Horizon*; SIO 56-72-69, 1, 99.1 mm (paratype), 27°07’ N, 117°02’ W, 0–2926 m, 29/30–XI–1951, R/V *Horizon*. Western Pacific: AMS 19608022, 1, 52.6 mm; SIO 51-87-60, 1, 150.4 mm (paratype), 25°30’ N, 115°16’ W, 21–III–1951, 1902 m, R/V *Paolina-T*. Indian: USMN 207612, 1, 81.6 mm (paratype), 4°52’ S, 60°02’ E, 0–2030 m, 23–VIII–1963, R/V *Anton Bruun*; ZMUC P. 6581, 1, 88.8 mm, (paratype), 5°28’ S, 130°39’ E, 23–III–1929, R/V *Dana*; ZMUC P. 6582, 1, 60.0 mm, (paratype), 44°18’ S, 166°46’ E, 17–I–1952, R/V *Galathea*; ZMUC P. 6583, 1, 91.0 mm, (paratype), collected with ZMUC P. 6582.

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TABLE 5.1. Morphometric data of *Dysalotus acanthobrychos* (n=1), *D. alcocki* (n=10) and *D. oligoscolus* (n=11).

Character	***Dysalotus acanthobrychos***	***Dysalotus alcocki***			***Dysalotus oligoscolus***		
	Holotype	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length (mm)	160.65	49.4–211.0	136.2	59.5	49.6–241.2	145.5	71.4
Head length (mm)	44.87	16.0–56.6	38.2	14.6	15.8–67.5	41.4	18.6
Percentage of HL							
Snout	10.7	9.5–13.7	11.1	1.2	8.5–12.9	11.1	1.2
Upper jaw	54.9	62.4–68.3	64.4	2.1	64.4–74.4	69.9	3.2
Lower jaw	64.8	75.3–81.4	78.7	2.4	66.8–88.1	80.0	6.0
Orbit width	14.7	9.9–14.9	12.0	1.5	11.4–16.0	13.6	1.4
Orbit height	12.4	8.9–11.0	9.9	0.8	9.3–13.7	11.7	1.6
Anterior nostril to eye	13.7	12.1–17.1	15.2	1.3	8.8–15.3	12.3	1.9
Posterior nostril to eye	6.9	6.7–11.0	9.3	1.3	4.0–8.6	6.5	1.3
Distance between nostrils	3.2	1.8–3.8	2.7	0.6	0.9–4.2	2.9	1.0
Interorbital distance	22.4	23.5–27.4	25.0	1.2	20.1–26.2	23.4	1.9
Head width	35.9	31.5–36.1	33.8	1.5	30.3–36.2	33.1	1.9
Cheek depth	6.0	5.6–10.5	7.1	1.5	3.6–8.0	5.7	1.1
Percentage of SL							
Head length	27.9	26.1–32.4	28.8	2.0	24.5–32.6	29.3	2.7
Body width	7.1	3.9–9.6	5.9	1.5	2.5–7.4	5.2	1.4
Insertion of pectoral fin	31.6	29.1–37.0	31.5	2.4	27.0–35.4	31.4	2.7
Insertion of pelvic fin	32.5	29.1–35.4	31.3	1.9	29.5–37.8	32.2	2.5
Pectoral-fin length	14.6	12.0–17.5	14.1	1.7	11.6–17.0	13.9	2.0
Pelvic-fin length	8.7	5.5–10.2	8.2	1.6	6.1–10.9	8.9	1.9
Origin of first dorsal fin	15.8	29.4–38.6	33.8	2.5	30.5–38.4	34.8	2.6
Base of first dorsal fin	16.1	12.4–17.1	15.7	1.6	12.8–22.1	16.8	3.4
First dorsal-fin depth	*	5.2–11.6	9.0	2.8	7.1–10.0	8.6	2.1

TABLE 5.1. (cont.)

Origin of second dorsal fin	51.2	48.0–55.5	52.2	2.1	49.8–55.7	53.2	2.0
Base of second dorsal fin	40.5	37.4–43.0	40.4	2.3	38.5–41.5	39.6	1.2
Second dorsal-fin depth	*	10.4–14.5	12.2	1.4	11.1–14.2	12.2	1.4
Origin of anal fin	14.5	48.4–54.4	51.0	1.9	49.8–54.1	52.4	1.5
Base of anal fin	39.1	33.4–43.1	40.6	3.4	36.3–41.1	39.4	1.9
Anal-fin depth	15.7	9.9–14.3	11.9	1.6	12.0–14.4	13.2	1.7
Peduncle depth	3.7	2.8–3.8	3.4	0.3	2.8–4.0	3.5	0.4
Peduncle length	7.8	7.6–10.5	8.4	1.0	7.5–9.1	8.2	0.8

TABLE 5.2. Meristic data of *Dysalotus acanthobrychos* (n=1), *D. alcocki* (n=12) and *D. oligoscolus* (n=11).

Character	*Dysalotus acanthobrychos*	*Dysalotus alcocki*		*Dysalotus oligoscolus*	
	Holotype	**Range**	**Mode**	**Range**	**Mode**
Fin-rays count					
First dorsal-fin rays	X	VIII–XI	X	VIII–XI	X
Second dorsal-fin rays	26	25–29	25	23–29	27
Anal-fin rays	26	25–29	27	23–27	27
Pectoral-fin rays	13	10—12	12	11–12	11, 12
Pelvic-fin rays	i, 5	i, 5	i, 5	I, 5	I, 5
Caudal-fin rays	ii+6+6+ii	ii, 6-6, 6-8,	ii, 6, 7, ii	ii, 6, 7-8, ii	ii, 6, 7, ii
Branchiostegal rays	7	7	7	7	7
Sensorial Pores					
Lateral line	41	40–44	43	41–43	43
Temporal	*	2	2	1, 2	2
Supratemporal	*	3	3	3	3
Otic	*	1, open	1, open	1, open	1, open
Supraorbital	*	4-5	5	5	5
Epiphyseal branch	*	2	2	2	2
Infraorbital	10	10–11	11	11	11
Preopercular	6	5–6	6	5–6	6
Mandibular	6	6	6	6	6
Fourth mandibular pore	1	1–2	1	1	1
Fifth mandibular pore	1	1	1	1	1

TABLE 5.3. Dentition data of *Dysalotus acanthobrychos* (n=1), *D. alcocki* (n=12) and *D. oligoscolus* (n=11).

Character	***Dysalotus acanthobrychos***	***Dysalotus alcocki***		***Dysalotus oligoscolus***	
	Holotype	**Range**	**Mode**	**Range**	**Mode**
Dentition					
Premaxilla	198	75–117	*	60–139	*
Dentary	199	76–126	*	67–132	*
Vomer	0	0	0	6–22	14
Palatine	19	2–13	9	1–3	2
Gill rakers					
Epibranhial	13	6–16	14	3–16	12
Ceratobranchial	17	11–25	17	8–27	26
Hypobranchial	0	0–3	0	0	0

FIGURE 5.1. Posterior part of body and caudal peduncle in (A) *Dysalotus oligoscolus* and (B) *Dysalotus alcocki* (modified from Jonhson and Cohen 1974).

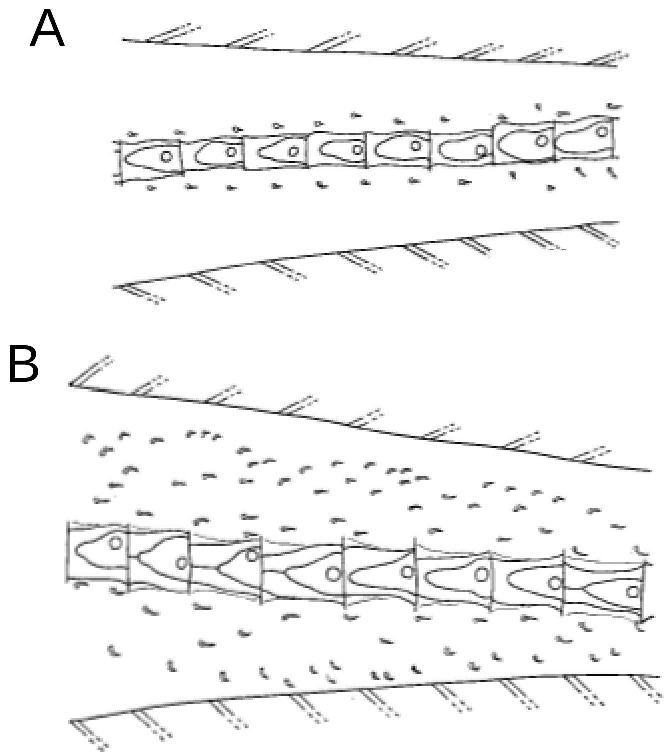


FIGURE 5.2. *Dysalotus acanthobrychos*, FMNH, 160.7 mm, holotype; in (A) body in lateral view; (B), head in lateral view.


A
B

FIGURE 5.3. Lateral view of head of (A) *Dysalotus alcocki*, USNM 207603, 207.1 mm, and (B) *Dysalotus oligoscolus*, ISH 1459/71, 117.0 mm, paratype.

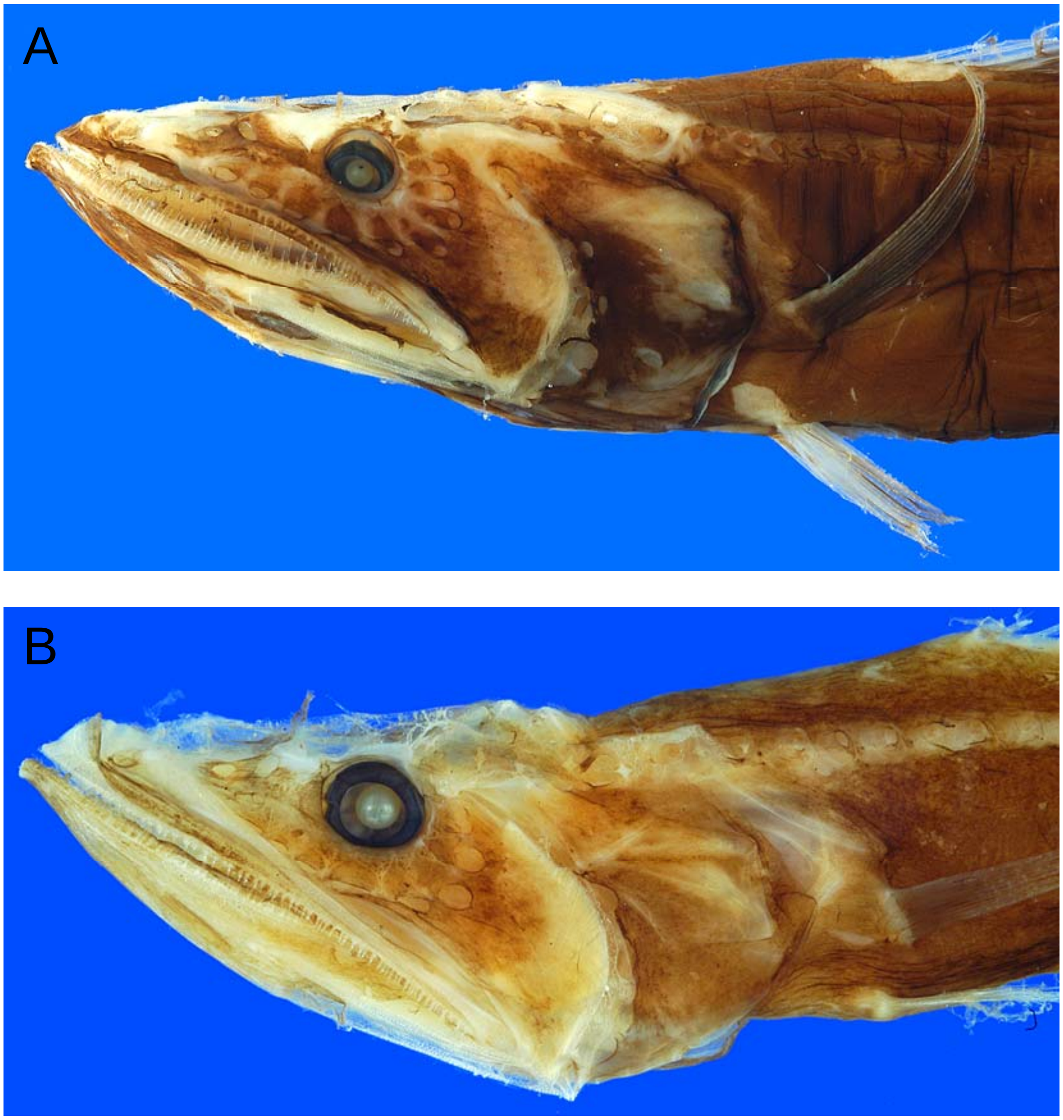
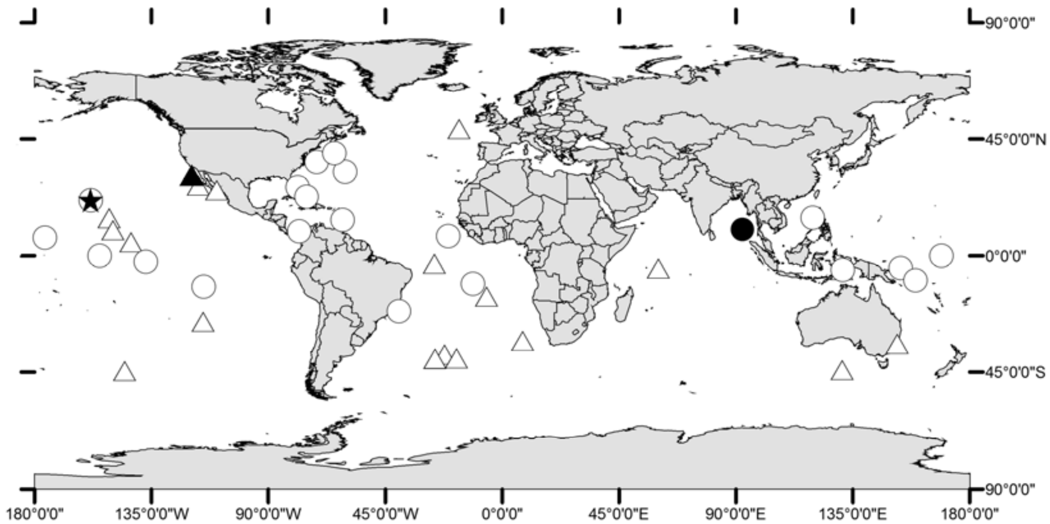

A
B

FIGURE 5.4. Distribution of the genus *Dysalotus*, circles stand for *D. alcocki*, triangles for *D. oligoscolus*, and star for D. *acanthobrychos*. Closed symbols indicate type localities. The paratypes of *D. oligoscolus* not examined herein but listed by Johnson and Cohen (1974) are included. Each point in the map may represent more than one lot.


90°0'0"
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0°0'0"
45°0'0"E
90°0'0"E
135°0'0"E
180°0'0"

CHAPTER 6 – GROSS MORPHOLOGY AND INNERVATION OF THE NEUROMASTS IN THE FAMILY CHIASMODONTIDAE

Abstract

Neuromasts are the mechanoreceptors that forms part of lateral line system in aquatic vertebrates, present on head and body. The canal neuromasts are found enclosed in canals that open to the environment via pores, and the superficial neuromasts are present on the surface of skin. Among the four genera that compromise the family Chiasmodontidae – *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus* – both enclosed and superficial neuromasts are present. Those neuromasts present an incredible variety of shapes, distribution, and innervation only comparable to a few other teleosteans. Neuromast patterns provide good taxonomic and phylogenetic characters for the group. The gross morphology of the lateral-line canals and the canal and superficial neuromasts are described, as well as their innervation, and is compared to other teleosts.

Introduction

The family Chiasmodontidae includes 34 species of meso- and bathypelagic fishes in the families *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus* (Chapters 2–5). The chiasmodontids have extreme aptations for life in the deep-sea, and capturing prey, which are explored in Chapter 7. One of the most remarkable characteristics of this family is the presence of a large number of neuromasts on the surface of head, along the body, and on the caudal fin, in addition to the neuromasts enclosed in the lateral-line system. The neuromasts varied in gross morphology and position among the genera, and some specific patterns were noted.

Neuromasts are the mechanoreceptors that form part of the lateral line system in aquatic vertebrates, and are present along head and body. They can be divided into two groups according to their position: the canal neuromasts are enclosed in the lateral-line canals; and the superficial neuromasts, are exposed on the skin surface. The superficial neuromasts usually are very different from the canal neuromasts in size and by having fewer hair and support cells, and may differ in development (Coombs et al. 1998).

Among the chiasmodontids both canal and superficial neuromasts are present, and there is a considerable variation in shapes and patterns among the genera, but relatively little diversity between the species. Descriptions are made in *Chiasmodon subniger*, *Dysalotus alcocki*, *Kali kerberti* and *Pseudoscopelus altipinnis*, which are good representatives of their genera, and in *Kali parri*, which has a unique pattern. The objectives of this chapter are to describe the gross morphology of both canal and superficial neuromasts, map the major groups and to determine their innervation. Specific variation of patterns and innervation is discussed in Chapter 6.

Material and methods

Terminology for the canal neuromasts follows Coombs et al. (1988). Counts of pores and neuromasts were made from anterior to posterior and are explained in the text, if necessary. Terminology for major groups of neuromasts is based on Sanzo's (1911) classification for the gobiids. Additional numbering of neuromasts groups is explained throughout the text. The terminology for nerves follows Northcutt et al. (2000) with the addition of some branches listed by Wongrat and Miller (1991). The identification of nerves was based on their position and track, meaning that no further histological investigation in the brain were made to determine the neurons from which they originate.

Neuromasts and nerves were examined in preserved specimens via direct observation and gross dissection using a Leica MZ8 stereomicroscope. To enhance differentiation of neuromasts and nerves, a temporary stain was made with 2% Methylene Blue (C.I. 52015) in alcoholic solution. The solution was carefully dropped on the region to be examined until the structure was temporarily stained. The advantages of using 2% Methylene Blue solution are similar to the use of Cyane Blue (Saruwatari et al. 1997), and includes the quick differentiation of nerves, neuromasts, pores of lateral line and myomeres, and the fact that Methylene Blue is soluble in ethanol 75% and water. After the use, the specimens completely recovered their original characteristics after a few hours to a couple days in the preservation solution. Techniques for permanent nerve staining in cleared and stained specimens were tried (e.g. Filipski and Wilson 1984; Song and Parenti 1995), but did not work satisfactory in some nerves, and had the major disadvantage that some structures of interests (i.e. neuromasts and muscles) were destroyed during the enzyme digestion process.

List of abbreviations.

an – anterior naris

buc – buccal ramus of the anterodorsal lateral line nerve

AV – anteroventral lateral line nerve

CIO – infraorbital canal neuromasts

CMD – mandibular canal neuromasts

COT – otic canal neuromasts

CPrO – preopercular canal neuromasts

CPO – postotic canal neuromasts

CSO – supraorbital canal neuromasts

CST – supratemporal canal neuromasts

CT – temporal canal neuromasts

CTR – trunk canal neuromasts

d – dorsal ramus of the posterior lateral line nerve

dav – deep subdivision of the anteroventral lateral line nerve

ib – inner buccal ramus of the anterodorsal lateral line nerve

l – lateral ramus of the posterior lateral line nerve

m – middle lateral line nerve

ob – outer buccal ramus of the anterodorsal lateral line nerve

op – opercle

or – otic lateral line nerve

p – posterior lateral line nerve

pn – posterior naris

pop – preopercle

ros – ramus opercularis superficialis of the

SPO – preorbital superficial neuromasts

sav – superficial subdivision of the anteroventral lateral line nerve

so – superficial ophthalmic ramus of the anterodorsal lateral line nerve

SSN – suborbital superficial neuromasts

SMD – mandibular superficial neuromasts

sav – superficial subdivision of the anteroventral lateral line nerve

SOP – opercular superficial neuromasts

SOC – occipital superficial neuromasts

SIO – interorbital superficial neuromasts

SBN – body superficial neuromasts

SCN – caudal superficial neuromasts

v – ventral ramus of the posterior lateral line nerve

Results

Both canal and superficial neuromasts are present in the four chiasmodontid genera: *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus* (Fig. 1). Canal neuromasts are included in the lateral system canals along the head and body. The superficial neuromasts are more concentrated on the head, but are also present on body and caudal fin. The superficial neuromasts vary in shape and for and a more detailed description of these groups and innervation is given below. Because of topological similarities, the descriptions are made in the following sequence: *Chiasmodon; Pseudoscopelus*; *Dysalotus*; *Kali*; and, if needed, *K. parri*.

Gross morphology

Canal neuromasts are diamond-shaped, not pigmented, and in most cases can only be visualized by dissection of the canal; except for the otic and postotic canals in *Dysalotus* and *Kali* (Fig. 2 A). The canal neuromasts are generally positioned between each two pores, and are named after the canal in which they are enclosed – although in some cases the neuromasts in the same canal were not innerved by the same nerves. Nine groups of canal neuromasts were recognized: supraorbital; otic; postotic; supratemporal;

temporal; infraorbital; preopercular; mandibular; and trunk canal.

Three basic shapes of superficial neuromasts were found: papillae, which are small and rounded neuromasts present in *Chiasmodon*, *Pseudoscopelus* and *Dysalotus* (Fig. 2 B); ovals, which are large and elongated neuromasts, in *Chiasmodon* and *Pseudoscopelus* (Fig. 2 C); and rods, which are enlarged neuromasts that project out of the skin, unique to *Kali* (Fig. 2 D). Eight general groups of superficial neuromasts were recognized, named herein after their position on body and innervation: preorbital, suborbital, mandibular, opercular, interorbital, occipital, body, and caudal-fin neuromasts. Schematics of the distribution of canal and superficial neuromasts among the chiasmodontids is presented in figures 6.3 to 6.9.

Canal Neuromasts

The lateral line canals are interconnected, and extend on the tip of snout, dorsal portion of cranium, face, preopercle, lower jaw and along flank to caudal fin.

The supraorbital canal is positioned on the anterior and dorsal surface of the head. It extends from the tip of the snout, pierces the nasal, the lateral edge of the frontal and is connected posteriorly to the otic canal. In *Chiasmodon* and *Pseudoscopelus*, the first and second pores are very small and the third pore is formed in the nasal. In the four genera, the third pore is limited by the nasal, remarkably larger, and covered by a thin membrane – i.e., it is not open to the environment. The remaining pores are on the frontal and parietal. *Kali* has five supraorbital canal neuromasts (CSO), *Chiasmodon* and *Pseudoscopelus*, six, and *Dysalotus*, seven.

The otic and postotic canals are continuous and without a clear limit – because of this they were treated solely as the otic canal in previous chapters. The otic and postotic neuromasts, however, can be differentiated by innervation. The otic/postotic canal pierces the anterior half of pterotic, on the dorsal surface of the head. It is connected anteriorly to the supraorbital, posteriorly to the temporal, and ventrally to the preopercular canals. The canal is open in *Dysalotus* and *Kali*, leaving the neuromasts exposed. *Kali* and *Dysalotus* have a single otic canal neuromast (COT), and *Chiasmodon* and *Pseudoscopelus*, two. *Chiasmodon*, *Dysalotus* and *Pseudoscopelus* have one postotic canal neuromast (CPO) and *Kali* lacks this neuromast.

The supratemporal canal is on the dorsal surface of the head. It branches from the postotic canal and pierces the extrascapular bone. In *Chiasmodon* it extends medially on the parietal, without piecing the bone, in *Dysalotus*, *Kali* and *Pseudoscopelus* it is restricted to the extrascapular. There are three supratemporal canal neuromasts (CST) in *Dysalotus* and *Pseudoscopelus*, and two in *Chiasmodon* and *Kali*.

The temporal canal pierces the ventral portion of the posttemporal. It is connected anteriorly to the postotic and posteriorly to the trunk canals. *Chiasmodon*, *Dysalotus* and *Pseudoscopelus* have two temporal canal neuromasts (CT), and *Kali* has a single neuromast.

The infraorbital canal is on the lateral side of head, posterior and ventral and slightly anterior to orbit. It is connected posterodorsally to the otic canal and is dead-end anteriorly. The first pore of the infraorbital canal is ventral to the posterior naris; the last pore can be between infraorbital 6 and the pterotic, dorsal to mid-eye in *Chiasmodon*, *Dysalotus* and *Kali* or anterodorsal to mid-eye in *Pseudoscopelus*. *Kali* has eight infraorbital canal neuromasts (CIO), *Chiasmodon* and *Pseudoscopelus* have 10, and

Dysalotus has 10 or 11.

The preopercular canal pierces the preopercular bone. It is connected dorsally to the otic canal, and ventrally to the mandibular canal. There are four preopercular canal neuromasts (CPrO) in *Kali*, five in *Chiasmodon* and *Pseudoscopelus*, and six in *Dysalotus*.

The mandibular canal pierces the angular and mandibular bones on the ventral part of the head, and extends from the anterior tip to the posterior angle of lower jaw. It is connected posteriorly to the preopercular canal. *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus* have six mandibular canal neuromasts (CMD).

The trunk canal is complete, extending along the lateral side of the body from head to caudal fin. The first pore is positioned on the supracleithrum, and it pierces the modified scales of the lateral line, which are embedded in the skin. In *Chiasmodon* and *Pseudoscopelus*, it extends to the base of the caudal-fin rays and the last scale of the trunk canal is disconnected, positioned on lower lobe of caudal fin. In *Dysalotus* and *Kali* the trunk canal extends to the caudal-fin fork.

Superficial Neuromasts

The superficial neuromasts are distributed on the dorsal part of head, face, opercle, lower jaw, dorsal part of body anterior to dorsal fin, along lateral line, and the caudal fin.

The preorbital superficial neuromasts (SPO) are located on the snout, anterior and/or anteroventral to orbit. They are divided into five groups, SPO1-5. In *Chiasmodon* and *Pseudoscopelus*, SPO1 is a triangular group of ovals on the dorsal and medial region of the snout, around the nasal bone or, in *Pseudoscopelus scutatus* and *Pseudoscopelus bothrorrhinos*, in a concave pit on the anterior portion of the snout. The SPO1 is on an irregular single row of papillae in *Dysalotus*, and on a single row of rods in *Kali*. In both cases the SPO1 is placed on the thin membrane that covers the nasal. The SPO2 is a group of ovals present only in *Chiasmodon* and *Pseudoscopelus*, positioned lateral and dorsal to the first pore of the supraorbital canal above the anterior part of maxilla. The SPO3 is a small group of papillae lateral to nasal, between the second pore of supraorbital canal and anterior naris in *Chiasmodon* and *Pseudoscopelus*; a group of papillae on an irregular longitudinal single row, lateral to the nasal bone, between the first pore and anterior nostril in *Dysalotus*; and a single vertical row of rods between infraorbital pores one and two in *Kali*. The neuromasts of SPO3 in *Dysalotus* are relatively smaller than in the other taxa. The SPO4 is a triangular group of ovals lateral on the snout, between the anterior and posterior naris, present only in *Chiasmodon* and *Pseudoscopelus*. The SPO5 is a group of ovals on the lateral part of snout, anterior to the orbit in *Chiasmodon* and *Pseudoscopelus*; and a longitudinal row of papillae and rods in *Dysalotus* and *Kali*, respectively.

The suborbital superficial neuromasts (SSN) are located on the face, posterior and ventral to orbit. The SSN are ovals in *Chiasmodon* and *Pseudoscopelus*, papillae in *Dysalotus,* and rods in *Kali*. In *Chiasmodon*, the SSN extends to the cheek anterior to the preopercle, dorsal to the upper jaw, and on infraorbital 3, and in *Pseudoscopelus* on infraorbital 2 and, in some species as *P. altipinnis*, infraorbital 1. In *Dysalotus*, SSN is a longitudinal row on the cheek, between the preopercle and the posterior part of the infraorbital canal. In all *Kali*, except *K. parri*, SSN is a short row dorsal to upper jaw and posterior to the infraorbital canal, and in *K. parri* the neuromasts are widespread on the cheek, posterior to the infraorbital canal, along the anterior edge of preopercle, and on a small area ventral to preopercle.

The mandibular superficial neuromasts (SMD) are positioned ventral and lateral on the lower jaw, and is divided into three groups, SMD1-3. The SMD are ovals in *Chiasmodon* and *Pseudoscopelus*, papillae in *Dysalotus*, and rods in *Kali*. In *Chiasmodon* and *Pseudoscopelus*, SMD1 is triangular and longitudinal, lateral on the dentary and dorsal to the mandibular canal. In *Pseudoscopelus* it extends anteriorly to the tip of snout, anterior to mandibular pore one, and in *Chiasmodon* it does not extend anterior to the second pore. The SMD2 is in one or two lateral rows, ventral to the mandibular canal on the dentary. The SMD3 is longitudinal, ventral to the mandibular of angular, between and around mandibular pores five and six. In *Dysalotus* and *Kali* (except *K. parri*), only SMD3 is present with few neuromasts; in *Kali parri* both SMD3 and 2 are present.

The opercular superficial neuromasts (SOP) are positioned on the opercle, and is divided into two groups, SOP1-2. The SOP are ovals in *Chiasmodon* and *Pseudoscopelus*, papillae in *Dysalotus* and rods in *Kali*. SOP1 is dorsal to the opercle. In *Chiasmodon* and *Dysalotus* it is in a single row parallel to the posterior edge of the preopercle, in *Pseudoscopelus* and *Kali* it is in a single row dorsal to the dorsal edge of the opercle, and in *Kali parri* it is in two rows parallel to the dorsal edge of opercle. The SOP2 is anterior and ventral to the opercle. In *Chiasmodon*, *Dysalotus*, *Kali* and in some species of *Pseudoscopelus*, such as *P. scriptus*, it is in a single irregular row anterior and parallel to the preopercle. In *P. altipinnis,* the SOP2 also extends along the ventral edge of the opercle. In *Kali* and *Pseudoscopelus* it reaches the subopercle.

The interorbital superficial neuromasts (SIO) are positioned on the dorsal part of the cranium and are divided into five groups, SIO1-4 and SIO'. The SIO1-4 are ovals in *Chiasmodon, Pseudoscopelus*, papillae in *Dysalotus*, and rods in *Kali*; SIO' is only present in *Chiasmodon* and *Pseudoscopelus*, and are papillae. The SIO1-4 are present in *Chiasmodon* and *Pseudoscopelus*, but only the SIO2 are present in *Kali* and *Dysalotus*. SIO1 is dorsal, on the anterior part of frontal, and it occupies a larger area in *Pseudoscopelus* than *Chiasmodon*. SIO2 is dorsolateral, on the pterotic, frontal, infraorbital six, and skin between the posterior naris and orbit. In *Pseudoscopelus*, SIO2 is elongated and is located between the posterior naris and eye, the region above the orbit, interorbital six, and the pterotic; in *Chiasmodon,* it is shorter and does not extend anterior to the orbit; in *Dysalotus* and *Kali* it is in a single row, between the pterotic and frontal. SIO3 is composed of two to four neuromasts on the posterolateral edge of the parietal, and a group of neuromasts on the posterior part of the frontal and sometimes on the supraoccipital; it also occupies a larger area in *Pseudoscopelus* than in *Chiasmodon*. SIO4 is dorsal, on the posteromedial half of the frontal and rarely on anterior parts of the parietal and supraoccipital. SIO' is dorsal on the frontal, posterior to SIO1 and on the skin that surrounds the supraorbital pore positioned between SIO1 and SIO3. All neuromasts are longitudinally arranged with the exception of a small neuromast on the anteromedial parts of SIO4 and SIO', where the neuromasts are remarkably smaller and transversely oriented.

The occipital superficial neuromasts (SOC) are in a single row, dorsal on the body between the head and first dorsal fin. The neuromasts are oval in *Chiasmodon* and *Pseudoscopelus*, papillae in *Dysalotus*, and rods in *Kali*.

The body superficial neuromasts (SBN) are positioned between the lateral-line pores, or in rows above and below the lateral-line canal. In *Chiasmodon* and *Pseudoscopelus*, the neuromasts between the lateral line pores are oval, and the dorsal and ventral rows are papillae; they are papillae in *Dysalotus*, and rods in *Kali*.

The caudal-fin superficial neuromasts (SCN) are divided into two groups SCN1-2. SCN1 is on the dorsal lobe of the caudal fin, between branched caudal-fin rays four and five; SCN2 is on the ventral lobe of the caudal fin between branched rays three and four. The neuromasts are papillae in *Chiasmodon*, *Pseudoscopelus* and *Dysalotus*, and rods in *Kali*.

Innervation

Nine rami of five lateral line nerves innervate the canal and superficial neuromasts in chiasmodontids: superficial ophthalmic and buccal rami of the anterodorsal lateral line nerve; anteroventral lateral line nerve; otic lateral line nerve; middle lateral line nerve; and dorsal, lateral and ventral rami of the posterior lateral line nerve. Schematics of innervation of neuromasts in chiasmodontids are in figures 6.9 to 6.17.

The anterodorsal lateral line nerve innervates the canal neuromasts CSO, most of the CIO, and the superficial neuromasts of SPO1-5 and SIO' (Figs. 9–11, 14–17). It exits the neurocranium via the trigeminal foramen, and immediately branches off into the superficial ophthalmic and buccal rami. The superficial ophthalmic ramus courses dorsally, along the ventral shelf of frontal in the orbit, and dorsally on the snout under the supraorbital canal. In the orbit capsule, it gives rise to three ramules that innervate the CSO and SIO'. It also innervates COT in *Kali parri* (Figs. 11 and 17). Anteriorly, it exits the orbit capsule, passing medial to the lateral ethmoid. In the snout, it enters the supraorbital canal, where it innervates the most anterior CSOs. Before reaching the nasal bone, it splits into two or three ramules that innervate the nasal and the first CSO.

The buccal ramus extends ventrally along the posterior and ventral margins of the orbit. The first ramule innervates three CIO in the infraorbitals 3 and 4. Next, it splits into the outer and inner buccal rami. The outer ramus courses medial and close to infraorbitals 2 and 1; it innervates all the ventral CIOs except for the first in *Dysalotus* and *Kali*. The inner ramus courses on the ventral margin of the orbit. In *Kali* and *Dysalotus*, the first CIO is innervated by a ramule of the inner ramus. After entering the snout, the inner ramus has a major dichotomy giving rise to two branches, one goes to the tip of snout and innervates SPO1-3, and the other courses dorsally and innervates SPO3-4. In *Dysalotus* and *Kali* the inner ramus also innervates the ascending process of the premaxilla.

The otic lateral line nerve innervates the dorsal portion of the CIO in infraorbitals 5 and 6, and the COT in *Chiasmodon*, *Dysalotus* and *Pseudoscopelus*. In *Kali parri*, it innervates CPO instead of COT (Figs. 11 and 17) – COT is innervated by the superficial ophthalmic ramus of the anterodorsal lateral line nerve. In *Chiasmodon* and *Pseudoscopelus*, it exits the neurocranium via its own foramen, which is slightly dorsal to the trigeminal foramen in the prootic. In *Dysalotus* and *Kali* it shares the trigeminal foramen with other nerves. It courses dorsally, giving rise to two ramules for the CIOs, passes thru a canal in the dermosphenotic and innervates the COT.

The anteroventral lateral line nerve is a member of the hyomandibular trunk, which also includes the sensory and motor fibers of the facial and sensory fibers of the trigeminal (Figs. 12–13). It innervates the CPrO, SSN, SMD and SOP. The hyomandibular trunk exits the neurocranium by the hyomandibular foramen, which is slightly posterior to the trigeminal foramen in the prootic. Initially it courses caudally, passing lateral to the sacullar capsule and medial to the hyomandibula. Before reaching the preopercle, it turns ventrally. Along the hyomandibula it gives rise to one to five ramules that pass thru foramina to the medial side, between the fibers of the A2 section of the adductor mandibulae muscle and innervate the SSN. The ramus opercularis superficialis also branches off along the hyomandibula, but courses caudally. It gives rise to two branches, one of which penetrates the preopercular canal to innervate the CPrOs, and the other passes medially to the preopercle to the opercle and innervates SOP1-2.

Before reaching the lower jaw, the anteroventral lateral line nerve passes laterally thru an enlarged foramen in the hyomandibula, dividing the fibers of the sections A2 (lateral) and A3 (medial) of the adductor mandibulae at their origin. After that it splits into the deep and superficial mandibular subdivisions, which penetrate the lower jaw via the angular. The deep mandibular subdivision passes again to the medial side of the hyomandibular nerve and follows parallel to the ventral edge of the hyomandibula to enter the lower jaw posteriorly. It courses between the fibers of the section Aw of the adductor mandibulae, medially to the angular and dentary. The deep mandibular subdivision gives rise to five ramules which innervate the CMD, and also has motor fibers for the intermandibularis muscle.

The superficial mandibular subsection enters the lower jaw dorsally, at the coronoid process of the angular. It passes thru a foramen and penetrates the mandibular canal. In the angular, it innervates the SMD3. Between the angular and dentary, it passes to the lateral side and splits into a dorsal and a ventral ramule, which innervate SMD1 and SMD2, respectively. In *Dysalotus* and *Kali* this split is not present as SMD 1 is not present, but the nerve still moves to the lateral side in *Kali*.

The middle lateral line nerve innervates the CST, CPO, SIO1-4, the anterior CT in *Chiasmodon*, *Dysalotus* and *Pseudoscopelus*, and the unique CT in *Kali* (Figs. 14–17). The middle lateral line nerve exits the neurocranium sharing the foramen for the vagus and glossophraryngeal nerves, in the exoccipital. It bends dorsally and passes between the fibers of the epaxial muscle. Between the posttemporal and the skull it splits into two rami, m1 and m2. The ramus m1 innervates CPO in *Chiasmodon*, *Dysalotus* and *Pseudoscopelus*, and the first CST in *Kali parri*. In *Chiasmodon* and *Pseudoscopelus* it also innervates SIO1–3, and SIO3 in *Dysalotus* and *Kali*. In *Chiasmodon* and *Pseudoscopelus*, it continues anteriorly, underneath a shelf formed by the lateral edge of the frontal, giving rise to several lateral ramules that innervate the anterior part of SIO2. A branch of the ramus m1 courses medially on the frontal and innervates SIO1. In *Dysalotus* and *Kali*, the ramus m1 does not extend anteriorly to the frontal. The ramus m2 innervates the anterior CT and CST in *Chiasmodon*, *Pseudoscopelus* and *Dysalotus*; in *Kali*, except *K. parri*, it innervates the single CT and the CST; and in *K. parri* it innervates the single CT and the second CST. In *Chiasmodon* and *Pseudoscopelus*, the ramus m2 passes thru a canal in the parietal, becomes exposed dorsally on neurocranium, and gives rise to several ramules which innervate SIO4. In *Kali*, except *K. parri*, and *Dysalotus* it is shorter and does not reach the parietal. In *Kali parri* the ramus m2 also courses inside a canal in the parietal, becomes exposed dorsally on neurocranium and, eventually, reaches the skin that recovers the epiphyseal branch of the supraorbital canal.

The posterior lateral line nerve innervates the posterior CTR, SOC, SBN, SCN and the posterior CT, when present. It exist the neurocranium sharing a foramen with the middle lateral line nerve, on the exoccipital. It courses caudally and, before reaching the supracleithurm, it gives rise to the dorsal ramus. Both the posterior lateral line nerve and the dorsal ramus course parallel and pass medial to the supracleitrhum, but the posterior lateral line nerve goes deep between the epaxial fibers, while the dorsal ramus is superficial.

The first ramule of the dorsal ramus innervates the posterior CT in *Chiasmodon* and *Pseudoscopelus*, then it branches again. A branch innervates the first CTR, and the SCO. The other branch innervates the next two to five CTR, and the SBNs around them. The major trunk of the posterior lateral line nerve continues deep on the body, along the transverse septum, and just lateral to the vertebrae. It gives rise to several ramules which innervate the posterior part of the CTR and SBN. Before reaching the caudal fin muscles, it moves laterally and becomes superficial. Finally, it divides into two branches that innervate the SCN-1 dorsally, the last CTR and SCN-2 ventrally.

Discussion

The origin and homology of neuromasts in Chiasmodontidae

The lateral-line canals in chiasmodontids are complete and a reduction in the number of neuromasts is only present in *Kali*. Allied to the late development of the superficial neuromasts in *Chiasmodon* (Shinagova, 1991), the idea that the superficial neuromasts in chiasmodontids are secondary and not derived from canal neuromasts is stretched, at least in most cases. In *Kali* there are only eight CIO neuromasts (vs. 10 in

Chiasmodon, *Dysalotus* and *Pseudoscopelus*), three CPrO (vs. five in *Chiasmodon* and *Pseudoscopelus* and six in *Dysalotus*), five CSO (vs. six in *Chiasmodon* and *Pseudoscopelus* and seven in *Dysalotus*), two CST (vs. three), and a single CT (vs. two), and, most species of *Kali*, CPO is absent.

The innervation of some groups of superficial neuromasts deserves considerable attention. First, is the position and innervation of SIO' group in *Chiasmodon* and *Pseudoscopelus*. The SIO' is positioned on the dorsal part of the skull, on the skin that delimits a pore of the supraorbital canal, and is also surrounded by the SIO1, 2 and 3, which are innervated by branches of the middle lateral line nerve; however, a ramule of the superficial ophthalmic ramus of the anterodorsal lateral line nerve innervates the SIO'. This ramule needs to pass thru a novel canal in the frontal that connects the ventral shelf of the orbit to the dorsal part of the neurocranium. Moreover, the superficial ophthalmic does not innervate any other superficial neuromast groups. For those reasons, the SIO' is hypothesized to be a primary neuromast, which originates from the supraorbital canal.

The second is a series of modifications in the canal neuromasts of the posterior part of the head in *Kali kerberti* and *K. parri*, which may suggest a series of evolutionary modifications. *Kali parri* is the only species in the genus *Kali* to have a CPO, but it has a different innervation from other chiasmodontids. In all species of *Kali*, the CPO is innervated by a ramus of the otic lateral line nerve (vs. the lateral ramus of the posterior lateral line nerve). In *Kali parri*, the COT is innervated by a ramule of the superficial ophthalmic ramus of the anterodorsal lateral line nerve (vs. the lateral ramus of the posterior lateral line nerve). The innervation of the first CPO by the ramus m1 of the middle lateral line nerve, instead of ramus m2 in *K. parri* is also intriguing. The ramus m1 innervates the COT in all other chiasmodontids, and the first CPO is innervated by ramus m2. Based on such innervation and the absence of CPO in the genus *Kali*, the following changes can be hypothesized: (1) a change in the innervation and the retention of the neuromasts in their original positions, followed by the deletion of CPO in all species of *Kali*, except *K. parri*; (2) a change on the neuromasts, which implies the addition of a CSO at the end of the canal, the lost of CPO and COT in all species of *Kali*, except *K. parri*, and the COT and CPO moved caudally in *K. parri* to replace the original CPO and lost CST, respectively; (3) both process, with the deletion of the original CPO with the addition of an CSO in all species of *Kali*, the original COT moved caudally in *K. parri*, combined to a change of innervation of the first CST. Any of those processes would result on a change of homology of COT, CPO and CST in *K. parri*.

Finally, although *Dysalotus* has seven CSO and *Pseudoscopelus* and *Chiasmodon*, six, only five of them are considered to be homologous based on their position, orientation and innervation. Among the chiasmodontids, two ramules perforate the orbital shelf of parietal to innervate the CSO on the part of the canal – among *Kali*, there is an extra ramule which perforates the pterotic and goes to the COT, as discussed above. In *Dysalotus*, however, the first ramule innervates three neuromasts (vs. one in *Chiasmodon* and *Pseudoscopelus*). Two neuromasts are considered to be a derived condition. In *Chiasmodon* and *Pseudoscopelus* the third anteriormost CSO is positioned above the posterior nostril and has a different orientation from the remaining. That neuromast is also considered to be a secondary condition. *Kali* is considered to have the plesiomorphic state.

The superficial neuromasts in Chiasmodontidae

Superficial neuromasts in fishes are widespread among teleosteans and are considered to have appeared multiple times. The primary superficial neuromasts developed as a result of the reduction of lateral-line canals, which fails to enclose the neuromasts in the embryo. In several cases, the primary superficial neuromasts takes the place of the canal neuromasts, being even more numerous. The secondary superficial neuromasts develop independently from the canal neuromasts; they can either originate from primary neuromasts or can arise in situ. The secondary canal neuromasts also develop later in the larvae or juveniles and are not necessarily associated to the reduction in the canal system (Coobs et al. 1998; Webb 1989). In *Chiasmodon*, the superficial neuromasts develop in juveniles between 38.3 and 66.0 mm, after the development of the canal neuromasts and the lateral-line canals are completely formed (Shinagova 1991). This model of development allied to the absence of reduction in the lateral-line system is indicative that chiasmodontids have secondary superficial neuromasts, although a deeper investigation in the genera *Dysalotus*, *Kali* and *Pseudoscopelus* is still needed.

Papillae-shaped superficial neuromasts are present in *Dysalotus*, *Chiasmodon* and *Pseudoscopelus* and appear to be the plesimorphic condition, similar to most superficial neuromasts found among the teleosts, such as Esocidae, Umbirdae, Ictaluridae and Cyprinidae (Nelson 1972; Puzdrowski 1989; Northcutt 2000). The oval neuromasts are unique to *Chiasmodon* and *Dysalotus*, and apparently are derived papillae. The rod neuromasts are unique to *Kali* and represent a synapomorphy for the genus. *Dysalotus* and *Kali* have superficial neuromasts distributed in single rows, which seems to be the plesiomorphic condition, while in *Chiasmodon* and *Pseudoscopelus* the neuromasts are widespread over broader areas, which also implies on further and more complex ramifications of the nerves and ramules.

In a very general way, the pattern found among teleostans is very similar, with the greatest concentration of neuromasts on the head and anterior part of body. This does not necessarily represent homology, but the need for further sensorial cells on the head. As a consequence, the innervation of superficial neuromasts varies among the different lineages. One of the most remarkable problems for comparisons is the divergence of terminology, even within the same family (see critiques made by Wongrat and Miller 1991). For this reason, the major groups identified by Sanzo (1911) in gobiids are used in this work to describe and compare the superficial neuromasts. For comparison purposes, the terminology of both neuromasts and innervation was expanded for other works, even where it has not been applied originally.

The chiasmodontids have eight of the nine series of superficial neuromasts found in gobiids: preorbital, suborbital, mandibular (= preoperculo-mandibular), opercular, interorbital, occipital (= anterior dorsal), body, and caudal-fin. Only absent group is the oculoscapular group, between the eye and the upper origin of pectoral fin (Wongrat and Miller 1991). Comparing the results presented herein, with the descriptions made by Wongrat and Miller (1991) for eleotrids, several differences and similarities among those two groups were found. The most remarkable difference is the strong reduction of the lateral-line canals in Gobioidei, which are restricted to the supraorbital, postorbital, supratemporal and preopercular canal, or even absent as in the eleotrids.

In regard to the innervation, in chiasmodonts the SSN is innervated exclusively by ramules of the anteroventral lateral line nerve versus the anteroventral lateral line nerve

(= truncus hyomandibularis) and the anterodorsal lateral line nerve (= truncus infraorbitalis?) in *Eleotris*. In chiasmodontids, the SMD is innervated exclusively by the superficial subdivision of the anteroventral lateral line nerve versus the presence of an extra subdivision (=ramus buccalis accesorius). The SPO in a single group, innervated by a single ramus of the posterior lateral line nerve in chiasmodontids, versus SPO in multiple groups, innervated by two rami of the posterior lateral-line nerve in eleotrids. The differences between chiasmodontids and eleotrids include: the innervation of superficial neuromasts include the SMD by the superficial subdivision of the anteroventral lateral line nerve exclusively, SOC divided in a dorsal and a ventral group (SOC1-2) and innervated by the ramus opercularis superficialis, the SPO on the dorsal part of the snout – SPO1 in chiasmodonds and groups s and r in eleotrids – innervated by the buccal ramus of the anterodorsal lateral line nerve (= truncus infraorbitalis).

Champsodontids compromise another group of teleosteans with a large number of superficial neuromasts widespread on the body. The group is of particular interest, since it was once considered to be the sister group of the chiasmodontids (Pietsch and Zabetian 1989; Pietsch 1990). This hypothesis was more recently refuted by both morphological and molecular evidence (Mooi and Johnson 1997; Chen 2001). The innervation of the lateral-line system in *Champsodon* was recently detailed by Nakae et al. (2006). Champsodontids also have some of the canals and canal neuromasts reduced: there are four CIO and CPO is absent, and the infraorbital canal is reduced and split into an anterior and posterior part. The trunk canal is more dorsal than in chiasmodontids, positioned on the epaxials slightly ventral to the dorsal fins (vs. at level of longitudinal septum in chiasmodontids), and does not reach the caudal fin. The CPrO is innervated by ramules of the anteroventral lateral line nerve (vs. a single branch of the anteroventral lateral line nerve courses inside the preopercular canal and innervate all CPrO).

Regarding superficial neuromasts, differences are even more remarkable. Although Nakae et al. (2006) did not attempt to describe those groups, it is very clear that the distribution of the superficial neuromasts in champsodontids is very different from the chiasmodontids. The SPO does not extend to the tip of the snout and a group of neuromasts innervated by the buccal ramus of the anterodorsal lateral line nerve extends dorsally and medially on the frontal. Some superficial neuromasts adjacent to the infraorbital canal are innervated by the outer buccal ramus of the anterodorsal lateral line nerve, which does not happen in chiasmodontids. The SSN extends to the pterotic (vs. restricted to cheek). Some SMD on the dentary are innervated by a deep subdivision of the anteroventral lateral line nerve in champsodontids (vs. deep subdivision of the anteroventral lateral line nerve innervates the CMD exclusively in chiasmodintids). Among the most significant differences in champsodontids, is a second series of SPO on the base of the second dorsal fin and a large number of neuromasts on the body, innervated by a network of ramules from the posterior lateral line nerve.

Tracking homology among the superficial neuromasts of chiasmodontids with other teleosteans is a difficult task. Although some groups of neuromasts are placed in similar positions, differences in innervation may indicate independent origins, as previously suggested by Coombs et al. (2008). In particular, the patterns present in chiasmodonds and champsodontids do not seem to be homologous, corroborating the previous hypothesis that those groups are not closely related (Mooi and Johnson 1997; Chen et al. 2003; Smith and Weeler 2004). Although the sister group of Chiasmodontidae has not been determined, recent data indicates that the family should be placed sister to the Scombroidei (Chen et al. 2003), which lacks superficial neuromasts. Therefore, the presence of superficial neuromasts in Chiasmodontidae probably represents a synapomorphy for the family; and differences among the shape, numbers and distribution of the superficial neuromasts are of phylogenetic significance within the genera and species.

Comparative Material

Chiasmodon braueri, LACM 36048-1, MNRJ 26701; *C. harteli*, BSKU 48916, ZMUC P. 6593, ZMUC P. 65166, ZMUC P. 6598, ZMUC P. 65101; *C. microcephalus*, MNRJ 26691; *C. niger*, USNM 367284, BMNH 1998.8.9.18365, BMNH 1922.5.26.1-3; *C. subniger*, LACM 32205-2; *Dysalotus alcocki*, USNM 207603, ZMUC P. 6584, ZMUC P. 6585, ZMUC P. 6586; *Kali colubrina*, MNRJ 26705, AMS I. 42761002; *K. indica*, LACM 30166-17, MCZ 15887; *K. kerberti*, AMNH 225946, LACM 31110-7, LACM 9633-12; *K. macrura*, LACM 30428-32, 30040-11; *K. macrodon*, USNM 207597; *K. parri*, ZMH 25096 (former ISH 2123b-71), UF 131503; *Pseudoscopelus altipinnis* ZMUC P. 6539, ZMUC P. 5645, MCZ 68460; *P. aphos*, USNM 29657; *P. astronesthidens*, MCZ 163443, MCZ 148307; *P. australis*, NNMZ P. 4307, NMNZ P. 40787, NMNZ P. 28657; *P. bothrorrhinos*, LACM 31524, LACM 56616-1; *P. cordilluminatus*, CAS 223102; *P. lavenbergi*, LACM 30573-1; *P. obtusifrons*, LACM 31528-1; *P. odontoglossum*, SIO 61-48; *P. parini*, LACM 44399-1, NMNZ P. 24463; *P. paxtoni*, NMNZ P. 28057; *P. pierbartus*, LACM 56615-1; MNRJ 26698, USNM 240687, ZMUB P. 1378; *P. sagamianus*, BMNH 1984.1.1.93; *P. scriptus*, MCZ 47850, ZMUC

65171; *P. scutatus*, MCZ 96854, USNM 235776.

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FIGURE 6.1. Posterior portion of head in (A) *Chiasmodon subniger* (LACM 32205-2); (B) *Dysalotus alcocki* (ZMUC P. 6586); (C) *Kali parri* (ISH 2123b-71); and (D) *Pseudoscopelus pierbartus* (USNM 240687). Arrows highlight some papillae; asterisks, oval, and crosses are rod neuromasts. Scale bar equals 2 mm.

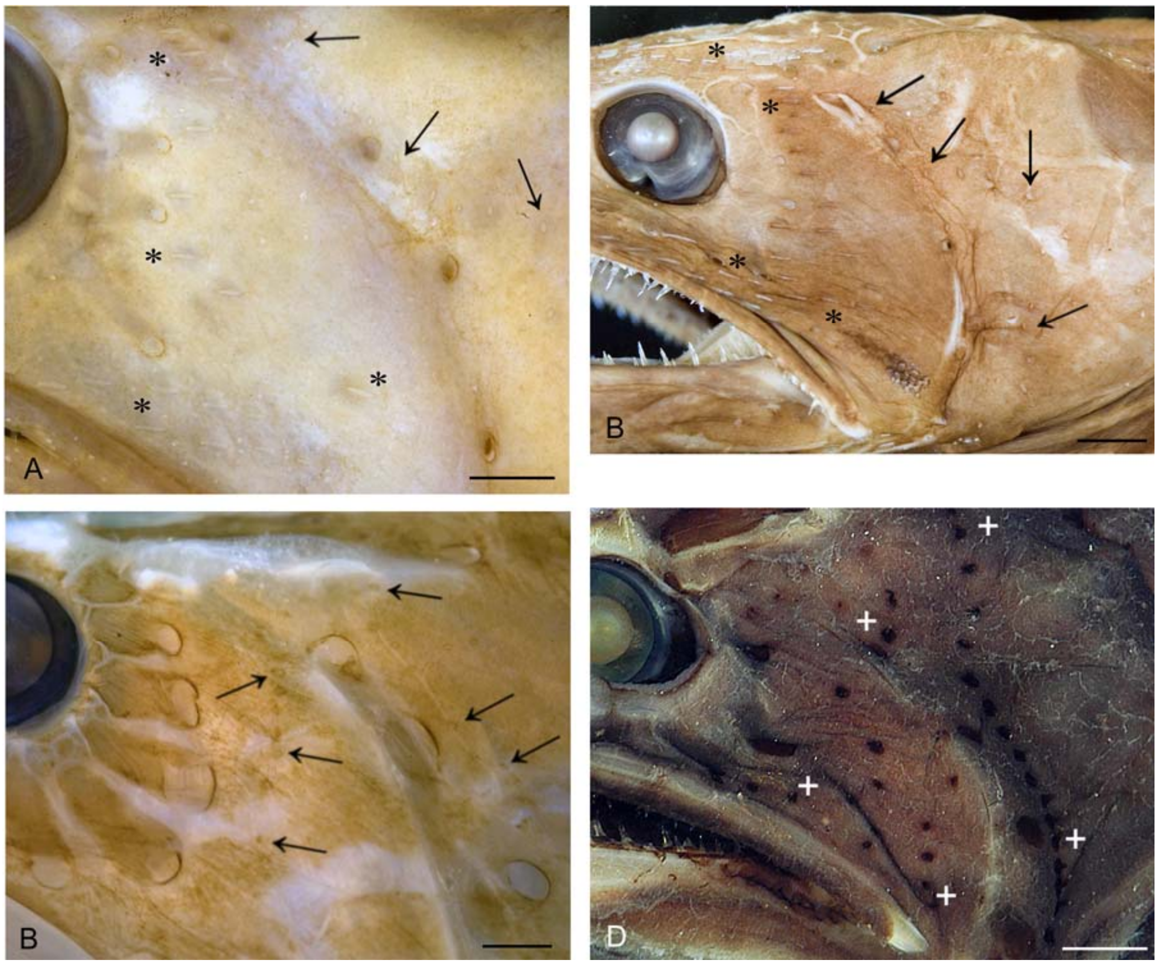
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FIGURE 6.2. Details of canal and superficial neuromasts: (A) canal neuromasts of the supraorbital canal in *Dysalotus alcocki* (ZMUC P. 6584); (B) papilla neuromast in opercular superficial group of *Pseudoscopelus australis* (NMNZ P. 28657); oval neuromast in suborbital superficial group of *Pseudoscopelus australis* (NMNZ P. 28657); and rod neuromast in body superficial group of *Kali kerberti* (AMNH 225946). Anterior to the left; bar equals 2 mm.

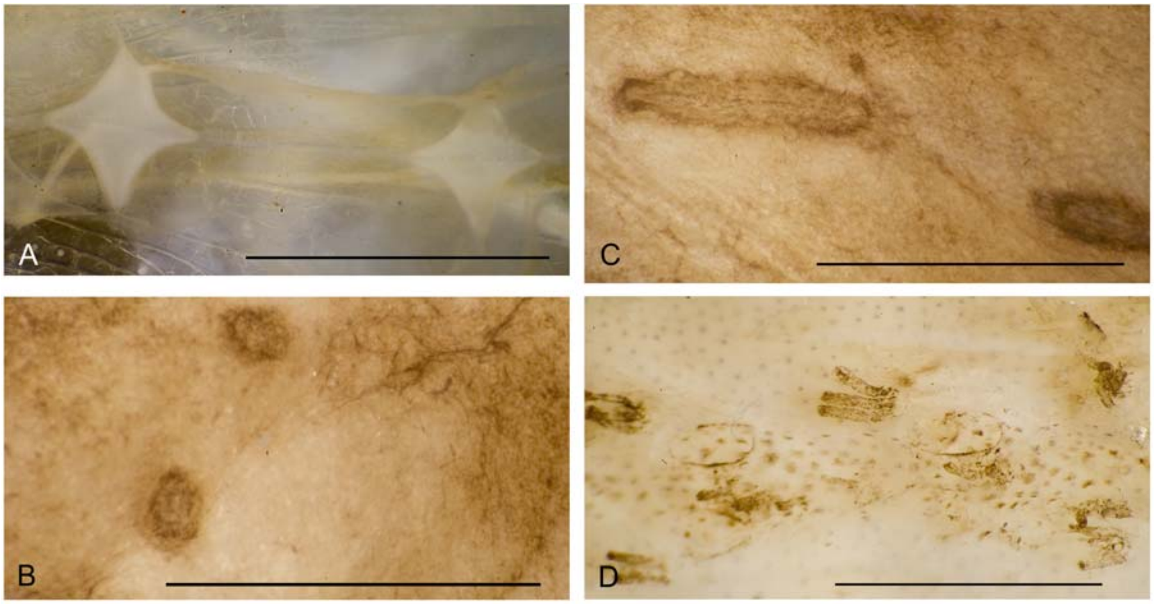
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FIGURE 6.3. Schematic of neuromasts in *Chiasmodon subniger* (LACM 32204-20): (A) lateral view of head, canal neuromasts; (B) lateral view of head, superficial neuromasts; (C) dorsal view, superficial (top) and canal (bottom) neuromasts. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

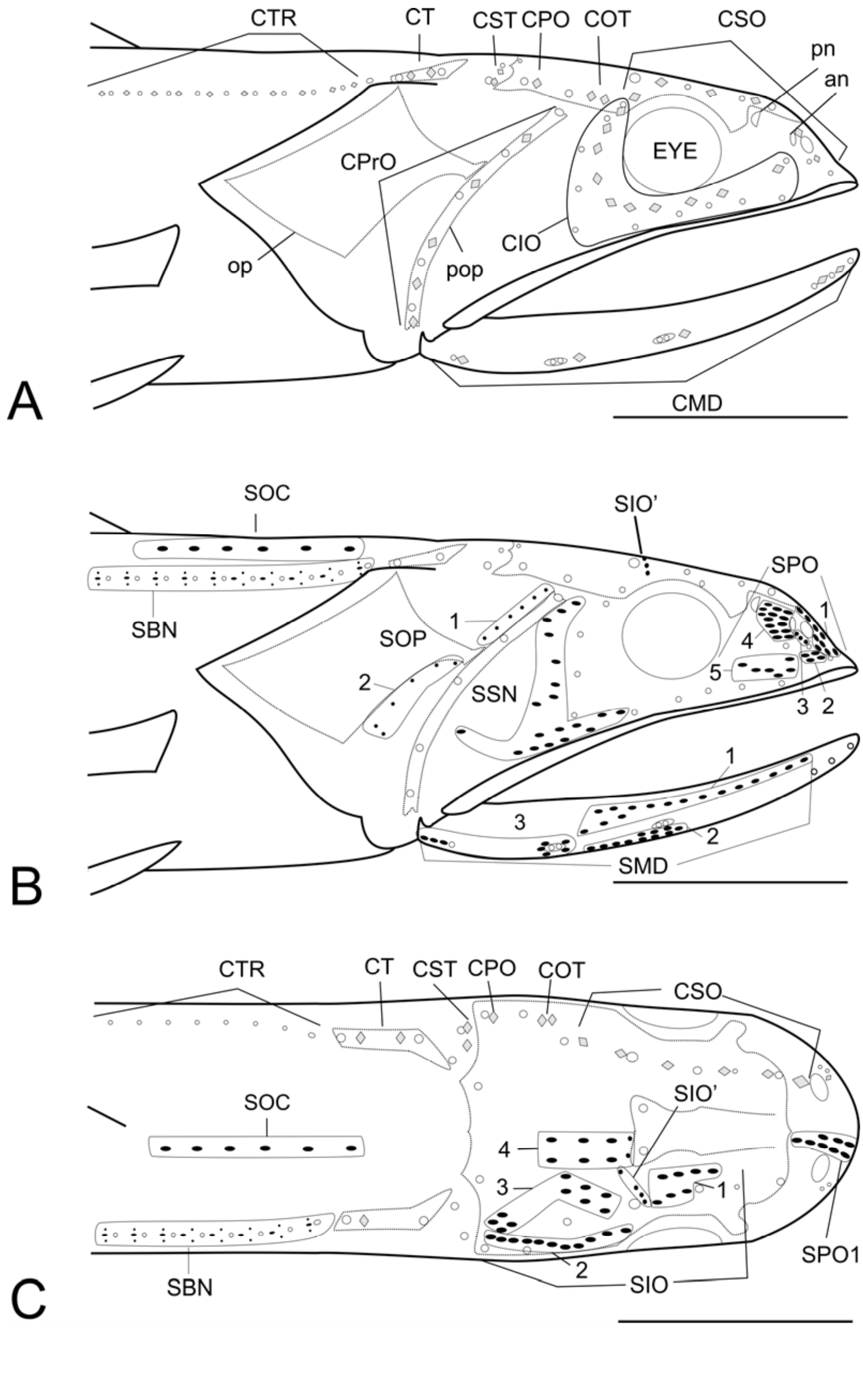

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FIGURE 6.4. Schematic of neuromasts in *Pseudoscopelus altipinnis* (ZMUC P. 6539): (A) lateral view of head, canal neuromasts; (B) lateral view of head, superficial neuromasts; (C) dorsal view, superficial (top) and canal (bottom) neuromasts. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

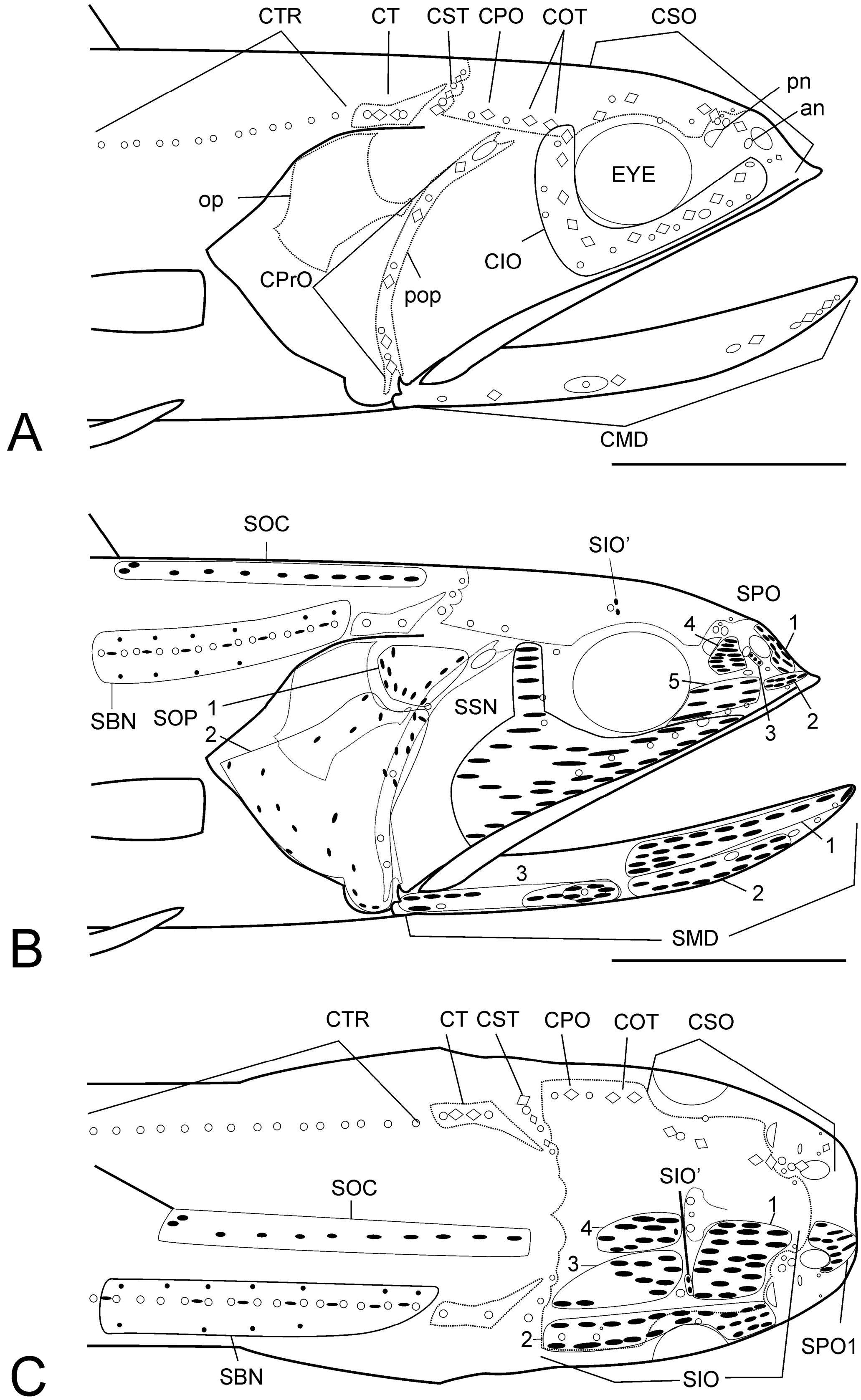
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FIGURE 6.5. Schematic of neuromasts in *Dysalotus alcocki* (ZMUC P. 6586): (A) lateral view of head, canal neuromasts; (B) lateral view of head, superficial neuromasts; (C) dorsal view, superficial (top) and canal (bottom) neuromasts. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

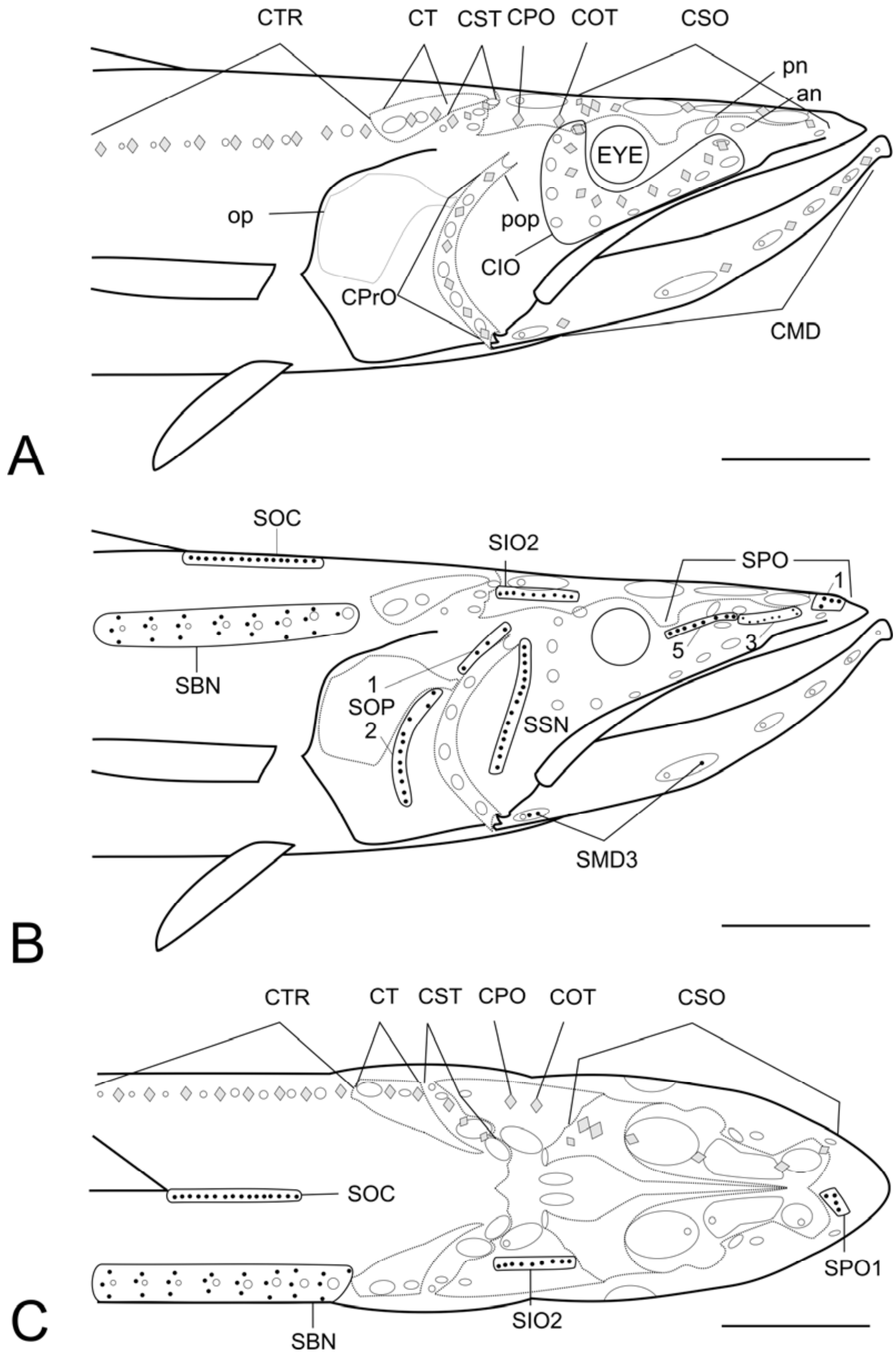
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FIGURE 6.6. Schematic of neuromasts in *Kali kerberti* (USNM 207614): (A) lateral view of head, canal neuromasts; (B) lateral view of head, superficial neuromasts; (C) dorsal view, superficial (top) and canal (bottom) neuromasts. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

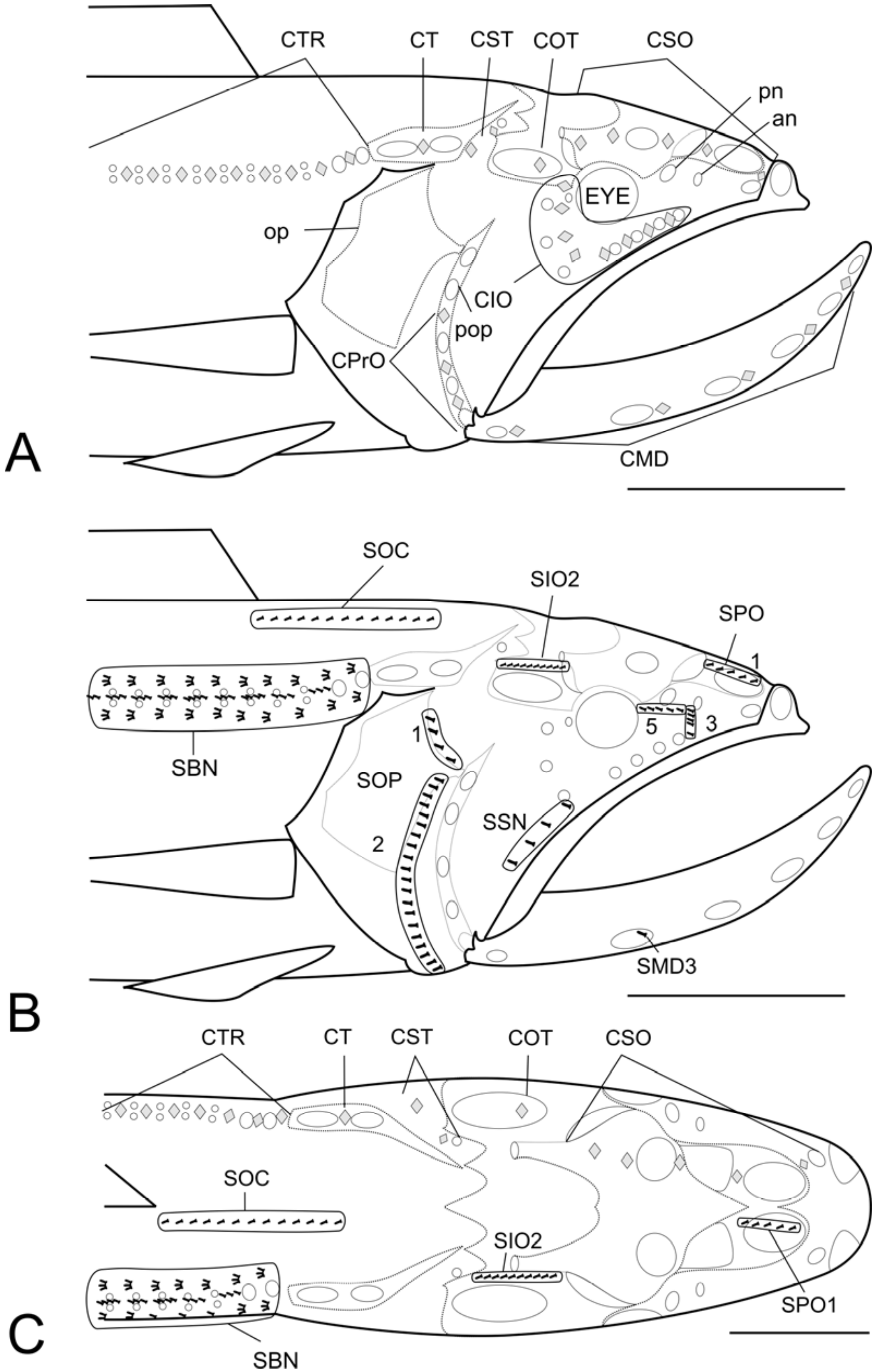
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FIGURE 6.7. Schematic of neuromasts in *Kali parri* (UF 131503): (A) lateral view of head, canal neuromasts; (B) lateral view of head, superficial neuromasts; (C) dorsal view, superficial (top) and canal (bottom) neuromasts. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

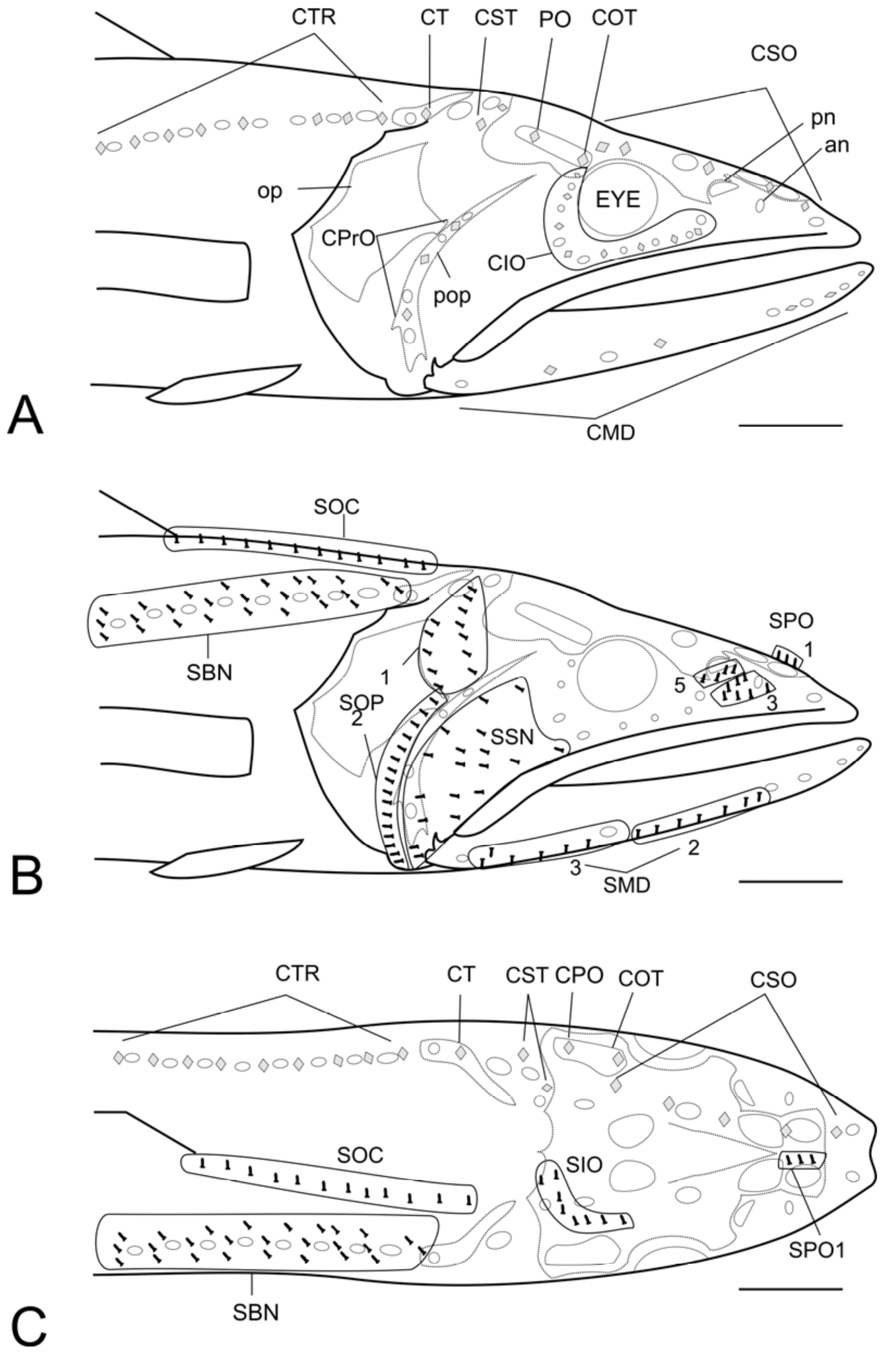
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FIGURE 6.8. Schematic of neuromasts on the caudal peduncle and caudal fin in (A) *Chiasmodon subniger* (LACM 32204-20), (B) *Dysalotus alcocki* ZMUC P. 6586, and (C) *Kali kerberti* (USNM 207614). Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

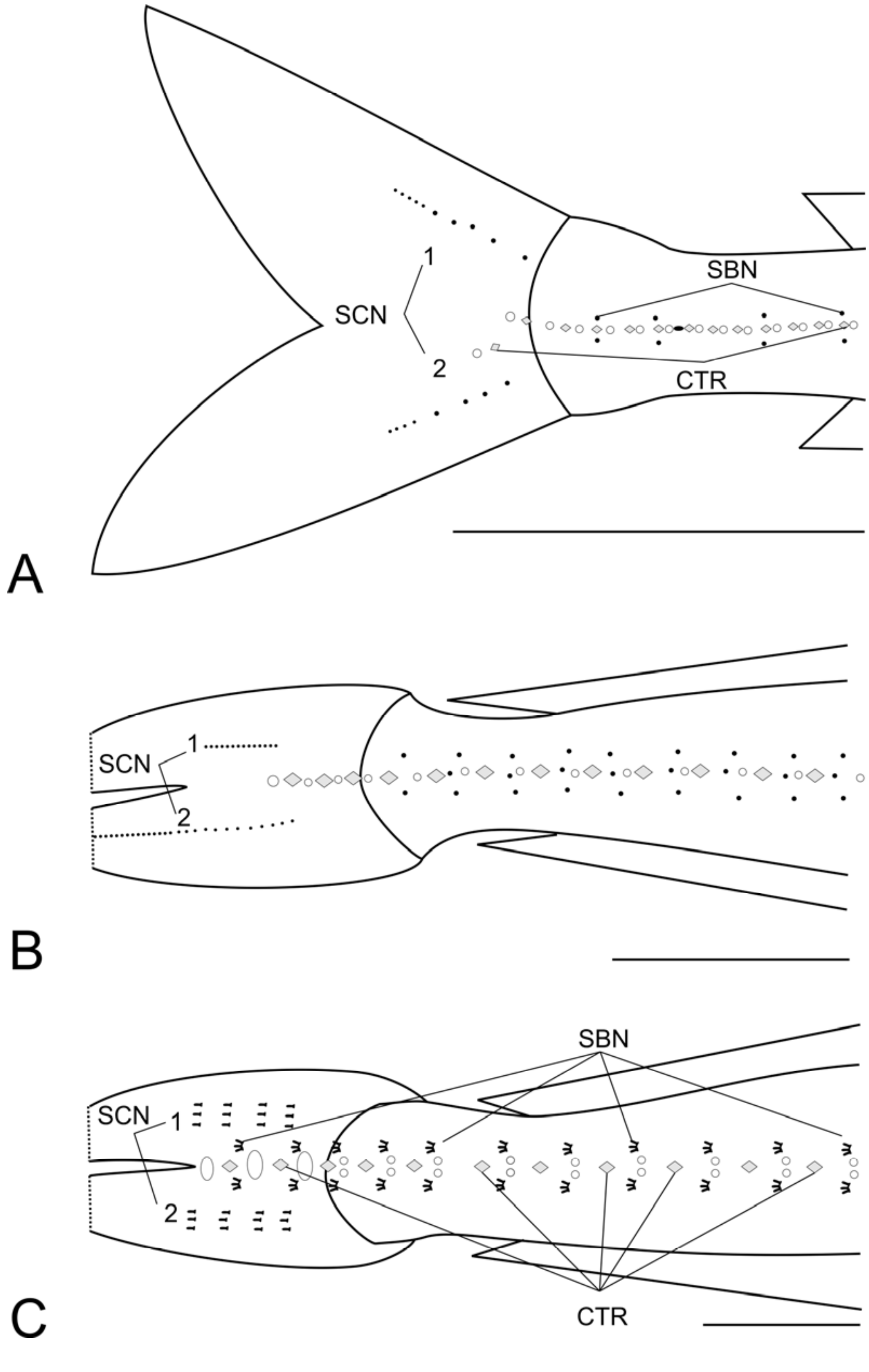
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FIGURE 6.9. Schematic of anterodorsal and otic lateral line nerves in *Chiasmodon subniger*: (A) complete track and branches of anterodorsal and otic lateral nerves; (B) superficial ophthalmic ramus of anterodorsal lateral line nerve and otic lateral nerve isolated; (C) buccal ramus of anterodorsal lateral line nerve isolated, with internal and outer buccal rami indicated. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

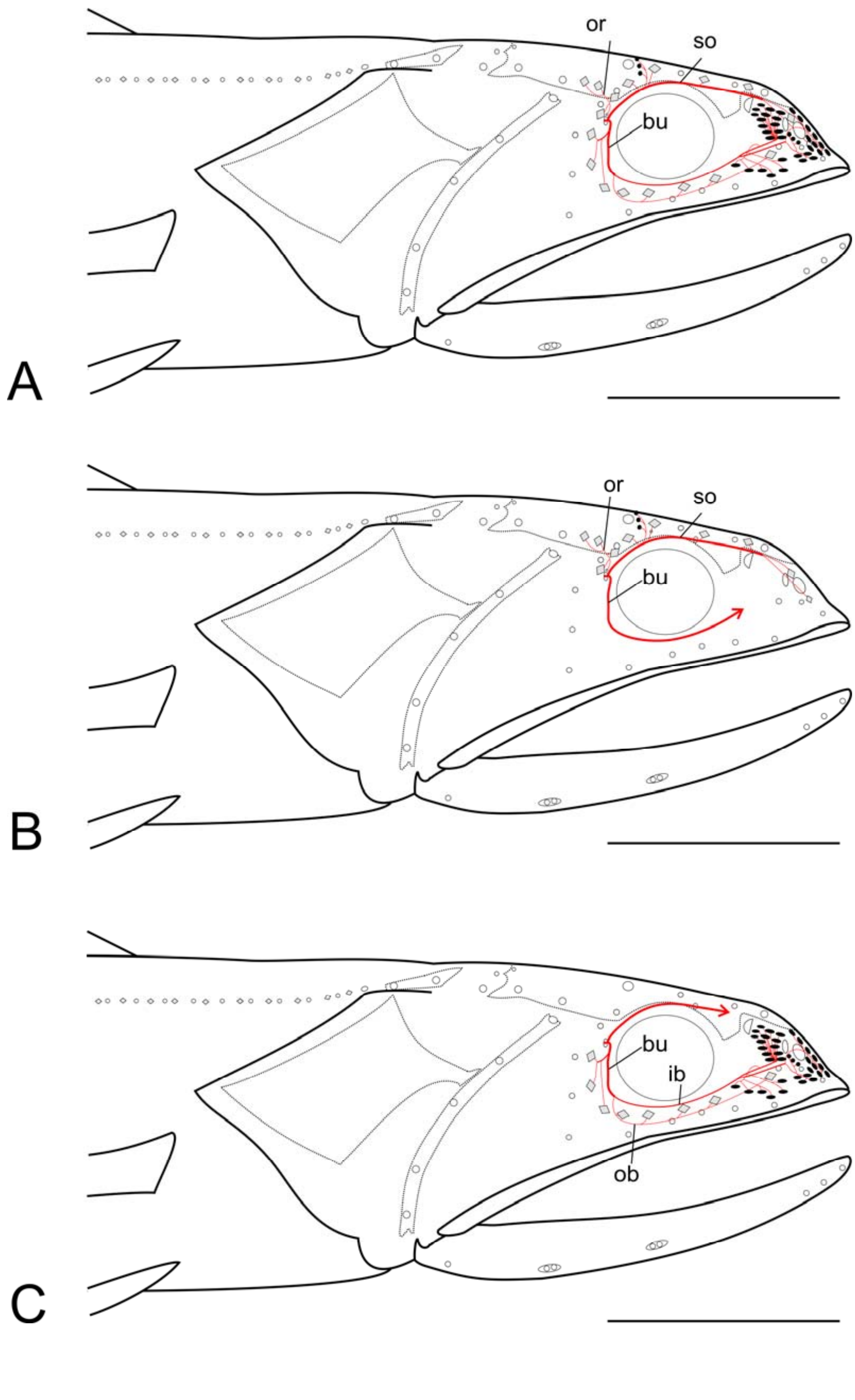

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FIGURE 6.10. Schematic of anterodorsal and otic lateral line nerves in *Pseudoscopelus altipinnis*: (A) complete track and branches of anterodorsal and otic lateral nerves; (B) superficial ophthalmic ramus of anterodorsal lateral line nerve and otic lateral nerve isolated; (C) buccal ramus of anterodorsal lateral line nerve isolated, with internal and outer buccal rami indicated. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

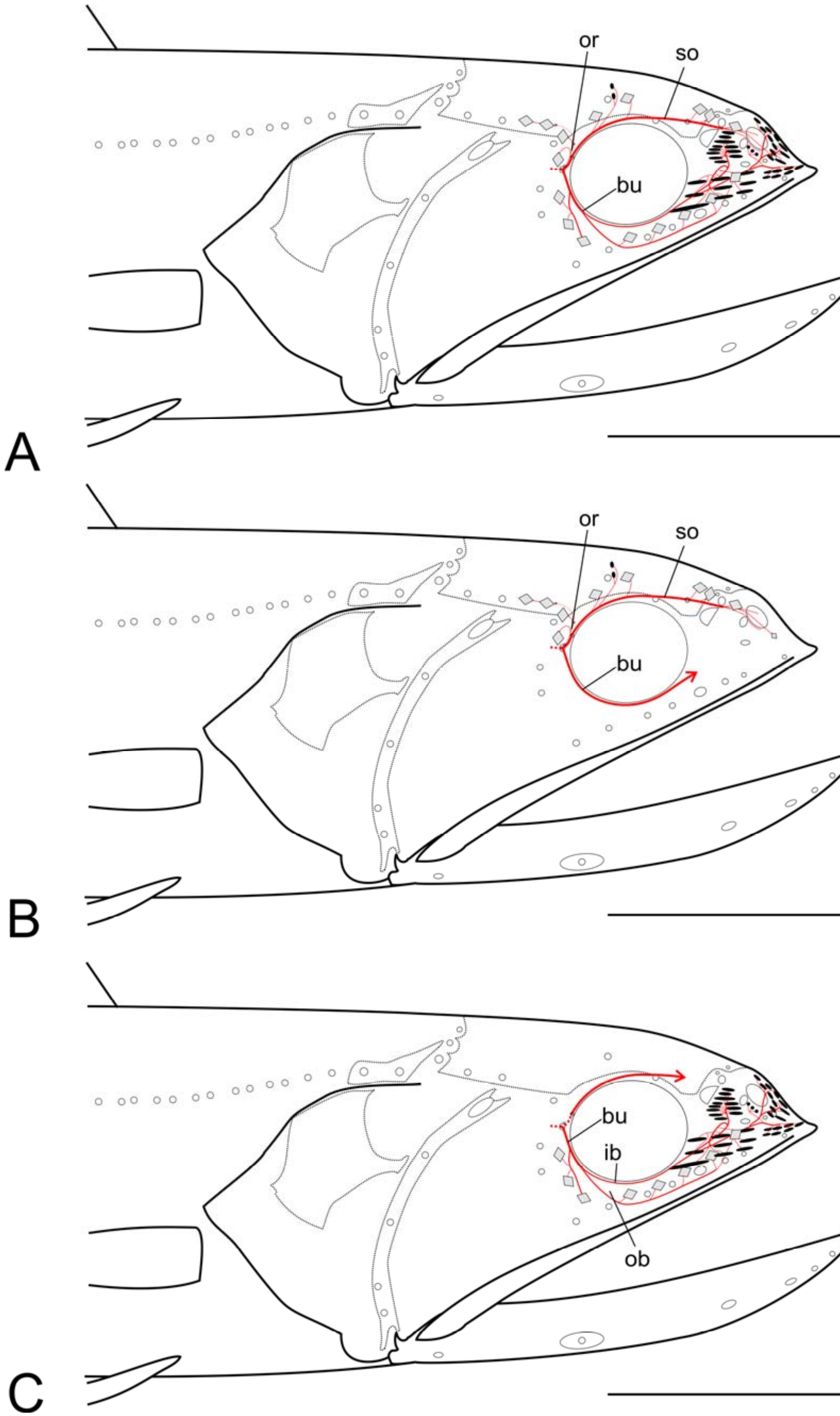

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FIGURE 6.11. Schematic of anterodorsal and otic lateral line nerves in (A) *Dysalotus alcocki*, (B) *Kali kerberti*, and (C) *Kali parri*. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

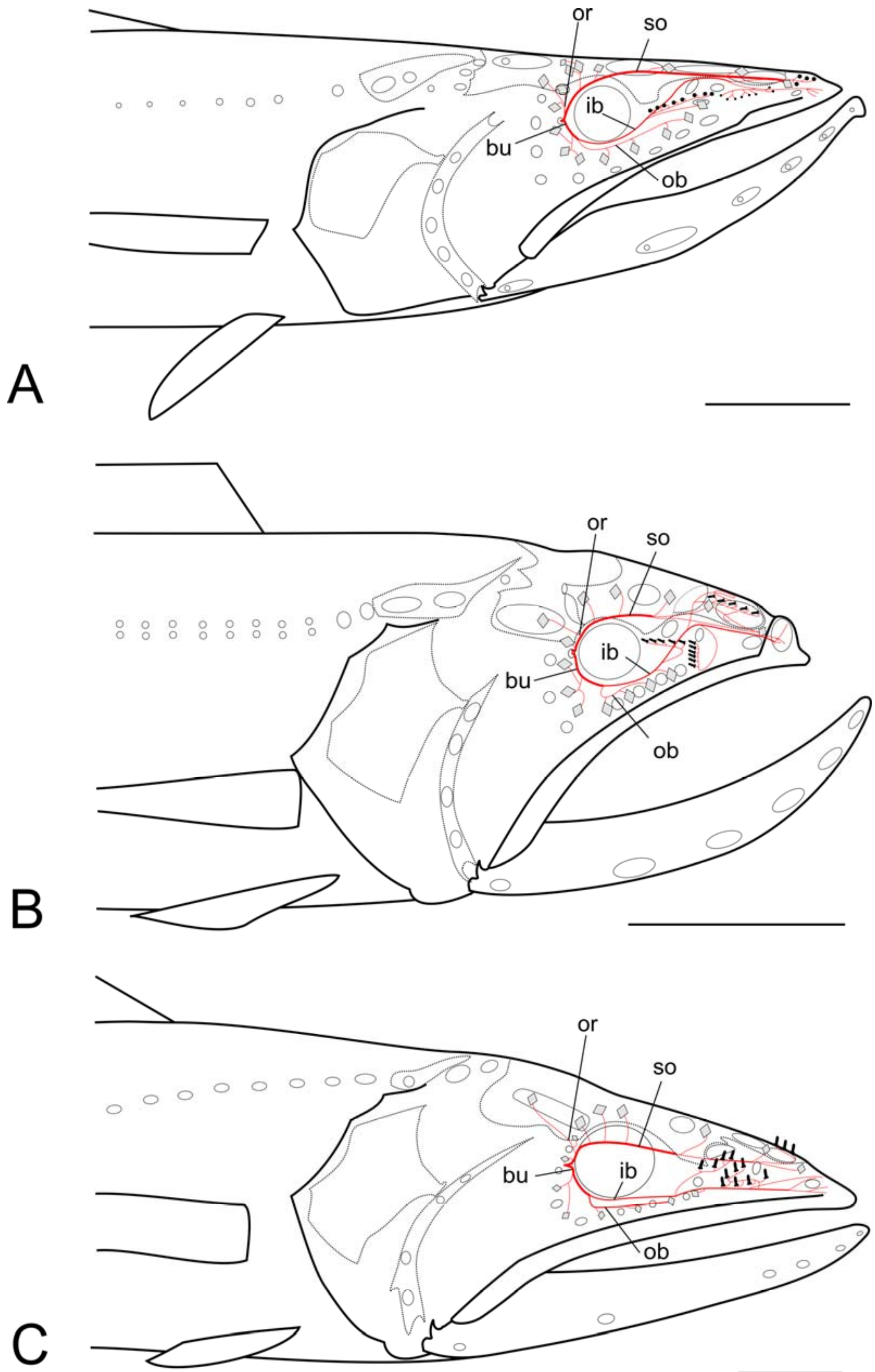

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FIGURE 6.12. Schematic of the anteroventral lateral line nerve in (A) *Chiasmodon subniger* and (B) *Pseudoscopelus altipinnis*. Medial view of lower jaw illustrated on bottom. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

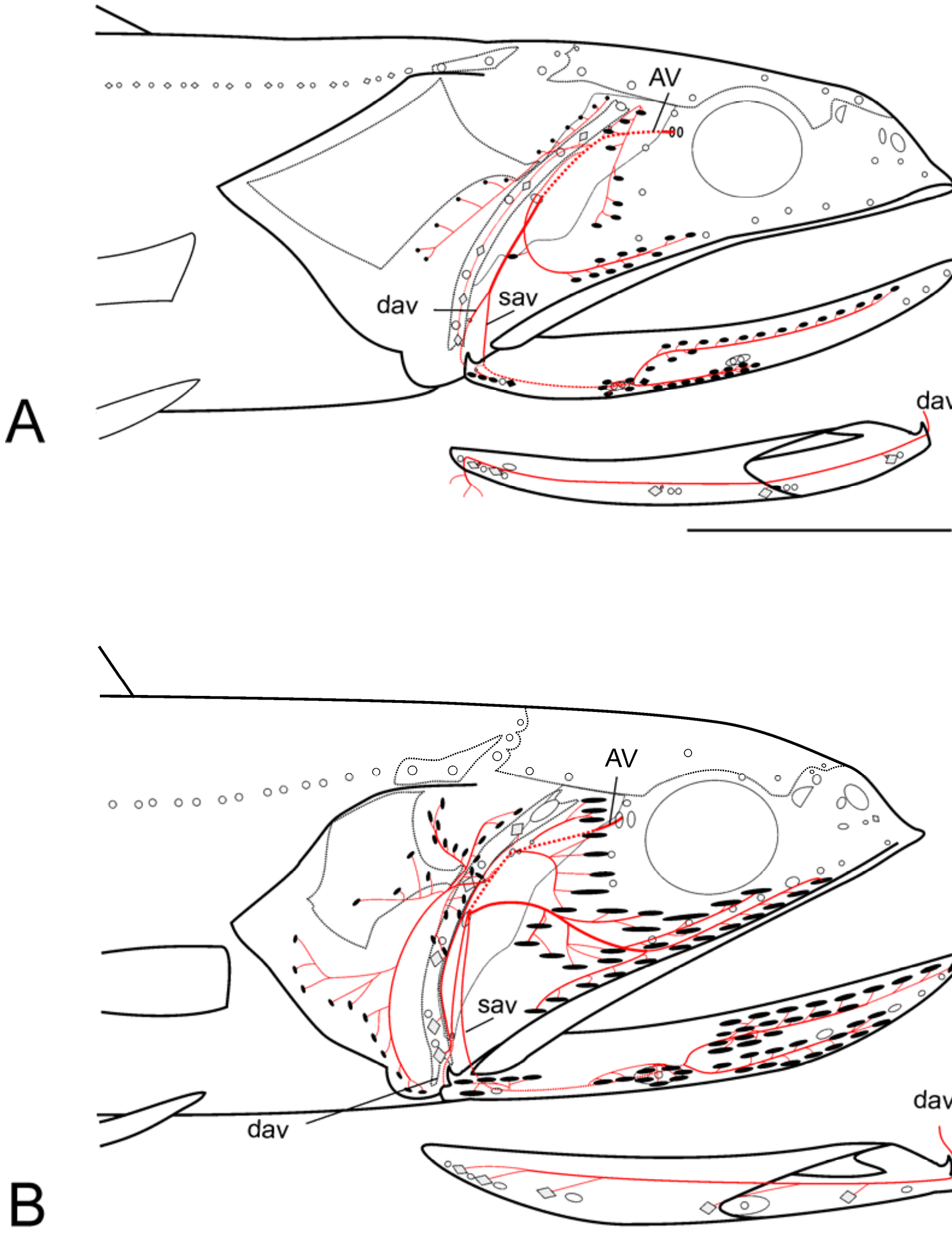

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FIGURE 6.13. Schematic of the anteroventral lateral line nerve in (A) *Dysalotus alcocki*, (B) *Kali kerberti*, and (C) *Kali parri*. Medial view of lower jaw illustrated on bottom. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

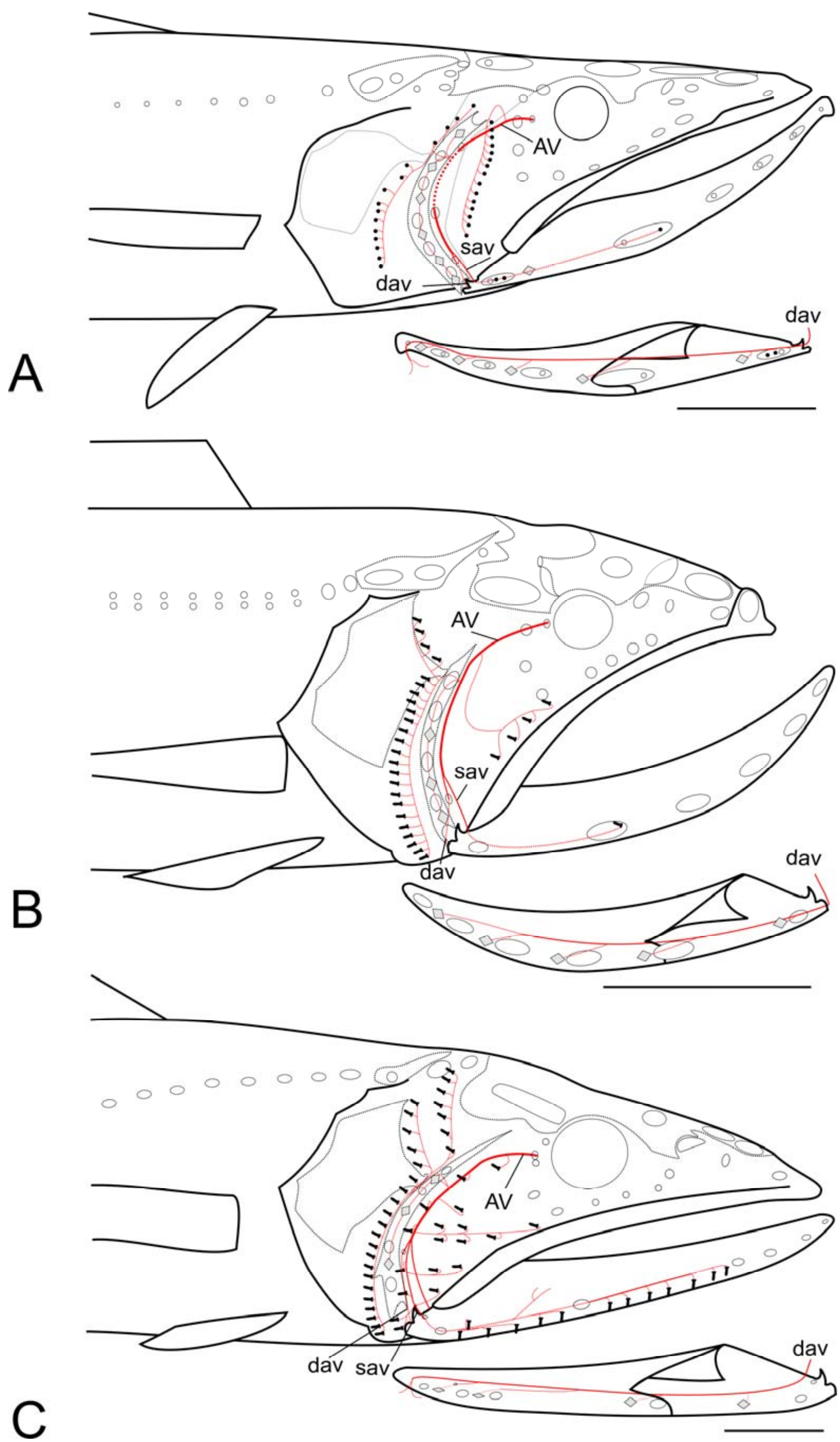
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FIGURE 6.14. (A), schematic of the anterior half of body of *Chiasmodon subniger* in lateral view, with the anterior part of the posterior lateral line nerve (p) and the posterior part of the middle lateral line nerve. (B), head of *Chiasmodon subniger* in dorsal view: on top, the complete track of the middle lateral line nerve and the dorsal neuromasts innervated by the dorsal ramus of the posterior lateral line nerve; on bottom, trunk of otic lateral line nerve and the superficial ophthalmic ramus of the anterodorsal lateral line nerve – notice the SOC', which is innervated by the anterodorsal lateral line nerve. (C), caudal peduncle and caudal fin of *Chiasmodon subniger*, with posterior portion of the posterior lateral line nerve. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

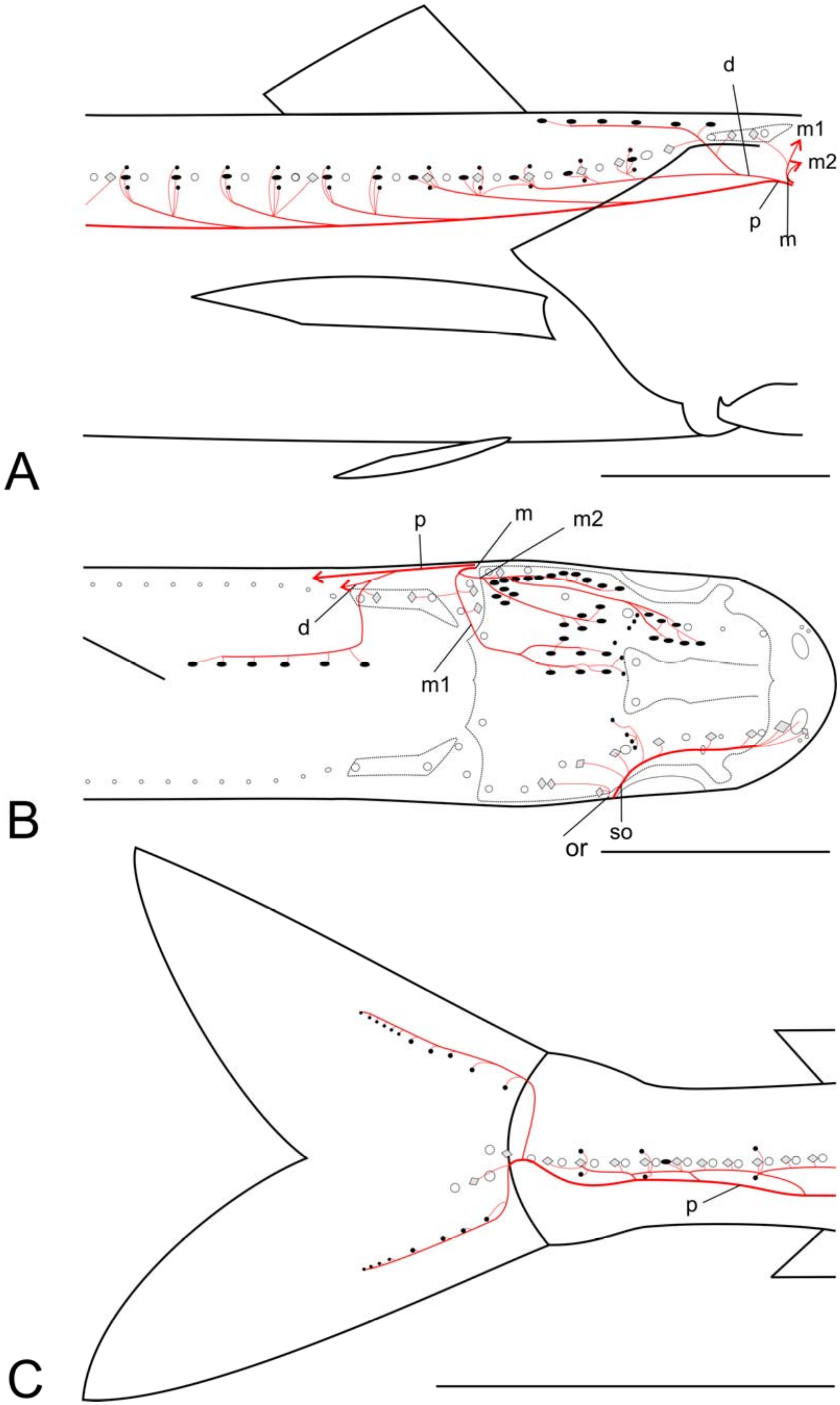
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FIGURE 6.15. (A), schematic of the anterior half of body of *Pseudoscopelus altipinnis* in lateral view, with the anterior part of the posterior lateral line nerve (p) and the posterior part of the middle lateral line nerve. (B), head of *Pseudoscopelus altipinnis* in dorsal view, on top, the complete track of the middle lateral line nerve and the dorsal neuromasts innervated by the posterior lateral line nerve; on bottom, track of otic lateral line nerve and the superficial ophthalmic ramus of the anterodorsal lateral line nerve – notice the SOC', which is innervated by the anterodorsal lateral line nerve. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.

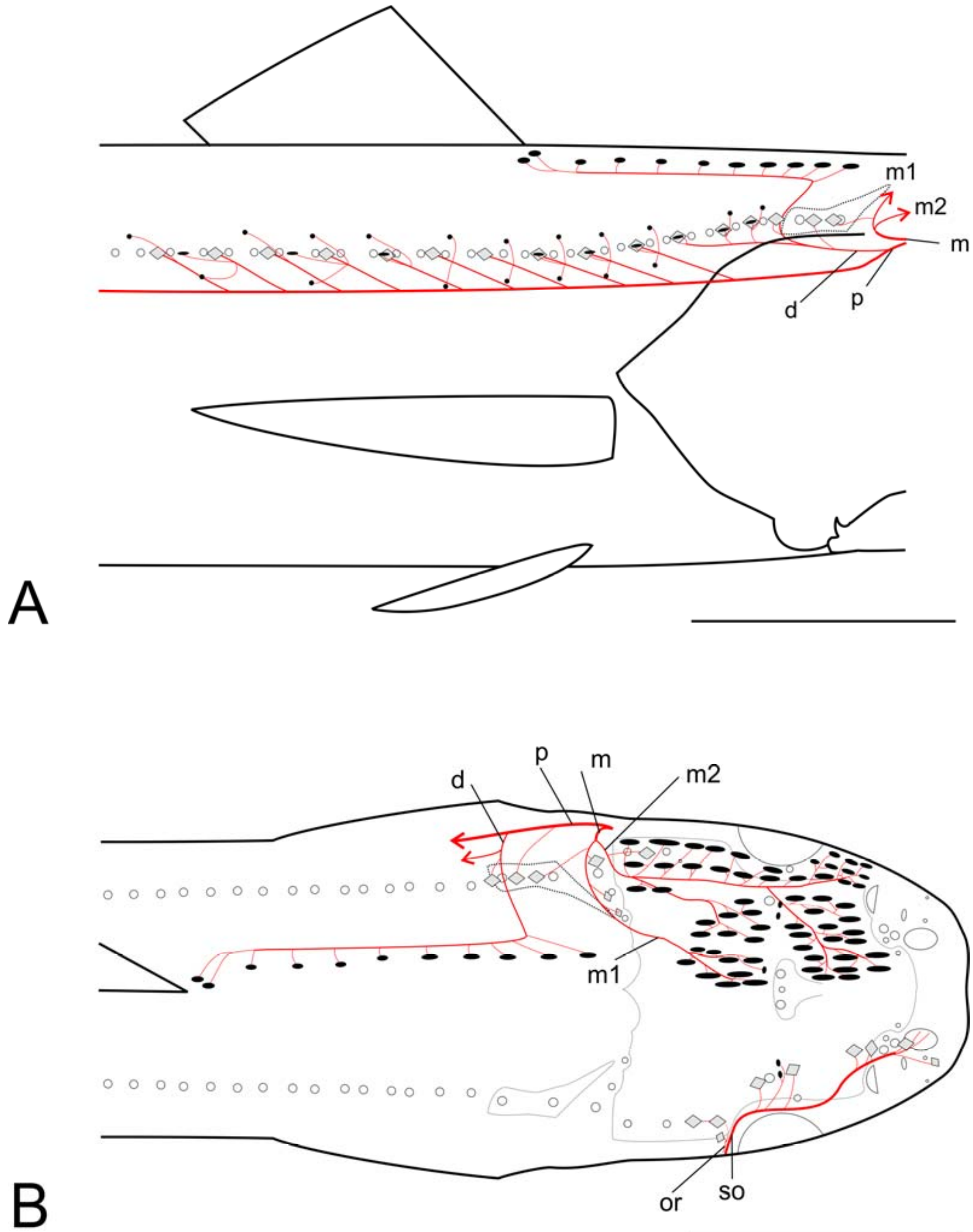
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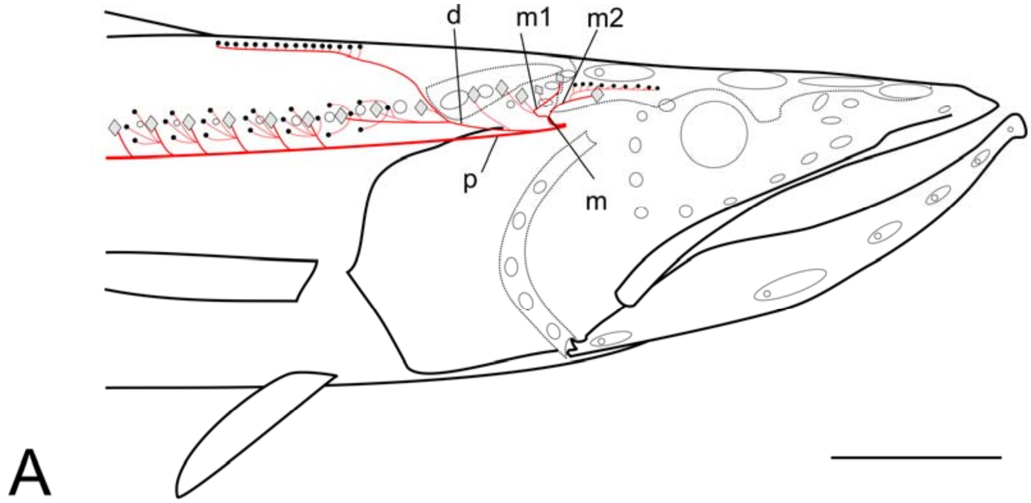
FIGURE 6.16. (A), schematic of the head of *Dysalotus alcocki* in lateral view, with the anterior part of the posterior lateral line nerve, dorsal ramus of posterior lateral line nerve, and the middle lateral line nerve. (B), head of *Dysalotus alcocki* in dorsal view: on top, the complete track of the middle lateral line nerve and the dorsal neuromasts innervated by the dorsal ramus of the posterior lateral line nerve (p); on bottom, track of otic lateral line nerve and the superficial ophthalmic ramus of the anterodorsal lateral line nerve. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.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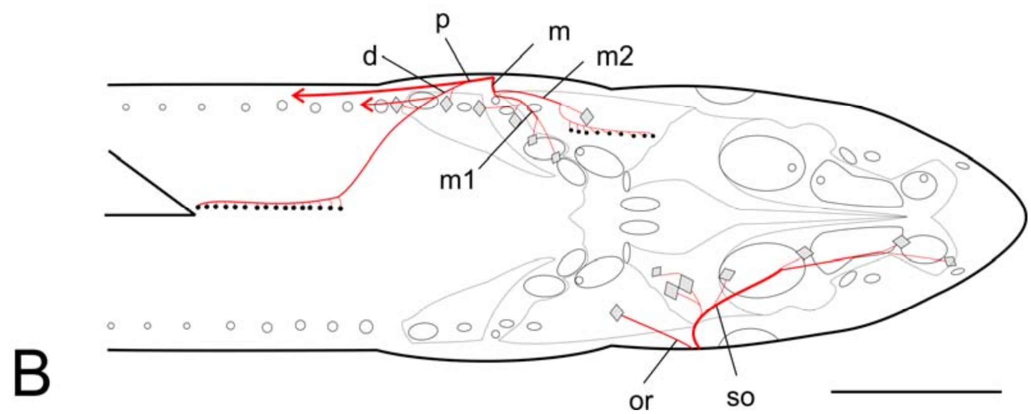
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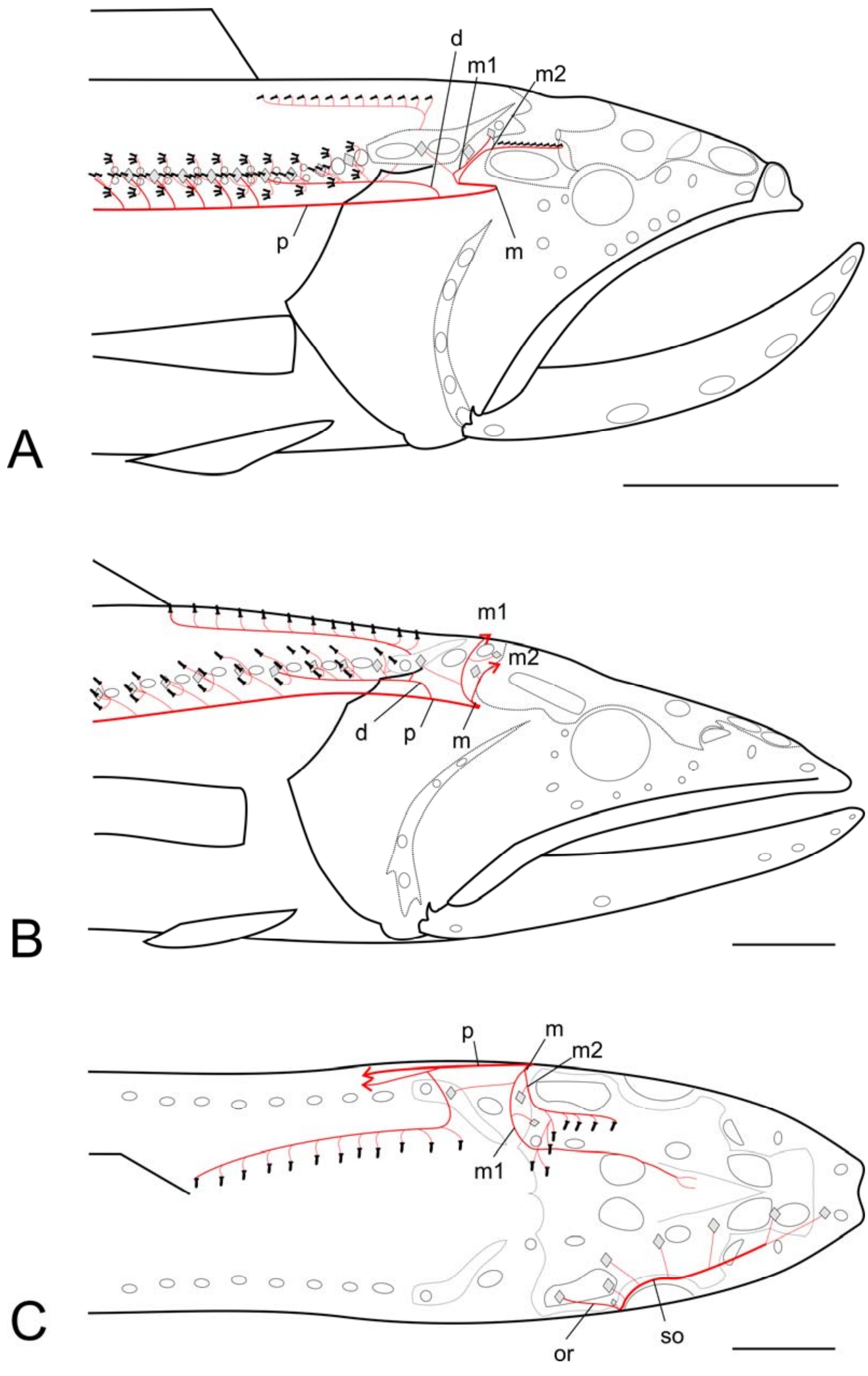
FIGURE 6.17. (A), schematic of the head of *Kali kerberti* and (B), *K. parri* in lateral view, with the anterior part of the posterior lateral line nerve, the dorsal ramus of the posterior lateral line never, and the middle lateral line nerve. (C), K. parri in dorsal view in dorsal view: on top, the complete track of the middle lateral line nerve (m) and the dorsal neuromasts innervated by the dorsal ramus of the posterior lateral line nerve; on bottom, track of otic lateral line nerve and the superficial ophthalmic ramus of the anterodorsal lateral line nerve. Canal neuromasts are in gray and superficial neuromasts in solid black; scale bar equals 10 mm.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CHAPTER 7 – THE PHYLOGENETIC RELATIONSHIPS OF THE FAMILY CHIASMODONTIDAE

Introduction

The family Chiasmodontidae comprises 33 species that inhabit the meso and bathypelagic regions of the Atlantic, Pacific, Indian and Southern Oceans (Chapters 2–6). The family includes four genera and an amazing diversity of aptations for deep-sea life: the photophores, when present, have a diversified pattern; the mouth is wide and has a great diversity of teeth ranging from numerous needle-like ones to huge fangs; and the skin is black and the dark pigmentation may extend to the cavities of body. The family is commonly referred to as the swallowers because of its enlarged mouth and the gargantuous voracity of some species that are able to swallow prey larger than their own bodies.

The genus *Chiasmodon* was erected by Johnson (1864), who regarded it as a member of the "Malacopterygian fishes". The family Chiasmodontidae was proposed by Jordan and Gilbert (1882) to include *Chiasmodon*, but Alcock (1890) and Garman (1889) still described *Ponerodon vastator* and *Chiasmodon subniger*, respectively, in the family Trachinidae. Norman (1929) produced the first revision for the family. Following, Smith (1965), Johnson (1969), Johnson and Cohen (1974); Lavenberg (1974) published generic revisions and the most important contributions to the taxonomy knowledge of Chiasmodontidae, establishing most of the synonyms followed until now. More recently, Prokofiev and Kukuev (2005, 2006a, b, c; 2008), and Melo (2008; this contribution) produced a series of taxonomic revisions and more recent species descriptions.

Despite the relatively large number of taxonomic works, very little attention has been given to the phylogenetic relationships of the chiasmodontids. Günther (1864) proposed that the chiasmodontids were members of the family Gadidae (Gadiformes), and Norman (1929) proposed a new division, the Chiasmodontiformes to include the Chiasmodontidae. Jordan and Gilbert (1882) proposed that the chiasmodontids were more related to the Trachinidae and Channichthyidae, and his ideas were shared by subsequent authors (e.g. Regan, 1913; Gosline, 1971).

The position of Chiasmodontids within the perciforms is not very well elucidated. Greenwoond et al. (1966) proposed that the chiasmodontids were a member of the Trachinoidei. This hypothesis was corroborated later by Pietsch and Zabetian (1986) and Piestch (1990), during their search for the sister groups of Ammodytidae and Uranoscopidae. According to their hypothesis the Chiasmodontidae and Champsodontidae were sister groups. Mooi and Johnson (1997), however, refuted this hypothesis, placing Champsodontide among the Scorpaeniformes. Recent attempts to elucidate the relationships of the Acanthomorpha using molecular data suggest that chiasmodontids are in a clade that includes the Scombroidei and Stromateoidei (Chen et al. 2003; Dettai and Lecointre 2005).

The monophyly of Chiasmodontidae has not been questioned nor tested, even though the four genera are extremely distinctive. Piestch (1989) only included *Chiasmodon* and *Pseudoscopelus* in his analysis – the same material was used by Pietsch and Zabetian (1990); Chen et al. (2003) only obtained sequences from a sample of *Kali*, and the same sequences were used by Dettai and Lecointre (2005).

Herein, the monophyly of the family Chiasmodontidae is corroborated by 24 synapomorphies, some of which include novel and complex morphological structures. Two groups are formed: the *Chiasmodon* group, composed of the genera *Chiasmodon* and *Pseudoscopelus* and supported by 18 synapomorphies; and the *Kali* group, composed of the genera *Dysalotus* and *Kali*, and supported by 22 synapomorphies. The monophyly of the genus *Chiasmodon* is supported by 16 synapomorphies; *Dysalotus*, by 18 synapomorphies; *Kali*, by 23 synapomorphies; and *Pseudoscopelus*, by 12 synapomorphies. A hypothesis of relationships among the species is also discussed.

Material and Methods

Representatives of 35 species of *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus* were used to examine characters of external morphology such as dentition, pigmentation, and the distribution of photophores and neuromasts; 28 species were used for internal morphological characters, such as muscles, bones, and innervation.

Prior to the enzymatic digestion during the process for clearing the muscles, the specimens were dissected under a Leica MZ-8 stereomicroscope for examination of musculature and innervation. A solution of Alcian Blue 2% was used to enhance some delicate muscles, nerves and the neuromasts, as described in Chapter 6. The specimens were cleared and stained for bone and caritlage using the method described by Taylor and Van Dyke (1985); for the most delicate specimens, Alcian Blue staining for cartilage in acetic acid solution was skipped. Terminology for the bones follows Weitzmann (1974), Stiassny (1986), Stiassny and Moore (1992) and Mooi and Johnson (1998); for the caudal-fin skeleton Fujita (199); for the muscles, Winterbotton (1974); for the canal neuromasts, Coombs et al. (1988); for the superficial neuromasts, Sanzo (1911) with modifications proposed in Chapter 6; for nerves, Northcutt et al. (2000), and for neuromasts, Melo et al. (2007).

To determine the character polarity, the outgroup analysis was used (Nixon and

Carpenter, 1993). The outgroups were chosen based on the available hypotheses of phylogenetic relationships of the family Chiasmodontidae: *Hoplostethus occidentalis* is a beryciform and a basal percomorph; *Diplectrum formosum*, a serranid and a generalized higher perciform, *Scomberomorus maculatus*, a scombrid; and *Bembrops anatirostris*, a percophid and a representitive of Trachinoidei. Multi-state characters were analyzed as ordered, when a sequence of transformation was observed, and are indicated in text. Variation of characters exclusive for the family or for specific genera were marked unknown (?) for the other groups (e.g. superficial neuromasts, photophores and characters of dentition) and are indicated on text. The absence of the groups of neuromasts groups were marled as unknown (?) in *Pseudoscopelus aphos* and, when absent, in *P. parini*, because of the hypothesis that some groups were secondary lost in those species.

A matrix of characters was organized using Mesquit version 1.12 (Maddison & Maddison 2006) and MacClade version 4.06 (Maddison & Maddison 2003). The phylogenetic analysis was performed in PAUP* version 4.0b10 (Swofford 2000), using the tree bisection algorithm of the heuristic search, with 1000 replications. A bootstrap analysis was performed in PAUP*, using 1000 heuristic replicates and the default commands. A decay analysis was performed in PAUP* using 20 replicates and the default commands, with the aid of TreeRot (Sorenson 1999) to produce the constraints trees. The character states were optimized by the accelerated transformation optimization (ACCTRAN, Swofford and Maddion, 1987), in accordance to the hypothesis of homology established a priori (de Pinna 1991).

List of abbreviations.

Osteology

CPNPU – Post-neural spinal cartilage of pleural centra

CPHY – Post-neural spinal cartilage of hypural

CPHPU – Post-haemal spinal caritlage of pleural centra

Neuromasts

SSN – suborbital superficial neuromasts

SMD – mandibular superficial neuromasts

SOP – opercular superficial neuromasts

SOC – occipital superficial neuromasts

SIO – interorbital superficial neuromasts

Photophores

apf – anteropreopercular photophores

if – isthmus photophores

lvf – lateral ventral-fin photophores

mxf – maxillary photophores

paf – pectoral-fin axillary photophores

pf – pectoral-fin photophores

ppf – posteropreopercular photophores

prcf – precaudal-fin photophores

prvf – preventral-fin photophores

ptvf – postventral-fin photophores

rtf – random trunk photophores

saf – anal-fin photophores

spf – suprapectoral-fin photophores

svf – supraventral-fin photophores

trf – transverse ventral-fin photophores

vaf– ventral-fin axillary photophores

vf – ventral-fin photophores

vnf – ventronasal photophores

Results

The matrix produced from 161 characters from bones, cartilages and tendons (osteology), dentition, muscles, neuromasts, photophores and other characteristics obtained for the phylogenetic analysis is presented in Table 7.1. The characters are as follows.

Characters

Cranium

1. Density of bones in head: compact and stout (0); fragile with widely separated trabeculae (1). In *Chiasmodon*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the bones forming the head are compact and well calcified; and in *Dysalotus* and *Kali*, they are fragile with trabeculae that can be observed by naked eye. (ci=1.0)

2. Pterospheoind (ordered): short (0); medium-sized (1); enlarged (2). In *Chiasmodon*, *Dysalotus*, *Kali*, *Pseudoscopelus aphos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the pterosphenoid is short and restricted to the medial and posterior margin of orbit; in *P. astronesthidens*, *P. australis*, *P. odontoglossum* and *P. parini*, the pterosphenoid is moderately developed and forms about half of the medial limit of the orbit; and in *P. altipinnis*, *P. bothrorrhinos*, *P. paxtoni* and *P. scutatus*, the pterosphenoid is enlarged, forming on most of the medial margin of orbit, and medially fused to the contralateral pterosphenoid. (ci=0.50)

3. Medial groove formed by crest on frontal (ordered): crest of frontal absent, groove absent (0); present, triangular, with straight medial border (1); present, with medial border gently curved (2); present, with border strongly curved, sigmoid (3). In *Bembrops* and *Diplectrum*, the crest of frontal is absent and the dorsal of the part cranium is flat; in *Chiasmodon*, *Dysalotus*, *Kali* and *Scomberomorus*, the crest is present on the frontal and it has a straight, medial border; and in *Pseudoscopelus astronesthidens*, *P. australis* and *P. odontoglossum*, the crest is present, and the medial border is gently curved; and in *P. altipinnis*, *P. aphos*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. parini*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, the crests is present and sigmoidal. In *Hoplostethus*, the crest is present, forming a groove of different than described above, and was coded as unknown (?). (ci=0.75)

4. Depth of groove formed by crest of frontal: shallow (0); moderately deep (1); very deep (2). In *Scomberomorus*, the groove formed by the crest of the frontal is shallow; in *Chiasmodon* and *Pseudoscopelus*, it is moderately deep; and in *Dysalotus*, *Kali* and *Hoplostethus*, the groove is very deep, formed by a great concavity of the middle shelf of the frontal. (ci=0.5)

5. Foramina in prootic (ordered): three (0); two (1); one (2). In *Chiasmodon*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, there are three foramina in the prootic, the hyomandibular and trigeminal foramina and a small (unnamed) foramen dorsal to the trigeminal foramen for the passage of the superficial ophthalmic ramus of the anterodorsal lateral line nerve; in *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon*, *Pseudoscopelus* and *Bembrops*, only the hyomandibular and the trigeminal foramina are present; and in *Kali colubrina*, *K. macrura* and *K. parri*, only the hyomandibular foramen is present. (ci=0.33)

6. Foramina in exoccipital: two (0); one (1). In *Dysalotus*, *Chiasmodon*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, there are two foramina in the exoccipital, the glossopharyngeal and vagus foramina; and in *Kali*, only the vagus foramen is present. (ci=1.0)

7. Size of parietal (ordered): normally developed (0); slightly reduced (1); extremely reduced (2). In *Chiasmodon*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the parietal is well developed and forms the posterolateral roof of the

neurocranium, and it is as long as the supraoccipital; in *Dysalotus* and *Kali parri*, the parietal is slightly shorter than the supraoccipital; and in *K. colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon* and *K. macrura*, the parietal is extremely reduced to a small circular bone and the epiotic forms posterolateral roof of the neurocranium. (ci=1.0)

8. Posterior wall of neurocranium: formed by supraoccipital, epiotics, exocippitals and basioccipital (0); formed by epiotics, exocipitals and basioccipital (1). In *Chiasmodon*, *Dysalotus*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the posterior wall of the neurocranium is formed dorsally by the supraoccipital, dorsolaterally by the epiotics, ventrolaterally by the exoccipitals and ventrally by the basioccipital; and in *Kali*, the posterior shelf of the supraoccipital is extremely reduced and does not contribute to the posterior wall of neurocranium, which is formed by the epiotics, exocipitals and basioccipital. (ci=1.0)

9. Connection between Baudelot’s ligament and second vertebra: absent (0); present (1). In *Dysalotus*, *Kali*, *Pseudoscopelus*, *Bembrops*, *Diplectrum, Hoplostethus,* and *Scomberomorus*, Baudelot’s ligament originates on the occiput of the basioccipital, passes through the epaxial musculature and inserts medially on the supracleithrum; and in *Chiasmodon*, the Baudelot’s ligament originates on the occiput of the basioccipital, passes ventrally to the first vertebra and connects to the basapophysis of the second vertebra, than passes thru the epaxial musculature and inserts on the supracleithrum. (ci=1.0)

Dermal bones

10. Shape of nasal: tubular (0); spoon-shaped (1); circular (2). In *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the nasal is elongated, forming a slender tube; in *Chiasmodon* and *Pseudoscopelus*, the nasal is spoon-shaped; and in *Kali* and *Dysalotus* is large and circular, with thin borders. (ci=1.0)

11. Position of nasal (ordered): dorsal (0); anterodorsal (1); anterior, facing forward (2). In *Kali*, *Dysalotus*, *Diplectrum*, *Bembrops*, *Hoplostethus* and *Scomberomorus*, the nasal is positioned on the dorsal part of the snout; in *Chiasmodon* and *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. paxtoni*, *P. parini*, *P. pierbartus*, *P. sagamianus* and *P. scriptus* it is positioned anterodorsally, in the concave snout; and in *P. bothrorrhinos* and *P. scutatus* it is positioned in a pit formed by the tip of the snout and faces anteriorly. (ci=1.0)

12. Position of Infraorbital 6 (ordered): ventral to dermosphenotic, infraorbital pore posterior to mid-eye (0); anterior to dermosphenotic, with small area contacting frontal, infraorbital pore posterior to mid-eye (1); anterior to dermosphenotic, forming the dorsal margin of orbit, infraorbital pore anterior to mid-eye (2). In *Dysalotus*, *Kali*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, infraorbital 6 is ventral to the dermosphenotic, its dorsal pore is posterior to mid-eye and the dorsal margin of the orbital is formed by the frontal; in *Chiasmodon*, infraorbital 6 is positioned anterior to the dermosphenotic and has a small area that contacts the frontal along the dorsal margin of

the eye, the pore is dorsal to mid-eye and most of the dorsal margin of the orbit is formed by the frontal; and in *Pseudoscopelus*, infraorbital 6 laterally contacts the margin of the frontal and forms the dorsal margin of the eye, its dorsal pore is positioned anterior to the mid-eye. (ci=1.0)

Opercular series

13. Preopercle: elongated, reaching otic dorsally (0); short, not reaching otic dorsally (1). In *Chiasmodon, Pseudoscopelus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the preopercle is long and dorsally articulates with the otic; and in *Kali*, *Dysalotus* and *Bembrops*, it is short, and does not reach the otic. (ci=0.5)

14. Articulating condyle of preopercle: absent (0); present (1). In *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the preopercle does not reach the surangular ventrally; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the preopercle reaches the surangular ventrally, and the ventral edge of the preopercle forms a condyle that articulates with the surangular during the opening and closing of mouth. (ci=1.0)

15. Shape of opercle: fan shaped (0); *U*-shaped (1); three-pronged (2). In *Chiasmodon*, *Pseudoscopelus altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. scutatus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the posterior margin of the opercle is fan-shaped with four angles; in *P. cephalus*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, the posterior edge of the opercle is *U*-shaped with upper and

lower lobes; and in *Kali* and *Dysalotus*, the posterior margin of the opercle is three-pronged. (ci=1.0)

16. Ossification of opercle, interopercle and subopercle: well ossified (0); not ossified, mostly membranous (1). In *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the opercle, interopercle and subopercle are well ossified, in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the margin of the opercle and interopercle are membranous and the subopercle is ossified only along a tendon that connects the subopercle to the surangular, ant the rest is membranous. (ci=1.0)

Jaws and Suspensorium

17. Length of maxilla and premaxilla: short, less than 50 % in head lenght (0); elongated, 60–87 % in head length and reaching close to angle of lower jaw (2). In *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the maxilla and premaxilla are short, not reaching the posterior angle of dentary; *Chiasmodon*, *Kali*, *Dysalotus* and *Pseudoscopelus*, the maxilla and premaxilla are elongated, reaching posterior angle of mouth. (ci=1.0)

18. Shape of upper and lower jaws in lateral view: gently arched (0); strongly arched (1). In *Chiasmodon*, *Pseudoscopelus*, *Dysalotus*, *Kali colubrina*, *K. parri*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the lower and upper jaw are slightly arched; and in *K. indica*, *K. kerberti*, *K. macrodon*, *K. macrura* and *K. falx*, the jaws are strongly arched. (ci=1.0)

19. Width of premaxilla: narrow (0); broad (2). In *Chiasmodon*, *Kali*, *Pseudoscopelus aphos*, *P. bothrorrhinos*, *P. cordilluminatus*, *P. pierbartus*, *P. obtusifrons*, *P. scutatus Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the premaxilla is narrow, premaxillary width 10–14% in length; and in *Dysalotus*, *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. sagamianus* and *P. scriptus*, the premaxilla and dentary are broad, premaxillary width 15–20% in length. (ci=0.33)

20. Ascending process of premaxilla (ordered): very elongated (0); reduced (1); extremely reduced (2). In *Bembrops*, *Diplectrum* and *Hoplostethus*, the ascending process of premaxilla is very elongated, and articulates with the ethmoid; in *Kali* and *Scomberomorus*, the ascending process is very reduced, and only articulates with the rostroid cartilage; and in *Chiasmodon*, *Dysalotus* and *Pseudoscopelus*, the premaxilla is almost a flat bone, and the ascending process is reduced to a small notch that articulates with the rostroid cartigale. The progressive reduction of the ascending process is considered to be a multi-step character in the evolution of the chiasmodontids. (ci=0.67)

21. Lateral surface of ascending process of premaxilla: flat (0); concave (1). In *Chiasmodon*, *Dysalotus*, *Kali colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon*, *K. macrura*, *K. parri*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the lateral surface of the ascending process of premaxilla is flat; and in *K. kerberti* and *K. macrodon*, the process is concave. (ci=1.0)

22. Supramaxilla: absent (0); present (1). In *Chiasmodon*, *Kali*, *Pseudoscopelus*, *Bembrops*, *Bembrops*, *Diplectrum* and *Scomberomorus*, the supramaxilla is present; and in *Dysalotus* and *Hoplostethus*, present. (ci=0.5)

23. Ventral notch in dentary: absent (0); present (1). In *Chiasmodon*, *Kali*, *Pseudoscopelus*, *Diplectrum*, the ventral notch in dentary is absent; and in *Bembrops*, *Dysalotus*, *Hoplostethus* and *Scomberomorus*, a notch ventral to the symphysis of dentaries is present. (ci=0.33)

24. Coronoid process of dentary (ordered): short (0); moderately elongated (1); very elongated (2). In *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus* the coronoid process of the dentary is short and the dentary articulates laterally with the angular; in *Chiasmodon* and *Pseudoscopelus* the coronoid process is moderately elongated, and a distinguishable triangular fenestra is formed between the dentary and angular; and in *Dysalotus* and *Kali* the coronoid process is very elongated, forming a wide fenestra between the dentary and angular. (ci=1.0)

25. Mesopterygoid: well developed (0); reduced (1). In *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the mesopteygoid has a wide shelf that forms the ventral margin of the orbit, and it articulates with the metapterygoid posteriorly and the palatine anterorventrally; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the mesopterygoid is reduced to a very thin shelf dorsal to the anterior process of the

metapterygoid (see character 26). (ci=1.0)

26. Metapterygoid: short and dorsal to quadrate (0); elongated, dorsally fused to the hyomandibular, and with anterior and ventral processes that articulates with palatine anteriorly, and anterior shelf of the quadrate, ventrally. In *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the metapterygoid articulates dorsally with the ventral margin of hyomandibular, posterior margin of mesopterygoid and the dorsal margin of quadrate; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the metapterydoid is caudally fused to the hyomandibular, has an anterior process that extends dorsal to the palatine and ventral to the reduced mesopterygoid, and a ventral process that extends along the ventral margin of the quadrate and forms a border that forms part of the articulation between the angular and the suspensorium. (ci=1.0)

Vertebral Column and ribs

Vertebrae

27. Number of vertebrae (ordered): less than 31 (0), 31 (0); 33–34 (1); 35–40 (2); 42–45 (3); 47–48 (4); 50 or more (5). In *Bembrops*, *Diplectrum*, *Hoplostethus* the vertebrae are 24, 26 and 28, respectively; in *Pseudoscopelus cephalus*, 31; in *Kali macrura*, 33–34; in *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. paxtoni*, *P. parini*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, *P. scutatus*, *Dysalotus* and *Kali colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon*, *K. parri*, 35–40; in *Chiasmodon asper*, *C. braueri*, *C. microcephalus*, *C. niger*, *C. pluriradiatus*, *C. subniger*, 42–45; in *C. harteli*,

47–48; and in *Scomberomorus*, 51. (ci=0.55)

28. Prezygapophyses: well-developed, articulating with the postzygapophyses of the anterior vertebra (0); poorly developed, not reaching the postzygapophyses of the anterior vertebra (1). In *Pseudoscopelus*, *Chiasmodon*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, both ventral and dorsal prezygapophyses are well developed, articulating with the postzygapophyses of the anterior vertebra; and in *Kali* and *Dysalotus*, the prezygapophyses are poorly developed and do not articulate with the postzygapophyses of the anterior vertebra. (ci=1.0)

29. Foramen for the spinal nerves on neural arch (ordered): present in all vertebrae (0); present only on pleural vertebra 3 (1); absent (2). In *Chiasmodon*, *Pseudoscopelus*, *Dysalotus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, each vertebra has a lateral foramen in the neural arch for the spinal nerve; in *Kali colubrina*, *K. macrodon* and *K. macrura*, a foramen is absent from most of the vertebrae, except for pleural vertebra 3, and in *K. falx*, *K. kerberti*, *K. indica* and *K. parri*, the foramen is absent in all vertebrae. In *Kali* the spinal nerves exit the neural canal via the indentation formed by the neural spines and the postzygapophyses. (ci=0.5)

Posterior vertebrae and caudal fin skeleton

30. Hemal spines and arches of vertebrae 2 and 3: not fused to centrum (0); fused to centra (1). In *Chiasmodon*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus*, *Scomberomorus*, the hemal arches and spines of vertebrae 2 and 3 are free from their

respective centra; and in *Kali* and *Dysalotus*, those haemal arches and spines are fused to the vertebral centrum. (ci=1.0)

31. Epurals (ordered): three, all well developed (0); three, epural 2 reduced (1); two epurals (2). In *Bembrops*, *Hoplostethus*, *Diplectrum*, *Chiasmodon*, *Pseudoscopelus*, *Kali colubrina* and *K. macrura*, the epurals are three; in *K. kerberti*, the epurals are three, but the epural 2 is reduced; and in *Dysalotus*, *K. falx*, *K. indica*, *K. macrodon*, and *K. parri*, the epurals are two. In *Scomberomorus* the epurals are two, but the fusion of epurals is not obvious as described above and the species was coded as unknown (?). (ci=0.29)

32. Hypurals 1, 2, 3, and 4: not fused (0); hypurals 1+2 and 3+4 fused to each other and to the ural centrum (1). In *Bembrops*, *Diplectrum*, *Chiasmodon*, *Dysalotus* and *Pseudoscopelus*, the hypurals 1, 2, 3 and 4 are not fused to each other, nor to the ural centrum. In *Kali*, hypurals 1+2 and 3+4 are fused to each other, and to the ural centrum at their base. In *Hoplostethus*, the hypurals are six, none of them fused; and in *Scomberomorus*, all elements are fused into a plate. (ci=0.5)

33. Hypural 5 (ordered): well developed (0); reduced (1); absent (2). In *Chiasmodon*, *Dysalotus*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus*, and *Scomberomorus*, the hypural 5 is well developed; in *Kali colubrina*, *K. indica*, *K. kerberti*, *K. macrura* and *K. parri*, the hypural 5 is reduced; and in *K. falx* and *K. macrodon*, absent or fused to hypurals 2+4. (ci=0.67)

34. Parahypural: free from ural centrum (0); fused to ural centrum (1). In *Chiasmodon*, *Dysalotus*, *Pseudoscopelus*, *Bembrops*, *Diplectrum, Hoplostethus* and *Scomberomorus*, the parahypural is free from the ural centrum; and in *Kali*, the parahypural is fused to the ural centrum. (ci=1.0)

35. CPNPU and CPHY 5: two elements (0); three elements (1). In *Chiasmodon*, *Dysalotus*, *Kali colubrina*, *K. falx*, *K. indica*, *K. macrura*, *K. parri*, *Hoplostethus*, *Scomberomorus* and *Diplectrum*, the post-neural elements are two, a CPNPU 2+3 and a CPHY; in *K. kerberti* and *K. macrodon*, the elements are three, CPNPU 2+3, CPNPU 3 and CPHY; and in *Bembrops*, one, CPNPU 2+3 and CPHY is absent. The number of CPNPU and CPHY is variable among the acanthomorphs (Fujima 1990): in *Hoplostethus*, several small elements; in *Scomberomorus*, three, CPNPU 2, 3 and CPHY, and in *Diplectrum*, two elements, the CNPHY and the interpleural cartilage. In the outgroup, the character was coded as unknown (?). (ci=1.0)

36. CPHPU: two elements (0); three elements (1). Among the chiasmodontids, there are two elements *Chiasmodon*, *Kali colubrina*, *K. macrura, K. parri* and *Pseudoscopelus*, CPHPU 2 and CPHPU 2+3; and in *Dysalotus*, *Kali falx*, *K. indica*, *K. kerberti*, and *K. macrodon*, there are three elements, CPHPU 1, 2 and 3. The number of CPHPU is variable among the Acanthomorpha (Fujima 1990): in *Bembrops*, only CPHPU 2+3 is present; in *Hoplostethus*, CPHPU 2+3 are fused, and an extra CPHPU 3 is present; in *Scomberomorus*, CPHPU 2 and 3 are separated; and in *Diplectrum*, a CPHPU 2+3 and a CPHPU 2 are present. In the outgroup the character was coded as unknown (?). (ci=0.33)

Ribs

37. Pleural ribs: thick, well developed (0); thin, poorly developed (1). In *Chiasmodon*, *Pseudoscopelus*, *Diplectrum*, *Bembrops*, *Hoplostethus* and *Scomberomorus*, the pleural ribs are normally developed, with a proximal expansion forming a shelf; and in *Dysalotus* and *Kali*, the pleural ribs are extremely thin, resembling in shape the epineurals. (ci=1.0)

38. Epipleural: absent (0); present on first pleural rib (1); present on second pleural rib (2). In *Dysalotus*, *Kali*, *Pseudoscopelus*, *Bremops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the epipleurals are absent; in *C. braueri*, *C. harteli*, *C. microcephalus*, *C. niger* and *C. pluriradiatus*, a single epipleural is present above the first pleural rib (third vertebra); and in *C. subniger*, a single epipleural is present on the second pleural rib (fourth vertebra). (ci=1.0)

Hyoid and Branchial arches

39. Foramen on ceratohyal: absent (0); present (1). In *Chiasmodon*, *Pseudoscopelus*, *Diplectrum* and *Scomberomorus*, a foramen in the ceratohyal is absent; and in *Dysalotus*, *Kali* and *Hoplostethus*, a foramen is present. (ci=0.5)

40. Proximal and distal ceratohyals: connected by cartilage (0); sutured by prongs (1). In *Kali*, *Dysalotus*, *Hoplostethus* and *Diplectrum*, the proximal and distal are connected by cartilage; and in *Chiasmodon*, *Pseudoscopelus* and *Scomberomorus*, the proximal and distal ceratohyals are connected by a suture formed by interconnecting prongs. (ci=0.5)

41. Branchiostegal rays: eight (0); seven (0); six (1). In *Hoplostethus*, the branchiostegal rays are eight; in *Chiasmodon*, *Dysalotus*, *Pseudoscopelus*, *Diplectrum* and *Scomberomorus*, seven; and in *Kali*, six. (ci=1.0)

42. Gill rakers on first arch: present (0); absent (1). In *Dysalotus*, *K. colubrina*, *K. kerberti*, *K. macrodon*, *K. macrura*, *K. parri*, *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, *P. scutatus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the gill rakers are present on the first arch; and in *Chiasmodon*, *K. falx*, *K. indica* and *P. australis*, they are absent. (ci=0.33)

43. Gill rakers on second arch (ordered): present (0); reduced in number (1); absent (2). In *Chiasmodon braueri*, *Dysalotus*, *K. colubrina*, *K. kerberti*, *K. macrodon*, *K. macrura*, *K. parri*, *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, *P. scutatus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the gill rakers are present on the elements of the second arch; in *C. harteli*, *C. niger* and *P. australis*, the rakers are fewer and restricted to the hypobranchial; and in *C. asper*, *C. microcephalus*, *C. pluriradiatus*, *C. subniger*, *K. falx* and *K. indica*, the gill rakers are absent. (ci=0.4)

44. Teeth on second brasibranchial: absent (0); present (1). In *Chiasmodon*

microcephalus, *C. subniger*, *Dysalotus*, *Kali*, *Bembrops*, *Diplectrum*, *Hoplostethus*, and *Scomberomorus*, teeth are absent on the second basibranchial; and in *C. asper*, *C. braueri*, *C. harteli*, *C. niger*, *C. pluriradiatus* and *Pseudoscopelus*, teeth are present. (ci=0.5)

45. Teeth on basihyal: absent (0); present (1). In *Chiasmodon*, *Dysalotus*, *Kali*, *Pseudoscopelus altipinnis*, *P. aphos*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. paxtoni*, *P. parini*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, *P. scutatus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, teeth are absent on the basihyal; and in *P. astronesthidens*, *P. australis* and *P. odontoglossum*, teeth are present. (ci=1.0)

46. Rod-like interarcual cartilage: present (0); reduced (1). In *Kali*, *Dysalotus*, *Bembrops*, *Diplectrum* and *Scomberomorus*, rod-like interarcual cartilage is well developed and links the uncinate process of the first epibranchial to the second pharyngobranchial; and in *Pseudoscopelus* and *Chiasmodon*, the rod-like interarcual cartilage is reduced, not connected to the first epibranchial. Johnson and Patterson (1993) listed the rod-like interarcual cartilage as a synapomorphy of the Perciformes (character 26). In *Hoplostethus*, the rod-like interarcual cartilage is absent and was coded as unknown (?). (ci=1.0)

47. Basibranchial 3: short, between basibranchial 2 and 3 (0); long, curved ventrally and passing underneath the basibranchial 4 (1) In *Bembrops*, *Diplectrum* and *Hoplostethus*,

basibranchial 3 is relatively short and extend between the basibranchials 2 and 4; and in *Chiasmodon*, *Dysalotus*, *Kali*, *Pseudoscopelus* and *Scomberomorus*, basibranchial 3 extends underneath the brasibranchial 4 and has a cartilaginous tip that curves ventrally. (ci=1.0)

48. Size of basihyal: elongated (0); short (1). In *Chiasmodon*, *Dysalotus*, *Kali kerberti*, *K. macrodon*, *K. macrura*, *K. parri*, *Pseudoscopelus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the basihyal is elongated; and in *Kali falx* and *K. indica*, the basihyal is short. (ci=1.0)

49. Shape of basihyal (ordered): straight (0); slightly arched (1); strongly arched (2) In *Chiasmodon*, *Dysalotus*, *Kali falx*, *K. indica*, *K. parri*, *Pseudoscopelus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the basihyal is straight; in *K. macrura*, the basihyal is slightly arched; and in *K. kerberti* and *K. macrodon*, the basihyal is strongly arched. (ci=1.0)

50. Ceratobranchial 1: free (0); connected to the internal part of mouth (1). In *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, ceratobranchial 1 is free; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, ceratobranchial 1 is connected by skin to the lateral wall of the mouth. (ci=1.0)

51. Platelets in distal portion of dorsal-fin element: absent (0); present (1). In *Chiasmodon*, *Dysalotus*, *Kali*, *Pseudoscopelus altipinnis*, *P. aphos*, *P. astronesthidens*, *P.*

australis, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. paxtoni*, *P. parini*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the platelets are absent; and in *P. bothrorrhinos* and *P. scutatus*, the distal portion of the pterygiofores of the first dorsal fin (= distal radials, see previous character) are modified into platelets, which are exposed in dorsal view. (ci=1.0)

Pectoral and Pelvic girdles

52. Anterior connection between pelvic and pectoral girdles: pelvic and pectoral girdle connected by a ligament (0); not connected (1). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the pelvic girdle of is dorsally inclined and anteriorly attached to the cleithrum or coracoid; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the pelvic girdle is flat and free-floating in the hypaxials and anterior and medial infracardinals, and only connected laterally to the postcleithrum by a thin fascia (see next character). Stiassny and Moore (1992) list this character as a synapomorphy for Perciformes (character 5); herein condition found herein for the chiasmodontids is considered to be a secondary reversion. (ci=1.0)

53. Lateral tendon between pelvic and pectoral girdles: present, connecting to cleithrum (0); present, connecting to postcleithrum (1). In *Kali*, *Dysalotus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the tendon extends from the lateral tip of pelvis to cleithrum; and in *Chiasmodon* and *Pseudoscopelus*, the tendon extends from the lateral tip of pelvis to the postcleithrum. The tendon between the pelvic girdle to the distal

postcleithrum was listed by Stiassny and Moore (1992) as a synapomorphy of Acanthomorpha (character 2) and a consequence of the forward position of the pelvic fin. The condition found in *Chiasmodon* and *Pseudoscopelus* is considered to be a secondary modification of that condition. (ci=1.0)

Pectoral Girdle

54. Scapular foramen: small (0); wide (1). In *Dysalotus*, *Kali*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the scapular foramen is moderately enlarged, not extending over an area larger than half of the scapula; and in *Chiasmodon* and *Pseudoscopelus*, the scapular foramen is enlarged and extends over an area larger than half of scapula. (ci=1.0)

55. Postcleithra 1 and 2: fused (0); separated (1). In *Dysalotus*, *Kali*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the postcleitra 1 and 2 are fused; and in *Chiasmodon* and *Pseudoscopelus*, the postcleithra 1 and 2 are separated. (ci=1.0)

56. Size of post-cleithrum 1: enlarged (0); reduced (1). In *Chiasmodon*, *Pseudoscopelus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the postcleithrum 1 is enlarged, and exposed in lateral view, posterior to the posterior plate of the cleithrum; and in *Dysalotus* and *Kali*, the postcleithrum (1 and 2 fused, see previous character) is small and laterally covered by the posterior plate of the cleithrum. (ci=1.0)

Pelvic girdle

57. Ligaments between the contralateral pelvic girdles: pelvic fins fused (0) medial

process overlapping or fused to the contralateral girdle (1); medial process not overlapping neither fused to the contralateral girdle (2). In *Hoplostethus*, the medial process of the pelvic girdle overlaps the process of the contralateral girdle; in *Diplectrum* and *Scomberomorus*, the collateral processes are sutured medially; and in the *Chiasmodon*, *Dysalotus*, *Kali*, *Pseudoscopelus* and *Bembrops*, the collateral process do not overlap and are not fused. Stiassny and Moore (1992) considered the non association of the pelvic halves as the plesiomorphic condition for Acanthomorpha, and described the overlapping and fusion as the apomorphic conditions (character 1). For a few groups in which there was no overlapping or fusion, it was considered a secondary reversion: percopsids, aphredoderioids, lampridiforms and in the fossil *Sphenocephalus*. Herein, the conditions found in the chiasmodontids are considered as a secondary reversion. (ci=0.67)

58. Anterior connection of the pelvic halves: connected by a tendon (0); connected by a cartilage (1); completely disconnected (2). In *Kali*, *Dysalotus*, *Diplectrum* and *Hoplostethus*, the pelvic halves are closely connected anteriorly by a tendinous ligament; in *Pseudoscopelus*, the pelvic girdles are anteriorly connected by a cartilaginous bridge; and in *Chiasmodon* and *Scomberomorus* the pelvic girdles are free anteriorly. (ci=0.67)

Dorsal fin

59. Insertion of first dorsal fin (ordered): between second and third vertebrae (0); between third and fourth vertebrae (1); between fourth and fifth vertebrae (2); between fifth and six vertebrae (3); between sixth and seventh vertebrae (4); and between seventh and

eighth vertebrae (5). In *Bembrops*, *Diplectrum* and *Hoplostethus*, the first dorsal fin inserts between the second and third vertebrae; in *Dysalotus* and *Scomberomorus*, the insertion is between the third and forth vertebrae; in *Kali falx*, *K. indica*, *K. kerberti* and *K. parri*, between the fourth and fifth vertebrae; in *K. colubrina*, *K. macrodon*, *K. macrura*, between the fifth and sixth vertebrae; in *Chiasmodon asper*, *C. braueri*; *C. harteli*, *C. niger*, *C. pluriradiatus*, *C. subniger* and *Pseudoscopelus*, between the sixth and seventh vertebrae; and in *C. microcephalus*, between the seventh and eighth vertebrae. (ci=0.56)

Anal Fin

60. Origin of anal fin: slightly posterior to the level of second dorsal fin (0); far posterior to the level of second dorsal fin (1). In *Dysalotus*, *Kali*, *Pseudoscopelus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the origin of the anal fin is a vertebra posterior to the origin of the dorsal fin; and in *Chiasmodon*, the anal fin originates four to five vertebrae posterior to the second dorsal. (ci=1.0)

61. Anal-fin proximal radials (ordered): enlarged, reaching and intercalating with the haemal spines (0); elongated anteriorly, but not reaching the level of the haemal spines, but extending proximally on body wall, lateral to the abdominal cavity (1); short, not extending lateral to the abdominal cavity (2). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the anal-fin proximal radials are very elongated, extending proximally between the neural spines, intercalating with them, being connected by ligament, at least anteriorly; in *Chiasmodon*, *Dysalotus*, *Kali macrura*, *K. parri* and *Pseudoscopelus*, the

proximal radials do not reach the neural spines, but are elongated anteriorly, and extend laterally to the expanded abdominal cavity; and in *K. colubrina*, *K. falx*, *K. indica*, and *K. macrodon*, the proximal radials are short and do not reach the extended abdominal cavity. (ci=0.67)

62. Length anal-fin proximal radials: gradually increasing/decreasing in size (0); third proximal radial much more elongated than the other radials (1). In *Chiasmodon*, *Dysalotus*, *Kali*, *Pseudoscopelus altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. scutatus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the proximal radials gradually increase in size anteriorly until the second, third, fourth or fifth radial, and than gradually decrease in size; and in *P. cephalus*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus*, and *P. scriptus*, the third proximal radial is very elongated, almost twice the length of the remaining radials. (ci=1.0)

Dentition

Teeth arrangement

63. Origin of replacement tooth: intraosseous (0); extraosseous (1). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the tooth development is intraosseous; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the development is extraosseous; and in *Bembrops*, is questionable. The modes of tooth development apparently evolved several times among the perciforms, but the extraosseus development is considered to be the plesiomorphic condition in osteichthyans (Trapani 2001). (ci=1.0)

64. Dentition type: homodont (0); heterodont (1). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the dentition is homodont. In *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the dentition is heterodont. (ci=1.0)

65. Series of teeth in premaxilla (ordered): one (0); two (1); three (3). In *Scomberomorus*, the premaxillary teeth are in a single series of a single row and in *Bembrops*, *Diplectrum* and *Hoplostethus*, in a single series of with a broad band of villiform teeth; in *Chiasmodon* and *Kali*, in two series (lateral and mesial); and in *Dysalotus* and *Pseudoscopelus*, in three series of one or three rows (lateral, middle, mesial; see chapter 3 and see next character). (ci=0.67)

66. Rows of teeth in middle and mesial series of premaxilla: one (0); three (1). This character refers to the specific distribution of teeth in the species of *Dysalotus* and *Pseudoscopelus* and was coded as unknown (?) in other groups. In *Pseudoscopelus obtusifrons*, *P. pierbartus*, the middle series is on a single row; and in *Dysalotus*, *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. odontoglossum*, *P. paxtoni*, *P. parini*, *P. sagamianus*, *P. scriptus*, *P. scutatus*, the middle and mesial series have three rows of teeth each. (ci=1.0)

67. Premaxillary teeth in mesial series in *Chiasmodon*: two to seven (0); one (1). This character describes the variation in the number of premaxillary teeth in the mesial series

within *Chiasmodon* and was coded as unknown (?) for in other groups (for description, see Chapter 2). In *Chiasmodon braueri*, *C. harteli*, *C. microcephalus*, *C. niger*, *C. subniger*, the premaxillary teeth in mesial series are two to seven; and in *C. asper* and *C. pluriradiatus*, one. (ci=1.0)

68. Premaxillary teeth in mesial row in *Kali* (ordered): more than nine (0); five to nine (1); four to five (2); three (3). This character describes the variation in the number of premaxillary teeth in the mesial series within *Kali* and was coded as unknown (?) in other groups. Although some variation is present, to simplify the description of the states, only the modes are being considered (for description, see Chapter 3). In *Kali parri*, the premaxillary teeth in mesial series are numerous, modally 15; in *K. colubrina* and *K. macrodon*, five to nine; and in *K. kerberti* and *K. macrura*, three to four; and in *K. indica* and *K. falx*, three. (ci=0.75)

69. Premaxillary teeth in mesial row in *Pseudoscopelus*: two to eight (0); more than 20 (1). This character describes the variation in the number of premaxillary teeth in the mesial series within *Pseudoscopelus* and was coded as unknown (?) in other groups (for description, see Chapter 4). In *Pseudoscopelus altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, the premaxillary teeth in mesial series are more than 20; and in *P. obtusifrons* and *P. pierbartus*, are two to eight. In *Chiasmodon*, the teeth in mesial row are less than eight; in *Kali*, are variable; and in *Dysalotus*, more than 20. (ci=1.0)

70. Dentary teeth in mesial row in *Kali* (ordered): more than ten (0); seven to eight (1); three (2). This character describes the variation in the number of premaxillary teeth in the mesial series within *Kali* and was coded as unknown (?) in other groups. Although some variation is present, for simplification of the states descriptions, only the modes are being considered (for description, see Chapter 2). In *Kali parri*, the dentary teeth in mesial series are numerous, modally 18; in *K. colubrina*, *K. kerberti*, *K. macrodon* and *K. macrura*, seven to eight; and in *K. indica* and *K. falx*, three. (ci=1.0)

Tooth morphology

71. Tooth: compact (0); hollow (1). In *Chiasmodon*¸ *Dysalotus*, *Kali* and *Pseudoscopelus*, the tooth is hollow; in *Bembrops, Diplectrum, Hoplostethus* and *Scomberomorus* the tooth is compact. (ci=1.0).

72. Dentary and premaxillary tooth crown (ordered): less than 10% of tooth length (0); 15–25% in tooth length (1); 35–47 % in tooth length (2). In *Chiasmodon*¸ *Dysalotus*, *Kali parri*, *Pseudoscopelus*, *Bembrops, Diplectrum, Hoplostethus* and *Scomberomorus*, the tooth crown is short and has less then 10 % in the tooth length; in *K. colubrina*, *K. macrura*, *K. indica*, *K. macrodon*, the tooth crown is moderately developed, 15–25 % in tooth length; and in *K. kerberti* and *K. falx*, the tooth crown is extremely developed and is 35–40% in tooth length. (ci=0.67)

73. Tooth attachment in dentary and premaxilla: ankylosed to bone or with anterior

attachment (0); ventral attachment (1). In *Chiasmodon*, *Dysalotus*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the teeth are either ankylosed to the bone or have an attachment that allow them to bend dorsally (types 1 and 4, sensu Fink 1981); and in *Kali*, the teeth, at least in the medial series, have a ventral attachment to the bone that allows them to bend dorsally and rotate around their own axis. Fink (1981) also described two other modes of attachment for the teleostans, which are also different to the condition present in *Kali*. (ci=1.0)

74. Teeth with ventral attachment in lateral series in lateral series of dentary and premaxilla: absent (0); present (1). This character refers to the teeth with ventral attachment (see previous character) in the lateral series. In *Chiasmodon*, *Kali colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon*, *Dysalotus*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the teeth with ventral attachment are absent in the lateral series; and in *K. macrura*, *K. parri*, the teeth with ventral attachment are present in both medial and lateral series, in dentary and premaxilla. (ci=0.5)

75. Recurved fangs in dentary and premaxilla: absent (0); present, extremely enlarged, 14–45% in premaxillary length, 15–47% in dentary length (1). In *Chiasmodon*, *Kali colubrina*, *K. parri*, *Dysalotus*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the extremely enlarged fangs are absent and the teeth are smaller than 10% in dentary and premaxillary length; and in *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon*, *K. macrura*, *K. normani*, extremely enlarged fangs are present on the premaxillary and dentary, 14–45% and 17–47 % on body length, respectively, not

allowing the mouth to be completely closed (ci=1.0)

76. Needle-like teeth in medial and mesial series of dentary and premaxilla: absent (0); present (1). In *Chiasmodon*, *Kali*, *Pseudoscopelus obtusifrons*, *P. pierbartus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the needle-like teeth are absent in premaxilla and dentary; and in *Dysalotus* and *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, the needle-like teeth are present in the medial and mesial series of premaxilla and mesial series of dentary. (ci=0.33)

77. Premaxillary canine: absent (0); present, small (1); present, enlarged (2); present, developed into fangs (3). In *Dysalotus*, *K. kerberti*, *K. macrodon*, *K. macrura*, *K. parri*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the canine is absent; in *Pseudoscopelus*, the premaxillary canine is present and reduced; in *Chiasmodon* and *Kali colubrina,* the premaxillary canine is and enlarged, and projects outside of the mouth; and in *K. indica* and *K. falx*, it is present and extremely enlarged. The premaxillary canine is a unicuspid tooth with a type 1 attachment on the anterior edge of the premaxillary head. The premaxillary canine present in *Kali* is apparently not homologous to that present in *Chiasmodon* and *Pseudoscopelus.* (ci=0.75)

78. Lateral accessory tooth: absent (0); present (1). In *Dysalotus*, *Kali*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, lateral accessory teeth are

absent; and in *Chiasmodon*, one or two small lateral accessory teeth are present beside the premaxillary canine. The lateral accessory tooth is a small, type 1, conical tooth, inserted lateral to the base of the premaxillary canine. (ci=1.0)

79. Premaxillary fang (ordered): absent (0); one present (1); two present (2). In *Dysalotus*, *Kali colubrina*, *K. falx*, *K. indica*, *K. parri*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the fang is absent; and in *Chiasmodon braueri*, *C. harteli*, *C. microcephalus*, *C. niger*, *C. subniger*, *K. kerberti*, *K. macrodon*, *K. macrura*, and *Pseudoscopelus*, a single fang is present; and in *C. asper* and *C. pluriradiatus*, two fangs are present. The premaxillary fang is a straight, type 4, conical tooth, inserted on the ventral shelf of the premaxillary head that is able to bend caudally and is posterior to the canine, if present. (ci=0.67)

80. Dentary canine: absent (0); present (1). In *Kali*, *Dysalotus*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the canine is absent on dentary; and in *Chiasmodon*, is present. The dentary canine is the largest tooth in lateral series, the only tooth in the series with type 1 attachment, conical and remains exposed when mouth closed. (ci=1.0)

81. Posterior teeth in lateral series of premaxilla: similar to adjacent teeth (0); one to three teeth modified (1); more than five teeth modified (2). In *Chiasmodon* and *Dysalotus* and *P. aphos*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, , *P. obtusifrons*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, *P. scutatus*, *Bembrops*, *Diplectrum*, *Hoplostethus*

and *Scomberomorus*, the teeth of the entire lateral row are all similar in shape and have a type 4 attachment to bone; in *P. altipinnis* and *P. paxtoni*, *P. lavenbergi* and *P. parini*, one to three teeth in the posterior part of premaxilla are stouter and have the type 1 attachment; and in *P. astronesthidens*, *P. australis*, *P. odontoglossum*, five to ten teeth in the posterior third of premaxilla are stouter and have are have type 1 attachment. Among the species of *Kali*, *K. macrura*, has teeth in the lateral series of premaxilla differentiated between the needle-like teeth and the ventral attachment to bone, therefore, not homologous to this character and coded as unknown (?) for that species; all other species have only a single kind of teeth along the entire series. (ci=1.0)

82. Needle-like teeth in lateral series: absent (0); present (1). This character refers to the needle-like teeth present on the lateral series in some species of *Kali*. In *Chiasmodon*, *Kali colubrina*, *K. colubrina*, *K. falx*, *K. indica*, *K. parri*, *Dysalotus*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the teeth in the lateral series of premaxilla and dentary are conical or recurved; and in *Kali kerberti*, *K. macrodon* and *K. macrura*, the teeth in the lateral series of premaxilla and dentary are needle-like. (ci=1.0)

83. Palatine teeth (ordered): absent (0); in single row (1); in two rows (2). In *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the palatine teeth are absent; in *Chiasmodon*, *Dysalotus*, *Kali*, *Pseudoscopelus altipinnis*, *P. aphos*, *P. australis*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. parini*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, the palatine teeth

are in a single row; and in *P. astronesthidens* and *P. odontoglossum*, the palatine teeth are in two rows. (ci=1.0)

Myology

Muscles of the cheek

84. Volume of section A2α of adductor mandibulae: moderately developed, covering most of the cheek but leaving the levator arcus palatini exposed dorsally and the adductor arcus palatini anteriorly (0); covering entire check (1). The A2α is the most lateral section of the adductor mandibulae, its origin is on the preopercle, hyomandubular, pterotic and/or dermosphenotic (see next character) and insertion on the ligamentum primordium. In *Diplectrum*, *Dysalotus* and *Kali macrura*, it covers A2α', if present, A2β, A3 and only the most ventral part of the levator arcus palatine, which remains mostly exposed laterally; and in *Chiasmodon*, *Pseudoscopelus* and *Kali parri*, *K. colubrina*, *K. falx*, *K. kerberti* and *K. indica Scomberomorus*, the section A2α occupies the entire cheek and covers all the medial muscles. (ci=0.33)

85. Origin of section A2α of adductor mandibulae (ordered): origin on anterior margin of preopercle and hyomandibula (0); anterior margin of preopercle, hyomandibula and anterolateral margin of pterotic (1); anterior margin of preopercle hyomandibula, anterolateral margin of pterotic, extending over dermosphenotic (2). The origin of the A2α includes a wide variety of sites: quadrate, sympletic, preopercle, hyomandibula, ectopterygoid, mesopterygoid, metapterygoid, infraorbitals, skull dorsolateral to the hyomandibular, prefrontal, palatine, ethmoid and parasphenoid (Winterbottom, 1974).

Among the chiasmodontids the insertion of Aα is the preopercle, and it extends ventrally over the A2β. In *Hoplostethus*, *Diplectrum* and *Dysalotus*, it is dorsally limited to the preopercle and hyomandibular; in *Chiasmodon*, *Kali parri*, *Kali kerberti*, *Pseudoscopelus*, it extends dorsally to the antero-lateral margin of pterotic, but not overlapping the dermosphenotic; and in *K. kerberti*, *K. colubrina*, *K. indica* and *Scomberomorus*, it extends over the dermosphenotic. (ci=0.5)

86. Section A2α' of adductor mandibulae (ordered): absent or fused with A2α (0); distinguished from A2α, but narrow (1); distinguished from A2α, and broad, of almost the same width as A2α (2). The A2α' is a subdivision of the A2α which can be distinguished from A2 by the direction of fibers, and deeper origin on preopercle and insertion on a mycomma with AW, and from A3 by the track of the ramus mandibularis of the trigeminal nerve. The origin of the A2α' is on the hyomandibular, and the insertion is on the ligamentum primordium, with A2α. (Wu and Shen, 2004). In *Hoplostethus*, *Diplectrum*, *Scomberomorus*, *Chiasmodon* and *Pseudoscopelus*, the A2α' is either absent or fused with A1α. In *Dysalotus* and *Kali*, the sections A2α, A2α' and A2β are separated; in *Dysalotus*, *K. macrura* and *K. falx*, A2α' is slender and composed by very few fibers; and in *Kali colubrina*, *K. indica*, *K. parri*, *K. kerberti* and *K. macrodon*, A2α' is broad, and is of the same width or slightly smaller than A2β. (ci=0.5)

87. Origin of A2β (ordered): short area, originating from area of half or less of the anterior margin of preopercle (0); broad area, originating from a broad area on anterior margin of preopercle (1). In *Kali*, *Dysalotus* *Diplectrum*, *Hoplostethus* and

Scomberomorus, the origin of A2β occupies a small area on preopercle; and in *Chiasmodon* and *Pseudoscopelus*, is broad, extending over almost entire length of preopercle. (ci=1.0)

88. Section A1β of adductor mandibulae: absent (0); present (1). In *Hoplostethus*, *Diplectrum* and *Scomberomorus*, the A1β is absent; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the A1β is present. The section A1β is a deep subdivision of the adductor mandibular, which lies on the palatal arch and is medial to the ramus mandibularis of the trigeminal; it originates from the hyomandibular and inserts dorsally on the maxilla (Winterbotton 1974). It deserves certain attention, because evolved independent times among the teleostans in several groups: Paracanthopterygii, *Astronesthes*, *Champsodon*, *Istiblenius*, *Johnius*, *Praealticus* and *Sarcocentron* (Rosen and Patterson, 1969; Gill and Mooi, 1993; Wu and Shen, 2004). In Paracanthopterygii the A1β is medial to the A2 and lateral to A3, but in chiasmodontids it is the deepest muscle of the cheek, medial to section A2 and A3. It also makes the author was the presence of this muscle that made Günther (1864) place the chiasmodontids among the gadids. (ci=1.0)

89. Insertion of section A1β of adductor mandibulae: on maxilla, posterior to mid-eye (0); on maxilla, anterior to mid-eye (1). In *Chiasmodon*, *Pseudoscopelus*, *Kali colubrina*, *K. indica* and *K. falx*, the A1β inserts on the premaxilla posterior to mid-eye; and in *Dysalotus*, *K. kerberti*, *K. macrodon*, *K. macrura* and *K. parri*, the insertion is anterior to mid-eye. Because A1β is absent in *Diplectrum*, *Hoplostethus* and *Scomberomorus*, it is

coded as unknown (?). (ci=0.33)

90. Tendon of A2α, A2β and A3: medial on angular, on meckelian fossa (0); lateral, on angular, on prearticular fossa (1). In *Chiasmodon*, *Dysalotus*, *Kali*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the tendon that serves as insertion for the sections A2α, A2β and A3 and the posterior part of ligamentum primordium inserts on the medial side of angular, on the meckelian fossa; and in *Pseudoscopelus*, the tendon inserts on the lateral side of angular, on the prearticular fossa. (ci=1.0)

Muscles of the head

91. Dilator operculi: medial to preopercle and lateral to hyomandibula (0); dorsal to preopercle and lateral to hyomandibula, overlapping it. (1). The dilator operculi originates on the pterotic and inserts dorsally on the articular process of the opercle. In *Chiasmodon*, *Pseudoscopelus Diplectrum*, *Hoplostethus* and *Scomberomorus*, it passes thru a fenestra formed laterally by the preopercle and medially by the hyomandibula; and in *Dysalotus* and *Kali*, the fenestra is absent and the dilator operculi passes dorsally to the preopercle, and lateral to the hyomandibula. (ci=1.0)

92. Intermandibularis: reaching symphysis of dentary anteriorly (0); not reaching symphysis of dentary anteriorly (1). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the intermantibularis anteriorly reaches the symphysis of the dentaries; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the intermandibularis does not reaches the symphysis of dentaries. (ci=1.0)

Muscles serving the hyoid and branchial arches

93. Anterior attachment of protractor hyoidei: anterior, close to symphysis of dentary (0); posterior, above or slightly posterior to attachment of intermandibularis (1). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the protractor hyoidei inserts medially on dentary, close to symphysis of dentaries; and in *Chiasmodon*, *Dysalotus, Kali* and *Pseudoscopelus*, the protractor hyoidei inserts medial on dentary, posterior or slightly above to attachment of intermandibularis. (ci=1.0)

94. Levator externus of first arch: normally developed (0); extremely reduced, with a few fibers (1). The origin of the levator externi is the pterotic and the insertion, the epibranchials. Among specialized acanthopterygians the levator externus for the third arch is frequently absent (Winterbottom, 1974). In *Diplectrum*, *Hoplostethus*, *Chiasmodon* and *Pseudoscopelus*, the levator externus for the first arch is well developed; and in *Kali* and *Dysalotus*, the levator externus of the first arch is extremely reduced, and with only a few fibers. (ci=1.0)

95. Origin of levator posterioris: dorsal to pterotic (0); ventral shelf of pterotic (1). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the levator posterioris originates on the dorsal part of pterotic and inserts on the fourth gill arch; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, originates on the ventral shelf of pterotic to insert on the fourth gill arch. The levator posterior is treated as a synapomorphy of the neoteleostans (Winterbottom, 1974). (ci=1.0)

96. Posterior attachment of the retractor dorsalis (ordered): first vertebra (0); third or fourth vertebra (1); fifth and sixth vertebrae (2); ninth vertebra (3). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the retractor dorsalis attaches to the first vertebra. In *Chiasmodon* and *Pseudoscopelus*, the retractor dorsalis connects to third or fourth vertebrae; in *Dysalotus*, *K. colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon* and *K. macrura*, the retractor dorsalis connects to the fifth or sixth vertebrae; and in *Kali parri*, the retractor dorsalis connects far posteriorly, on the ninth vertebrae. The retractror dorsalis is a paired muscle that connects the upper pharyngeals to the vertebrae; it is a synapomorphy of Neoteleostei and has an important role in manipulating food; the origin of the retractor dorsalis can be any of the first to sixteenth vertebrae and the insertion exclusively on the third and the insertion on the third infrapharyngobranchial in acanthomorphs (Lauder and Lien, 1983). (ci=0.75)

97. Connection of retractor dorsalis on vertebra: centrum (0); basapophysis (1). In *Dysalotus*, *Kali*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the retractor dorsalis connects ventrally, to the centrum; and in *Pseudoscopelus* and *Chiasmodon*, the retractor dorsalis connects laterally, to the anterior edge of the basapophysis. (ci=1.0)

Muscles between the pectoral girdle and the skull

98. Levator posterior, protractor pectoralis: present (0); absent (1). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the levator posterior, protractor pectoralis are present; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the levator posterior, protractor

pectoralis are absent. The levator posterior, protractor pectoralis are part of a complex that connects the cranium to posterior part of gill arch and to pectoral girdle (Winterbotton, 1974). Among the chiasmodontids, those muscles are absent, and the pectoral girdle is dorsally connected to the body by the fibers of the epaxial musculature and by the Baudelot's ligament. (ci=1.0)

99. Heads of pharyngoclavicularis internus: one (0); two (1). In *K. colubrina*, *K. indica*, *K. macrura*, *K. parri*, *Pseudoscopelus bothrorrhinos*, *P. scutatus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the pharyngoclavicularis internus has a single head that inserts on the lateral process of the pharyngobranchial; and in *Chiasmodon*, *Dysalotus*, *K. kerberti*, *K. macrodon*, *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. paxtoni*, *P. parini*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, the pharyngoclavicularis internus has two heads that insert on the lateral process and the body of the lower pharyngobranchial. The origin of the pharingoclavicularis internus is on the anterior face of cleithrum (Winterbottom, 1974). (ci=0.2)

100. Obliquus ventralis of arches 1 and 2: present (0); absent (1). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the obliquus ventralis is present on the first, second and third gill arches; and in *Chiasmodon*, *Dysalotus*, *Kali* and *Pseudoscopelus*, the obliquus ventralis is absent on the first and second arches and present only on the third arch. The obluquus ventralis is a muscle that connects the hypobranchial to the ceratobranchial on each arch, and is absent on the fourth arch (Winterbotton, 1974).

(ci=1.0)

Muscles of the Pectoral fin

101. Origin of the abductor superficialis pelvicus: medially in midline of pelvis (0); lateral to midline of pelvis (1). In *Dysalotus*, *Kali* and *Pseudoscopelus*, the abductor superficialis pelvicus originates from midline of the pelvis; and in *Chiasmodon*, the abductor superficialis pelvicus originates laterally. The abductor superficialis pelvicus is a muscle in the ventral side of the pelvis, which originates medially and inserts onto the base of the pelvic-fin rays (Winterbotton, 1974). (ci=1.0)

Muscles of the Caudal fin

102. Interradials: fibers oblique to caudal-fin rays (0); fibers transverse to caudal-fin rays (1). In *Dysalotus*, *Kali*, *Diplectrum* and *Hoplostethus*, the interradials and composed by fibers that are transverse and originate on the bases of the caudal-fin rays and insert on the adjacent ray; and in *Chiasmodon* and *Pseudoscopelus*, the interradials are composed of longitudinal fibers that originate on the proximal caudal-fin rays and insert on the distal caudal-fin rays. In *Scomberomorus*, the caudal fin is highly modified and this character was coded as unknown (?). (ci=1.0)

103. Origin of flexor dorsalis and flexor ventralis inferior: second vertebra before centrum (0); third vertebra before centrum (1). In *Kali*, *Dysalotus*, *Pseudoscopelus*, *Diplectrum* and *Hoplostethus*, the flexor dorsalis and flexor ventralis inferior originate on the spines, arches and body of the vertebra 2; and in *Chiasmodon*, the flexor dorsalis and

flexor ventralis inferior originate on the spines, arches and body of the vertebra 3. All species, the flexor dorsalis and flexor ventralis inferior insert on the middle rays of the upper and lower lobes of the caudal fin respectively. In *Scomberomorus*, the caudal fin is highly modified and this character was coded as unknown (?). (ci=1.0)

The body musculature

104. Infracardinalis anterior: narrow and elongated (0); broad and elongated (1). The infracardinalis anterior is a ventral and anterior muscle that connects the ventral tip of cleithrum to the pelvis. In *Dysalotus*, *Kali*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, it is a narrow, elongated muscle that has a small point of attachment into both the cleithrum and the pelvis; and in *Chiasmodon* and *Pseudoscopelus*, it is broad, with a broad point of insertion on the cleithrum and pelvis. (ci=1.0)

105. Infracardinalis medius: thin (0); broad (1). In *Dysalotus*, *Kali*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the infracardinalis medius is a narrow bundle that forms the ventral wall of body between the pelvic and anal fins; and in *Chiasmodon* and *Pseudoscopelus*, the infracardinalis medius is a broad bundle that contributes to the ventral and for the lateral wall of the body between the pelvic and anal fins. (ci=1.0)

106. Hypaxial musculature (ordered): obliquus superioris and obliquus inferiors sections of the hypaxial connected (0); obliquus inferioris partially disconnected from obliquus superioris anteriorly, broad (1); obliquus inferioris completely disconnected from obliquus superioris anteriorly, reduced to a narrow bundle of fibers along body (2). In

Diplectrum, *Hoplostethus*, *Scomberomorus*, the fibers of the hypaxial musculature are continuous and not clearly differentiated; in *Dysalotus* and *Kali*, the obliquus inferioris is broad and partially disconnected from the obliquus superioris, with a connection made by some fibers and the myosepta; and in *Chiasmodon* and *Pseudoscopelus*, the obliquus inferioris on the abdominal cavity is reduced to a narrow bundle of fibers, the fibers are completely disconnected. Differences on the orientation of the fibers of the hypaxial musculature allow it to be differentiated into the obliquus superioris and obliquus inferioris sections (Winterbottom 1974). (ci=1.0)

Laterosensory system

Lateral line canal

107. Lateral line: continuous (0); last scale disconnected from lateral line, on lower lobe of caudal fin (1). In *Dysalotus*, *Kali*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the lateral line scales are continuous; and in *Chiasmodon* and *Pseudoscopelus*, the last scale is disconnected from the lateral line and moved to the lower lobe of caudal fin. (ci=1.0)

108. Extension of lateral line: ending at base of caudal-fin rays (0); extends to caudal-fin fork. In *Chiasmodon*, *Pseudoscopelus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the lateral line ends at the base of the caudal-fin rays; or in *Chiasmodon* and *Pseudoscopelus*, at the loose scale on ventral lobe of caudal fin (see previous character); and in *Kali* and *Dysalotus*, the lateral line extends to the tip of the medial caudal fin rays, which forms the fork. (ci=1.0)

109. Pores of trunk lateral line canal (ordered): one pore, perforating the scale (0); two pores, perforating the scales (1); scales not perforated, a pore opening between each between the scales (2). In *Dysalotus*, *Diplectrum* and *Hoplostethus*, a pore perforates each scale on the trunk canal of the lateral line system; in *Kali*, two longitudinal pores are present per scale; and in *Chiasmodon* and *Pseudoscopelus*, the scales are not perforated, and one or two pores are present between each scale. (ci=1.0)

110. Infraorbital pores (ordered): eight to nine (0); 10 to 11 (1); 11 to 12 (2); 13 to 14 (3). In *Dysalotus*, the infraorbital pores are eight; in *Kali*, ten to 11; *Chiasmodon subniger* and *Pseudoscopelus*, 11 to 12; in *C. asper*, *C. braueri*, *C. harteli*, *C. microcephalus*, *C. niger* and *C. pluriradiatus*, 13 to 14. This character was coded as unknown (?) in the outgroup, because in *Bembrops* and *Scomberomorus*, the infraorbital canal is reduced; and in *Diplectrum* and *Hoplostethus* the pores are many are tinny. (ci=0.75)

111. Lateral line canals: simple (0); widened (1). In *Chiasmodon*, *Pseudoscopelus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the lateral line canals of head and body are simple (=narrow); and in *Kali* and *Dysalotus*, the canals are widened. (ci=0.5)

112. Supratemporal canal: does not extend over temporal (0); extending over temporal (1). In *Dysalotus*, *Kali*, *Diplectrum*, *Bembrops*, *Hoplostethus* and *Scomberomorus*, the supratemporal canal is limited by the extrascapular and does not reach the neurocranium; and in *Chiasmodon*, the supratemporal canal extends on the temporal bone. (ci=1.0)

Canal Neuromasts

113. Supraorbital canal neuromasts (ordered): five (0); six (1); seven (2). *Kali* and *Diplectrum*, the supraorbital canal neuromasts are five; *Chiasmodon*, *Pseudoscopelus* and *Dysalotus*, *six*; and *Hoplostethus*, seven. Although *Chiasmodon*, *Pseudoscopelus* and *Dysalotus* have the same number of neuromasts, the arrangement of the neuromasts found in *Chiasmodon* and *Pseudoscopelus*, is different to *Dysalotus* suggesting that they a neuromast evolved independently in those groups (see Chapter 6 for further discussion). The canal neuromasts could not be observed in *Bembrops* and *Scomberomorus* and were coded as unknown (?). (ci=0.67)

114. Otic canal neuromasts: two (0); one (1). In *Chiasmodon*, *Pseudoscopelus*, *Diplectrum* and *Hoplostethus*, the neuromasts the otic canal neuromasts are two; and in *Dysalotus* and *Kali*, one. The canal neuromasts could not be observed in *Bembrops* and *Scomberomorus* and were coded as unknown (?). (ci=1.0)

115. Postotic canal neuromasts: one (0); absent (1). In *Chiasmodon*, *Dysalotus*, *Kali parri*, *Pseudoscopelus*, *Diplectrum* and *Hoplostethus*, the postotic canal neuromast is one; and in *K. colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon* and *K. macrura*, absent. A discussion regarding the homology of the postotic canal neuromasts in *K. parri* and the remaining chiasmodontids is given in Chapter 6. The canal neuromasts could not be observed in *Bembrops* and *Scomberomorus* and were coded as unknown (?). (ci=1.0)

116. Supratemporal canal neuromast: one (0); two (1); three (2). In *Hoplostethus*, the supratemporal canal neuromast is one; *Kali* and *Diplectrum*, two; and in *Chiasmodon*, *Dysalotus* and *Pseudoscopelus*, three. The canal neuromasts could not be observed in *Bembrops* and *Scomberomorus* and were coded as unknown (?). (ci=0.67)

117. Temporal canal neuromasts: two (0); one (1). In *Chiasmodon*, *Dysalotus*, *Pseudoscopelus*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the temporal canal neuromasts are two; and in *Kali*, one. The canal neuromasts could not be observed in *Bembrops* and *Scomberomorus* and were coded as unknown (?). (ci=1.0)

118. Preopercular canal neuromasts: six (0), five (1); three (2). In *Dysalotus*, *Diplectrum* and *Hoplostethus*, the preopercular canal neuromasts are six; and in *Chiasmodon* and *Pseudoscopelus*, five; and in *Kali*, three. The canal neuromasts could not be observed in *Bembrops* and *Scomberomorus* and were coded as unknown (?). (ci=1.0)

119. Infraorbital canal neuromasts: eight (0); 10 (1); 11 (2). In *Kali*, the infraorbital canal neuromasts are eight; *Chiasmodon*, *Pseudoscopelus*, *Diplectrum* and *Hoplostethus*, 10; and *Dysalotus*, 11. The canal neuromasts could not be observed in *Bembrops* and *Scomberomorus* and were coded as unknown (?). (ci=1.0)

Superficial Neuromasts

120. Superficial neuromasts: absent (0); present (1). In *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the superficial neuromasts are absent; and in *Chiasmodon*, *Dysalotus*,

Kali and *Pseudoscopelus*, the superficial neuromasts are present, arranged into seven groups: preorbital, suborbital, mandibular, opercular, interorbital, occipital, body, and caudal-fin superficial neuromasts. For definition of groups, terminology and innervation see also Chapter 6. The following characters referring to the patterns of superficial neuromasts were coded as unknown (?) in the outgroup. (ci=1.0)

121. Shape of superficial neuromasts: only papillae present (0); papillae and ovals present (1); papillae absent, rods present (2). In *Dysalotus*, only the papillae are present; in *Chiasmodon* and *Pseudoscopelus*, both the papillae the oval neuromasts are present; and in *Kali*, only the rods are present. (ci=1.0)

Superficial Neuromasts groups

122. SOC: only SOC 1, 3 and 5 present (0); SOC 1, 2, 3, 4 and 5 present (1). In *Dysalotus* and *Kali*, only SOC 1, 3 and 5 are present; and *Chiasmodon* and *Pseudoscopelus*, SOC 1-5 are present. (ci=1.0)

123. SOC1: in straight row over nasal (0); in small patch on top of snout (1); on abroad area on anterodorsal part of snout (2). In *Dysalotus*, SOC1 is on a short, straight row on nasal; in *Kali*, SOC1 is on a small patch on top of snout; and in *Chiasmodon* and *Pseudoscopelus*, SOC1 is on a broad area on the anterodorsal part of snout. (ci=1.0)

124. SOC 3: in short straight row lateral to nasal (0); in group of neuromasts ventral to the anterior nostril (1). In *Chiasmodon* and *Pseudoscopelus*, SOC3 is short straight row

lateral to the nasal; and in *Dysalotus* and *Kali*, SOC3 is on a patch of neuromasts ventral to the anterior nostril. (ci=0.5)

125. SOC 5: in small group between the anterior and posterior nostrils (0); in single row between the posterior nostril and the eye (1); on the infraorbital 1, not reaching the anterior margin of eye (1); on the infraorbital 1, reaching the anterior orbit of eye (3). In *Kali parri*, the SOC is in a small group between the anterior and posterior nostrils; in *Dysalotus*, *K. colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon* and *K. macrura*, the SOC is in a single row between the posterior nostril and the eye; in *Chiasmodon*, the SOC in a group on the infraorbital 1, but it does not extend to the anterior margin of eye, and in *Pseudoscopelus*, the SOC in a group on infraorbital 1, that extends to the anterior margin of eye. (ci=1.0)

126. SSN: on dorsal part of cheek, exclusively (0); dorsal to posterior part of upper jaw, exclusively (1); covering most of the cheek, but not overlapping the infraorbitals, innervated by several rami of the anteroventral lateral line nerve (2); covering most of the cheek and including the dorsal and ventral part of the eye, and dorsal to the upper jaw, and overlaps the infraorbital bones (3). In *Dysalotus*, the SSN is restricted to single row of neuromasts on the dorsal part of cheek, innervated by a dorsal ramus of the anteroventral lateral line nerve; in *Kali colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon*, *K. macrura* and *K. normani*, the SSN is restricted to a single row on the cheek, dorsal to the posterior half of the upper jaw, and it is innervated by a medial ramus of the anteroventral lateral line nerve; in *K. parri*, the SSN covers most of the cheek, but

does not overlap the infraorbitals, and it is innervated by several rami of the anteroventral lateral line nerve, including major dorsal and medial rami; and in *Chiasmodon* and *Pseudoscopelus*, the SSN covers most of the cheek, including the region posterior and ventral to orbit (see next character) and it is innervated by a dorsal and a medial rami of the anteroventral lateral line nerve. (ci=1.0)

127. Anterior distribution of SSN: not reaching the posterior margin of eye (0); not extending beyond the mid-eye (1); extending anterior to mid-eye (2). In *Dysalotus* and *Kali*, the SSN is entirely restricted to posterior to the orbit; in *Chiasmodon*, the SSN extends along the posteroventral part of orbit, but does not reach the mid-eye; and in *Pseudoscopelus*, SSN extends ventrally between the upper jaw and the infraorbital canal extends beyond the mid-eye, reaching infraorbital 1. (ci=1.0)

128. Connection between SSN and SOC 5: discontinuous (0); continuous (1). In *Chiasmodon*, *Dysalotus*, *Kali*, *Pseudoscopelus aphos*, *P. astronesthidens*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. pierbartus*, *P. sagamianus* and *P. scriptus*, the SSN and SOC5 are discontinuous; and in *P. altipinnis*, *P. australis*, *P. bothrorrhinos*, *P. parini*, *P. paxtoni* and *P. scutatus*, the SSN extends anteriorly between the infraorbital canal and the ventral margin of eye and is continuous with SOC5. (ci=0.33)

129. SMD: only SMD 3 present (0); only SMD 2 and 3 present (1); SMD 1, 2 and 3 present (2). In *Dysalotus* and *Kali colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon*

and *K. macrura*, only SMD 3 is present and it is restricted to the posterior part of the lower jaw; in *K. parri*, SMD 2 and 3 are present, and it extends along the posterior and anteroventral part of the lower jaw; and in *Chiasmodon* and *Pseudoscopelus*, SMD 1, 2 and 3 are present and extend along the posterior, ventral and dorsal parts of the lower jaw. (ci=1.0)

130. Distribution of SOP 1: absent (0); parallel to dorsal margin of opercle (1); parallel to posterior margin of preopercle (2); on a *V*-shaped row, parallel to dorsal margin of opercle and posterior margin of preopercle (3); widespread on area between dorsal margin of opercle and posterior margin of preopercle (4). In *Chiasmodon asper* and *C. pluriradiatus* the SOP 1 is absent; in *Dysalotus* and *C. braueri*, *C. harteli*, *C. microcephalus*, *C. niger* and *C. subniger*, SOP 1 is parallel to the posterior margin of preopercle; in *K. colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon*, *K. macrura*, *Pseudoscopelus aphos*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus* and *P. scriptus*, SOP 1 is parallel to the dorsal margin of the opercle; in *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni* and *P. scutatus*, SOP 1 is in a *V*-shaped row that extends dorsal to the opercle and posterior to the preopercle; and in *K. parri*, SOP 1 is widespread between the dorsal margin of opercle and posterior margin of preopercle. (ci=0.8)

131. SOP 2: in single row parallel to anterior margin of opercle, not extending over opercle, interopercle and to subopercle (0); in single row parallel to anterior margin of opercle, reaching subopercle, but not extending over opercle and interopercle (1); in

single row parallel to anterior margin of opercle, reaching subopercle and extending over interopercle (2); widespread over opercle, interopercle and subopercle (3). In *Chiasmodon* and *Dysalotus*, SOP 2 is in a short row parallel to the anterior margin of the opercle, and it does not reach the subopercle; in *Kali*, SOP 2 is in a single row that reaches the subopercle; in *Pseudoscopelus aphos*, *P. bothrorrhinos*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, SOP2 extends along the anterior margin of the opercle, subopercle, and on the posterior margin of the interopercle; and in *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. lavenbergi*, *P. odontoglossum*, *P. paxtoni* and *P. parini*, SOP 2 is widespread on the opercle, interopercle and subopercle. In *Chiasmodon*, *Dysalotus* and *Kali*, there is a major branch of the anteroventral lateral line nerve that courses along the anterior margin of opercle and innervates the single row of SOP2. In *Pseudoscopelus*, there are two or three ramifications to innervate the neuromasts on posterior margin of interopercle and those on opercle. (ci=1.0)

132. SIO: only the SIO 2 present (1); SIO 1, 2, 3, 4 present (2). In *Dysalotus* and *Kali*, only SIO 2 is present and is restricted to the pterotic; and in *Chiasmodon* and *Pseudoscopelus*, SIO 1, 2, 3, 4 are present on pterotic, parietals, supraoccipital and frontals. (ci=1.0)

133. SIO 1: restricted to posterior half of frontal (0); SIO1 on posterior and anterior parts of frontal (1). This character refers to the distribution of SIO1 and 2 in *Chiasmodon* and *Pseudoscopelus* and was coded as unknown (?) in the other groups. In *Chiasmodon*, SIO

1 is restricted to the posterior part of frontal, and does not extend anteriorly; and in *Pseudoscopelus*, SIO 1 extends on the entire frontal, reaching the medial and anterior margins. (ci=1.0)

134. SIO 2: restricted to pterotic and posterior are of frontal (0); SIO 2 extending along pterotic and lateral shelf of frontal. This character refers to the distribution of SIO1 and 2 in *Chiasmodon* and *Pseudoscopelus*. In *Chiasmodon*, SIO 2 is restricted to the pterotic and posterior margin of frontal and does not extend anterior to the mid-eye; and in *Pseudoscopelus*, SIO 2 extends on pterotic and along the lateral margin of frontal extending anterior to the mid-eye. (ci=1.0)

135. SIO': absent (0), present (1). In *Dysalotus* and *Kali*, SIO' is absent; and in *Chiasmodon* and *Pseudoscopelus*, present. (ci=1.0)

Photophores

136. Photophores: absent (0); present as white lines (1); photophores present as discrete, circular organs (2). In *Chiasmodon*, *Dysalotus*, *Kali*, *Pseudoscopelus aphos*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the photophores are absent; in *P. parini,* the photophores are present as white lines on body; and in *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, *P. scutatus*, the photophores are present as discrete, small organs along body. The following characters refer to the groups of photophores among the species of *Pseudoscopelus*. The

following characters referring to the patterns of photophores were coded as unknown (?) in the outgroup, *Chiasmodon*, *Dysalotus*, *Kali*, *P. aphos* and when absent in *P. parini*. (ci=1.0)

Photophore groups

137. *apf*: absent (0); present (1). In *P. cephalus*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus* and *P. scriptus*, is absent; and in *Pseudoscopelus altipinnis*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. lavenbergi*, *P. odontoglossum*, *P. paxtoni* and *P. scutatus*, present. (ci=1.0)

138. *mxf*: absent (0); present, in irregular row of photophores, not continuous with *apf* (1); present, in single regular row of photophores, continuous with *apf*, (2). In *P. bothrorrhinos*, *P. lavenbergi* and *P. scutatus*, *mxf* is absent; in *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. odontoglossum* and *P. paxtoni*, present in an irregular row of photophores, and discontinuous with the apf; and in *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus* and *P. scriptus*, present in a single regular row of neuromasts, continuous with the apf. In *P. cephalus*, the *mxf* is present but its shape could not be conclusively verified and was coded as unknown (?). (ci=1.0)

139. *ppf*: absent (0); present (1). In *Pseudoscopelus australis*, *P. lavenbergi* and *P. paxtoni*, the ppf is absent; and in *P. altipinnis*, *P. astronesthidens*, *P. bothrorrhinos*, *P. cordilluminatus*, *P. obtusifrons*, *P. odontoglossum*, *P. pierbartus*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, present. The presence or absence of the *ppf* in *P. cephalus* could

not be conclusively verified and was coded as unknown (?). (ci=0.33)

140. *vnf*: absent (0); present (1). In *Pseudoscopelus bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. pierbartus*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, the *vnf* is absent; and in *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. paxtoni*, present. (ci=0.5)

Photophores on body

141. *pf* and *paf*: absent (0); present (1). In *Pseudoscopelus bothrorrhinos* and *P. scutatus*, the *pf* and *paf* are absent; and in *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus* and *P. scriptus*, present. (ci=1.0)

142. *prcf*: present as a longitudinal line (0); present, oval shaped or three-pronged (1); present, *U*-shaped (2). In *Pseudoscopelus parini*, the *prcf* is in a longitudinal line; in *P. altipinnis*, *P. australis*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, the *prcf* is oval or three-pronged; and in *P. astronesthidens* and *P. odontoglossum*, the *prcf* is U-shaped. (ci=1.0)

143. *if* and *prvf*: discontinuous (0); continuous (1) In *Pseudoscopelus aphos altipinnis*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. lavenbergi*, *P. parini*, *P. paxtoni* and *P. scutatus*, the *if* and *prvf* are discontinuous and form two separated groups; and in *P.*

cephalus, *P. cordilluminatus*, *P. obtusifrons*, *P. odontoglossum*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, the *if* and *prvf* are continuous and form a single, irregular line. (ci=0.33)

144. *prvf* and *ptvf*: discontinuous (1); continuous (2). In *Pseudoscopelus altipinnis*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. parini P. paxtoni*, *P. pierbartus*, *P. sagamianus* and *P. scriptus*, the *prvf* and *ptvf* are discontinuous and form two separated groups; and in *P. bothrorrhinos* and *P. scutatus*, the *prvf* and *ptvf* are continuous and form a single irregular line. (ci=1.0)

145. *trf*: absent (0); present in single, irregular row with widely spaced photophores (1); present in single row with closely spaced and a medial cluster of photophores (2); present in a broad band of two or three closely spaced photophores (3). In *Pseudoscopelus astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. odontoglossum* and *P. scutatus*, the *rtf* is absent; in *P. altipinnis* and *P. paxtoni*, the rtf is in a single, irregular row, with widely spaced and few photophores; in *P. cephalus*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, the *rtf* is present in a single continuous row, with a medial cluster of photophores; and in *P. lavenbergi*, the *rtf* is present in a broad band of three to five photophores. (ci=1.0)

146. *saf*: incomplete anteriorly and posteriorly (0); complete anteriorly and incomplete posteriorly (1); complete anteriorly and posteriorly (2). In *Pseudoscopelus*

astronesthidens, *P. australis*, *P. odontoglossum* and *P. parini*, the *saf* is not connected anteriorly and posteriorly; in *P. altipinnis*, *P. bothrorrhinos*, *P. lavenbergi*, *P. obtusifrons*, *P. pierbartus* and *P. scutatus*, the *saf* is complete anteriorly, and incomplete posteriorly; and in *P. cephalus*, *P. cordilluminatus*, *P. paxtoni*, *P. sagamianus* and *P. scriptus*, the *saf* is complete anteriorly and posteriorly. (ci=0.67)

147. Anterior extension of *saf*: not reaching the level of anus (0); reaching the level of anus (1); extending anterior to the level of anus (2). In *Pseudoscopelus altipinnis*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. scriptus* and *P. scutatus*, the *saf* anteriorly does not reach the level of anus; in *P. obtusifrons* and *P. pierbartus*, the *saf* reaches the level of anus; and in *P. cephalus*, *P. cordilluminatus* and *P. sagamianus*, the *saf* extends anterior to the level of anus. (ci=1.0)

148. *spf*: absent (0); present (1). In *Pseudoscopelus altipinnis*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. odontoglossum*, *P. paxtoni*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, the *spf* is absent; and in *P. obtusifrons* and the *P. pierbartus*, present. (ci=1.0)

149. *svf*: absent (0); present (1). In *Pseudoscopelus altipinnis*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus* and *P. scriptus*, the *svf* is absent; and in *P. bothrorrhinos* and *P. scutatus*, present. (ci=1.0)

150. *vaf*: absent (0); present (1). In *Pseudoscopelus bothrorrhinos* and *P. scutatus*, the *vaf* is absent; and in *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus* and *P. scriptus*, present. (ci=1.0)

151. *vf*: absent (0); present (1). In *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. lavenbergi*, *P. odontoglossum* and *P. scutatus*, the *vf* is absent; in P. *altipinnis*, *P. cephalus*, *P. cordilluminatus*, *P. obtusifrons*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus*, *P. scriptus*, present. (ci=0.5)

152. Photophores group *lvf*: absent (0); present (1). In *Pseudoscopelus altipinnis*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. odontoglossum*, *P. paxtoni*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, the *lvf* is absent; and in *P. obtusifrons* and *P. pierbartus*, present. (ci=1.0)

Miscellaneous

153. Internal color of buccal cavity (ordered): pale (0); dusky, with widely spaced melanophores (1); black, with condensed melanophores (2). In *Dysalotus*, *Kali colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon*, *K. macrura*, *Pseudoscopelus aphos*, *P. bothrorrhinos*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. scriptus*, *P. scutatus*, *Bembrops*, *Diplectrum* and *Scomberomorus*, the buccal cavity is pale; in *Chiasmodon*, the buccal cavity is dusky, with melanophores widely spaced; and in *K. parri*, *P. altipinnis*,

P. astronesthidens, *P. australis*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. sagamianus* and *Hoplostethus*, the buccal cavity is black, including the gill arches, but not the filaments. (ci=0.22)

154. Color of peritoneum (ordered): pale (0); dusky (1); black (2). In *Dysalotus*, *Pseudoscopelus aphos*, *P. bothrorrhinos*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. scriptus* and *P. scutatus*, the peritoneum is pale; in C*hiasmodon*, *Kali colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon*, and *K. macrura*, the peritoneum is dusky, with widely spaced melanophores; and in *K. parri*, *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni* and *P. sagamianus*, the peritoneum is black. (ci=0.22)

155. Prickles on juveniles: absent (0); present (1). In *Kali*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the prickles are absent on juveniles; and in *Chiasmodon*, *Dysalotus* and *Pseudoscopelus*, small prickles are present on the juveniles. The prickles are small scale-like structures that differ in gross morphology from the scales by being totally embedded in the skin (vs. embedded in the skin only posteriorly, mostly exposed) and by the smooth surface (vs. surface with a well defined center, the focus, and ridges and grooves forming the circuli, radii, and annuli). (ci=0.5)

156. Prickles in adults: absent (0); present, small (1); present, enlarged (2). In *Kali*, *Pseudoscopelus*, *Chiasmodon braueri*, *C. harteli*, *C. microcephalus*, *C. niger* and *C. subniger*, the prickles are absent on adults; in *C. asper* and *C. pluriradiatus*, tinny

prickles are present on head and body of adults; and in *Dysalotus*, enlarged prickes are present on the posterior half of body. (ci=1.0)

157. Shape of snout: triangular (0); moderately blunt (1); concave (2). In *Kali*, *Dysalotus* *Diplectrum* and *Scomberomorus*, the snout is triangular; in *Chiasmodon*, *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus*, *P. scriptus* and *Hoplostethus*, the snout is moderately blunt; and in *P. bothrorrhinos* and *P. scutatus*, the tip of the snout is concave. (ci=0.67)

158. Caudal-fin rays: i+7+8+i (0), ii+6+7+ii or ii+6+6+ii (1). In *Chiasmodon* and *Pseudoscopelus*, the caudal fin rays are usually i+7+8+i; and in *Kali* and *Dysalotus*, ii+6+7+ii or ii+6+6+ii. (ci=1.0)

159. Pectoral-fin rays: 20 or more (0); 15–16 (1); 12–14 (2); 10–11 (3). In *Scomberomorus* and *Bembrops*, pectoral-fin rays are 20 or more; in *C. asper*, *C. pluriradiatus* and *Diplectrum*, 15–16; and in *Pseudoscopelus*, *C. braueri*, *C. harteli*, *C. microcephalus*, *C. niger*, *C. subniger*, and *Hoplostethus*, 12–14; and in *Dysalotus* and *Kali*, 10–11. (ci=0.6)

160. Peritoneum cavity: not extending beyond anal-fin insertion (0); extending posterior to anal-fin insertion (1). In *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the peritoneum cavity does not extend beyond the insertion of the anal fin; and in

Chiasmodon, *Dysalotus*, *Kali* and *Pseudoscopelus*, it extends posterior to the insertion of the anal fin. (ci=1.0)

161. Swim bladder: filled with air (0); filled with fat (1). In *Chiasmodon*, *Dysalotus*, *Bembrops*, *Diplectrum*, *Hoplostethus* and *Scomberomorus*, the swim bladder is filled with air; and in *Kali* and *Dysalotus*, is filled with globules of fat. (ci=1.0)

Phylogenetic Analysis

The Phylogenetic analysis resulted in 12 trees with 338 steps (CI = 0.704; RI = 0.911), illustrated in Figure 7.1 and 7.2. The unambiguous state changes are presented in Table 7.2, and the characters are discussed below.

The family Chiasmodontidae is divided into two major clades: the *Chiasmodon* group; and the *Kali* group. The *Chiasmodon* group includes the genera *Chiasmodon* and *Pseudoscopelus*, and the *Kali* group includes the genera *Dysalotus* and *Kali.* The present hypothesis agrees with the placement of *Myersiscus* as a synonym of *Pseudoscopelus* (de Beaufort & Chapman 1951); *Dolichodon Odontonema*, *Hemicyclodon* and *Gargaropteron* of *Kali* (Smith 1965; Johnson & Cohen 1974), and the placement of *Dysalotus macrodon* in *Kali*.

Discussion

The monophyly of Chiasmodontidae

The monophyly of Chiasmodontidae is well supported by 24 synapomorphies:

condyle formed on ventral edge of preopercle (character 14); opercular bones poorly ossified and mostly membranous (character 16); elongated maxilla and premaxilla (character 17); elongated coronoid process of dentary is elongated, forming fenestra on the lateral symphysis of between dentary and angular (character 24); reduced mesopterygoid (character 25); enlarged metapterygoid (character 26); ceratobranchial of first gill arch connected by skin to the internal wall of mouth (character 50); pelvic fin loose, not connected anteriorly to the pectoral girdle (character 52); short anal-fin proximal radials (character 61); origin of replacement tooth extraosseous (Character 63); heterodont dentition (character 64); premaxillary teeth in two or three series of a single or multiple rows (character 65); tooth hollow (character 71); palatine teeth in single row (character 83); section A1β of adductor mandibulae present (character 88); intermandibularis not reaching symphysis of dentary anteriorly (character 92); anterior attachment of protractor hyoidei posterior, above or slightly posterior to attachment of intermandibularis (character 93); origin of levator posterioris in ventral shelf of pterotic (character 95); posterior attachment of the retractor dorsalis (character 96); absence of the gill arch muscles levator posterior, protractor pectoralis (character 98), and obliquus ventralis of arches 1 and 2 (character 100); the loose hypaxial musculature (character 106); the superficial neuromasts (character 120); and the peritoneum cavity extending posterior to the anal-fin insertion (character 160).

The *Chiasmodon* clade

The Chiasmodon clade is composed of the mesopelagic genera *Chiasmodon* and

Pseudoscopelus. It is well supported by 18 synapomorphies: the spoon shaped nasal (character 10), anterodorsal on head (character 11); teeth on second brasibranchial present (character 44, reversal in *Chiasmodon subniger*); rod-like interarcual cartilage reduced (character 46); lateral tendon between pelvic girdle connecting to the postcleithrum (character 53); postcleithra 1 and 2 separated (character 55); origin of first dorsal fin between sixth and seventh or between seventh and eighth vertebrae (character 59); one or two premaxillary fangs (character 79); broad origin of A2β on anterior margin of preopercle (character 87); retractor dorsalis connected to the basaphophysis (character 97); fibers of interadialis transversal to caudal fin rays (character 102); infracardinalis anterior broad and elongated (character 104); infracardinalis medius broad (character 105); last lateral-line scale loose on lower lobe of caudal fin (character 107); lateral-line scales not perforated (character 109); infraorbital pores 11–14 (character 110); five preopercular canal neuromasts (character 118); snout moderately blunt or concave (character 156).

The genus *Chiasmodon*

The genus *Chiasmodon* includes seven species. The monophyly of *Chiasmodon* (clade C1) is supported by 16 synapomorphies: connection of Baudelot's ligament to the basapophysis of second vertebra between basioccipital and cleithrum (character 9); 42 to 48 vertebrae (character 27); epipleural present on first or second pleural rib (character 38); gill rakers on first arch absent (character 42); origin of anal far posterior to the level of the insertion of second dorsal fin (character 60); presence of the premaxillary moderately canine enlarged and slightly sigmoid (character 77), lateral accessory tooth present (character 78); dentary canine present (character 80); lateral origin of the abductor superficialis pelvicus (character 101); origin of flexor dorsalis and flexor ventralis on third vertebra before centrum (character 103); hypaxial muscle obliquus inferioris reduced and disconnected from obliquus superioris (character 106); Infraorbital pores 13–14 (character 110; reverse in *C. subniger*); Supratemporal canal extending on temporal (character 112); buccal cavity and peritoneum dusky (character 152 and 153);

The species of *Chiasmodon* are morphologically very conservative, and the clades C2, C3 and C3 are poorly supported by characters of dentition and gill rakers. *Chiasmodon braueri* is the most basal species in the family. The clade C2 includes *C. asper*, *C. harteli*, *C. microcephalus*, *C. niger*, *C. pluriradiatus* and *C. subniger*, and is supported by a single synapomorphy: the reduction of gill rakers on the second arch (character 43). The clade C2 includes *C. asper*, *C. microcephalus*, *C. pluriradiatus* and *C. subniger*, and is supported by a single synapomorphy: the absence of gill rakers in on the second arch (character 43, state 2). The clade C3 includes *C. microcephalus* and *C. subniger* and is supported by a single synapomorphy: the absence of teeth in the basibranchial (character 44, homoplastic with the outgroup). The clade is C4 is formed by *C. asper* and *C. pluriradiatus*, two very similar species, and is well supported by five synapomorphies: a single premaxillary tooth in medial series (character 67); two premaxillary fangs (character 79); SOP 1 absent (character 130); prickles present in adults (character 156), and 15–16 pectoral fin rays (character 159).

It is noteworthy that the fewer infraorbital pores in *Chiasmodon subniger* (character 110), was understood as a reversion and an autapomorphy, and that the character that supports the clade C3 is reversal from the state found in the outgroup.

The genus *Pseudoscopelus*

The genus *Pseudoscopelus* (clade P1) includes 16 species. The monophyly of *Pseudoscopelus* is supported by 12 synapomorphies: medial border of crest of frontals curved (character 3); infraorbital 6 forming the dorsal margin of the orbit, and its pore anterior to mid-eye (character 23); a cartilaginous anterior connection of the pelvic halves (character 58); three series of teeth in premaxilla (character 65, homoplastic with *Dysalotus*); needle-like teeth in medial and mesial series of dentary and premaxilla (character 76; homoplastic with *Dysalotus*); premaxillary canine small (character 77); tendon of A2α, A2β and A3 lateral on angular, inserting on prearticular fossa (character 90); SOC extending anterior margin of eye (character 125); SSN extending ventrally between the upper jaw and the infraorbital canal, reaching infraorbital 1(character 127); SOP 2 reaching the subopercle (character 131); SIO 1 extends on the entire frontal (character 133); SIO 2 extending anterior to the mid-eye (character 134).

The clade P2 is composed of *Pseudoscopelus altipinnis*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. pierbartus*, *P. sagamianus*, *P. scriptus* and *P. scutatus*, and is supported by a single synapomorphy: photophores present (character 136). The clade P3 is composed by *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. bothrorrhinos*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni* and *P. scutatus*, and is supported by a two synapomorphies: the SSN extending anteriorly and continuous with SOC 5 (character 128; reversal in *P. astronesthidens*, *P. lavenbergi* and *P. odontoglossum*); and SOP 1 on a *V*-shaped row, parallel to dorsal margin of opercle and posterior margin of preopercle (character 130; reversal in *P. parini*).

The clade P4 includes *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. lavenbergi*, *P. odontoglossum*, *P. parini* and *P. paxtoni*, and is supported by six synapomorphies: the broad premaxilla (character 19; homoplastic with *P. cephalus*, *P. sagamianus*, *P. scriptus* and *Dysalotus*); one to three posterior premaxillary teeth in lateral series stout and ankylosed to bone (character 81, state 1); SOP 2 widespread over opercle, interopercle and subopercle (character 131, state 3); *ppf* present (character 140); and the buccal cavity and peritoneum black (characters 153, state 3, and 154; both homoplastic with *P. sagamianus*, *Kali parri* and *Hoplostethus*).

The clade P5 is composed by *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. odontoglossum*, *P. parini* and *P. paxtoni*, and is supported by a single synapomorphy: photophore *mxf* in an irregular row of photophores, and discontinuous with the *apf* (character 138, state 1)

The clade P6 includes *P. altipinnis* and *P. paxtoni*, and is supported three synapomorphies: the enlarged pterosphenoid, forming great part of the medial limit of the orbit and fused to contralateral in ventral midline (character 2, state 2; homoplastic with *P. bothrorrhinos* and *P. scutatus*); *trf* in single, irregular row with widely spaced photophores (character 145, state 1); *vf* absent (character 151). The clade P7 includes *P. astronesthidens*, *P. australis*, *P. odontoglossum* and *P. parini*, and is supported by a single synapomorphy: *saf* incomplete anteriorly and posteriorly (character 146, state 0). The clade P8 is composed by *P. astronesthidens*, *P. australis* and *P. odontoglossum*, and is supported by three synapomorphies: medial border of crest of frontals gently curved (character 3, state 2); teeth on basihyal present (character 45); five or more teeth on posterior third of lateral series of premaxilla stout and with type 1 attachment (character 81, state 2). The clade P9 includes *P. astronesthidens* and *P. odontoglossum*, and is supported by four synapomorphies: the palatine teeth in two rows (character 83, state 2); SSN and SOC 5 discontinuous (character 128; homoplastic with *Chiasmodon*, *Dysalotus*, *Kali*, *Pseudoscopelus aphos*, *P. astronesthidens*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. pierbartus*, *P. sagamianus* and *P. scriptus*); and ppf present (character 139, homoplastic with *P. altipinnis*, *P. bothrorrhinos*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus*, *P. scriptus* and *P. scutatus*); and *prcf* is *U*-shaped (character 142, state 2).

The clade P10 includes *Pseudoscopelus bothrorrhinos* and *P. scutatus* and is supported by nine synapomorphies: the enlarged pterosphenoid, forming great part of the medial limit of the orbit and fused to contralateral in ventral midline (character 2, state 2; homoplastic with *P. altipinnis* and *P. paxtoni*); nasal anterior, facing forward (character 11, state 2); platelets in distal portion of dorsal-fin element (character 51); pharyngoclavicularis internus with a single head (character 99, homoplastic in *Kali*); *pf* and *paf* absent (character 141, state 0); *prvf* and *ptvf* are continuous and form a single irregular line (character 144); *svf* present (character 149); *vaf* absent (character 150); tip of snout concave (character 157, state 2).

The clade P11 includes *Pseudoscopelus cephalus*, *P. cordilluminatus*, *P. obtusifrons*, *P. pierbartus*, *P. sagamianus* and *P. scriptus* and is supported by two synapomorphies: opercle *Y*-shaped (character 15, state 1); the third proximal radial the largest (character 62), *apf* absent (character 137, state 0); *if* and *prv* are continuous and form a single, irregular line (character 143, state 1; homoplastic with *P. altipinnis* and *P. odontoglossum*); and *trf* in single row with closely spaced and a medial cluster of photophores (character 145, state 2). The clade P 12 includes *P. obtusifrons*, *P. pierbartus* and is supported by teeth in middle and mesial series of premaxilla in single row (character 66); premaxillary teeth in mesial row two to eight (character 69); needle-like teeth are in premaxilla and dentary absent (character 76); *saf* extending to the level of anus (character 147, state 1); *spf* (character 148); photophores group *lvf* (character 152).

Remarks

The genus *Pseudoscopelus* was earlier diagnosed by the presence of mucous pits along body (Lütken 1892). The mucous pits were later identified as photophores by Beebe (1931) and since than, the presence of photophores has been largely used as the major diagnostic for the genus (e.g. Lavenberg 1974; Mooi and Paxton 2001; Pokofiev & Kukuev 2005).

Most species of *Pseudoscopelus* have small discrete photophores organized in lines on head and body, but in *P. parini* the photophores are vestigial and in *P. aphos* they are completely absent. Even after the description of those two species, subsequent authors still diagnose *Pseudoscopelus* by the presence of photophores (e.g. Spitz 2007; Prokofiev and Kukuev 2008). The existence of photophores in some species has been so overwhelming that Johnson and Keene (1986, 1990) did not included *Pseudoscopelus* in Chiasmodontidae, and a few authors (e.g. Smith 1965; Spitz 2007) suggested the erection of a new family to include *Pseudoscopelus*.

According to the present hypothesis both the family Chiasmodontidae and the *Chiasmodon* group are well supported. Removing the species of *Pseudoscopelus* with photophores would make Chiasmodontidae paraphyletic and polyphyletic, and would lead to a possible paraphyletic family – depending on the inclusion or not of *P. parini*, a species with vestigial photophores.

Lavenberg (1974) noticed the many similarities between *Pseudoscopelus* and *Chiasmodon* and suggested that *Pseudoscopelus* arose from a *Chiasmodon*-like ancestor. Although he opted to keep the status of both genera, he also mentioned that further investigations of the genus *Chiasmodon* could cause the collapse of *Pseudoscopelus*.

According to the present hypothesis, a new family should not be erected to include *Pseudoscopelus*; and *Chiasmodon* and *Pseudoscopelus* should remain as two distinct genera. Melo et al. (2007) tentatively proposed a new diagnosis to the genus which would include all species: the dorsal margin of the orbit is formed by infraorbital 6 and the position of the last infraorbital pore in the dorsal edge of the orbit is anterior to the middle of the pupil. That diagnostic characteristic is listed herein as one of the synapomorphies for the genus.

The existence of two species of *Pseudoscopelus* lacking photophores or with vestigial ones is an interesting problem which leads to three hypothesis: 1) the photophores are a synapomorphy of the genus and were secondary lost in *P. aphos* and reduced in *P. parini*; 2) *P. aphos* and *P. parini* have a basal position in the genus, and the condition found in *P. parini* represents an intermediate stage; and 3) the photophores had an independent origin in *P. parini*. According to the present analysis, *P. aphos* has a basal position in the family and the photophores are not a synapomorphy of *Pseudoscopelus*, but of the more inclusive clade P1. The second conclusion is that the discrete photophores were secondary lost in *P. parini*.

Among the species of *Pseudoscopelus*, Lavenberg (1974) proposed the existence of four species groups [none of his species were described and the names are not valid according to the ICZN (1999)]. The *obtusifrons* group includes *P. obtusifrons* and an species not considered valid (see Chapter 4); the *legandi* group, includes *P. bothrorrhinos* and *P. scutatus*; the *clarkei* group includes *P. parini*; *P. australis*, and *P. astronesthidens*; the *altipinnis* group includes *P. altipinnis*, *P. sagamianus*, *P. lavenbergi*, *P. scriptus* and *P. stellatus* [herein considered a junior synonym of *P. scriptus*]. Of those groups, only *legandi* group is corroborated herein as defined [= clade P10], and the other groups are considered to be paraphyletic and/or polyphyletic.

Prokofiev and Kukuev (2007, 2008) proposed the existence of a group diagnosed by the black buccal cavity: *Pseudoscopelus altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis* and *P. lavenbergi*. First of all, it should be pointed out that the black buccal cavity was misinterpreted in *P. aphos*, *P. parini* and *Kali parri*. The buccal cavity in *P. aphos* is pale, and in *P. parini* and *K. parri*, it is black. Later, Prokofiev (2009:19) assumed that the dark buccal cavity "was formed in North Pacific population [of *P. sagamianus*, sic] independently", and mentioned that *P. sagamianus* had some morphological characteristics divergent from the black-mouthed group, but did not list them. The results agree in part with those conclusions if the misinterpretations are taken in consideration. *Pseudoscopelus altipinnis*, *P. astronesthidens*, *P. australis*, *P. lavenbergi*, *P. parini* and the undescribed species *P. paxtoni* and *P. odontoglossum* form a monophyletic group that is supported by six synapomorphies, including the color of mouth (clade P4).

Prokofiev and Kukuev (2006) described the "superspecies" *Pseudoscopelus astronesthidens* to include *P. astronesthidens* and *P. australis*. They diagnosed it with 12 characteristics, most of them without a phylogenetic significance and present in other *Pseudoscopelus*. Two of the given diagnostic characters, however, have phylogenetic significance and are synapomorphies of the clade P8, which also includes the undescribed species *P. odontoglossum*: the enlarged premaxillary teeth in the posterior part of the marginal row and the presence of teeth on the tongue [=basihyal].

Melo (submitted, Chapter 4) proposed the existence of six groups, based mostly on photophore pattern, dentition and external morphology, and pointed out that those groups were for merely taxonomic purposed and did not necessarily represent phylogeny. The cladistic analysis supports the existence of five of those groups: *P. scriptus* group (clade P11); *P. altipinnis* group (clade P6); *P. scutatus* group (clade P10); *P. astronesthidens* group (clade P 8); and *P. lavenbergi* group (with a single species). The only species group that did not have its monophyly supported was the *P. aphos* group, which included *P. aphos* and *P. parini*. The *P. aphos* group was diagnosed by the absence of photophores, a reversal in *P. parini*.

The *Kali* group

The Kali group is composed of *Dysalotus* and *Kali*. It is well supported by 22 synapomorphies: bones of neurocranium fragile (character 1); parietal reduced (character 7); nasal widened (character 10); preopercle not contacting the otic dorsally (character

13); opercle three-pronged (character 15); coronoid process of dentary elongated (character 24); prezygapophysis poorly developed (character 28); the hemal spines and arches of vertebrae 2 and 3 fused to centrum (character 30); epural 2 reduced or absent (character 31, reversal in *Kali colubrina* and *K. macrura*); pleural ribs poorly developed (character 37); foramen on ceratohyal present (character 39; homoplastic with *Scomberomorus*); postcleithrum 1+2 reduced and overlapped by posterior plate of the cleithrum (character 56); section A2α of adductor mandibulae distinguished from A2α' (character 86); dilator operculi passing dorsally to the preopercle, and lateral to the hyomandibula (character 91); the levator externus of the first arch is extremely reduced (character 94); retractor dorsalis connecting posterior to the fifth vertebra (character 96); the lateral line extends to caudal fin fork (character 108); lateral line canals widened (character 111); otic canal neuromast one (character 114); SOC3 on a patch of neuromasts ventral to the anterior nostril (character 124); SOC is in a single row between the posterior nostril and the eye (character 125, reversal in *K. parri*); caudal-fin rays ii+6+7+ii or ii+6+6+ii (character 158); pectoral-fin rays 10–11 (character 159, state 3); Swim bladder filled with fat (character 161).

The genus *Dysalotus*

The genus *Dysalotus* includes three species. The monophyly of *Dysalotus* is corroborated by 18 synapomorphies: premaxilla broad (character 19, homoplastic with *P. altipinnis*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. lavenbergi*, *P. odontoglossum*, *P. parini*, *P. paxtoni*, *P. sagamianus* and *P. scriptus*); ascending process of premaxilla extremely reduced (character 20, homoplastic with *Pseudoscopelus*); supramaxilla present (character 22, homoplastic with *Hoplostethus*) ventral notch in dentary present (character 23, homoplastic with *Bembrops* and *Scomberomorus*); Post-haemal spinal caritlage of pleural centra (CPHPU) with three elements, CPHPU 1, 2 and 3 (character 36, homoplastic with *Kali falx*, *K. indica*, *K. kerberti*, and *K. macrodon*); insertion of first dorsal fin between the third and forth vertebrae (character 59, homoplastic with *Scomberomorus*); three series of teeth in premaxilla (character 65, homoplastic with *Pseudoscopelus*); needle-like teeth in medial and mesial series of dentary and premaxilla (character 76, homoplastic with *Pseudoscopelus*); infraorbital pores are eight (character 110); three supratemporal canal neuromast (character 116); 11 infraorbital canal neuromasts (character 119); SOC1 is on a short, straight row on nasal (character 123, state 0); the SSN is restricted to single row of neuromasts on the dorsal part of cheek (character 126, state 0); SOP 1 parallel to the posterior margin of preopercle (character 130, homoplastic with *Chiasmodon braueri*, *C. harteli*, *C. microcephalus*, *C. niger* and *C. subniger*); enlarged prickles present in juveniles and adults (characters 155 and 156, state 2). branchiostegal rays seven (character 41); tooth with a ventral attachment to the bone that allows them to bend dorsally and rotate around their own axis (character 73); and origin of section A2α of adductor mandibulae enlarged (character 85).

The genus *Kali*

The genus *Kali* (clade K1) includes seven species. The monophyly of *Kali* is supported by 23 synapomorphies: a single foramen in the exoccipital (character 6);

posterior wall of neurocranium lacking the supraoccipital (character 8); the ascending process of the premaxilla is very reduced (character 20, homoplastic with *Scomberomorus*); hypurals 1+2 and 3+4 fused to each other, and to the ural centrum at their base (character 32); hypural 5 reduced or lost (character 33); parahypural fused to ural centrum (character 34); section A2α' of adductor mandibulae broad (character 86, reversal in *K. macrura* and *K. falx*); two longitudinal pores are present per scale of the trunk lateral line canal (character 109, state 1); supraorbital canal neuromasts five (character 113, homoplastic with *Diplectrum*); temporal canal neuromasts one (character 117); preopercular canal neuromasts three (character 118, state 2); infraorbital canal neuromasts eight (character 119, state 0); SOC1 is on a small patch on top of snout (character 123, state 1); SOP 2 in a single row that reaches the subopercle (character 131, state 1).

The clade K2 includes *K. colubrina*, *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon* and *K. macrura*, and is supported by five synapomorphies: parietal extremely reduced (character 7, state 2); anal-fin proximal radials short (character 61, state 2); dentary teeth in mesial row less than seven (character 70, state 1); dentary and premaxillary tooth crown enlarged, 15% or more in tooth crown (character 72, state 1); postotic canal neuromasts absent (character 115). The clade K3 includes *K. kerberti*, *K. falx*, *K. indica*, *K. macrodon* and *K. macrura* and is supported by three synapomorphies: jaws strongly arched (character 18); and extremely enlarged fangs are present on the premaxillary and dentary (character 75).

The clade K4 includes *K. falx* and *K. indica* and is supported by seven synapomorphies: foramen for spinal nerves absent in all vertebrae (character 29, homoplastic with *K. kerberti* and *K. parri*); gill rakers on first arch absent (character 42, homoplastic with *Chiasmodon* and *P. australis*); gill rakers on second arch (character 43, homoplastic with *C. asper*, *C. microcephalus*, *C. pluriradiatus* and *C. subniger*); basihyal short (character 48); premaxillary teeth in mesial row three (character 68, state 3); dentary teeth in mesial row three (character 70, state 2); premaxillary canine extremely enlarged (character 77, state 2).

The clade K5 includes *K. kerberti*, *K. macrodon* and *K. macrura*, and is supported by three synapomorphies: basihyal arched (character 49); a premaxillary fang present (character 79, homoplastic with *Chiasmodon braueri*, *C. harteli*, *C. microcephalus*, *C. niger*, *C. subniger*, and *Pseudoscopelus*); needle-like teeth in lateral series present (character 82). The clade K6 includes *K. kerberti* and *K. macrodon*, and is supported by four synapomorphies: lateral surface of ascending process of premaxilla concave (character 21); post-neural spinal cartilage of pleural centra and hypural 5 with three elements (character 35, state 1); basihyal strongly arched (character 49, state 2); and pharyngoclavicularis internus with two heads (character 99, homoplastic with *Chiasmodon*, *Dysalotus*, *P. altipinnis*, *P. aphos*, *P. astronesthidens*, *P. australis*, *P. cephalus*, *P. cordilluminatus*, *P. lavenbergi*, *P. obtusifrons*, *P. odontoglossum*, *P. paxtoni*, *P. parini*, *P. pierbartus*, *P. sagamianus* and *P. scriptus*).

Comparative material

Outgroup
Bembrops anatirostris – AUM 24897
Diplectrum formosum – AUM 16069
Hoplostethus occidentalis – AUM 25858
Scomberomorus maculates – AUM 46134

Ingroup
Chiasmodon asper – SIO 68-483-60; HUM 143753
Chiasmodon braueri – NMNZ 31317 (cs)
Chiasmodon harteli – HUMZ 126543 (cs); MCZ 65530 (cs); MCZ 65527 (cs)
Chiasmodon microcephalus – MCZ 97611 (cs); SAIB 63772 (cs)
Chiasmodon niger – MCZ 69742 (cs)
Chiasmodon pluriradiatus – MCZ 41378 (cs); USNM 367248 (cs)
Chiasmodon subniger – LACM 3220420 (cs); UW 48713 (cs)
Dysalotus alcocki – MCZ 60807 (cs), ZUMC 6584 (cs)
Kali colubrina – MNRJ 26705 (cs)
Kali kerberti – USNM 207614 (cs); UW 21249 (cs)
Kali falx – USNM 392646 (cs)
Kali indica – MCZ 158887 (cs)
Kali macrodon – USNM 207597 (cs)
Kali macrura –UW 21247 (cs)
Kali parri – UF 131503 (cs)
Pseudoscopelus altipinnis – USNM 202255 (cs); ZMUC 6539 (cs)
Pseudoscopelus aphos – USNM 26957 (cs)
Pseudoscopelus astronesthidens – MCZ 163443 (cs)
Pseudoscopelus australis – NMNZ P. 4307
Pseudoscopelus bothrorrhinos – LACM 56616-1 (cs)
Pseudoscopelus cephalus – USNM 93142
Pseudoscopelus cordilluminatus – MCZ 161017
Pseudoscopelus lavenbergi –LACM 30573-1 (cs)
Pseudoscopelus obtusifrons – BMNH 2003.5.13.113, NMNZ P. 20074
Pseudoscopelus odontoglossum – SIO 73-311 (cs)
Pseudoscopelus parini – LACM 44399-1 (cs)
Pseudoscopelus paxtoni – NMNZ P. 18068 (cs)
Pseudoscopelus pierbartus – USNM 24068 (cs); LACM 56615-1 (cs)
Pseudoscopelus sagamianus – BMNH 1984.1.1.93 (cs)
Pseudoscopelus scriptus – MCZ 68449 (cs)
Pseudoscopelus scutatus – MCZ 96854 (cs)

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TABLE 7.1. Data matrix of characters obtained for the phylogenetic analysis

---

Hoplostethus
00?2000000000000000001100000000000?001000000?0000000000100000000????0?00000000
000000000??000000000000000000?102000010???????????????0????????????????220020100
Diplectrum
000?0000000000000000000000000000?000010000000000000000000000????0?00000000
000000000??000000000000000000?000001001 0???????????????0????????????????000000200
Scomberomorus
0011000000000000000010010006000?1000?000110000010000000000021000000????0?00000000
000000000?000000000000??0000???00???????0???????????????0????????????????000000000
Bembrops
000?100000001000000000000000000000?00001000000000000?000200?000?0????0?00000000
0000?????????????????????????00???????0???????????????0??????????????????000?000
Chiasmodon braueri
0011000012110101100200011140000000000010111010110010111102241 10111?0??1?0000021
1100111011000110111111111112102301100201?1112023102101001 0???????????????111010
210
Chiasmodon microcephalus
00110000121101011002000111400000000000101112001100101111022511 0111?0??1?0000021
11001110110001101111111111121023011002011111202310210100 10???????????????111010
210
Chiasmodon niger
0011000012110101100200011140000000000010111110110010111102241 10111?0??1?0000021
11001110110001101111111111121023011002011111202310210100 10???????????????111010
210
Chiasmodon pluriradiatus
00110000121101011002000111400000000000101112101100101111022411 0111?1??1?0000021
21001110110001101111111111121023011002011111202310200100 10???????????????111110
110
Chiasmodon asper
0??1??0012110101100200 0???4?????????0???11210??0010???????4110111?1??1?00000212100
1??0?1???1???????1?????21023011002011111202310200100 10???????????????111110110
Chiasmodon harteli
00110000121101011002000111500000000000101111101100101111022411 0111?0??1?0000021
11001110110001101111111111121023011002011111202310210100 10???????????????111010
210
Chiasmodon subniger
00110000121101011002000111400000000000201112001100101111022411 0111?0??1?0000021
11001110110001101111111111121022011002011111202310210100 10???????????????111010
210
Pseudoscopelus altipinnis
0231100002120101101200011130000000000000110010?1001011110214010 1121??11?0000110
1010111011010110111111010111102200100201111120332123311112111111101200011 02210
10210

TABLE 7.1. (cont.)

Pseudoscopelus aphos
0031100002120101100200011130000000000000110010?10010111102140101121??11?0000110
1000111011010110 1?1111?????1022001002011111203320222111 10???????????????0010102
10
Pseudoscopelus astronesthidens
012110000212010110120001113000000000000011001111001011110214010112 1??11?0000110
1020211011010110111111010111102200100201111120332023311112111112000000001002210
10210
Pseudoscopelus australis
0121100002120101101200011130000000000000111111110010111102140101121??11?0000110
1020111011010110111111010111102200100201111120332123311112110111000000001002210
10210
Pseudoscopelus bothrorrhinos
02?11000022201011002000111300000000000000110010110011111102140101121??11?0000110
1000111011010110111101010111102200100201111120332123211112101001010100100000 10
20210
Pseudoscopelus cephalus
0?311?00021201?110120001??10????????0???10010??0010????????0111121??11?0000110100
01????1???1???????1??????102200100201111120332?2??111?20??01110222001 10??101021?
Pseudoscopelus cordilluminatus
0?311?000212011110020001??30????????0???10010??0010???????40111121??11?0000110100
01????1???1???????1??????1022001002011111203320222111120210111022200110001010210
Pseudoscopelus lavenbergi
0031100002120101101200011130000000??00011001011001011110214010112 1??11?00001101
0101110110101101111110101111022001002011111203320233111121001110031000 10022101
0210
Pseudoscopelus obtusifrons
0?311?0002120111100200011130????????0???10010??0010???????40111120??01?0000010100
01????1???1???????1??????1022001002011111203320222111120211111021110111001010210
Pseudoscopelus odontoglossum
0121100002120101101200011130000000??000110011110010111102140101121??11?00001101
020211011010 1???1???1??????10220010020111112033202331111211111210000000100221010
210
Pseudoscopelus parini
0131100002120101101200011130000000000000110010110010111102140101121??11?0000110
101011101101011011111101011110220010020111112033212331111 1????1000?00??1??12101
0210
Pseudoscopelus paxtoni
0231100002120101101200011130000000000000110010110010111102140101121??11?0000110
1010111011010110111111010111102200100201111120332123311112101110011000110221 0
10210
Pseudoscopelus pierbartus
0031100?02120111100200011130000000000000110010110010111102140111120??01?0000010
1000111011010110111111010111102200100201111120332022211112021011102111011100 10
10210

TABLE 7.1. (cont.)

Pseudoscopelus sagamianus
00311000021201011012000111300000000000001100101100101111021401111 21??11?0000110
10001????1???1???????1??????102200100201111120332022211111202101110222001102210 10
210

Pseudoscopelus scriptus
003110000212011110120001113000000000000011001011001011110214011112 1??11?0000110
10001110110101101111110101111022001002011111203320222111112021011102200011000 10
10210

Pseudoscopelus scutatus
02311000022201011002000111300000000000001100101100111 1???2?40101121??11?00001101
00011101101011011110101011110220010020111112033212321111210100101010010000010 2
0210

Dysalotus alcocki
101210100100112110120112113 1?12000011010100000100101000120101011 21?01100000100
0000100101101111120111000001010010110200210001100001 00??00???????????????001201
311

Kali colubrina
1012212101001121100100021131110111001010200000100101000120302011 1??111?1110002
00000112201001111120101000001011110011112012011110002 10??00???????????????01000
1311

Kali falx
10121121010011211101000211312121210110102120001101010001202020111??3?212101030
0000112101001111120111000001011110011112012011110002 10??00???????????????010001
311

Kali indica
10121121010011211101000211312121110110102120001101010001202020111??3?121101030
0000112201001111120101000001011110011112012011110002 10??00???????????????010001
311

Kali kerberti
10121121010011211101100211312111111110102000001021010001203020111??2?112101000
1001112201101111120111000001011110011112012011110002 10??00???????????????010001
311

Kali macrodon
10121121010011211101100211311121211110102000001021010001202020111??1?111101000
1001112201101111120111000001011110011112012011110002 10??00???????????????010001
311

Kali macrura
10122121010011211101000211211101110010102000001011010001203010111??2?111111000
10?110110110111113010100000101111001111201201111000210??00???????????????010001
311

Kali parri
10122111010011211001000211312121110010102000001001010001202010111??0?100110000
00001122011011111301010000010111100101120120110200141 0??00???????????????220001
311

Table 7.2. Unambiguous character state changes. Changes were identified with the aid of MacClade version 4.06 (Maddison & Maddison 2003). Arranged as follows: character: change.

Chiasmodontidae
14: 0->1
16: 0->1
17: 0->1
24: 0->1
25: 0->1
26: 0->1
50: 0->1
52: 0->1
61: 0->1
63: 0->1
64: 0->1
65: 0->1
71: 0->1
83: 0->1
88: 0->1
92: 0->1
93: 0->1
95: 0->1
96: 0->1
98: 0->1
100: 0->1
106: 0->1
120: 0->1
160: 0->1

Chiasmodon group
11: 0->1
12: 0->1
44: 0->1
46: 0->1
53: 0->1
54: 0->1
55: 0->1
59: 1/2->4
79: 0->1
87: 0->1
97: 0->1
102: 0->1
104: 0->1
105: 0->1
107: 0->1
109: 0->2
118: 0->1
157: 0->1

Clade C1 -- *Chiasmodon*
9: 0->1
27: 3->4
38: 0->1
42: 0->1
60: 0->1
78: 0->1
80: 0->1
101: 0->1
103: 0->1
106: 1->2
110: 2->3
112: 0->1
153: 0->1
154: 0->1

Clade C 2
no unambiguous changes
Clade C4
44: 1->0

Clade C5
67: 0->1
79: 1->2
130: 1->0
156: 0->1
159: 2->1

Chiasmodon microcephalus
59: 4->5

Chiasmodon subniger
38: 1->2
110: 3->2

Clade P1 – *Pseudoscopelus*
3: 1->3
12: 1->2
65: 1->2
76: 0->1
90: 0->1
131: 0->2

Clade P2
136: 0->2

Clade P3
130: 2->3

Clade P4
19: 0->1
81: 0->1
131: 2->3
140: 0->1
153: 0->2
154: 0->2

Clade P5
138: 0->1

Clade P6
2: 1->2
145: 0->1
151: 0->1

Clade P7
146: 1->0

Clade P8
3: 3->2
45: 0->1
81: 1->2

Clade P9
83: 1->2
128: 1->0
142: 1->2

TABLE 7.2. (cont.)

Clade P10
2: 0/1->2
11: 1->2
51: 0->1
99: 1->0
141: 1->0
144: 0->1
149: 0->1
150: 1->0
157: 1->2

Clade P11
15: 0->1
62: 0->1

Clade P13
66: 1->0
69: 1->0
76: 1->0
147: 0->1
148: 0->1
152: 0->1

Pseudoscopelus altipinnis
143: 0->1
146: 1->2

Pseudoscopelus odontoglossum
143: 0->1

Pseudoscopelus australis
42: 0->1
43: 0->1

Pseudoscopelus parini
136: 2->1

Pseudoscopelus lavenbergi
145: 0->3

Pseudoscopelus obtusifrons
137: 0->2
140: 0->1

Kali group
1: 0->1
7: 0->1
13: 0->1
15: 0->2
24: 1->2
28: 0->1
30: 0->1
31: 0->1/2
37: 0->1
56: 0->1
86: 0->1
91: 0->1
94: 0->1
96: 1->2
108: 0->1
111: 0->1
114: 0->1
158: 0->1
161: 0->1

Clade K1 – *Kali*
6: 0->1
8: 0->1
32: 0->1
33: 0->1
34: 0->1
39: 0->1
41: 1->2
73: 0->1
85: 0/1->2
86: 1->2
109: 0->1
113: 1->0
117: 0->1
118: 0->2
131: 0->1
154: 0->1

Clade K2
7: 1->2
61: 1->2
68: 0->1
70: 0->1
72: 0->1
115: 0->1

Clade K3
18: 0->1
69: 1->2
75: 0->1

Clade K4
29: 1->2
42: 0->1
43: 0->2
48: 0->1
68: 2->3
71: 1->2
77: 0->3

Clade K5
49: 0->1
79: 0->1
82: 0->1

Clade K6
21: 0->1
35: 0->1
49: 1->2
99: 0->1

Kali colubrina
31: 1/2->0
77: 0->2

Kali falx
33: 1->2
72: 1->2
86: 2->1
99: 0->1

Kali kerberti
29: 1->2
72: 1->2

Kali macrodon
33: 1->2
68: 2->1

Kali macrura
27: 3->2
31: 1/2->0
61: 2->1
74: 0->1
84: 1->0
85: 2->1
86: 2->1
96: 2->3

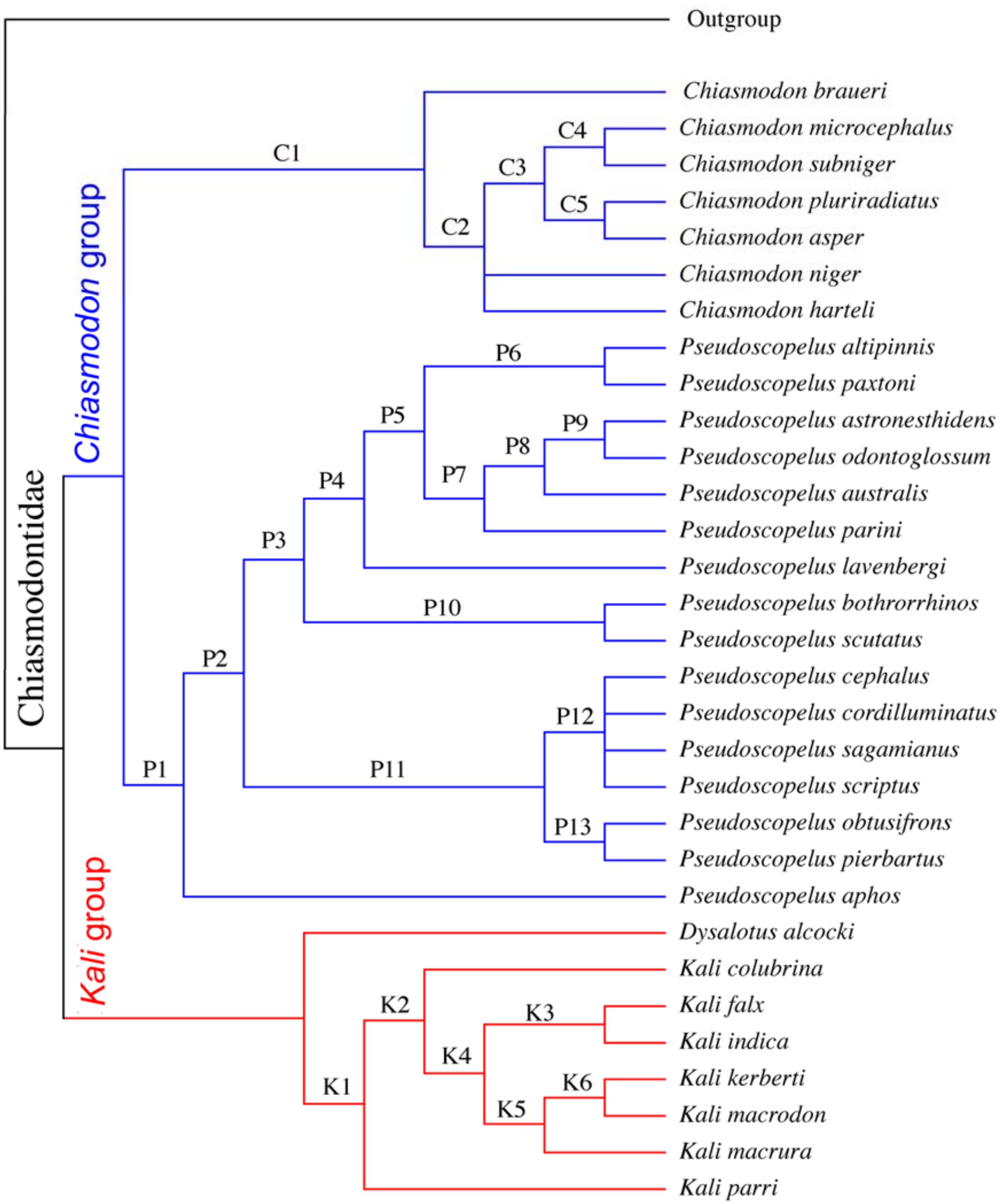
TABLE 7.2. (cont.)

Kali parri
29: 1->2
74: 0->1
96: 2->3
125: 1->0
129: 0->1
153: 0->2
154: 1->2

Dysalotus alcocki
19: 0->1
22: 0->1
36: 0->1
65: 1->2
76: 0->1
110: 1->0

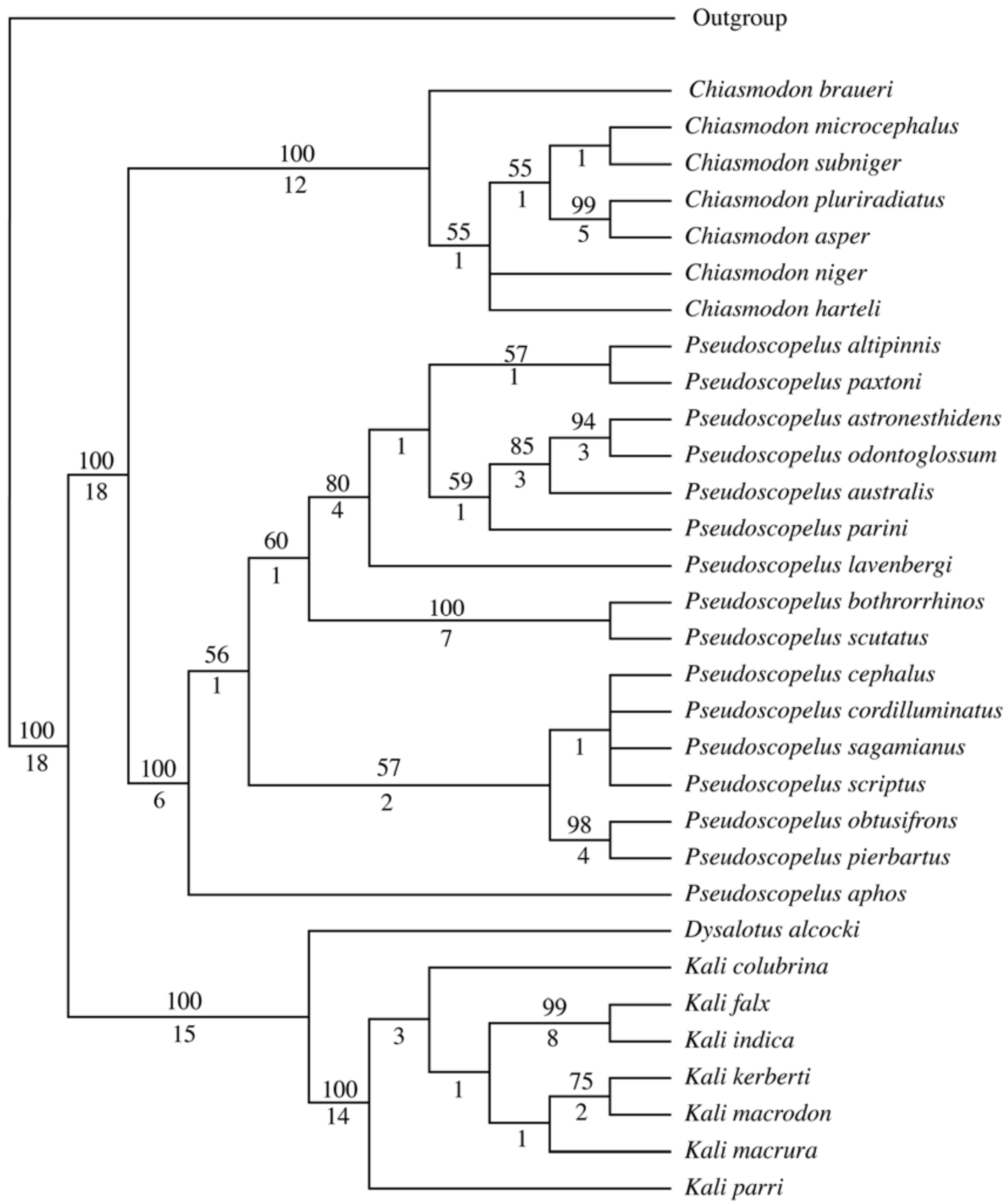
156: 0->2

FIGURE 7.1. Phylogenetic hypothesis of relationships of the family Chiasmodontidae with the proposed classification. Strict consensus of 12 most parsimonious trees with 338 steps (CI = 0.704; RI = 0.911). Clade names and numbers are on top of branches.



Outgroup
Chiasmodontidae
Chiasmodon group
Kali group
C1
C2
C3
C4
C5
Chiasmodon braueri
Chiasmodon microcephalus
Chiasmodon subniger
Chiasmodon pluriradiatus
Chiasmodon asper
Chiasmodon niger
Chiasmodon harteli
P1
P2
P3
P4
P5
P6
P7
P8
P9
P10
P11
P12
P13
Pseudoscopelus altipinnis
Pseudoscopelus paxtoni
Pseudoscopelus astronesthidens
Pseudoscopelus odontoglossum
Pseudoscopelus australis
Pseudoscopelus parini
Pseudoscopelus lavenbergi
Pseudoscopelus bothrorrhinos
Pseudoscopelus scutatus
Pseudoscopelus cephalus
Pseudoscopelus cordilluminatus
Pseudoscopelus sagamianus
Pseudoscopelus scriptus
Pseudoscopelus obtusifrons
Pseudoscopelus pierbartus
Pseudoscopelus aphos
K1
K2
K3
K4
K5
K6
Dysalotus alcocki
Kali colubrina
Kali falx
Kali indica
Kali kerberti
Kali macrodon
Kali macrura
Kali parri

Figure 7.1. Phylogenetic hypothesis of relationships of the family Chiasmodontidae. Strict consensus of 12 most parsimonious trees with 338 steps (CI = 0.704; RI = 0.911). Numbers on top of clades are the Bootstrap values, and number on bottom are the Decay values.


Outgroup
Chiasmodon braueri
Chiasmodon microcephalus
Chiasmodon subniger
Chiasmodon pluriradiatus
Chiasmodon asper
Chiasmodon niger
Chiasmodon harteli
Pseudoscopelus altipinnis
Pseudoscopelus paxtoni
Pseudoscopelus astronesthidens
Pseudoscopelus odontoglossum
Pseudoscopelus australis
Pseudoscopelus parini
Pseudoscopelus lavenbergi
Pseudoscopelus bothrorrhinos
Pseudoscopelus scutatus
Pseudoscopelus cephalus
Pseudoscopelus cordilluminatus
Pseudoscopelus sagamianus
Pseudoscopelus scriptus
Pseudoscopelus obtusifrons
Pseudoscopelus pierbartus
Pseudoscopelus aphos
Dysalotus alcocki
Kali colubrina
Kali falx
Kali indica
Kali kerberti
Kali macrodon
Kali macrura
Kali parri