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Phylogenetic Systematics of the Family Pentacerotidae (Actinopterygii: Order Perciformes)

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Table of contents

Abstract

The osteologic and myologic characteristics of the family Pentacerotidae are described in detail. The family Pentacerotidae is a monophyletic group supported by 11 synapomorphies found in all family members. Of their synapomorphies, two (the second infraorbital and endopterygoid articulate with lateral ethmoid conditions) are considerably rare in percoids and strongly support the monophyly of the family. A comparison of 44 transformation series among all species revealed four equally parsimonious trees, and a strict consensus tree was adopted. On the basis of the inferred phylogenetic relationships of the Pentacerotidae, this family was cladistically classified into two subfamilies and seven genera: Histiopterinae (*Histiopterus*, *Evistias*, *Zanclistius*, *Pentaceropsis*, *Paristiopterus*, and *Parazanclistius*) and Pentacerotinae (*Pentaceros*). The center of origin of pentacerotids was inferred to be the Southern Australian region. I propose that the two families, Ostracoberycidae and Chaetodontidae, are closely related with Pentacerotidae.

Key words: Phylogeny, Pentacerotidae, monophyly, cladistic classification, zoogeography

I. Introduction

The family Pentacerotidae, commonly called armorheads, is classified into the perciform suborder Percoidei (*sensu* Nelson, 2006). This family comprises 7 genera and approximately 12 species (*sensu* Nelson, 2006) that inhabit the bottoms of shallow to deep waters in the subantarctic to temperate waters of the Indo-Pacific and southwestern Atlantic (e.g., Hardy, 1983a; Hoese et al., 2006; Nelson, 2006). Pentacerotidae is characterized by exposed tubercles on the head, strong body compression, and absent supramaxillae (e.g., Hardy, 1983a). This family includes species such as *Pseudopentaceros wheeleri*, Kusakari-tsubodai in Japanese, which is commercially valuable as a fishery resource (Boehlert and Sasaki, 1988; Seki and Somerton, 1994).

Pentacerotidae have been variously classified by previous ichthyologists (Table. 1). For example, Jordan (1907) recognized eight genera (*Histiopterus*, *Evistias*, *Zanclistius*, *Richardsonia* [=*Paristiopterus*], *Quinquarius* and *Quadrarius* [=*Pentaceros*], *Gilchristia* [=*Pseudopentaceros*] and *Pentaceropsis*) and two subfamilies, Histiopterinae and Quinquariinae (=Pentacerotinae), in the Histiopteridae, which is the previous name of this family. Smith (1964) subdivided Pentacerotidae into the subfamilies Histiopterinae and Pentacerotinae, and recognized five genera (*Histiopterus*, *Zanclistius*, and *Paristiopterus* in the subfamily Histiopterinae, and *Pentaceropsis* and *Pentaceros* in subfamily Pentacerotinae). Hardy (1983a, b) recognized eight genera in the family and subdivided the family into three subfamilies: Histiopterinae (including *Histiopterus*, *Zanclistius*, *Evistias*, and *Parazanclistius*), Paristiopterinae (including *Paristiopterus* and *Pentaceropsis*), and Pentacerotinae (including *Pentaceros* and *Pseudopentaceros*). The classification of the family has not been adequately evaluated, because the interrelationships of the family have not yet been reconstructed, which can provide the basis of the classification. In addition, the monophyly of Pentacerotidae has not been evaluated on the basis of the concept of synapomorphy.

The purposes of the present study are to describe the comparative anatomy of the family Pentacerotidae based on osteologic and myologic observations, to verify and estimate the monophyly of the Pentacerotidae, to reconstruct the phylogenetic relationships within the Pentacerotidae, and to propose a classification of the family based on the phylogenetic relationships. The zoogeography of pentacerotids and taxa closely related with the family are also discussed on the basis of anatomic observations and reconstructed phylogenetic relationships, and comparison of the synapomorphy of the family and derived characters found in the Percoidei.

TABLE 1. Major previous classification recognized in Pentacerotidae.

Author	Subfamily	Genus
Jordan (1907)	Histiopterinae	*Histiopterus*, *Evistias*, *Zanclistius*, and *Richardsonia*
	Quinquariinae	*Quinquarius*, *Quadrarius*, *Gilchristia*, and *Pentaceropsis*
Smith (1964)	Histiopterinae	*Histiopterus*, *Zanclistius*, and *Paristiopterus*
	Pentacerotinae	*Pentaceropsis* and *Pentaceros*
Hardy (1983a, b)	Histiopterinae	*Histiopterus*, *Zanclistius*, *Evistias*, and *Parazanclistius*
	Paristiopterinae	*Paristiopterus* and *Pentaceropsis*
	Pentacerotinae	*Pentaceros* and *Pseudopentaceros*

II. Materials and Methods

The osteologic and myologic examinations were made on specimens stained with the Alizarin Red-S and Alcian Blue, and under a stereomicroscope with a camera lucida (Leica MZ-7.5 and MZ-9.5). The terminology generally follows that used in the recent literature regarding percoids, e.g., Sasaki (1989) and Kim (2002) for osteology, and Winterbottom (1974) for myology. The definitions of higher taxonomic categories in the materials list are in accordance with Nelson (2006). Measurements and counts were made according to Hubbs and Lagler (1958). Standard length is abbreviated as SL. Institutional abbreviations follow Eschmeyer (1998), except for the Hokkaido University Museum, Hakodate, Japan (HUMZ), and the South African Institute for Aquatic Biodiversity, National Research Foundation, Grahamstown, South Africa (SAIAB). The materials examined for anatomy and abbreviations used in this study are listed below.

Materials used for dissection and observation.

Perciformes

Percoidei

Pentacerotidae. *Histiopterus typus* (Temminck and Schlegel, 1844), HUMZ 72430 (145 mm SL); *Evistias acutirostris* (Temminck and Schlegel, 1844), HUMZ 97737, 114459 (123.3, 143 mm SL); *Zanclistius elevatus* (Ramsay and Ogilby, 1888), NMNZ P.010834 (180.3 mm SL); *Pentaceropsis recurvirostris* (Richardson, 1845), NMV A 1294, A 1305 (200.9, 190.7 mm SL); *Paristiopterus labiosus* (Günther, 1872), AMS I.23955-001 (175.8 mm SL); *P. gallipavo* (Whitley, 1944), HUMZ 33215 (288.3 mm SL); *Parazanclistius hutchinsi* (Hardy, 1983), HUMZ 33239 (196.5 mm SL); *Pentaceros capensis* (Cuvier, 1829), SAIAB 8292 (142.5, 254.2 mm SL); *P. decacanthus* (Günther, 1859), NMNZ P.021397, P.032853 (190.8, 183.7 mm SL); *P. japonicus* (Steindachner, 1883), HUMZ 36478, 90278 (143.1, 114.0 mm SL); *P. quinquespinis* (Parin and Kotlyar, 1988), HUMZ 164613 (214.4 mm SL); *Pseudopentaceros richardsoni* (Smith, 1844), NMNZ P.15180 (319.9 mm SL); *P. wheeleri* (Hardy, 1983), HUMZ 147629 (261.0 mm SL).

Latidae. *Lates mariae* (Steindachner, 1909), HUMZ 125944 (97.7 mm SL).

Percichthyidae. *Coreoperca herzi* (Herzenstein, 1896), CNUC 37660 (139.8 mm SL).

Acropomatidae. *Synagrops japonicus* (Döderlein, 1883), HUMZ 79944 (107.7 mm SL); *Doederleinia berycoides* (Hilgendorf, 1879), HUMZ 79421 (135.8 mm SL).

Ostracoberycidae. *Ostracoberyx dorygenys* (Fowler, 1934), HUMZ 143188, 193736 (72.8, 76.2 mm SL); *O. paxtoni* (Quéro and Ozouf-Costaz, 1991), AMS I.27693-005 (88.8 mm SL).

Banjosidae. *Banjos banjos* (Richardson, 1846), HUMZ 199907 (85.6 mm SL).

Centrarchidae. *Lepomis macrochirus* (Rafinesque, 1819), HUMZ 119326 (97.4 mm SL).

Lutjanidae. *Macolor macularis* (Fowler, 1931), HUMZ 63074 (123.4 mm SL).

Pempheridae. *Pempheris japonica* (Döderlein, 1883), HUMZ 49213 (100.2 mm SL).

Chaetodontidae. *Chaetodon modestus* (Temminck and Schlegel, 1844), HUMZ 199873, 199875 (95.5, 89.7 mm SL).

Kyphosidae. *Microcanthus strigatus* (Cuvier, 1831), HUMZ 105899 (107.8 mm SL).

Anatomic abbreviations.

The following abbreviations are used in the Figures.

Bones and cartilages

ACP, ascending process of premaxillary; ACT, actinost; ALP, alveolar process; ANG, anguloarticular; ARP, articular process; ASK, accessory subpelvic keel; BB, basibranchial; BO, basioccipital; BR, branchiostegal ray; BSP, basisphenoid; CB, ceratobranchial; CC, cranial condyle; CH, ceratohyal; CIHPU, interhemal spine cartilage of preural centra; CINPU, inter-neural spine cartilage of centra; CLE, cleithrum; COM, coronomeckelian; COR, coracoid; CPEP, post-epural cartilage; CPHPU, post-hemal spine cartilage of preural centra; CPHY, post-hypural cartilage; DEN, dentary; DHH, dorsal hypohyal; DP, distal pterygiophore; EB, epibranchial; ECP, ectopterygoid; EH, epihyal; ETH, ethmoid; EO, epiotic; EN, epineural; ENP, endopterygoid; EP, epural; EXO, exoccipital; FRO, frontal; HB, hypobranchial; HS, hemal spine; HY, hypural; HYO, hyomandibular; IAC, interarcual cartilage; IC, intercalar; IH, interhyal; IO, infraorbital; IOP, interopercle; LET, lateral ethmoid; LP, lateral process of maxilla; MAX, maxillary; MEC, meckelian cartilage; MEP, metapterygoid; NA, nasal; NS, neural spine; OP, opercle; PA, parietal; PAL, palatine; PB, pharyngobranchial; PC, premaxillary condyle; PCL, postcleithra; PHY, parhypural; PMP, postmaxillary process; POP, preopercle; PP, postpelvic process; PR, pleural rib; PRM, premaxilla; PRO, prootic; PRPT, proximal pterygiophore; PS, parasphenoid; PT, posttemporal; PTO, pterotic; PTS, pterosphenoid; PU, preural centrum; PV, pelvic girdle; QUA, quadrate; RC, rostral cartilage; RET, retroarticular; SBP, subpelvic process; SCA, scapula; SCL, supracleithrum; SN; supraneural; SO, supraoccipital; SOP, subopercle; SPO, sphenotic; SS, subocular shelf; ST, supratemporal; STA, stay; SYM, symplectic; UN, uroneural; US, urostyle; V, vomer; VHH, ventral hypohyal.

Muscles and ligaments

A1–3 and Aw, adductor mandibular sections 1–3 and w; AAP, adductor arcus palatini; ABP, abductor profundus; ABS, abductor superficialis; ABSP, abductor superficialis pelvicus; AD, adductor; ADP, adductor profundus; ADPP, adductor profundus pelvicus; ADR, adductor radialis; ADS, adductor superficialis; ADSP, adductor superficialis pelvicus; AH, adductor hyomandibulae; AO, adductor operculi; ARD, arrector dorsalis; ARDP, arrector doorsalis pelvicus; ARV, arrector ventralis; ARVP, arrector ventralis pelvicus; BL, Baudelot's ligament; CO, coracoradialis; DO, dilatator operculi; DED, depressores dorsales; DEA, depressores anales; EPAX, epaxialis; ERA, errectores anales; ERD, erectores dorsales; EXP, extensor proprius; FD, flexor dorsalis; FDS, flexor dorsalis superior: FV, flexor ventralis; FVE, flexor ventralis externus; FVI, flexor ventralis inferior; HAB 1–2, hyohyoidei abductors section 1–2; HAD, hyohyoidei adductores; HL, hypochordal longitudinalis; HPAX, hypaxialis; IFCP, infracarinalis posterior; IFM, infracarinalis medius; IM, intermandibularis; INA, inclinatores anales; IND, inclinatores dorsales; INT, interradialis; LAP, levator arcus palatini; LAS, lateral superficialis; LE, levatores externi; LEP, levator posterior; LO, levator operculi; LI, levatores interni; LP, ligamentum primordium; OBD, obliqui dorsales; OBP, obliquus posterior; OBS, obliquus superioris; OBI, obliquus inferioris; OBV, obliqui ventrales; PH, protractor hyoidei; PCE, pharyngoclavicularis externus; PCI, pharyngoclavicularis internus; PP, protractor pectoralis; RC, rectus communis; RD, retractor dorsalis; RV, rectus ventralis; SO, sphincter esophagi; SPCA, supracarinalis anterior; SPCP, supracarinalis posterior; STH, sternohyoideus; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior; TEB2, transversus epibranchialis 2; TPB2, transversus pharyngobranchialis 2; TVA, transversus ventralis anterior; TVP, transversus ventralis posterior.

III. Systematic Methodology

The cladistic methodology formulated by Hennig (1966) was adopted for estimation of the phylogenetic relationships of the Pentacerotidae. Outgroup comparisons were used to determine the character polarity (Watrous and Wheeler, 1981; Wiley, 1981).

The pentacerotids belong to the suborder Percoidei (Nelson, 2006), but taxa closely related with the Pentacerotidae have not been adequately examined. The suborder Percoidei is used as an outgroup for the determination of character polarity, because the suborder is considered to be the most primitive group within the order Perciformes (e.g., Johnson, 1993; Mooi, 1993; Imamura and Yabe, 2002). Typical percoid characters are treated as outgroup conditions, based on the percoid taxa examined in this study and in the literature (e.g., Matsubara, 1943; Yabe, 1985; Sasaki, 1989; Tyler et al., 1989; Johnson and Patterson, 1993; Ishida, 1994; Imamura, 2000; Kim, 2002).

When all pentacerotids commonly have the same characters and they are not found in typical percoids, such characters are treated as apomorphic, as discussed under "Synapomorphies of Pentacerotidae". Transformation series (TS) recognized in this study are divided into two categories. When the character variation within the Pentacerotidae is recognized in a TS and the character polarity is determinable, the TS is discussed under "Character recognition". Unpolarized characters, autapomorphic characters recognized only in terminal taxa, and characters considered to have intraspecific variations having no effect on the determination of the relationship are discussed under the other category, "Other variations".

The data were analyzed using PAUP* 4.0b10 (Swofford, 2002), including ACCTRAN and DELTRAN optimizations and the heuristic search option. Character evolution was assumed as "ordered" (Wagner parsimony: Farris, 1970) when character order was decidable, or "unordered" (Fitch parsimony: Fitch, 1971) when character order was equivocal due to many modifications. When characters in an outgroup are not specified, a question mark (?) is coded for the conditions in the data matrix.

IV. Comparative Anatomy

1. Osteology

1-1. Circumorbital bones

(Figs. 1, 2)

Description

The circumorbital bones comprise six infraorbitals. They form a serial tubular structure for the infraorbital sensory canal, which is continuous with the tubular structures of the head. Many exposed tubercles are present on the lateral surface of the infraorbitals in all pentacerotids, except for *Paristiopterus gallipavo* and *Pentaceropsis*.

The first infraorbital (=lachrymal), the largest bone among the circumorbital bones, is situated anterior to the second infraorbital and connects posteriorly with the second infraorbital bone. The first infraorbital partially overlaps with the anterior portion of the maxilla anteriorly. This bone is L-shape in *Histiopterus*, *Zanclistius*, *Evistias*, and *Parazanclistius* (Fig. 1A–D); robust and triangular in *Paristiopterus* (Fig. 1E–F); rod- like in *Pentaceropsis* (Fig. 2A); square in *Pentaceros* (Fig. 2B–E); and sharp and triangular in *Pseudopentaceros* (Fig. 2F–G). Several bridges cover the sensory canal running through the first infraorbital.

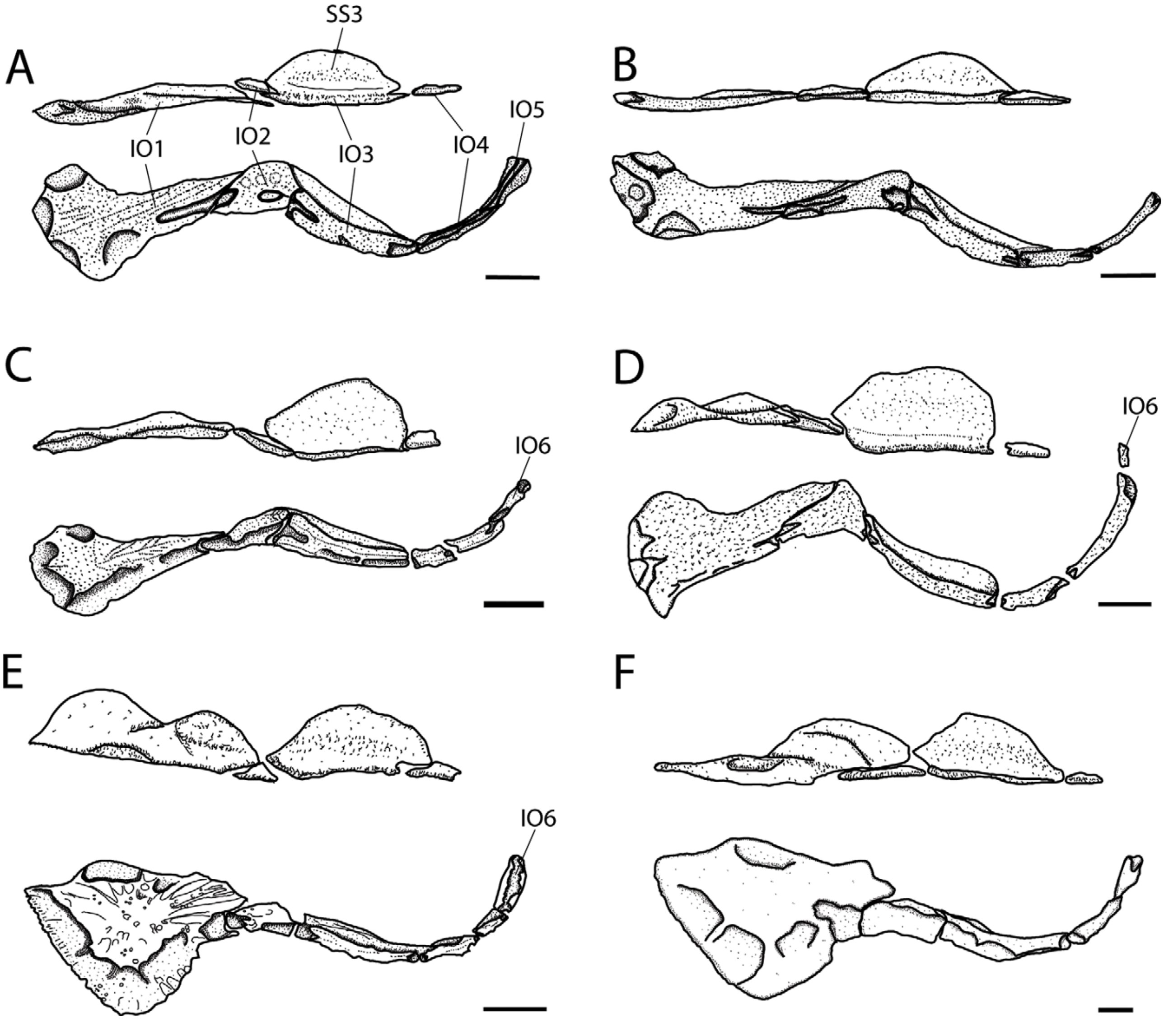

FIGURE 1. Dorsal (above) and lateral (below) aspects of circumorbital bones. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*. Dorsal aspects of IO5 and IO6 are not shown. IO6 of A, B, and F are figured with the neurocranium. B and E are shown as mirror images. Scale bar = 5 mm.

The second infraorbital is a rectangular or triangular bone, and located posterior to the first infraorbital. It articulates with the lateral ethmoid anteromedially. The bone has a well-developed subocular shelf dorsomedially and also a simple ridge dorsolaterally in *Pentaceros* and *Pseudopentaceros*, whereas the shelf and ridge are absent in the others.

The third infraorbital is a rod-like bone. This bone is firmly attached to the second infraorbital anteriorly and to the fourth infraorbital posteriorly. It has a well-developed subocular shelf in all pentacerotids, except for *Pentaceropsis recurvirostris* in which the shelf is completely lacking. The shelf is pointed anteromedially and articulates with the lateral ethmoid.

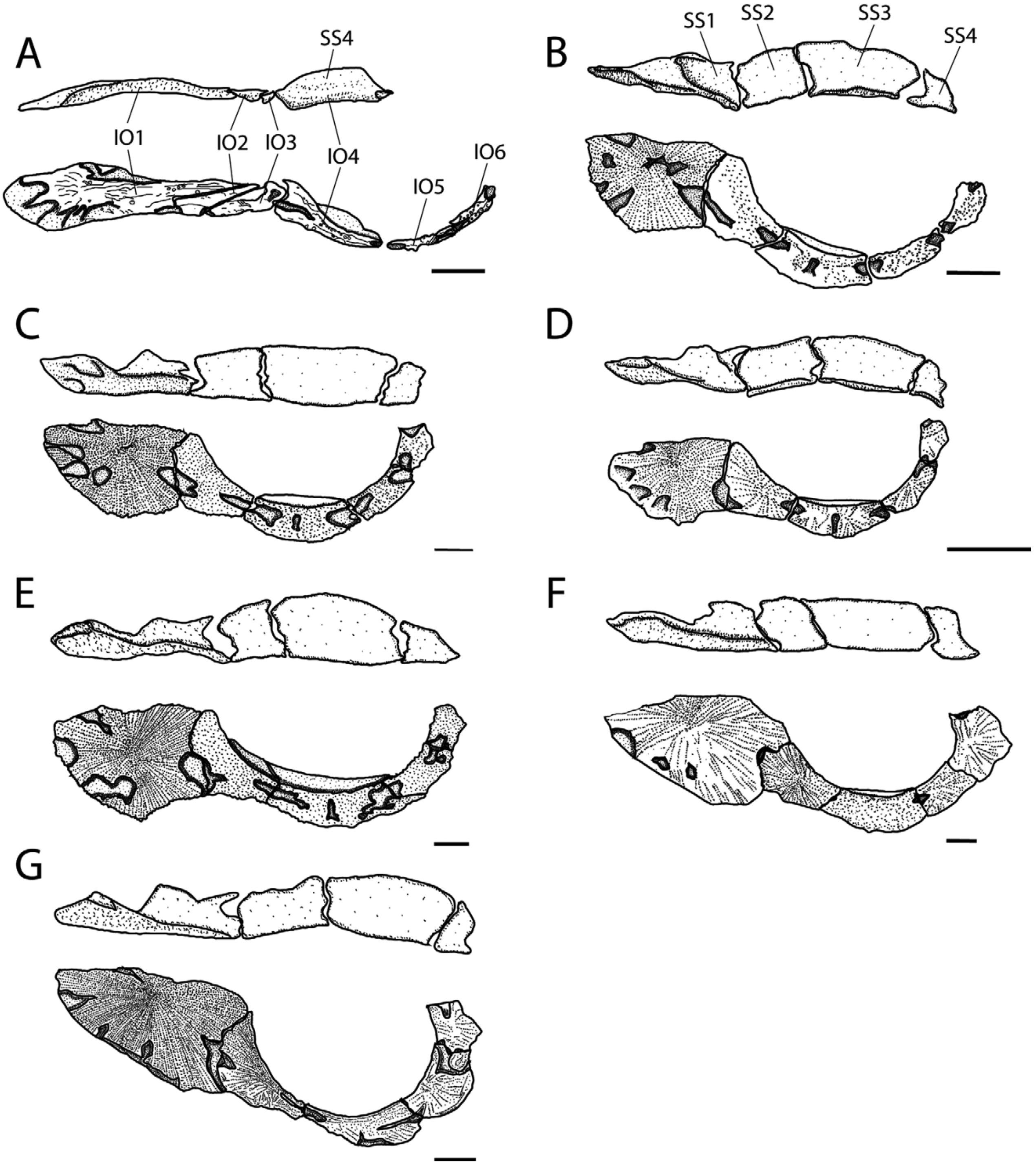

FIGURE 2. Dorsal (above) and lateral (below) aspects of circumorbital bones. A, *Pentaceropsis recurvirostris*; B, *Pentaceros capensis*; C, *P. decacanthus*; D, *P. japonicus*; E, *P. quinquespinis*; F, *Pseudopentaceros richardsoni*; G, *P. wheeleri*. Dorsal aspects of IO5 and IO6 are not shown. IO6 of B to G is figured with the neurocranium. A to C and F are shown as mirror images. Scale bar = 5 mm.

The fourth infraorbital is a tubular bone. It is sutured with the third infraorbital anteriorly and with the fifth infraorbital posteriorly. This bone has a well-developed subocular shelf in *Pentaceropsis*, *Pentaceros*, and *Pseudopentaceros*, whereas a distinct shelf is absent in the others. The posteroventral margin of this bone is sutured with the preopercle in *Pentaceros* and *Pseudopentaceros*, whereas it is adjacent to the preopercle in the others.

The fifth infraorbital is a tubular bone. This bone is attached to the fourth infraorbital ventrally and to the six infraorbital dorsally. This bone have a well-developed subocular shelf in *Pentaceros* and *Pseudopentaceros*, while a distinct shelf is absent in the others.

The sixth infraorbital (=dermosphenotic) is situated on the sphenotic and is loosely connected to the frontal. It is firmly attached to the sphenotic in *Pentaceros* and *Pseudopentaceros,* whereas it is loosely attached to the sphenotic in the others. The sensory canal of this bone is continuous with the canal of the frontal and pterotic.

Synapomorphies of Pentacerotidae

SA 1. Second infraorbital articulating with the lateral ethmoid.

The pentacerotids have a second infraorbital that articulates with the lateral ethmoid anteromedially. This is a derived character, because in the primitive condition in typical percoids, the lateral ethmoid usually articulates with first infraorbital, but not with the second infraorbital (e.g., Gosline, 1984; Yabe, 1985; pers. obs.).

Character recognition

TS 1. Exposed tubercles on the infraorbitals. (0: absent; 1: present)

Ingroup. Many exposed tubercles are present on the lateral surface of the infraorbitals in all pentacerotids (character 1-1), except for *Paristiopterus gallipavo* and *Pentaceropsis* (character 1-0).

Outgroup. The exposed tubercles on the infraorbitals are typically absent (character 1-0) in percoids (e.g., Gregory, 1933; Imamura, 1996; pers. obs.).

TS 2. First infraorbital shape. (1: L-shape; 2: robust and triangular; 3: rod like; 4: square; 5: sharp and triangular) (unordered)

Ingroup. The first infraorbital is L-shaped in *Histiopterus*, *Zanclistius*, *Evistias*, and *Parazanclistius* (character 2-1); robust and triangular in *Paristiopterus* (character 2-2); rod-like in *Pentaceropsis* (character 2-3); square in *Pentaceros* (character 2-4); and sharp and triangular in *Pseudopentaceros* (character 2-5).

Outgroup. The first infraorbital has various shapes in percoids. For example, it is round in the mullids, rod-like in the acropomatids *Doederleinia* and *Synagrops*, and the epigonid *Florenciella*; square in the banjosid *Banjos* and centrarchid *Lepomis*; sharp and triangular in the ostracoberycid *Ostracoberyx*; and triangular in the latid *Lates* and chaetodontid *Chaetodon* (e.g., Mok and Shen, 1983; Prokofiev, 2007b; pers. obs.). Therefore, a typical percoid condition cannot be determined and outgroup condition is coded as “?”.

TS 3. Subocular shelf on the second infraorbital. (0: absent; 1: present)

Ingroup. The subocular shelf is present on the second infraorbital in *Pentaceros* and *Pseudopentaceros* (character 3-1), whereas it is absent in the others (character 3-0).

Outgroup. The shelf is absent on the second infraorbital in typical percoids (character 3-0) (e.g., Smith and Bailey, 1962; Johnson, 1980; Gosline, 1984; Kim, 2002; pers. obs.).

TS 4. Subocular shelf on the fourth infraorbital. (0: absent; 1: present)

Ingroup. The subocular shelf is present on the fourth infraorbital in *Pentaceropsis*, *Pentaceros*, and *Pseudopentaceros* (character 4-1), whereas a distinct shelf is absent in the others (character 4-0).

Outgroup. The shelf is absent on the fourth infraorbital in typical percoids (character 4-0) (e.g., Gosline, 1984; Westneat, 1993; Carpenter and Johnson, 2002; pers. obs.).

TS 5. Connection between the fourth infraorbital and preopercle. (0: separated; 1: sutured)

Ingroup. The posteroventral margin of the fourth infraorbital is sutured with the preopercle in *Pentaceros* and *Pseudopentaceros* (character 5-1), whereas these bones are separated in the others (character 5-0).

Outgroup. The fourth infraorbital is separated from the preopercle in typical percoids (character 5-0) (e.g., Gosline, 1968; Imamura, 1996; pers. obs.).

TS 6. Subocular shelf on the fifth infraorbital. (0: absent; 1: present)

Ingroup. The subocular shelf is present on the fifth infraorbital in *Pentaceros* and *Pseudopentaceros* (character 6-1), whereas a distinct shelf is absent in the others (character 6-0).

Outgroup. The subocular shelf is absent on the fifth infraorbital in typical percoids (character 6-0) (e.g., Smith and Bailey, 1962; Gosline, 1984; pers. obs.).

TS 7. Connection between the fifth infraorbital and sphenotic. (0: loosely attached; 1: firmly attached)

Ingroup. The fifth infraorbital is loosely attached to the sphenotic in most pentacerotids (character 7-0), while it is firmly attached to the sphenotic in *Pentaceros* and *Pseudopentaceros* (character 7-1).

Outgroup. The fifth infraorbital is loosely attached to the sphenotic in typical percoids (character 7-0) (e.g., Sasaki, 1989; Imamura, 1996; pers. obs.).

Other variations

Subocular shelf on the *third infraorbital*. The subocular shelf is present on the third infraorbital in most pentacerotids, as well as in typical percoids (e.g., Baldwin and Johnson, 1993; pers. obs.), while it is lacking in *Pentaceropsis recurvirostris*. Therefore, the latter condition can be treated as an autapomorphy of *Pentaceropsis recurvirostris* and is not used for phylogenetic analysis.

1-2. Neurocranium

(Figs. 3–13)

Description

The neurocranium comprises 6 unpaired elements (vomer, ethmoid, parasphenoid, basisphenoid, supraoccipital, and basioccipital) and 11 paired elements (nasal, lateral ethmoid, frontal, pterosphenoid, sphenotic, prootic, parietal, pterotic, epiotic, intercalar, and exoccipital).

The nasal bone is a flat tubular bone, and has a simple sensory canal continuous with the supraorbital sensory canal on the frontal bone. The bone is connected with the frontal and lateral ethmoid posteriorly. This bone is firmly attached to the ethmoid posteromedially in *Pentaceros* and *Pseudopentaceros*, whereas it is loosely attached in the others. Many exposed tubercles are present on the dorsal surface of the nasal in all pentacerotids, except for *Paristiopterus* and *Pentaceropsis*.

The vomer is a triangular bone situated on the anteroventral region of the neurocranium. This bone is connected with the ethmoid and lateral ethmoid dorsally, and the parasphenoid posteriorly. It is also connected with the palatine by a strong ligament anterolaterally. The vomer possesses villiform teeth anteroventrally in *Pentaceros* and *Pseudopentaceros*, whereas it lacks teeth in other pentacerotids.

The ethmoid forms the anterior border of the neurocranium. The bone is connected with the vomer anteriorly, the lateral ethmoid laterally and the frontal posteriorly. This bone bears an anterior projection; the projection is sharp in most pentacerotids, whereas it is blunt in *Pentaceropsis*, *Pentaceros,* and *Pseudopentaceros*. The ethmoid-maxillary ligament connects the anterior process of ethmoid and lateral process of the maxillary. This ligament is also connected with the ventral surface of the nasal bone in *Pentaceros* and *Pseudopentaceros,* whereas it is free from the nasal bone in the others. Many exposed tubercles are present on the dorsal surface of the ethmoid in *Pentaceros capensis*, whereas they are absent in other pentacerotids.

The lateral ethmoid is a triangular bone that connects with the frontal bone dorsally, the ethmoid anteriorly, and the parasphenoid ventrally. This bone articulates with the dorsal process of the second and third infraorbitals laterally. Many exposed tubercles are present on the lateral surface of the lateral ethmoid in all pentacerotids, except for *Paristiopterus* and *Pentaceropsis*.

The frontal is the largest bone in the dorsal skull roof. It is connected with the ethmoid, nasal, and lateral ethmoid anteriorly; the supraoccipital, parietal, and pterotic posteriorly; and the sixth infraorbital, sphenotic, and pterotic posteroventrally. The supraorbital sensory canal penetrates this bone, and is continuous with the canal of the nasal anteriorly, and those of the sixth infraorbital and pterotic bones laterally. Many exposed tubercles are present on the dorsolateral surface of the frontal bone.

The parietal is a triangular bone on the posterodorsal region of the neurocranium. It is attached to the frontal anteriorly, the pterotic laterally, the epiotic posteriorly, and the supraoccipital medially. Many exposed tubercles are present on the lateral surface of the parietal in all pentacerotids, except for *Paristiopterus* and *Pentaceropsis*.

The sphenotic is located on the posterodorsal corner of the orbit. It is usually connected with the frontal anteromedially, the pterotic posteriorly, the pterosphenoid anteroventrally, the prootic ventrally, and the sixth infraorbital dorsally.

The pterosphenoid is a square shape bone situated below the posterodorsal wall of the orbit. It is connected with the frontal dorsally, the sphenotic laterally, and the prootic and basisphenoid ventrally.

The parasphenoid is a long bone situated on the ventral portion of the neurocranium. It is usually sutured with the vomer and lateral ethmoid anteriorly, the prootic posteriorly, and the basioccipital posteriorly.

The basisphenoid is located on the posteroventral margin of the orbit, and is usually sutured with the prootic and pterosphenoid of both sides posteriorly, and the parasphenoid anteroventrally.

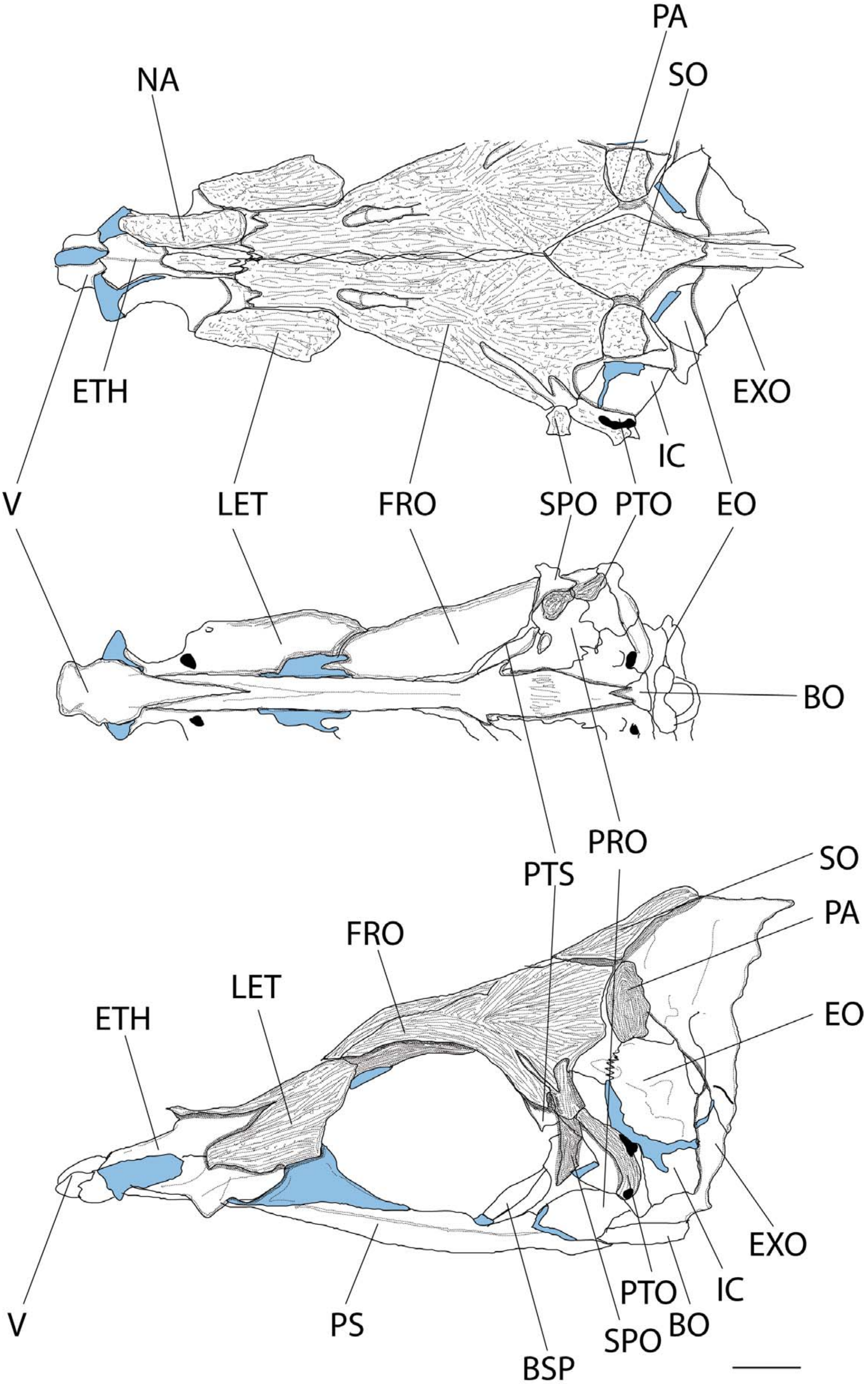

FIGURE 3. Neurocranium of *Histiopterus typus* in the dorsal (upper), ventral (middle), and lateral (lower) aspects. Scale bar = 5 mm.

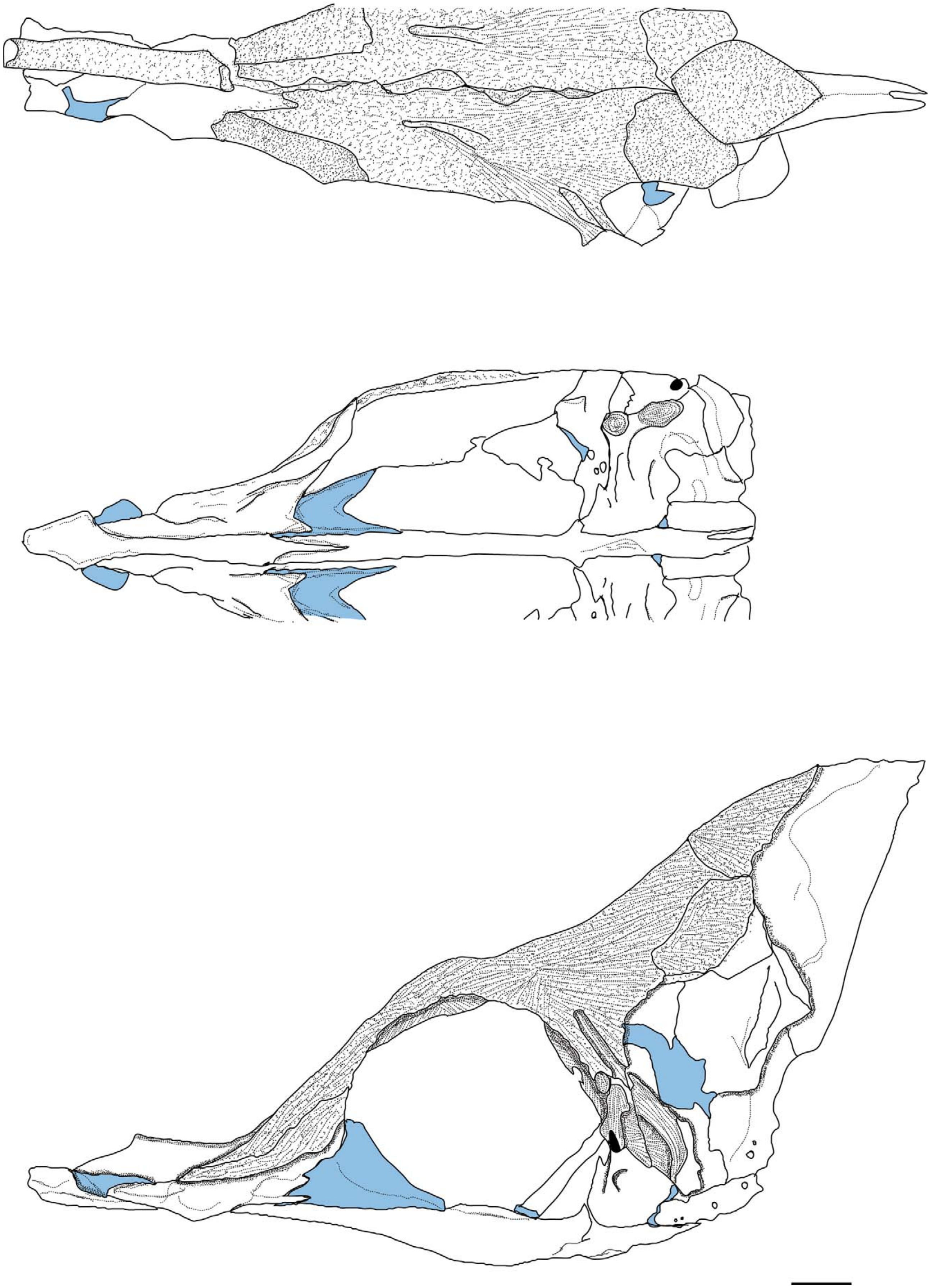

FIGURE 4. Neurocranium of *Zanclistius elevatus* in the dorsal (upper), ventral (middle), and lateral (lower) aspects. Shown as a mirror image. Scale bar = 5 mm.

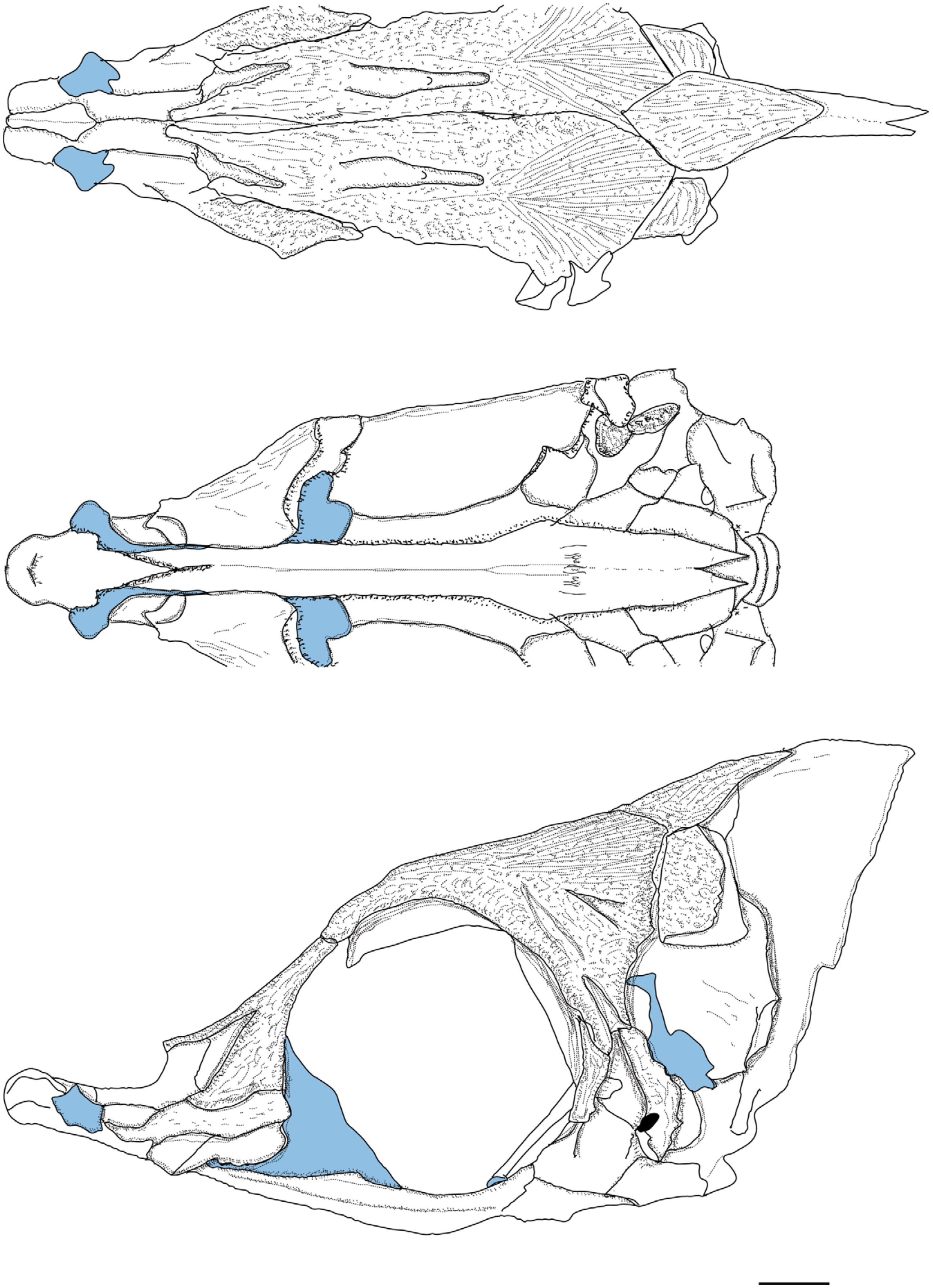

FIGURE 5. Neurocranium of *Evistias acutirostris* in the dorsal (upper), ventral (middle), and lateral (lower) aspects. Scale bar = 5 mm.

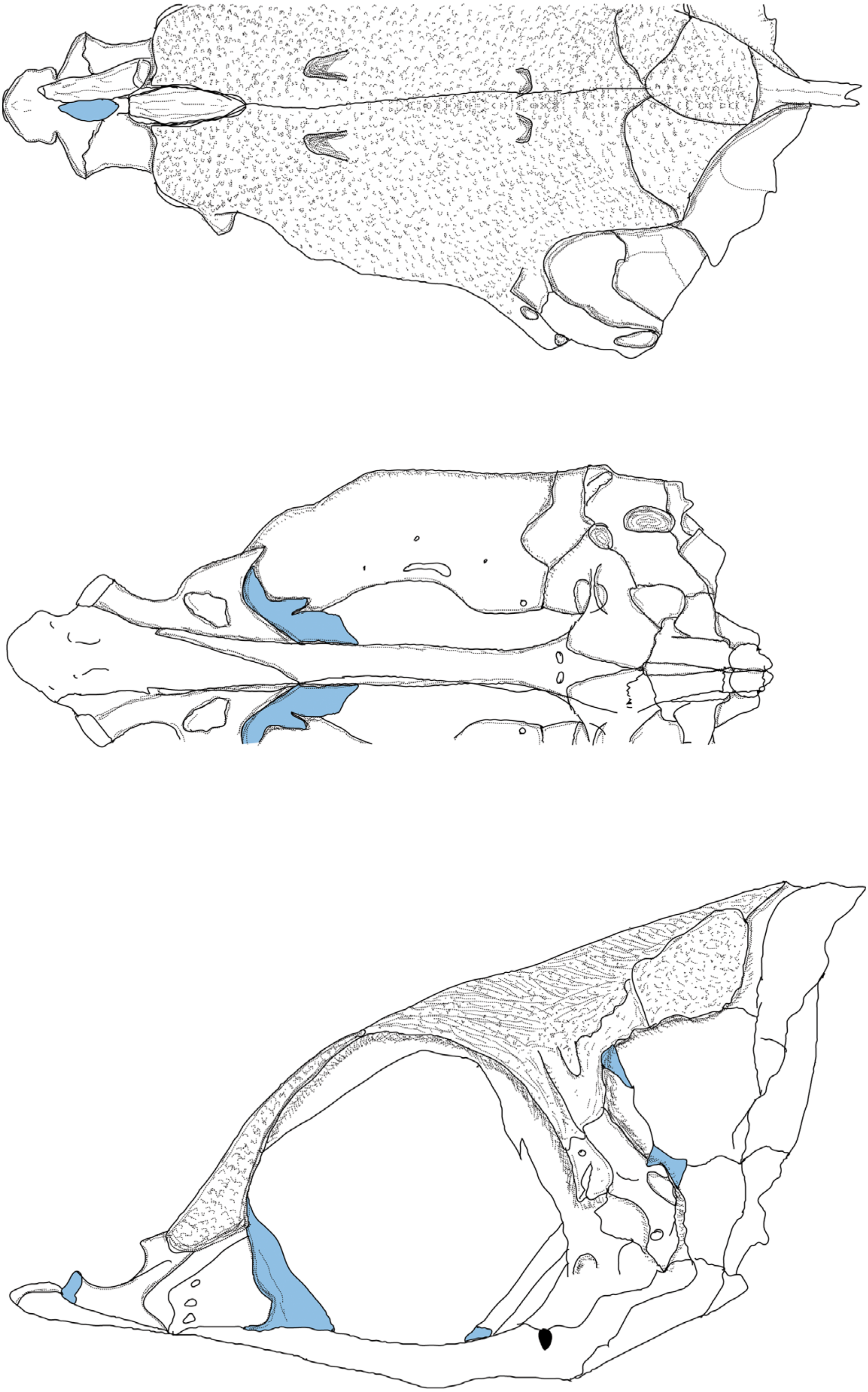

FIGURE 6. Neurocranium of *Parazanclistius hutchinsi* in the dorsal (upper), ventral (middle), and lateral (lower) aspects. Scale bar = 5 mm.

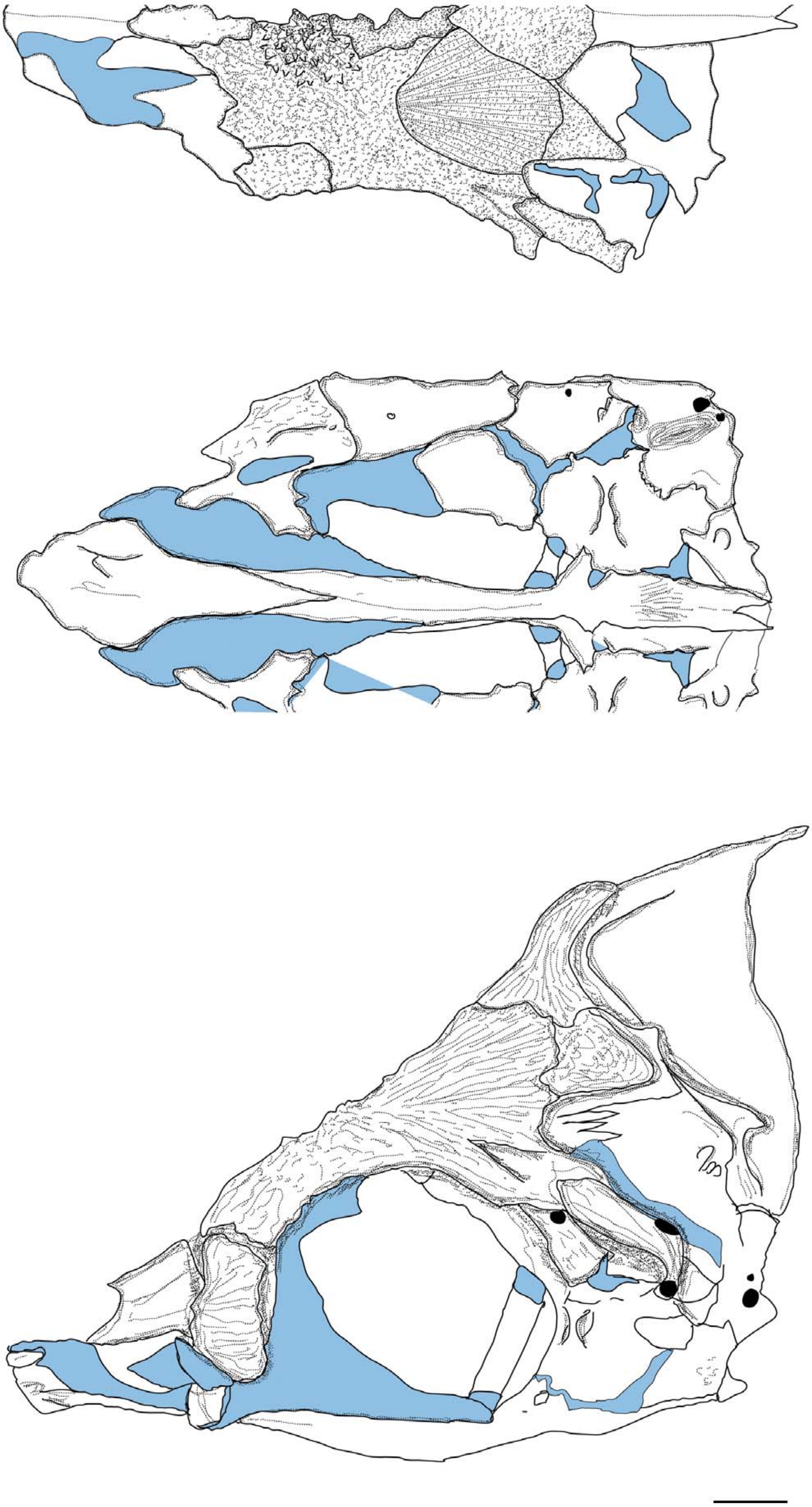

FIGURE 7. Neurocranium of *Paristiopterus labiosus* in the dorsal (upper), ventral (middle), and lateral (lower) aspects. Shown as a mirror image. Scale bar = 5 mm.

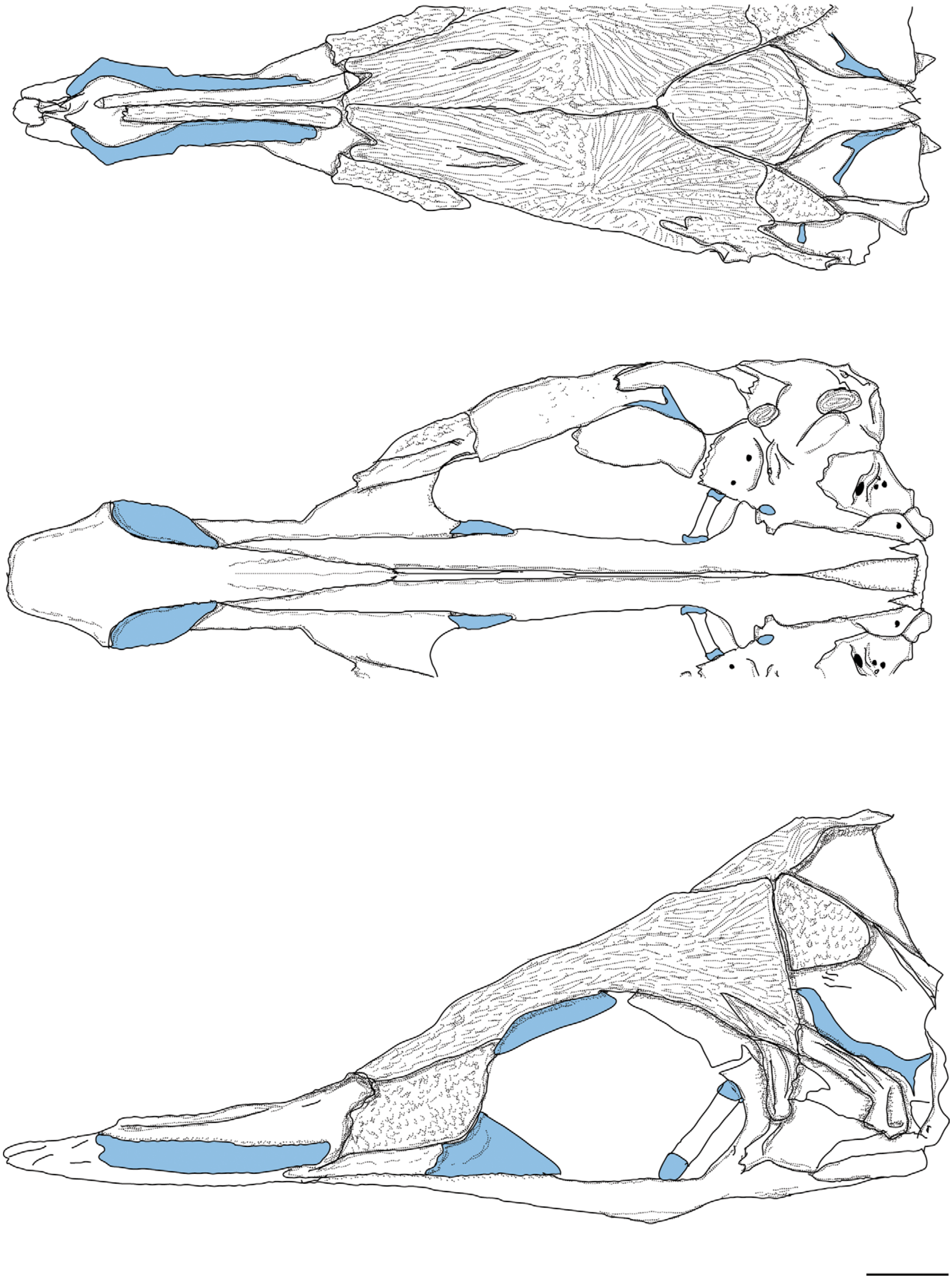

FIGURE 8. Neurocranium of *Pentaceropsis recurvirostris* in the dorsal (upper), ventral (middle), and lateral (lower) aspects. Shown as a mirror image. Scale bar = 5 mm.

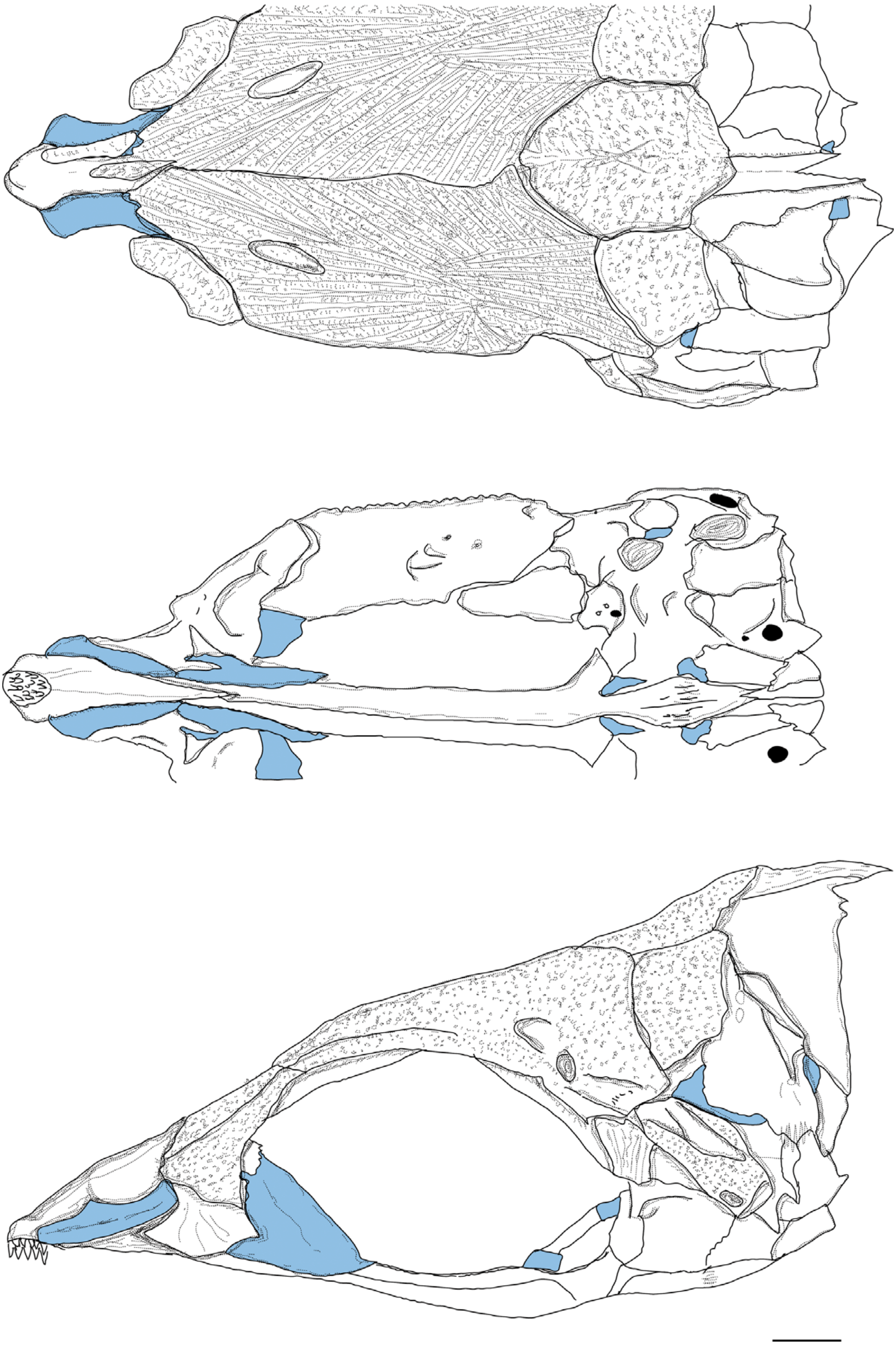

FIGURE 9. Neurocranium of *Pentaceros capensis* in the dorsal (upper), ventral (middle) and lateral (lower) aspects. Shown as a mirror image. Scale bar = 5 mm.

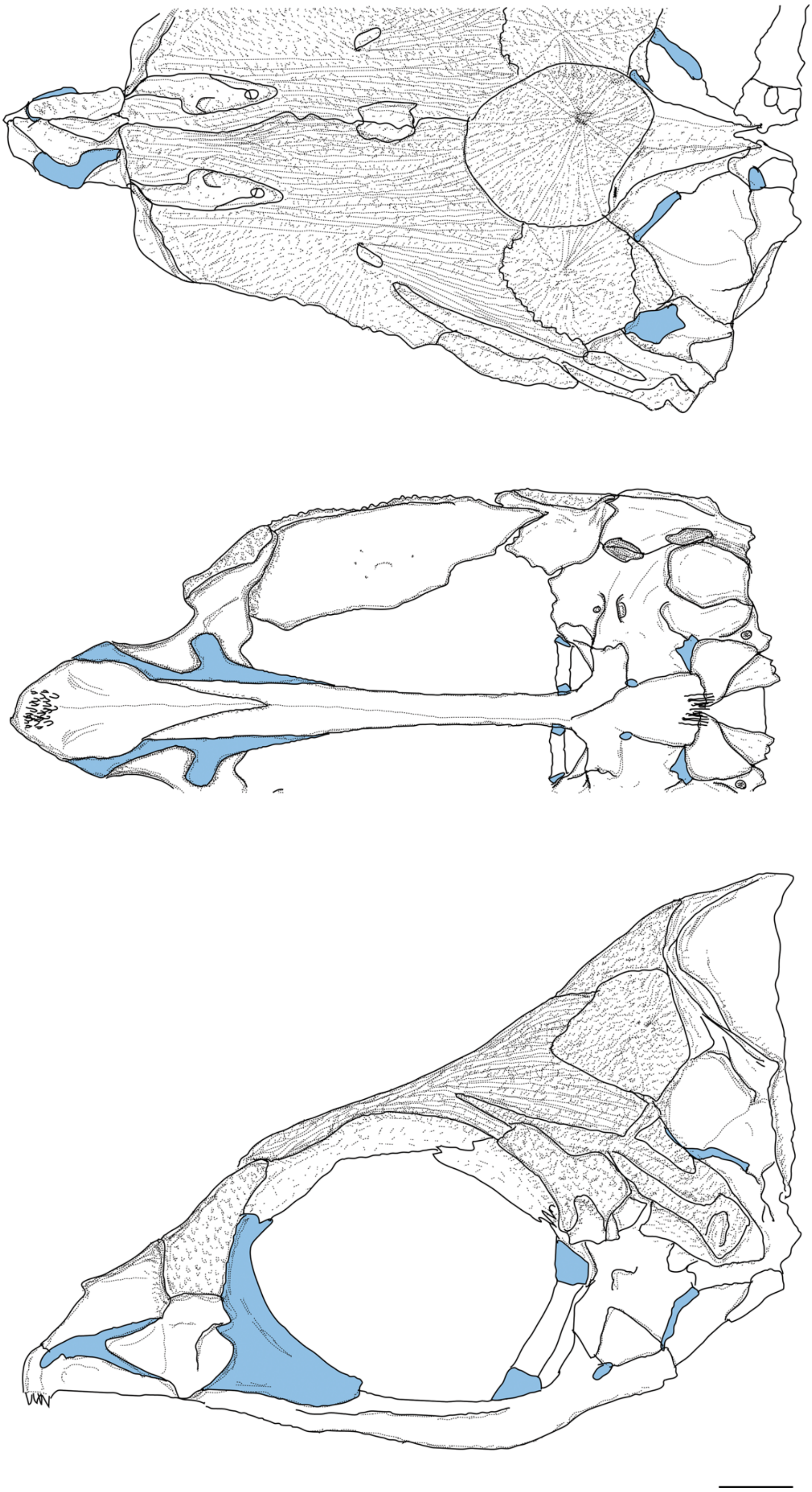

FIGURE 10. Neurocranium of *Pentaceros decacanthus* in the dorsal (upper), ventral (middle), and lateral (lower) aspects. Shown as a mirror image. Scale bar = 5 mm.

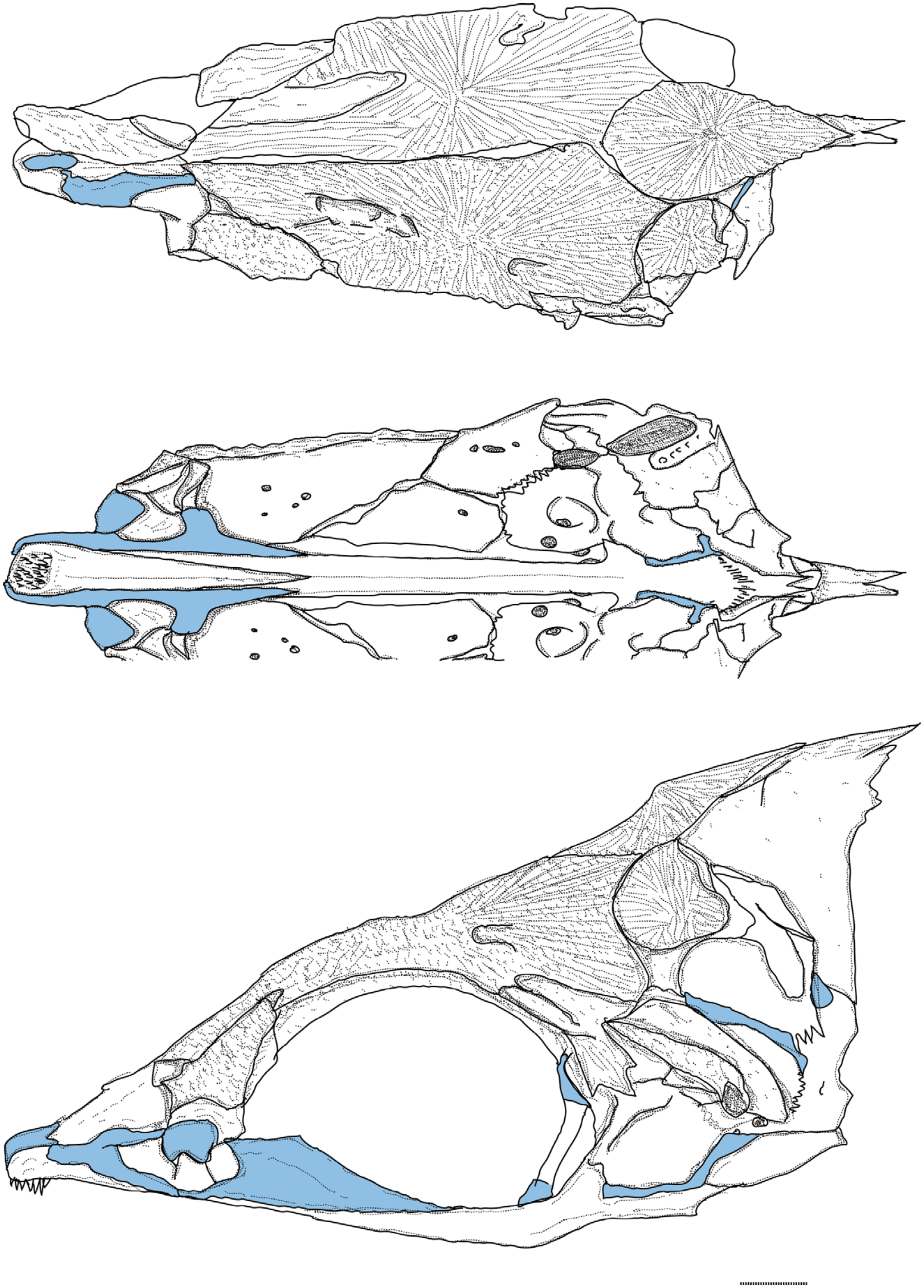

FIGURE 11. Neurocranium of *Pentaceros japonicus* in the dorsal (upper), ventral (middle), and lateral (lower) aspects. Scale bar = 5 mm.

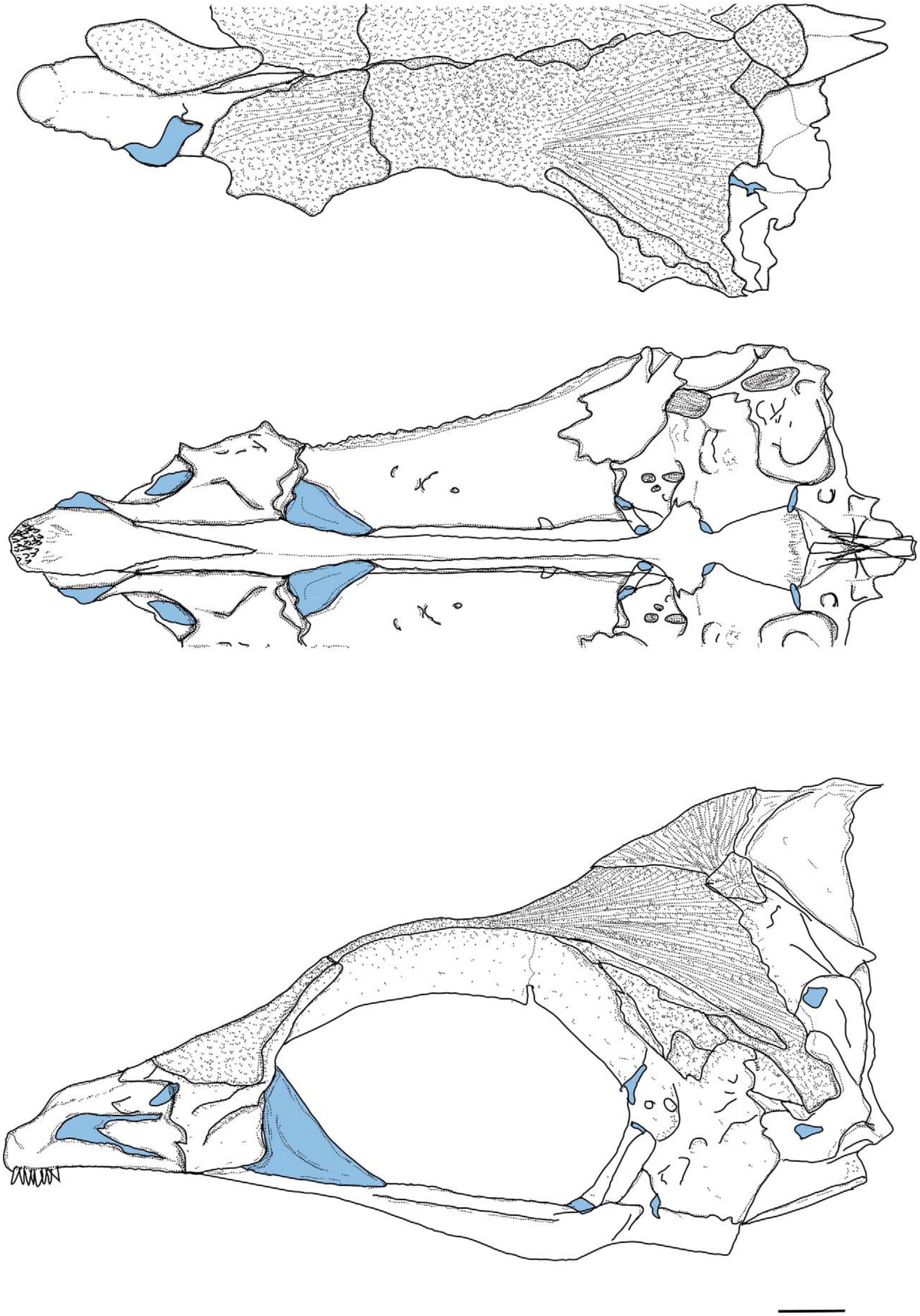

FIGURE 12. Neurocranium of *Pentaceros quinquespinis* in the dorsal (upper), ventral (middle), and lateral (lower) aspects. Scale bar = 5 mm.

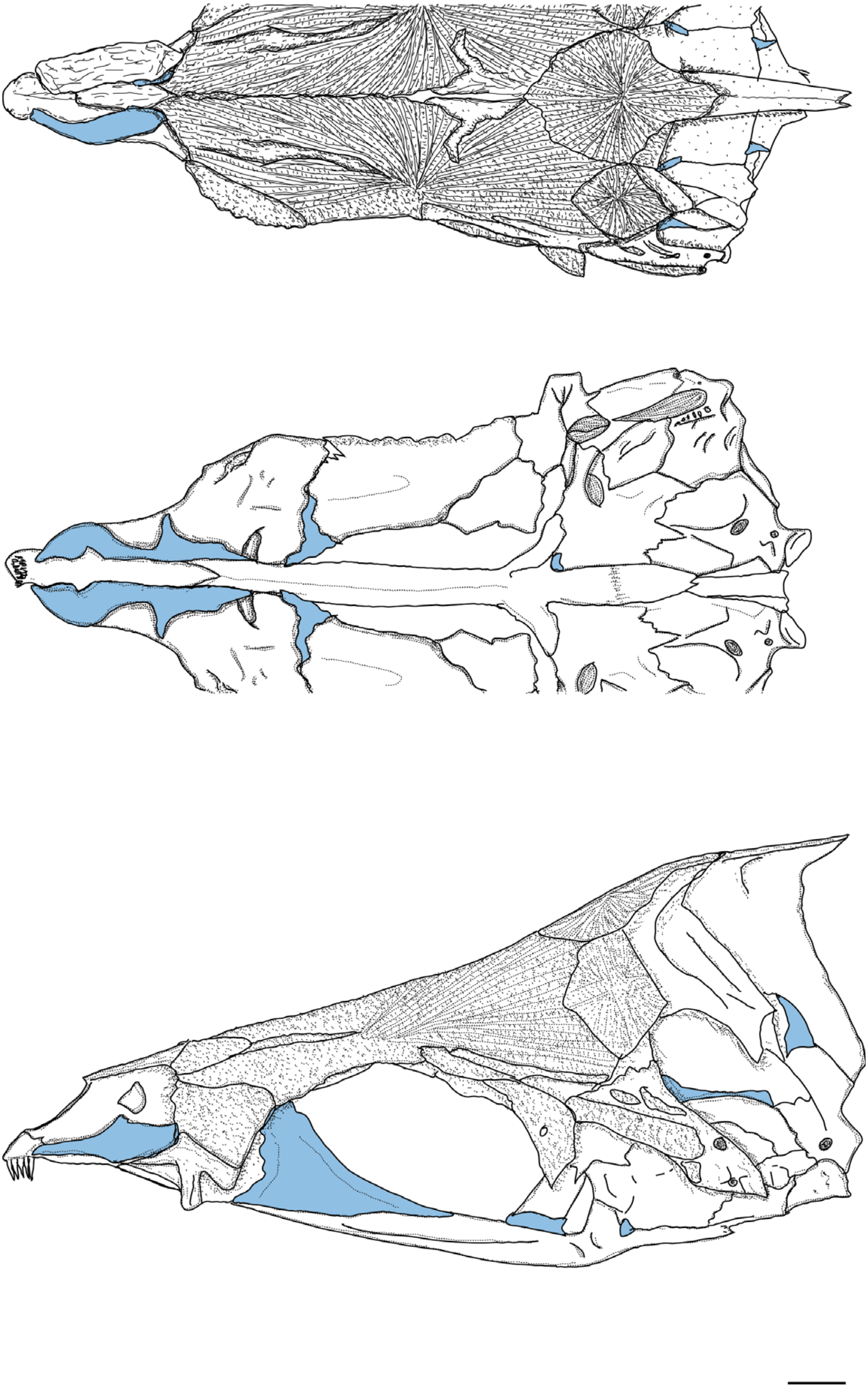

FIGURE 13. Neurocranium of *Pseudopentaceros wheeleri* in the dorsal (upper), ventral (middle), and lateral (lower) aspects. Scale bar = 5 mm.

The prootic is a square bone that forms the posteroventral region of the neurocranium. It is connected with the pterosphenoid anteriorly; the basisphenoid anteromedially; the basioccipital, exoccipital, and intercalar posteriorly; the sphenotic and pterotic dorsally; and the parasphenoid ventrally. The anteroventral region of this bone is connected to the first pharyngobranchial. This bone has two trigeminofacial chambers, located in the anterodorsal region of the bone, through which the trigeminal and facial nerves separately pass. These foramina are covered with a broad bridge. The prootic possesses an elongated socket for articulation with the cartilaginous condyle of the hyomandibula posterodorsally.

The pterotic comprises a pair of rectangular bones, situated on the dorsolateral region of the neurocranium. It is connected with the frontal and sphenotic bones anteriorly, the parietal and epioccipital bones medially, and the prootic and intercalar bones ventrally. The temporal sensory canal passes through the tubular structure of this bone, and continues in the supratemporal sensory canal posteriorly, the preoperculo-mandibular sensory canal laterally, and the frontal sensory canal anteriorly. It possesses a socket for articulation with the cartilaginous condyle of the hyomandibula anterodorsally.

The epiotic is a triangular bone located on the posterior margin of the neurocranium. This bone is attached to the parietal bone dorsally, the supraoccipital medially, the pterotic ventrally and the exoccipital posteriorly. This bone is also connected to the dorsal limb of the posttemporal.

The intercalar occupies the posterolateral region of the neurocranium. It connects with the prootic anteriorly, the pterotic laterally, and the exoccipital medially. The posteromedial region of the intercalar forms a facet for connection with the ventral limb of the posttemporal.

The supraoccipital forms the posteromedial roof of the neurocranium, and is connected with the frontal anteriorly, the parietal and epiotic laterally, and the exoccipital ventrally. The supraoccipital crest is well developed dorsally (high and stout). The posterior tip of the supraoccipital crest is forked and sandwiches the first supraneural bilaterally.

The exoccipital is situated on the posteromedial wall of the neurocranium. This bone is connected with the supraoccipital dorsally, the prootic anteriorly, the intercalar and pterotic dorsolaterally, and the basioccipital ventrally. It has a posterior condyle for articulation with the first vertebra.

The basioccipital lies on the posteroventral position of the neurocranium, and is connected with the exoccipital dorsally, the prootic anteriorly, and the parasphenoid ventrally. It has a posterior condyle for articulation with the first vertebra. This bone provides the origin of Baudelot’s ligament laterally.

Synapomorphies of Pentacerotidae

SA 2. Many exposed tubercles are present on the dorsal and lateral surfaces of the head (including frontal, supraoccipital and pterotic).

Many exposed tubercles are present on the dorsal and lateral surfaces of the head (including frontal, supraoccipital, and pterotic) in pentacerotids. The exposed tubercles are absent on the head in typical percoids (e.g., Gregory, 1933; Imamura, 1996; pers. obs.). The exposed tubercles are present in pentacerotids, and are therefore a synapomorphy.

SA 3. Supraoccipital crest high and stout.

The supraoccipital crest is low and thin in typical percoids (e.g., Gosline, 1985; Yabe, 1985; Sasaki, 1989; Tyler et al., 1989; pers. obs.), while the supraoccipital crest is high and stout in pentacerotids. This condition is a synapomorphy of the family.

Character recognition

TS 8. Connection between nasal and ethmoid. (0: loosely attached; 1: firmly attached)

Ingroup. The nasal bone is firmly attached to the ethmoid posteromedially in *Pentaceros* and *Pseudopentaceros* (character 8-1), whereas it is loosely attached to the ethmoid in the others (character 8-0).

Outgroup. The nasal bone is loosely attached to the ethmoid in typical percoids (character 8-0) (e.g., Tominaga, 1968; Sasaki, 1989; Imamura, 1996; pers. obs.).

TS 9. Exposed tubercles on the nasal, lateral ethmoid, and parietal bones. (0: absent; 1: present)

Ingroup. Many exposed tubercles are present on the lateral or dorsal surface of the nasal, lateral ethmoid, and parietal bones in all pentacerotids (character 9-1), except for *Paristiopterus* and *Pentaceropsis* (character 9-0).

Outgroup. These exposed tubercles are typically absent (character 9-0) in percoids (e.g., Gregory, 1933; Imamura, 1996; pers. obs.).

TS 10. Teeth on vomer. (0: present; 1: absent)

Ingroup. Teeth are present on the vomer in *Pentaceros* and *Pseudopentaceros* (character 10-0), whereas they are absent in other pentacerotids (character 10-1).

Outgroup. The vomerine teeth are typically present in percoids (character 10-0) (e.g., Katayama, 1959; Yabe, 1985; Prokofiev, 2007b; pers. obs.).

TS 11. Ethmoid projection. (0: sharp; 1: blunt)

Ingroup. The ethmoid projection is sharp in most pentacerotids (character 11-0), whereas it is blunt in *Pentaceropsis*, *Pentaceros*, and *Pseudopentaceros* (character 11-1).

Outgroup. The ethmoid projection is sharp in typical percoids (character 11-0) (e.g., Sasaki, 1989; Otero, 2004; pers. obs.).

TS 12. Ethmoid-maxillary ligament. (0: free from nasal; 1: connected with nasal)

Ingroup. The ethmoid-maxillary ligament is connected with the ventral surface of the nasal bone in *Pentaceros* and *Pseudopentaceros* (character 12-1), whereas it is free from the nasal bone in the others (character 12-0).

Outgroup. The ethmoid-maxillary ligament is typically free from the nasal bone in percoids (character 12-0) (e.g., Yabe, 1985; Shinohara, 1994; pers. obs.).

Other variations.

Exposed tubercles on the ethmoid. Exposed tubercles are absent on the ethmoid in most pentacerotids, as well as in typical percoids, (e.g., Gregory, 1933; Imamura, 1996; pers. obs.), while this bone has many exposed tubercles dorsally in *Pentaceros capensis*. Because the latter condition is an autapomorphy of *Pentaceros capensis*, however it is not used for the phylogenetic analysis.

1-3. Jaws

(Figs. 14–17)

Description

The jaws consist of the premaxilla and maxilla in the upper jaw, and the dentary, anguloarticular, retroarticular, and coronomeckelian in the lower jaw. A supramaxilla is absent. Cartilaginous elements, the rostral cartilage in the upper jaw, and Meckelian cartilages in the lower jaw are also present.

The premaxilla is an L-shaped bone situated on the anterior portion of the upper jaw region. This bone has three processes: a process formed by the ascending and articular processes, an alveolar process, and a postmaxillary process. The ascending and articular processes continue to form a common process lacking a distinct notch. This process is attached with the rostral cartilage medially. The rostral cartilage articulates with the ethmoid medially. The alveolar process has villiform teeth medially in all pentacerotids, whereas enlarged cylindrical teeth are also present in *Paristiopterus*. The triangular postmaxillary process is situated on the posterodorsal region of the premaxilla. This process is attached to the maxilla medially.

The maxilla is a rod-like bone situated on the posterodorsal of the premaxilla. This bone consists of a head bearing a lateral process, premaxillary and cranial condyles, and an enlarged shaft like posterior part with a small ventral process. The lateral process and premaxillary condyle is ventromedially directed and forms a deep groove. A long and slender ligament interconnects the lateral process and the anterior process of the ethmoid, and the other short ligament interconnects the lateral process and the anterior tip of the nasal bone. The cranial condyle extends dorsally. It articulates with the premaxillary condyle anteromedially and is connected with the vomer anterolaterally. The basal portion of the cranial condyle is connected with the anterior process of the palatine. The ventral process on the posteroventral portion of the maxilla is connected with the alveolar process of the premaxilla posteriorly. The ligamentum primordium is inserted onto the anterolateral surface of the shaft of the maxilla, and a tendon from the adductor mandibulae section 1 is inserted onto the posterior surface of the premaxillary condyle.

The dentary is a boomerang-shaped bone situated on the anterior margin of the lower jaw. It has villiform teeth dorsomedially in all pentacerotids, while it also has cylindrical teeth in *Paristiopterus*. This bone has a well-developed groove medially, onto which the adductor mandibulae section w is inserted. The preoperculo-mandibular sensory canal runs in the ventral tubular structure of this bone, and is continuous with the angular

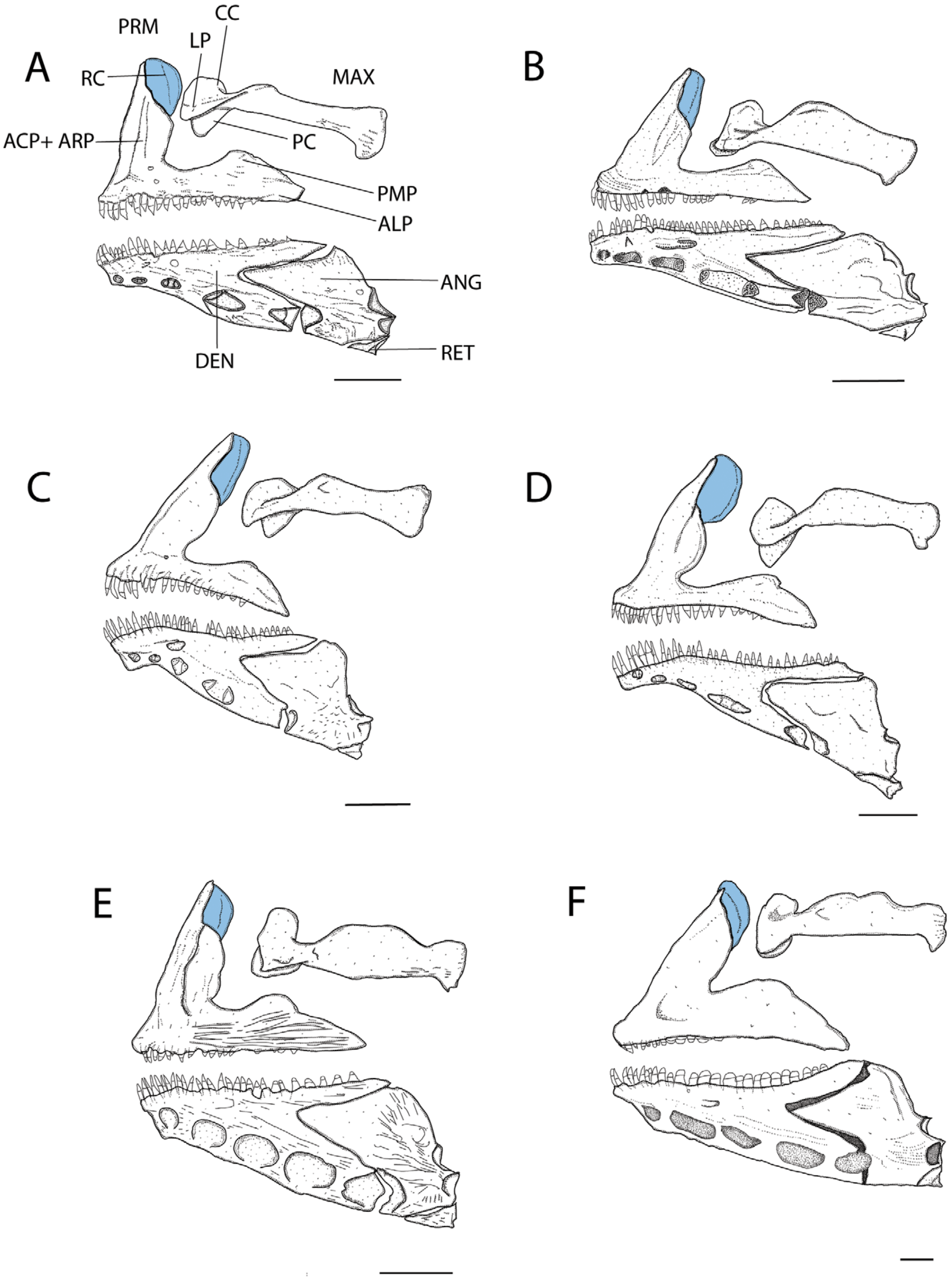

FIGURE 14. Lateral aspects of jaws. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*. B and E are shown as mirror images. Scale bar = 5 mm.

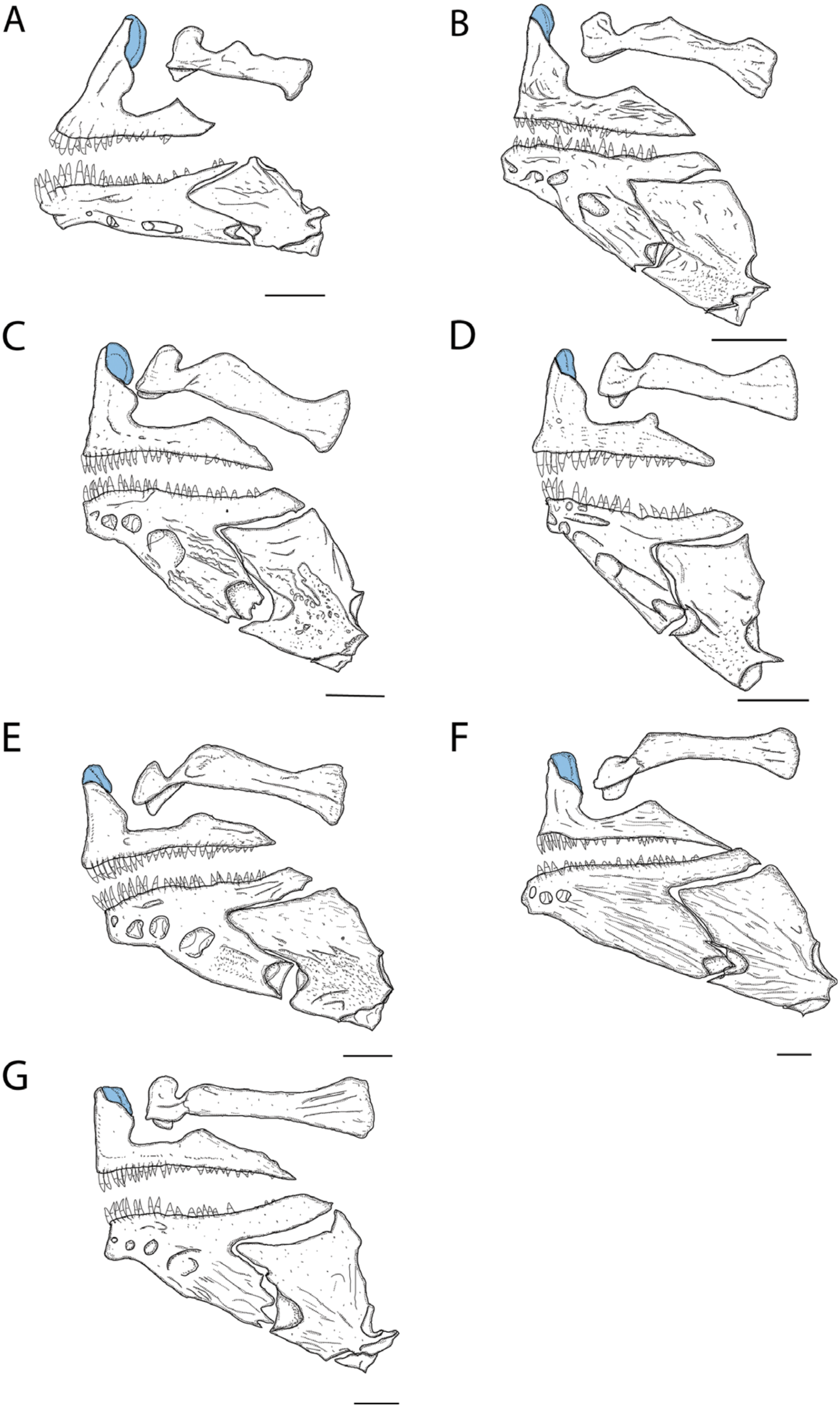

FIGURE 15. Lateral aspects of the jaws. A, *Pentaceropsis recurvirostris*; B, *Pentaceros capensis*; C, *P. decacanthus*; D, *P. japonicus*; E, *P. quinquespinis*; F, *Pseudopentaceros richardsoni*; G, *P. wheeleri*. A to C and F are shown as mirror images. Scale bar = 5 mm.

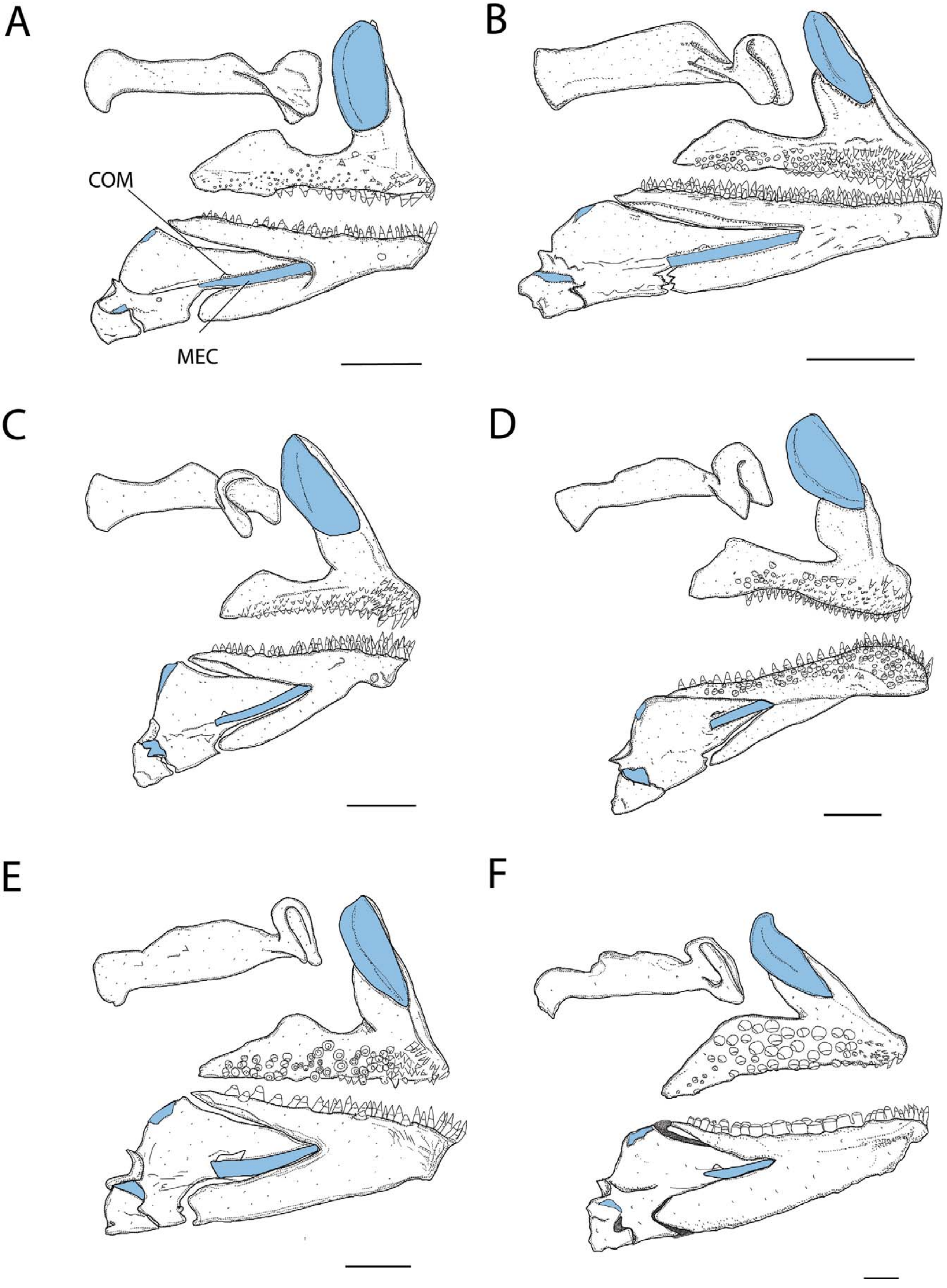

FIGURE 16. Medial aspects of the jaws. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*. B and E are shown as mirror images. Scale bar = 5 mm.

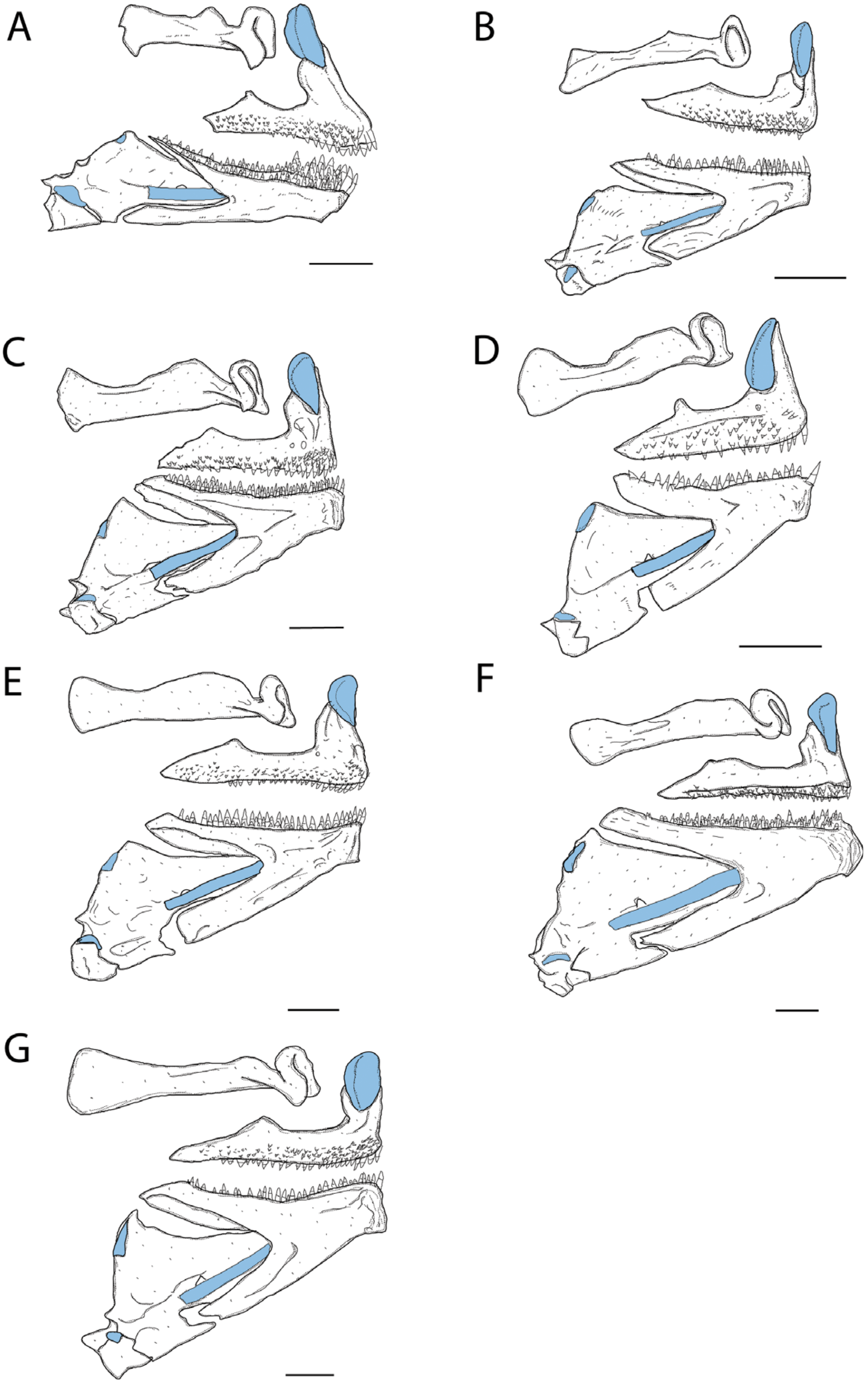

FIGURE 17. Medial aspects of the jaws. A, *Pentaceropsis recurvirostris*; B, *Pentaceros capensis*; C, *P. decacanthus*; D, *P. japonicus*; E, *P. quinquespinis*; F, *Pseudopentaceros richardsoni*; G, *P. wheeleri*. A to C and F are shown as mirror images. Scale bar = 5 mm.

posteriorly. Four large pores are present on the lateral surface of this tubular structure. The dentary is connected with the anguloarticular posteriorly and the Meckelian cartilage medially. Many exposed tubercles are present on the lateral surface of the dentary in *Pentaceros* and *Pseudopentaceros*, whereas they are absent in the others.

The anguloarticular is a wedge-shape bone that occupies the posterior region of the lower jaw. The anterior projection of this bone is inserted into the deep notch of the dentary. This bone has a glenoid cavity dorsolaterally for articulation with the quadrate. The margin of this glenoid cavity has a developed edge. The preoperculo-mandibular sensory canal runs in the tubular structure of this bone ventromedially. The anguloarticular bone is attached to the retroarticular ventrally. Many exposed tubercles are present on the lateral surface of the anguloarticular in *Pentaceros* and *Pseudopentaceros*, whereas they are absent in the others.

The retroarticular forms the posteroventral corner of the lower jaw. It is connected with the anguloarticular posteromedially and has a strong ligamentous connection with the interopercle.

The Meckelian cartilage is a slender rod-like bone, lying on the medial surface of the lower jaw. A tendon extending from the adductor mandibulae section 3 inserts below this bone.

The coronomeckelian is a tiny bone situated between the anguloarticular bone and the Meckelian cartilage. A tendon extending from the adductor mandibulae section 2 inserts into this bone.

Synapomorphies of Pentacerotidae

SA 4. Ascending and articular processes continuous.

The ascending and articular processes continue to form a common process lacking a distinct notch in pentacerotids. A notch between the ascending process and cranial condyle is present in typical percoids (e.g., Fraser, 1968; Tominaga, 1968; Sasaki, 1989; Imamura, 1996; pers. obs.). The lack of the notch is considered a synapomorphy.

SA 5. Supramaxilla absent.

The supramaxilla is primitively present in percoids (e.g., Tominaga, 1968; Baldwin and Johnson, 1993; Kim, 2002; pers. obs.), and the absence of such supramaxilla is regarded as an apomorphy. The supramaxilla is absent in pentacerotids.

SA 6. Distal ends of premaxilla and maxilla articurate.

The distal ends of the premaxillary and maxillary bones have a specialized articulation in pentacerotids. In most typical percoids, the distal ends of the premaxilla and maxilla are not articulated (e.g., Sasaki, 1989; Kim, 2002; pers. obs.). Thus, the former condition can be regarded as a synapomorphy.

Character recognition

TS 13. Exposed tubercles on dentary and anguloarticular bones. (0: absent; 1: present)

Ingroup. Many exposed tubercles are present on the lateral surface of the dentary and anguloarticular bones in *Pentaceros* and *Pseudopentaceros* (character 13-1), whereas they are absent in the others (character 13-0).

Outgroup. The exposed tubercles are typically absent on the dentary and anguloarticular in percoids (character 13-0) (e.g., Gregory, 1933; Fraser, 1972; Imamura, 1996; pers. obs.).

TS 14. Teeth on jaws. (0: villiform; 1: villiform and enlarged cylindrical)

Ingroup. Villiform teeth are present in both jaws in most pentacerotids (character 14-0), whereas the jaws also have enlarged cylindrical teeth in *Paristiopterus* (character 14-1).

Outgroup. The jaws only have villiform and/or small conical teeth in typical percoids (character 14-0) (e.g., Tominaga, 1968; Sasaki, 1989; pers. obs.).

1-4. Suspensorium and opercular bones

(Figs. 18–21)

Description

The suspensorium consists of seven elements: the palatine, ectopterygoid, endopterygoid, metapterygoid, quadrate, symplectic, and hyomandibular. The opercular consists of four elements; the preopercle, opercle, interopercle, and subopercle.

The palatine is a stick-like bone situated on the anterior portion of the suspensorium. It possesses a cartilaginous cap anteriorly. The anterior portion of the palatine extends and articulates with the head region of the maxilla anteroventrally. It has a well-developed socket for articulation with the ethmoid cartilage anterodorsally. The palatine also articulates with the lateral ethmoid posterodorsally and is connected with the endopterygoid and ectopterygoid posteriorly. A large facet, articulating with the head of the lateral ethmoid, is present on the middle part of the palatine in *Paristiopterus labiosus* and *P. gallipavo* (Figs. 18E, F), while it is absent in the others. The palatine lacks teeth.

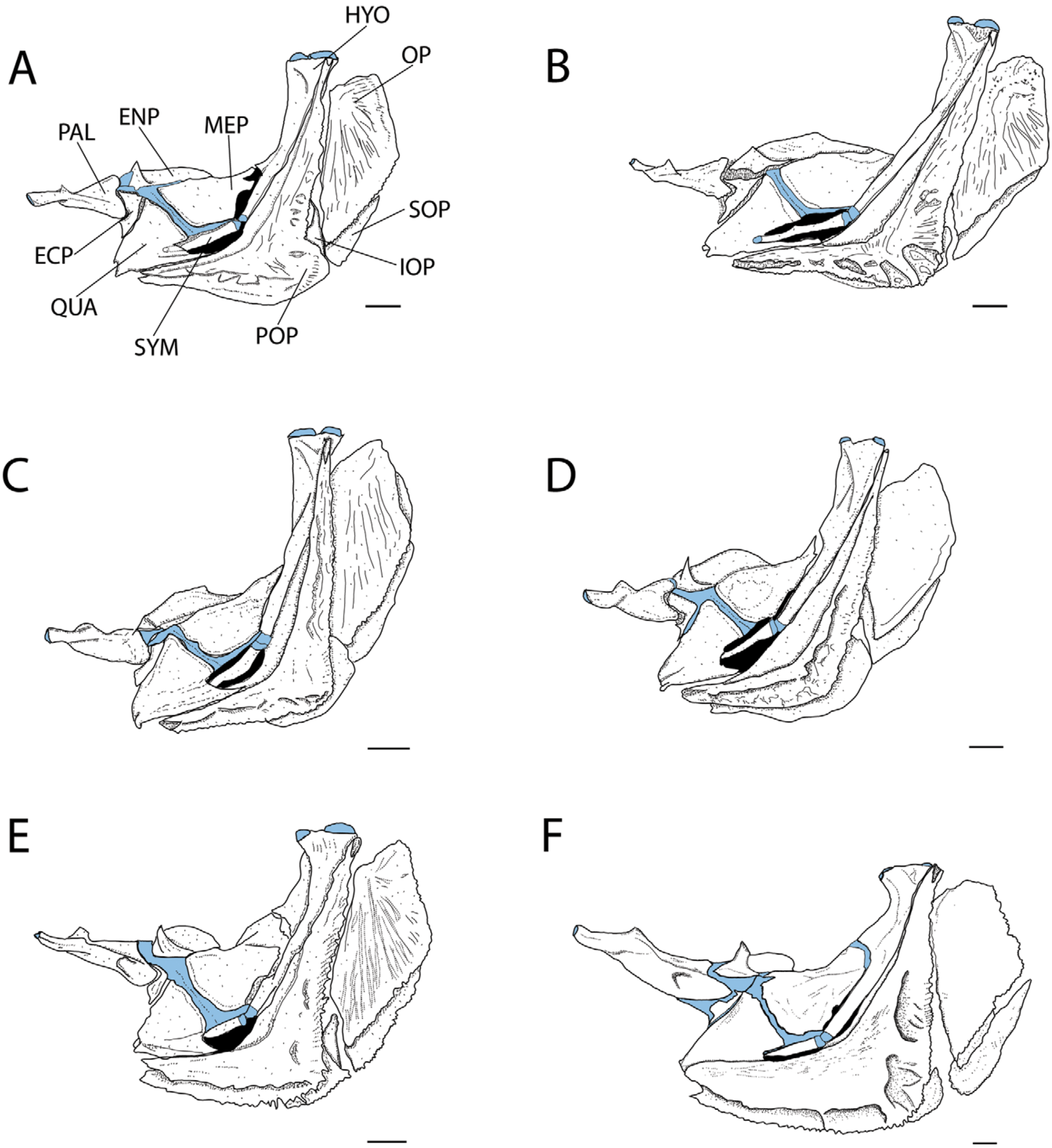

FIGURE 18. Lateral aspects of the suspensorium and opercular bones. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*. B and E are shown as mirror images. Scale bar = 5 mm.

The ectopterygoid is a small boomerang-shaped or triangular bone. This bone is connected with the endopterygoid via a narrow cartilage dorsally and with the palatine anteriorly. A short triangular extension from the posteroventral portion of this bone runs along the anterior edge of the quadrate.

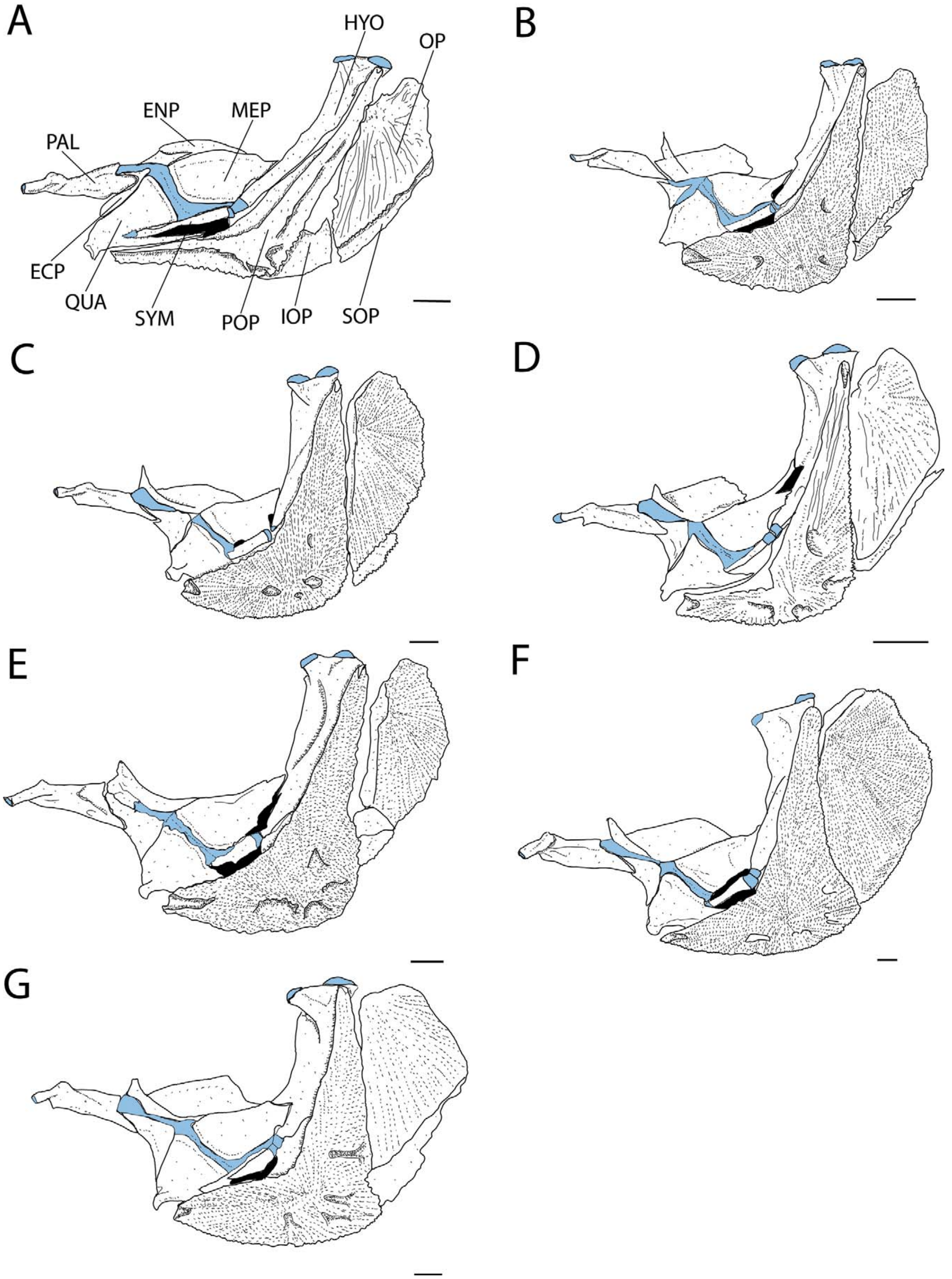

FIGURE 19. Lateral aspects of the suspensorium and opercular bones. A. *Pentaceropsis recurvirostris*; B, *Pentaceros capensis*; C, *P. decacanthus*; D, *P. japonicus*; E, *P. quinquespinis*; F, *Pseudopentaceros richardsoni*; G. *P. wheeleri*. A to C and E are shown as mirror images. Scale bar = 5 mm.

The endopterygoid is a thin oval bone situated below the orbit, and has a strong projection anterodorsally, which articulates with the lateral ethmoid. The bone is connected with the palatine anterodorsally and the metapterygoid posteroventrally.

The metapterygoid is a fan-shaped bone attached to the quadrate and sympletic via a narrow cartilaginous band anteroventrally and ventrally, respectively. It possesses a laminar process, the metapterygoid lamina, dorsolaterally. The bone is connected to the anteroventral part of the hyomandibula and posterior pointed tip of the endopterygoid. The metapterygoid has an ascending process posterodorsally, forming a space where the lateral part of the levator arcus palatini inserts with hyomandibula.

The quadrate is a triangular bone situated on the ventral region of the suspensorium. This bone is connected with the ectopterygoid anteriorly, the metapterygoid dorsally, the preopercle posteriorly, and the symplectic medially. This bone has a condyle for articulation with the anguloarticular anteroventrally.

The symplectic is a stick-like bone. It overlaps with the quadrate anterolaterally and connected to the metapterygoid by a narrow cartilage dorsally. The symplectic has a cartilaginous cap on its anterior tip and a cartilaginous socket posteriorly for articulation with the interhyal.

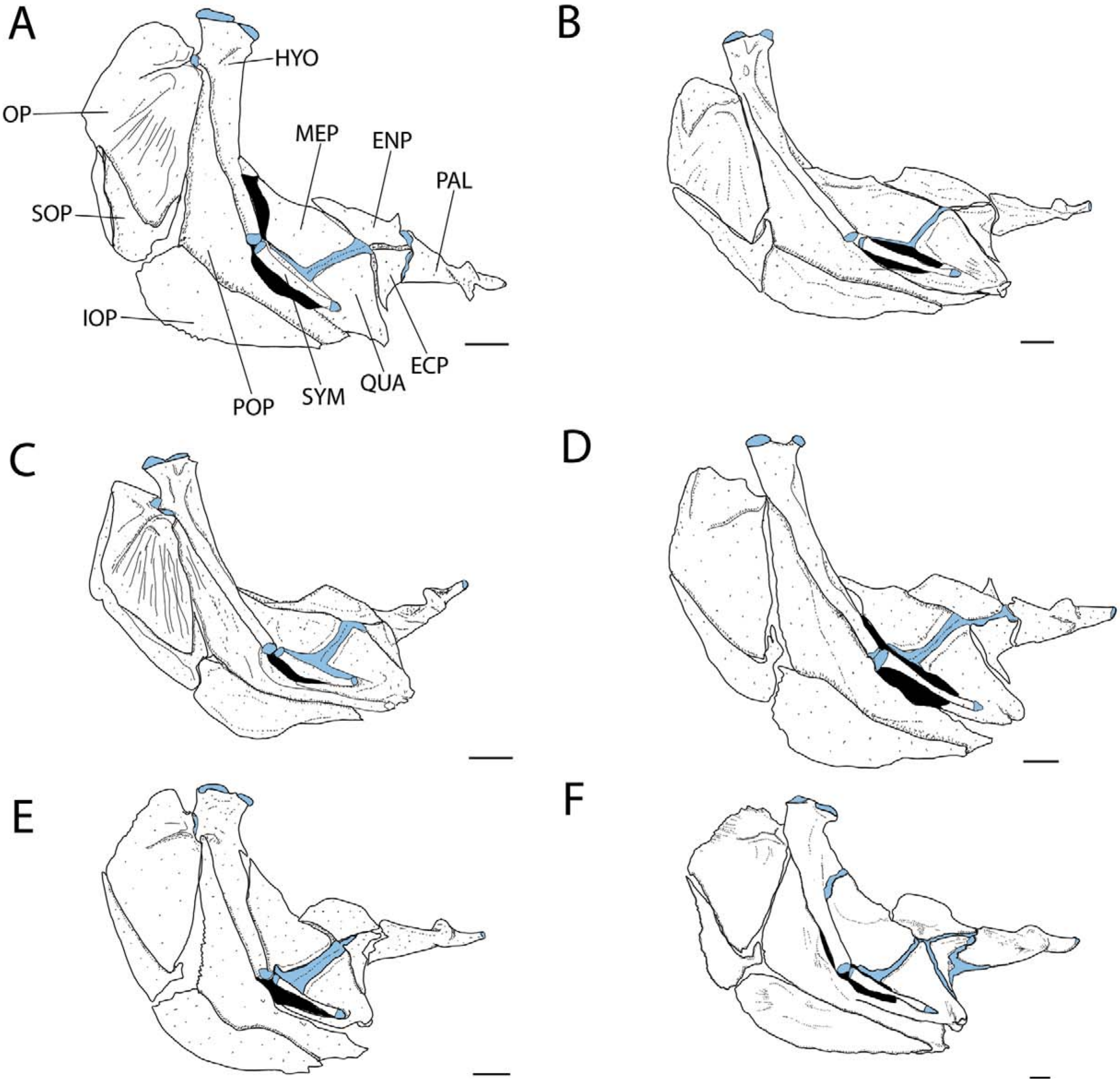

FIGURE 20. Medial aspects of the suspensorium and opercular bones. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*. B and E are shown as mirror images. Scale bar = 5 mm.

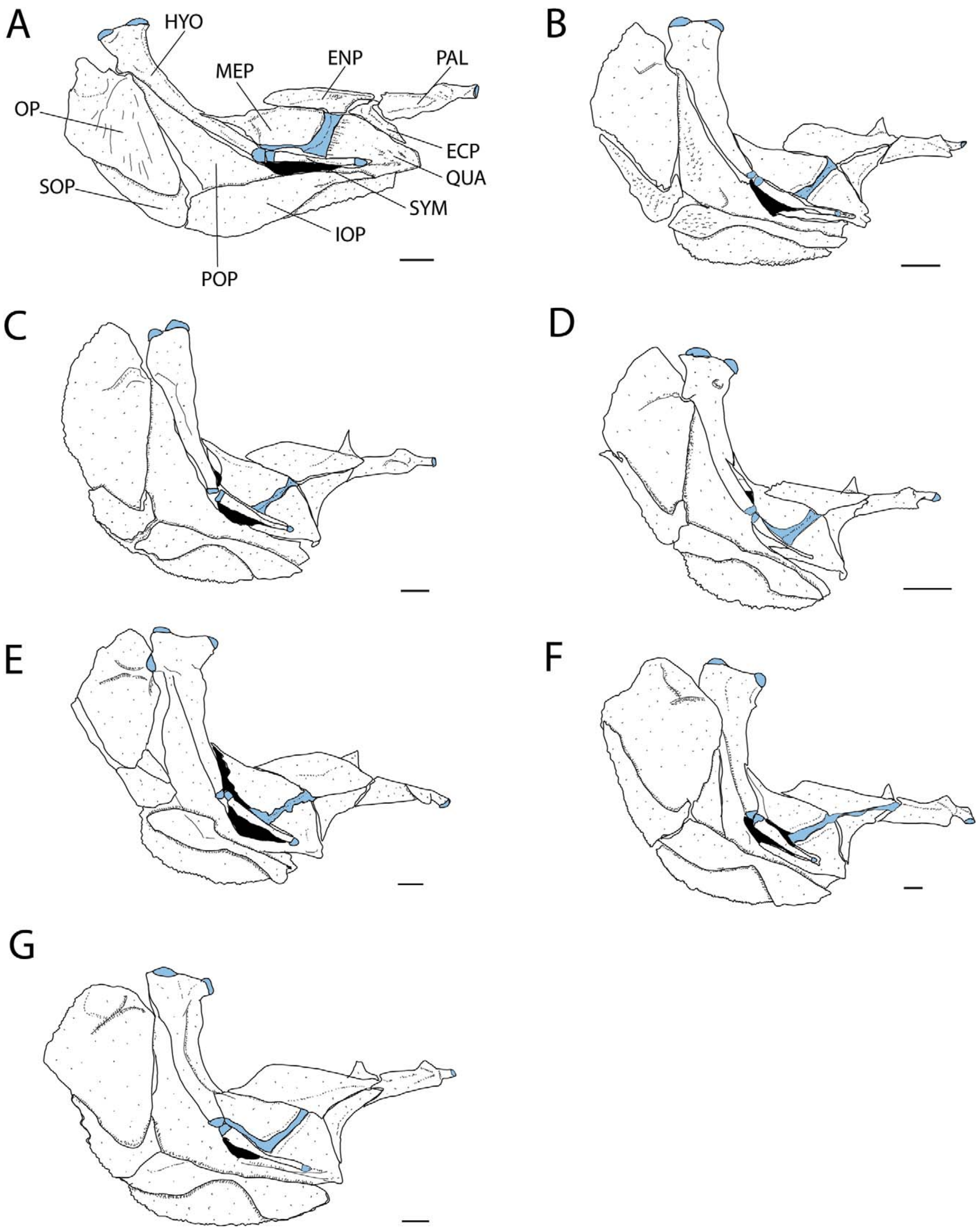

FIGURE 21. Medial aspects of the suspensorium and opercular bones. A. *Pentaceropsis recurvirostris*; B, *Pentaceros capensis*; C, *P. decacanthus*; D, *P. japonicus*; E, *P. quinquespinis*; F, *Pseudopentaceros richardsoni*; G. *P. wheeleri*. A to C and F are shown as mirror images. Scale bar = 5mm.

The hyomandibula is situated on the posterodorsal region of the suspensorium and forms a long shaft ventrally. A low ridge, serving as the levator arcus palatini and a tendon from the third infraorbital, is present along the shaft on the ventral portion of the hyomandibula. The hyomandibula has two dorsal condyles articulating with a facet formed by the prootic and sphenotic, and a facet formed by the pterotic, and has a posterodorsal condyle articulating with a facet on the anterodorsal corner of the opercle. It is sutured to the metapterygoid anteroventrally and is firmly attached to the preopercle posteriorly. It is also attached to the symplectic and interhyal ventromedially.

The preopercle is a crescent-shaped bone that has a supporting structure for the preoperculo-mandibular sensory canal. The canal is continuous with that of the anguloarticular anteroventrally and that of the pterotic dorsally. The sensory canal runs along a series of grooves and is partly covered by narrow bony bridges in *Histiopterus typus*, *Zanclistius elevatus*, *Evistias acutirostris*, *Parazanclistius hutchinsi*, *Paristiopterus labiosus*, *P. gallipavo*, and *Pentaceropsis recurvirostris*, whereas it penetrates a series of tubular structures with some openings in *Pentaceros capensis, P, decacanthus, P. japonicus*, *P. quinquespinis*, *Pseudopentaceros richardsoni*, and *P. wheeleri*. It is attached to the hyomandibula and quadrate anteriorly, and the opercle, subopercle, and interopercle posteriorly. This bone has a serrated posterior margin, but no preopercular spines. Many exposed tubercles are present on the lateral surface of the preopercle in all pentacerotids, except for *Paristiopterus gallipavo*.

The opercle is a thick, bow-shaped bone that articulates with the hyomandibular anteriorly. This bone overlaps with the subopercle ventromedially. Spines are absent in this bone. Many exposed tubercles are present on the lateral surface of the opercle in all pentacerotids, except for *Parazanclistius* and *Paristiopterus gallipavo* in which they are lacking.

The subopercle is a crescent-shaped bone situated on the posterior portion of the opercular region. It is attached to the opercle ventrally, the anteroventral margin of the preopercle anteriorly, and the interopercle anterolaterally. The ventral portion of the subopercle is unossified.

The interopercle is an elongated bone situated medial to the ventral portion of the preopercle. The interopercle is thick in all pentacerotids, except for *Pentaceros* and *Pseudopentaceros* in which it is thin. It is connected with the retroarticular anteriorly via a strong ligament. The ventral margin of the interopercle is weakly expanded in *Histiopterus*, *Zanclistius*, *Paristiopterus*, and *Pentaceropsis*, while it is concave in *Pentaceros* and *Pseudopentaceros*.

Synapomorphies of Pentacerotidae

SA 7. Palatine teeth are absent.

The palatine teeth are present in most typical percoids (e.g., Johnson, 1980; Kim, 2002; Imamura, 2004; Otero, 2004; pers. obs.), whereas the palatine teeth are absent in pentacerotids; therefore, this condition is a synapomorphy.

SA 8. Endopterygoid articulating with the lateral ethmoid.

The endopterygoid articulates with the lateral ethmoid in all pentacerotids. This condition is a synapomorphy, because in the typical percoids the palatine usually articulates with the lateral ethmoid, and not the endopterygoid (e.g., Gosline, 1984; Sasaki, 1989; Kim, 2002; pers. obs.).

Character recognition

TS 15. Facets on the palatine. (0: absent; 1: present)

Ingroup. A large facet for articulation with the head of the lateral ethmoid is present on the middle part of the palatine in *Paristiopterus labiosus* and *P. gallipavo* (character 15-1), while it is absent in the others (character 15-0).

Outgroup. A facet is absent on the middle part of the palatine in typical percoids (character 15-0) (e.g., Sasaki, 1989; Kim, 2002; pers. obs.).

TS 16. Sensory canal on the preopercle. (0: covered by narrow bridges; 1: covered by wide bridges)

Ingroup. The preopercular sensory canal runs through a series of grooves partly covered by narrow bony bridges on the lateral side of preopercle in *Histiopterus*, *Zanclistius*, *Evistias*, *Parazanclistius*, *Paristiopterus*, and *Pentaceropsis* (character 16-0), whereas it penetrates a tubular structure of the preopercle in *Pentaceros* and *Pseudopentaceros* (character 16-1).

Outgroup. The preopercle sensory canal runs through a groove-like structure of the preopercle partly covered by narrow bridges (character 16-0) in typical percoids (e.g., Westneat, 1993; Otero, 2004; Prokofiev, 2007a: pers. obs.).

TS 17. Exposed tubercles on opercle. (0: absent; 1: present)

Ingroup. Many exposed tubercles are present on the lateral surface of the opercle in all pentacerotids (character 17-1), except for *Parazanclistius* and *Paristiopterus gallipavo* (character 17-0).

Outgroup. The tubercles on the opercle are typically absent (character 17-0) in percoids (e.g., Gregory, 1933; Imamura, 1996; pers. obs.).

TS 18. Interopercle. (0: thick; 1: thin)

Ingroup. The interopercle is thick in all pentacerotids (character 18-0), except for *Pentaceros* and *Pseudopentaceros* in which it is thin (character 18-1).

Outgroup. The interopercle is thick in typical percoids (character 18-0) (e.g., Gregory, 1933; Johnson, 1980; Gill and Mooi, 1993; pers. obs.).

TS 19. Ventral margin of interopercle. (0: expand; 1: concaved)

Ingroup. The ventral margin of the interopercle is weakly expanded in *Histiopterus*, *Zanclistius*, *Evistias*, *Paristiopterus*, and *Pentaceropsis* (character 19-0), while it is concave in *Pentaceros* and *Pseudopentaceros* (character 19-1).

Outgroup. The ventral margin of the interopercle is expanded in typical percoids (character 19-0) (e.g., Carnevale, 2006; Prokofiev, 2007a; pers. obs.).

Other variations.

None.

1-5. Hyoid arch

(Figs. 22–28)

Description

The hyoid arch, situated on the ventrolateral portion of the head, consists of the hypohyals, ceratohyal, epihyal, interhyal, branchiostegal rays, urohyal, and basihyal.

The hypohyals comprise two (dorsal and ventral) elements. The dorsal hypohyal is a triangular bone located on the anterodorsal portion of the hyoid arch. This bone is connected to the ventral hypohyal anteroventrally and the ceratohyal posteriorly by a cartilaginous intervention. The ventral hypohyal is a rectangular bone situated on the anteroventral portion of the hyoid arch. This bone is connected to the dorsal hypohyal dorsally and the ceratohyal posteriorly by a cartilaginous intervention.

The ceratohyal is a large, flattened bone situated in the middle portion of the hyoid arch. This bone is connected to the hypohyals anteriorly and the epihyal posteriorly by the cartilaginous intervention. This bone suspends four or five branchiostegal rays ventrally. The ceratohyal has a large beryciform foramen dorsally. The dorsal margin of this bone is covered with narrow cartilage, which is continuous with the cartilage between the ceratohyal and epihyal.

The epihyal is a triangular bone located on the posterior part of the hyoid arch. This bone attaches to the ceratohyal by the cartilaginous intervention. This bone suspends two branchiostegal rays ventrolaterally. The posterior corner of the epihyal articulates with the interhyal dorsally.

The interhyal is a short and rod-like bone that interconnects the hyoid arch and suspensorium. It possesses a cartilaginous cap dorsally and ventrally. The interhyal articulates with the epihyal ventrally and with a cartilaginous socket surrounded by the hyomandibular, symplectic, and preopercle dorsally.

The branchiostegal rays, long and slender elements, are situated on the ventral region of the hyoid arch. There are seven branchiostegal rays in all pentacerotids, except for *Pseudopentaceros wheeleri*, which has seven or eight. The anterior three rays are supported by the anteromedial region of the ceratohyal, the middle two by the posterolateral region of the ceratohyal, and the posterior two by the lateral region of the epihyal ventrally.

The urohyal (Fig. 27) is a thin plate-like bone, lying on the midline below the basibranchials. This bone connects with the ventral hypohyals on both sides by strong ligaments anteriorly. It attaches to the first basibranchial dorsally.

The basihyal (Fig. 28) is a simple rod-like bone situated on the anterior tip of the hyoid arch. This bone has a cartilaginous cap anteriorly and is connected with the first basibranchial by a strong ligament posteroventrally.

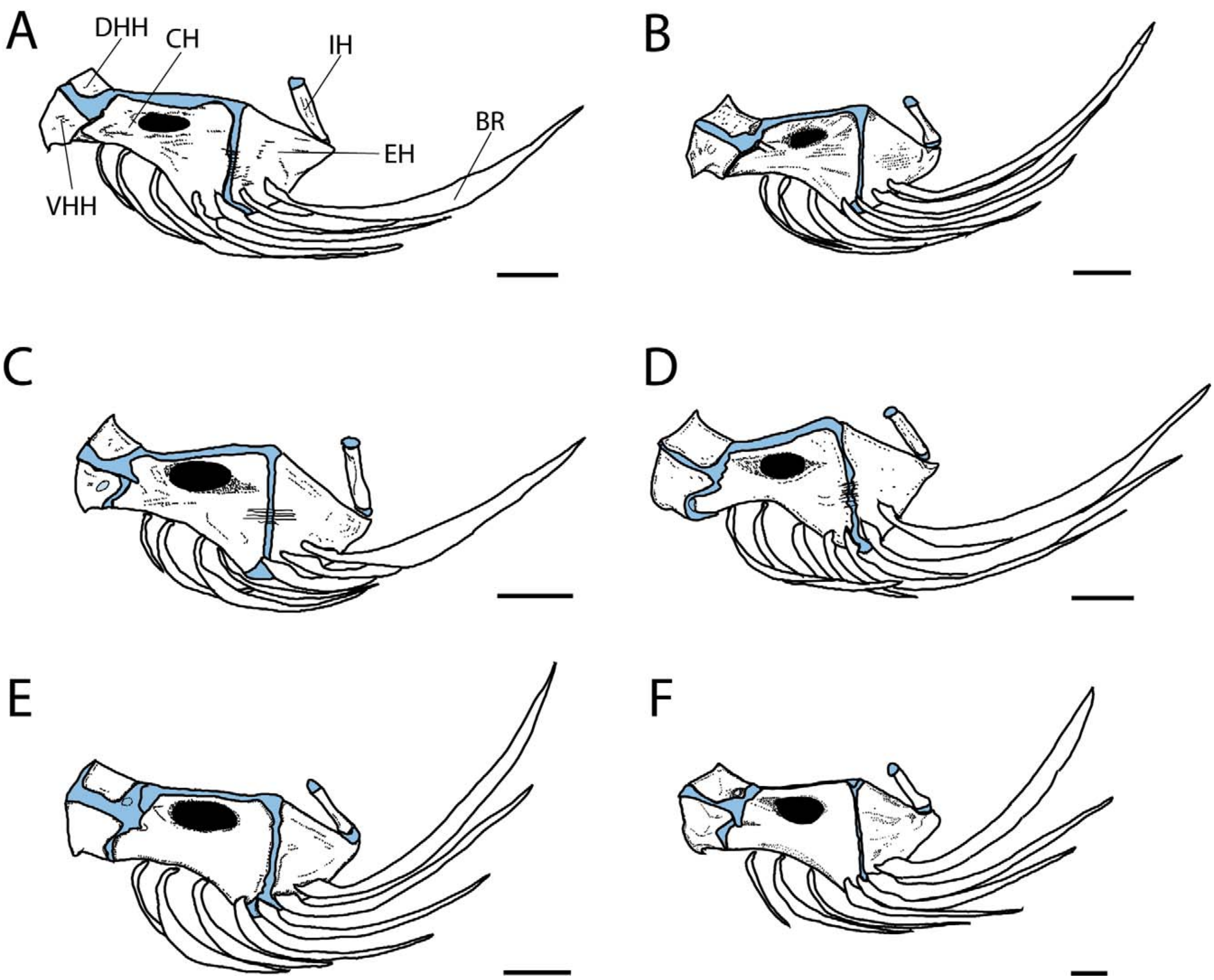

FIGURE 22. Lateral aspects of the hyoid arch. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*. B and E are shown as mirror images. Scale bar = 5 mm.

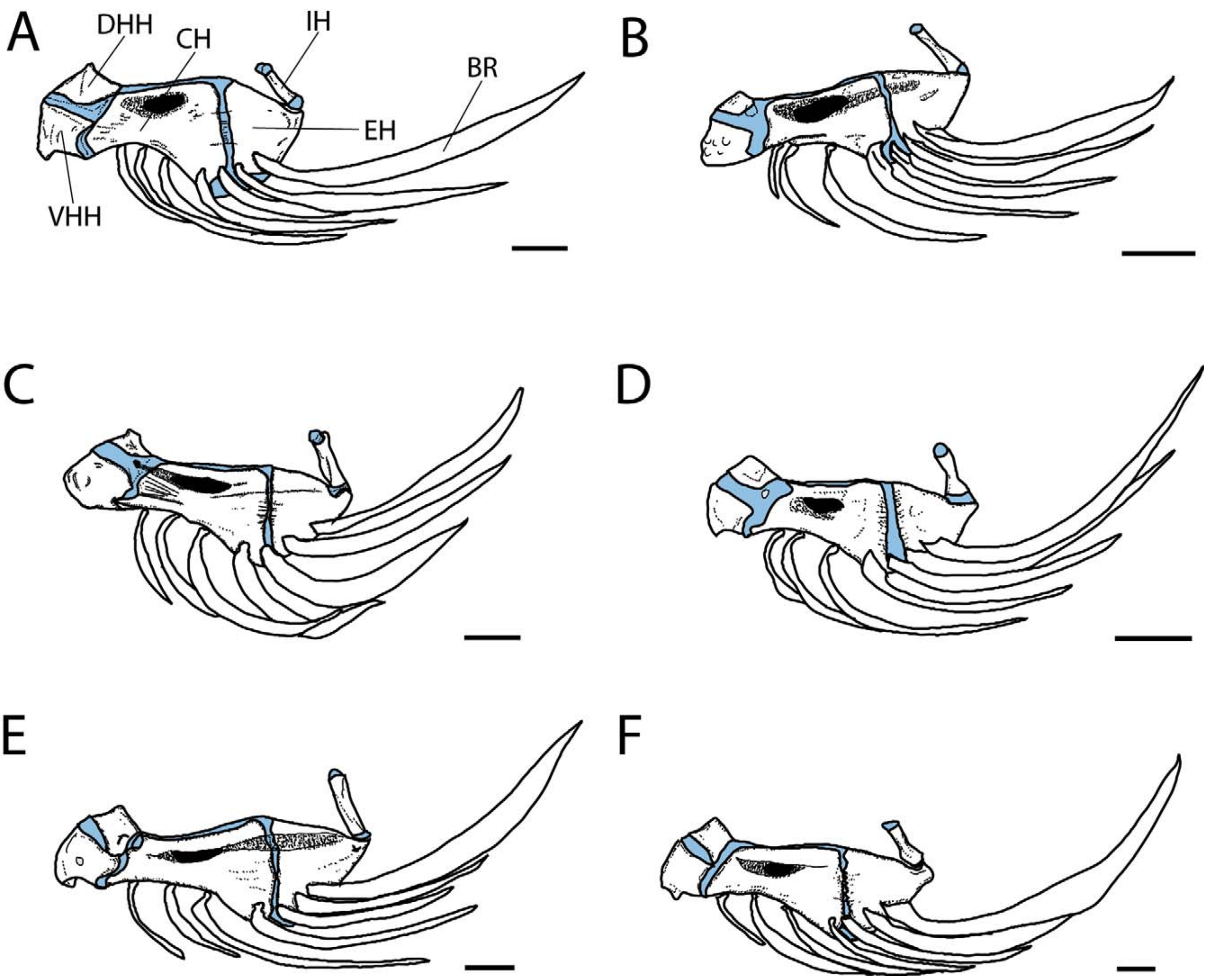

FIGURE 23. Lateral aspects of the hyoid arch. A, *Pentaceropsis recurvirostris*; B, *Pentaceros capensis*; C, *P. decacanthus*; D, *P. japonicus*; E, *P. quinquespinis*; F, *Pseudopentaceros richardsoni*. A to C and F are shown as mirror images. Scales bar = 5 mm.

Synapomorphies of Pentacerotidae

None.

Character recognition

No variations were recognized that were useful for the phylogenetic analysis.

Other variations

Eight branchiostegal rays (Fig. 26). There are seven branchiostegal rays in all pentacerotids, as well as in typical percoids (e.g., McAllister, 1968; Johnson, 1984), except for one species (*Pseudopentaceros wheeleri* HUMZ 147629, Fig. 26A), which has eight. Therefore, the eight-ray condition is considered a derived character. This variation is intraspecific in one species, however, and has no effect on reconstruction of the phylogenetic relationships. Accordingly, the variation is not included in the analysis.

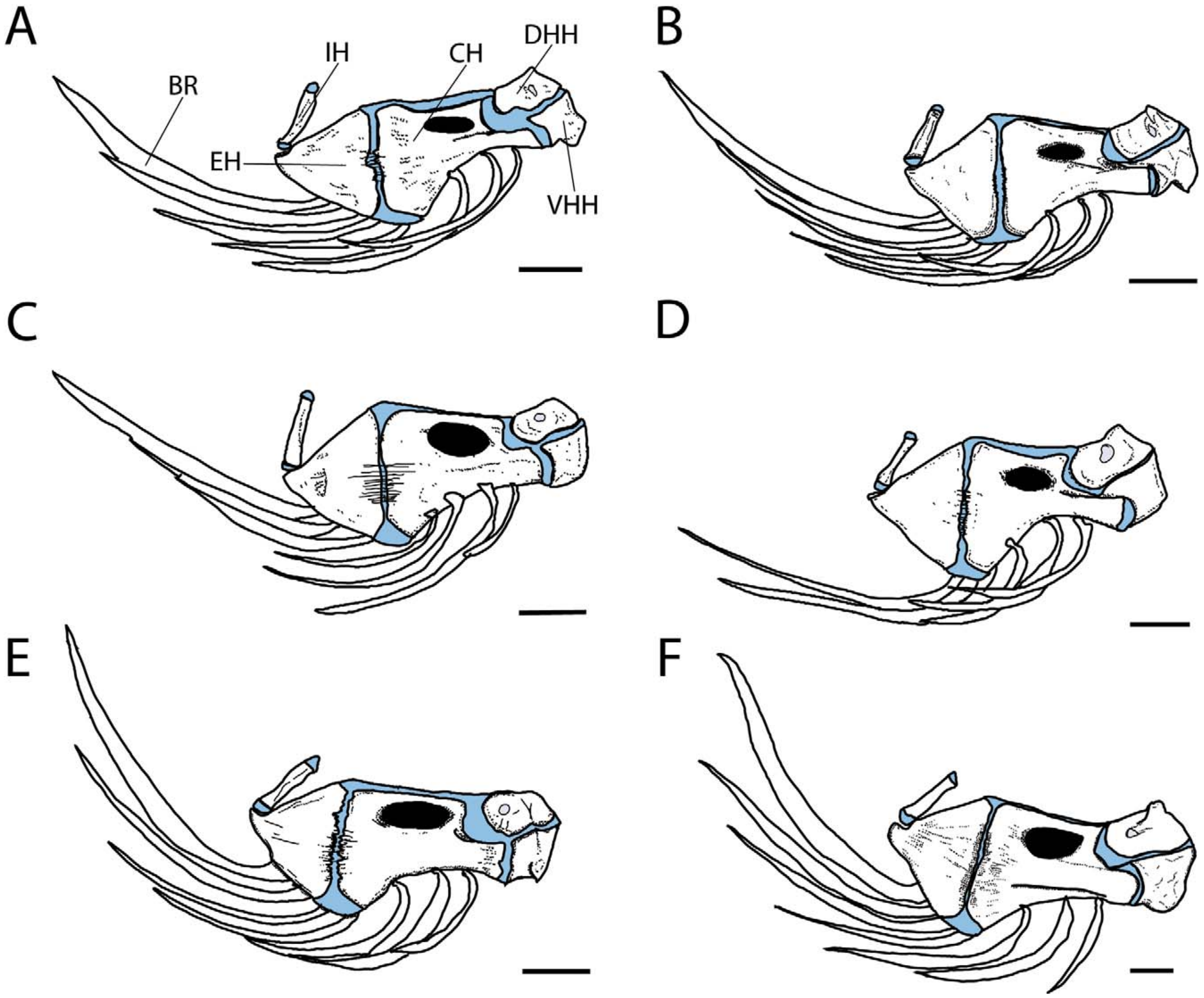

FIGURE 24. Medial aspects of the hyoid arch. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*. B and E are shown as mirror images. Scale bar = 5 mm.

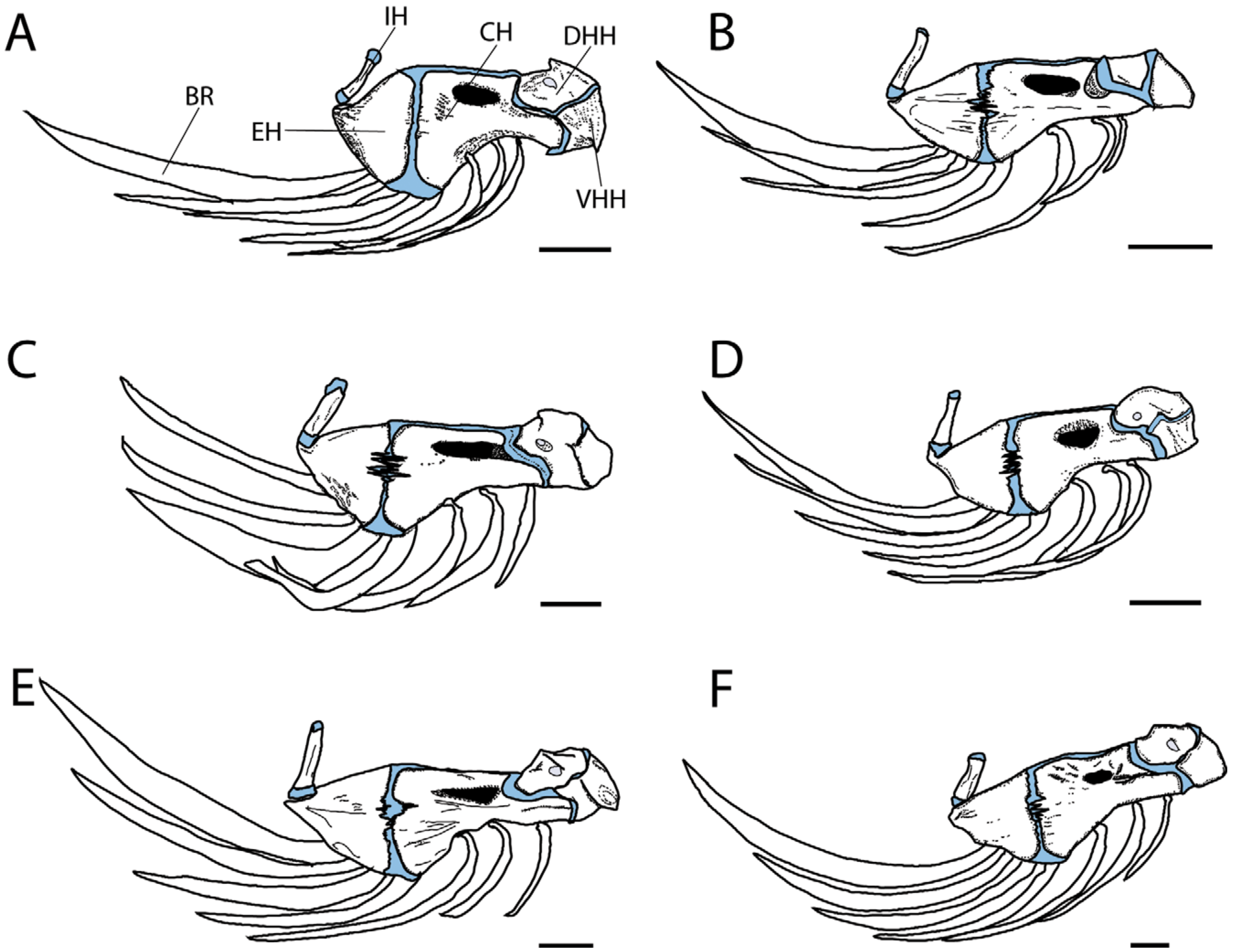

FIGURE 25. Medial aspects of the hyoid arch. A, *Pentaceropsis recurvirostris*; B, *Pentaceros capensis*; C, *P. decacanthus*; D, *P. japonicus*; E, *P. quinquespinis*; F, *Pseudopentaceros richardsoni*. A to C and F are shown as mirror images. Scale bar = 5 mm.

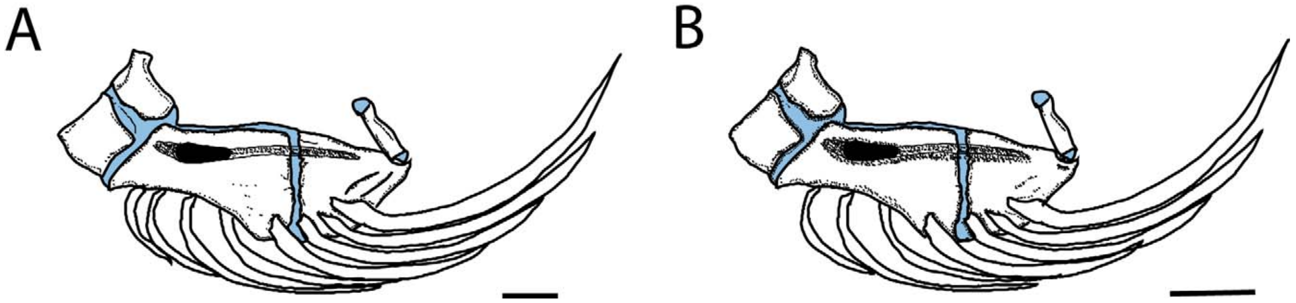

FIGURE 26. Lateral aspects of the hyoid arch in *Pseudopentaceros* HUMZ 147629; B, HUMZ 146164. Scale bar = 5 mm.

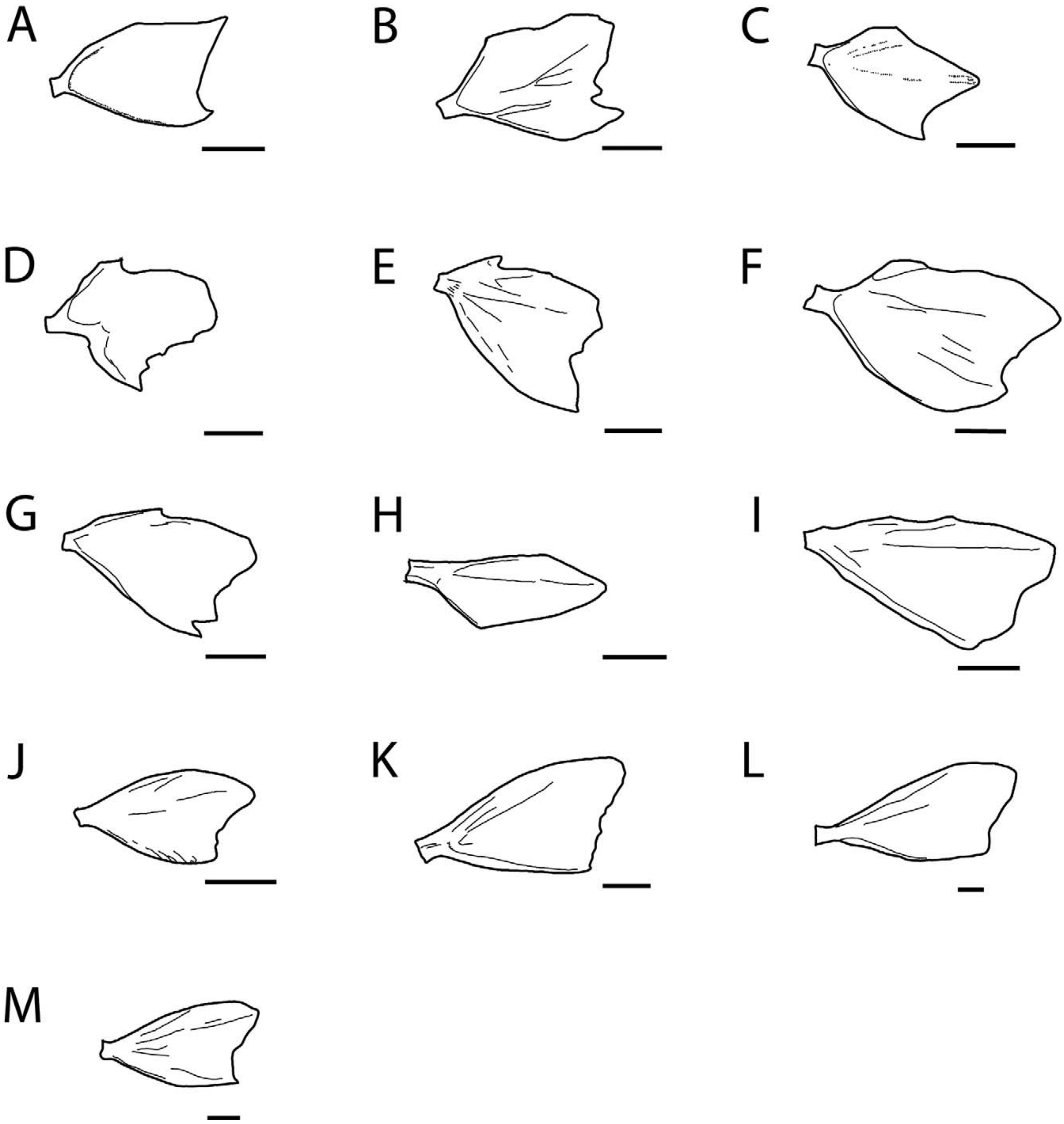

FIGURE 27. Lateral aspects of urohyal. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*; G, *Pentaceropsis recurvirostris*; H, *Pentaceros capensis*; I, *P. decacanthus*; J, *P. japonicus*; K, *P. quinquespinis*; L, *Pseudopentaceros richardsoni*; M, *P. wheeleri*. B, E, G, H, I, and L are shown as mirror images. Scale bar = 5 mm.

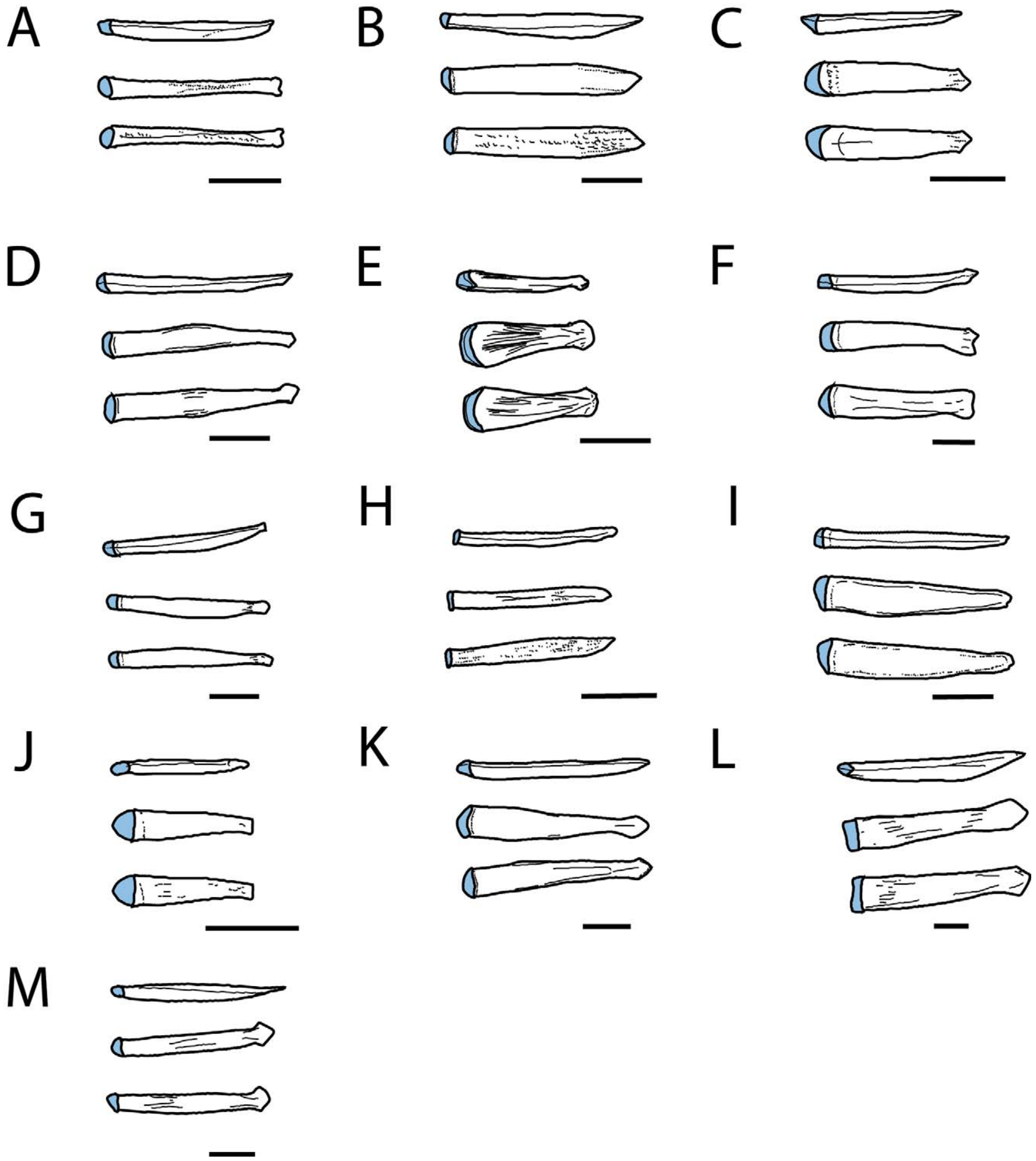

FIGURE 28. Lateral (top), dorsal (center) and ventral (bottom) aspects of basihyal. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*; G, *Pentaceropsis recurvirostris*; H, *Pentaceros capensis*; I, *P. decacanthus*; J, *P. japonicus*; K, *P. quinquespinis*; L, *Pseudopentaceros richardsoni*; M, *P. wheeleri*. B, E, G, H, I, and L are shown as mirror images. Scaale bar = 5 mm.

1-6. Branchial arch

(Figs. 29, 30)

Description

The branchial arch comprises two (lower and upper) elements. The lower element includes three medial basibranchials, three pairs of hypobranchials, and five pairs of ceratobranchials; the upper element contains four pairs of epibranchials, and four pairs of pharyngobranchials. A long interarcual cartilage is present between the first epibranchial and second pharyngobranchial.

The basibranchials are three plate-like bones and one central cartilage. These elements are situated on the midline of the oral floor. The first basibranchial is a pointed rod-like bone. This bone has a tiny cartilaginous cap anteriorly. It is connected with the basihyal via a strong ligament anterodorsally and with the second basibranchial posteriorly by a cartilaginous intervention. The second basibranchial is a rod-like bone situated between the first and third hypobranchials. The second basibranchial is connected with the third basibranchial posteriorly by a cartilaginous intervention. The third basibranchial is a wedge-like bone covered with a cartilaginous cap posteriorly. This bone is connected with the second basibranchial anteriorly. The posterior portion of the third basibranchial is situated below the central cartilage.

The hypobranchials are three paired bones becoming progressively smaller posteriorly. The first hypobranchial has an anteriorly-pointed projection laterally and is connected with the dorsal hypohyals by a strong ligament. It articulates with a cartilage between the first and second basibranchials anteriorly and with the first ceratobranchial posteriorly. The second hypobranchial is a stick-like bone that and articulates with a cartilage between the second and third basibranchials anteriorly and with the second ceratobranchials posteriorly. The third hypobranchial is a crescent-shape bone that is connected with the posterior part of the third basibranchial anteriorly and with the third ceratobranchial posteriorly.

The ceratobranchials comprise four pairs of rod-like bones and a pair of triangular-toothed bones. The first to third ceratobranchials articulate with the hypobranchial facets anteriorly and with the epibranchial facets posteriorly on the anterior three arches. The fourth ceratobranchial articulates with the central cartilage anteriorly and with the fourth epibranchial posteriorly. It bears a small canine tooth row posteriorly only in *Pentaceros quinquespinis* (Fig. 29K), while it lacks the tooth row in the others. The fifth ceratobranchial is situated on the posteroventral region of the branchial arch and bears a tooth plate dorsally. This bone is projecting anteriorly and connected with the central cartilage by a strong ligament.

The epibranchials are four paired rod-like bones without tooth plates, and situated between the pharyngobranchials and ceratobranchials. The first epibranchial articulates with the first pharyngobranchial medially and the first ceratobranchial laterally. This bone has an uncinate process, which articulates with the interarcual cartilage medially. The second epibranchial articulates with the ventral region of the second pharyngobranchial and the lateral region of the third pharyngobranchial medially, and with the second ceratobranchial laterally. The third epibranchial articulates with the posterolateral region of the third pharyngobranchial and the anterolateral region of the fourth pharyngobranchial medially in most pentacerotids, whereas this bone articulates only with the anterolateral region of the fourth pharyngobranchial medially in *Zanclistius elevatus*. This bone also articulates with the third ceratobranchial laterally. The fourth epibranchial articulates with the posterior corner of the third pharyngobranchial and the anterolateral region of the fourth pharyngobranchial medially in most pentacerotids, while it articulate only with the anterolateral region of the fourth pharyngobranchial medially in *Zanclistius elevatus*. This bone also articulates with the fourth ceratobranchial laterally.

The pharyngobranchials are a pair of small and toothless bones (first), and three pairs of toothed bones (second to fourth). The first pharyngobranchial is a stick-like bone and connected with the prootic of the neurocranium dorsally and with the first epibranchial ventrally. The second pharyngobranchial is a flat bone connected with the second epibranchial laterally and with the interarcual cartilage anteriorly. In addition to a tooth plate on the second pharyngobranchial, this bone has an autogenous tooth plate at the articulatory portion with the second epibranchial ventrally in *Pentaceros capensis*, *P. decacanthus*, *P. japonicus*, *Pseudopentaceros richardsoni*, and *P. wheeleri*, while it lacks such a tooth plate in the others. The third pharyngobranchial is the largest element in the upper branchial arch. This bone is fused with the fourth pharyngobranchial only in *Paristiopterus gallipavo* (Fig. 30F), while it is separated from the fourth pharyngobranchial in the others. The fourth pharyngobranchial is a circle-like bone, having a tooth plate on its oral surface. It is continuous with the third pharyngobranchial only in *Paristiopterus gallipavo*.

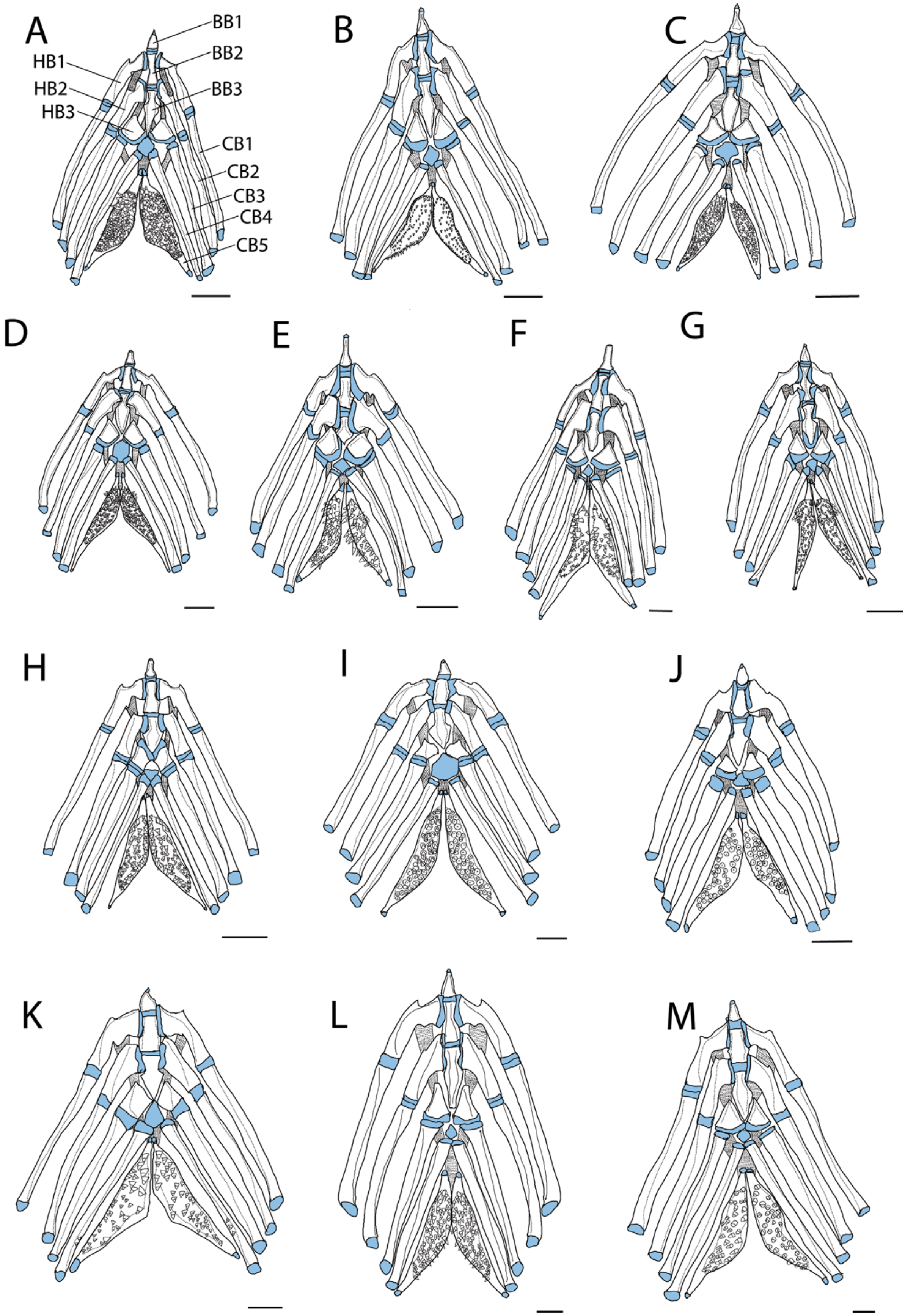

FIGURE 29. Dorsal aspects of the lower branchial arch. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*; G, *Pentaceropsis recurvirostris*; H, *Pentaceros capensis*; I, *P. decacanthus*; J, *P. japonicus*; K, *P. quinquespinis*; L, *Pseudopentaceros richardsoni*; M, *P. wheeleri*. B, E, G, H, I, and L are shown as mirror images. Scale bar = 5 mm.

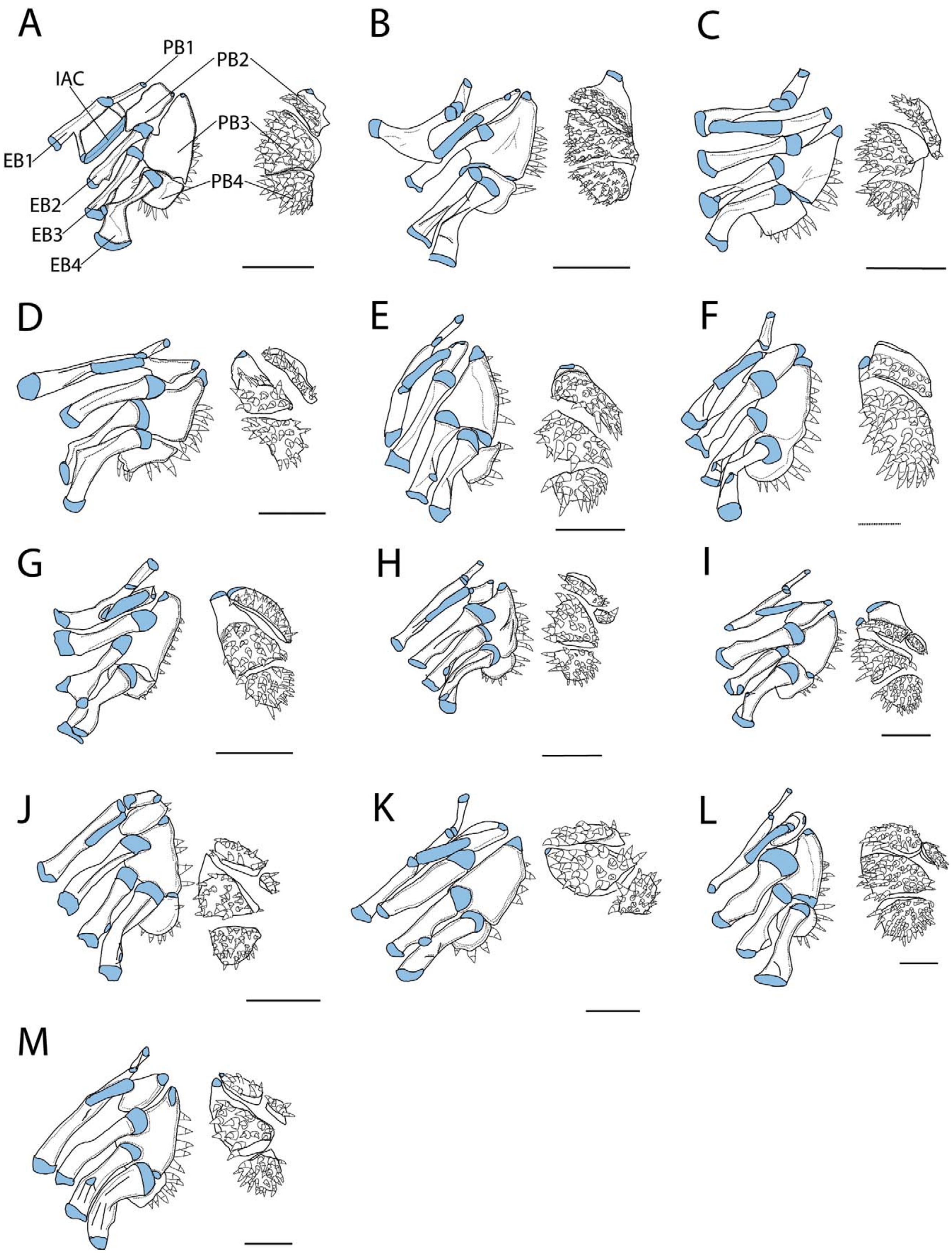

FIGURE 30. Dorsal aspects of the upper branchial and the ventral aspect of its tooth-plate. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*; G, *Pentaceropsis recurvirostris*; H, *Pentaceros capensis*; I, *P. decacanthus*; J, *P. japonicus*; K, *P. quinquespinis*; L, *Pseudopentaceros richardsoni*; M, *P. wheeleri*. B, E, G, H, I, and L are shown as mirror images. Scale bar = 5 mm.

Synapomorphies of Pentacerotidae

SA 9. Absence of a tooth plate on the third epibranchial.

The third epibranchial tooth plate is present in most typical percoid (e.g., Tominaga, 1968; Kim, 2002; Imamura, 2004; Otero, 2004; pers. obs.), whereas the epibranchial tooth plate is lacking in pentacerotids, and is therefore a synapomorphy.

Character recognition

TS 20. Autogenous tooth plate on the second pharyngobranchial toothplate. (0: present; 1: absent)

Ingroup. The second pharyngobranchial has an autogenous tooth plate at the articulatory portion with the second epibranchial ventrally in *Pentaceros capensis*, *P. decacanthus*, *P. japonicus*, *Pseudopentaceros richardsoni*, and *P. wheeleri* (character 20-0), while it lacks such a tooth plate in the others (character 20-1).

Outgroup. The second pharyngobranchial typically has an autogenous tooth plate in the percoids (character 20-0) (e.g., Stiassny, 1991; Imamura, 2004; pers. obs.).

Other variations.

Small canine tooth row on the fourth ceratobranchial. A small canine tooth row is present on the fourth ceratobranchial posteriorly in *Pentaceros quinquespinis*. In contrast, such a tooth row is absent in other pentacerotids. The former condition is regarded as an apomorphy, because it is not found in typical percoids (e.g., Sasaki, 1989; Imamura, 1996; Kim, 2002; pers. obs.). It is an autapomorphy of *Pentaceros quinquespinnis*, however, and is therefore excluded from the phylogenetic analysis.

The third pharyngobranchial is fused with the fourth pharyngobranchial. The third pharyngobranchial is separated from the fourth pharyngobranchial in most pentacerotids, as well as in typical percoids (e.g., Tominaga, 1968; Yabe, 1985; Sasaki, 1989; pers. obs.), while these bones are fused each other in *Paristiopterus gallipavo*. Therefore, the latter condition can be treated as an autapomorphy of *Paristiopterus gallipavo* and is not used for the phylogenetic analysis.

1-7. Pectoral girdle

(Figs. 31–34)

Description

The pectoral girdle is comprised of the supratemporals, posttemporal, supracleithrum, cleithrum, scapula, coracoid, actinosts, and postcleithra.

The supratemporals (=extrascapula) are situated on the posterodorsal region of the head. The bones are loosely attached to the posterolateral region of the neurocranium in many pentacerotids, whereas it is firmly attached to the posterolateral region of the neurocranium in *Pentaceros* and *Pseudopentaceros*. The bones are firmly connected with the parietal laterally and the pterotic ventrally in *Histiopterus*, *Zanclistius*, *Evistias*, *Parazanclistius*, and *Paristiopterus*, and with the pterotic laterally in *Pentaceros* and *Pseudopentaceros*. They are also firmly connected with the posttemporal ventrally. Many exposed tubercles are present on the lateral surface of the supratemporals in all pentacerotids, except for *Parazanclistius*, *Paristiopterus*, and *Pentaceropsis*. Two supratemporals are present in *Pentaceros*, *Pseudopentaceros*, and a specimen of *Histiopterus typus* (HUMZ 72430, 200078); three bones in *Paristiopterus*, *Pentaceropsis* and a specimen of *H. typus* (HUMZ 199821, 200034); and four bones in *Zanclistius* and *Parazanclistius*. The bones are narrow and tubular in *Histiopterus*, *Zanclistius*, *Evistias*, *Parazanclistius*, and *Paristiopterus* (Fig. 31), whereas they are wide and disk-like with tubular structure in *Pentaceros* and *Pseudopentaceros* (Fig. 32). They support the temporal sensory canal; the canal is supported by the lowermost supratemporal and is continuous with that in the pterotic anteriorly and that of the posttemporal posteriorly, and is branched in this bone to form an additional sensory canal supported by upper supratemporal(s). The additional canal is further branched to form many subcanals and their openings in *Histiopterus*, *Zanclistius*, *Evistias*, and *Pentaceropsis*, while it is not branched in other pentacerotids.

The posttemporal is a tubular bone situated between the supratemporal and supracleithrum. This bone is anteriorly forked to form the dorsal and ventral limbs. The dorsal limb is connected with the epiotic dorsomedially. The ventral limb is connected with the intercalar posteroventrally by a ligament. This bone is penetrated by the temporal sensory canal, which is continuous with that in the lowermost supratemporal anteriorly and that in the

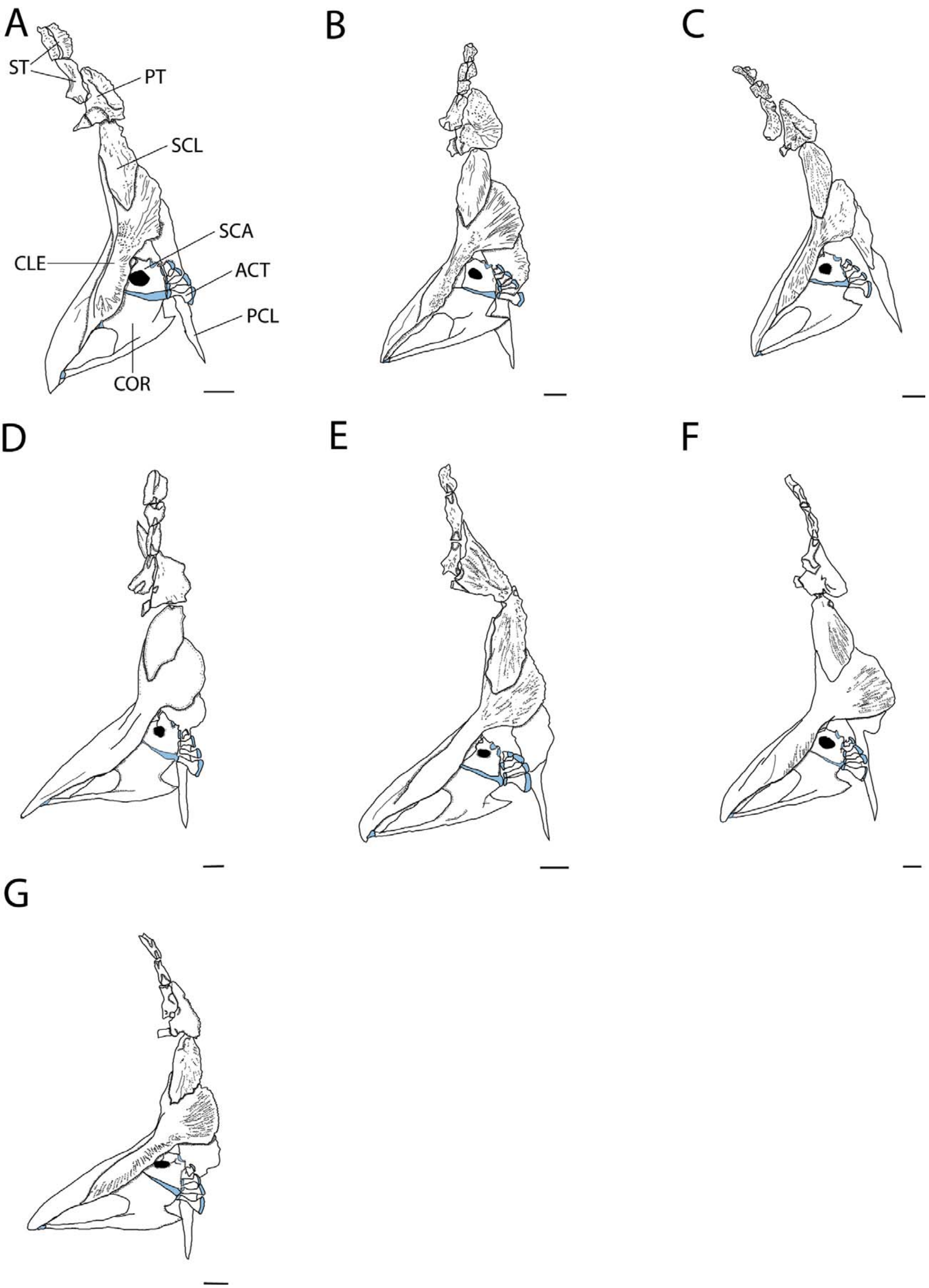

FIGURE 31. Lateral aspects of the pectoral girdle. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*; G, *Pentaceropsis recurvirostris*. B, E, and G are shown as mirror images. Scale bar = 5 mm.

supracleithrum posteriorly. In the posttemporal, the canal is branched intricately to form several subcanals and their openings in *Histiopterus*, *Zanclistius*, *Evistias*, *Parazanclistius*, *Paristiopterus*, and *Pentaceropsis*, whereas such subcanals or openings are absent in the others. Many exposed tubercles are present on the lateral surface of the posttemporal in *Histiopterus*, *Zanclistius*, *Evistias*, *Paristiopterus labiosus*, *Pentaceros*, and *Pseudopentaceros*, while they are absent in *Parazanclistius*, *Paristiopterus gallipavo*, and *Pentaceropsis*.

The supracleithrum is a shield-like bone that attached with the cleithrum ventromedially. It articulates with the posttemporal anterodorsally. It has a short tubular structure on the anterodorsal corner where the temporal sensory canal connects to lateral line on the body. This bone is connected with Baudelot's ligament medially. Many exposed tubercles are present on the lateral surface of the supracleithrum in all pentacerotids, except for *Parazanclistius*.

The cleithrum is wing-like and is the largest bone in the pectoral girdle. It is connected with the supracleithrum dorsolaterally, with the scapula posterodorsally, the coracoid posteroventrally, and the postcleithrum dorsomedially. Many exposed tubercles are present on the lateral surface of the cleithrum in all pentacerotids, except for *Parazanclistius*.

The scapula is a rectangular bone with a large scapular foramen anteriorly for the passage of nerves and vessels. It is sutured to the cleithrum anteriorly, and connected with three actinosts posteriorly and with the scapula ventrally via a narrow cartilaginous band.

The coracoid is an anchor-like bone situated on the ventrolateral region of the pectoral girdle. This bone has the long anterior process loosely connected with the cleithrum anterodorsally by the cartilaginous intervention, and has the beak-like process reaching the postcleithrum region.

The actinosts are comprised of four column-like bones supporting the pectoral fin rays posteriorly. The upper three actinosts articulate with the scapula anteriorly, and the lowermost one articulates with the cartilaginous band between the scapula and coracoid anteriorly.

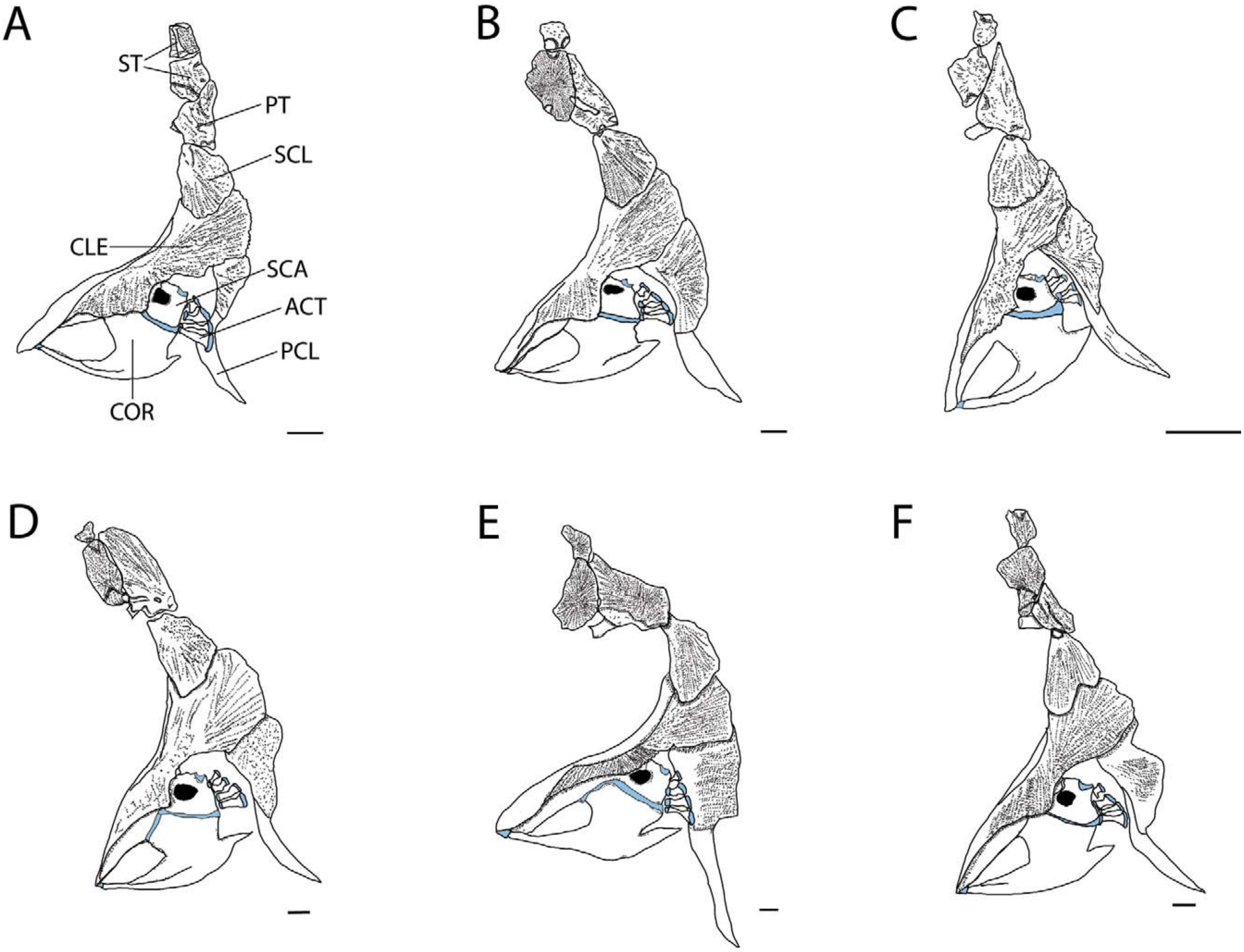

FIGURE 32. Lateral aspects of the pectoral girdle. A, *Pentaceros capensis*; B, *P. decacanthus*; C, *P. japonicus*; D, *P. quinquespinis*; E, *Pseudopentaceros richardsoni*; F, *P. wheeleri*. A, B, and E are shown as mirror images. Scale bar = 5 mm.

The postcleithra are comprised of two long leaf-like bones and situated on the posterior region of the pectoral girdle. The upper postcleithrum is connected with the medial surface of the posterior process of the cleithrum dorsolaterally and with the lower postcleithrum ventromedially.

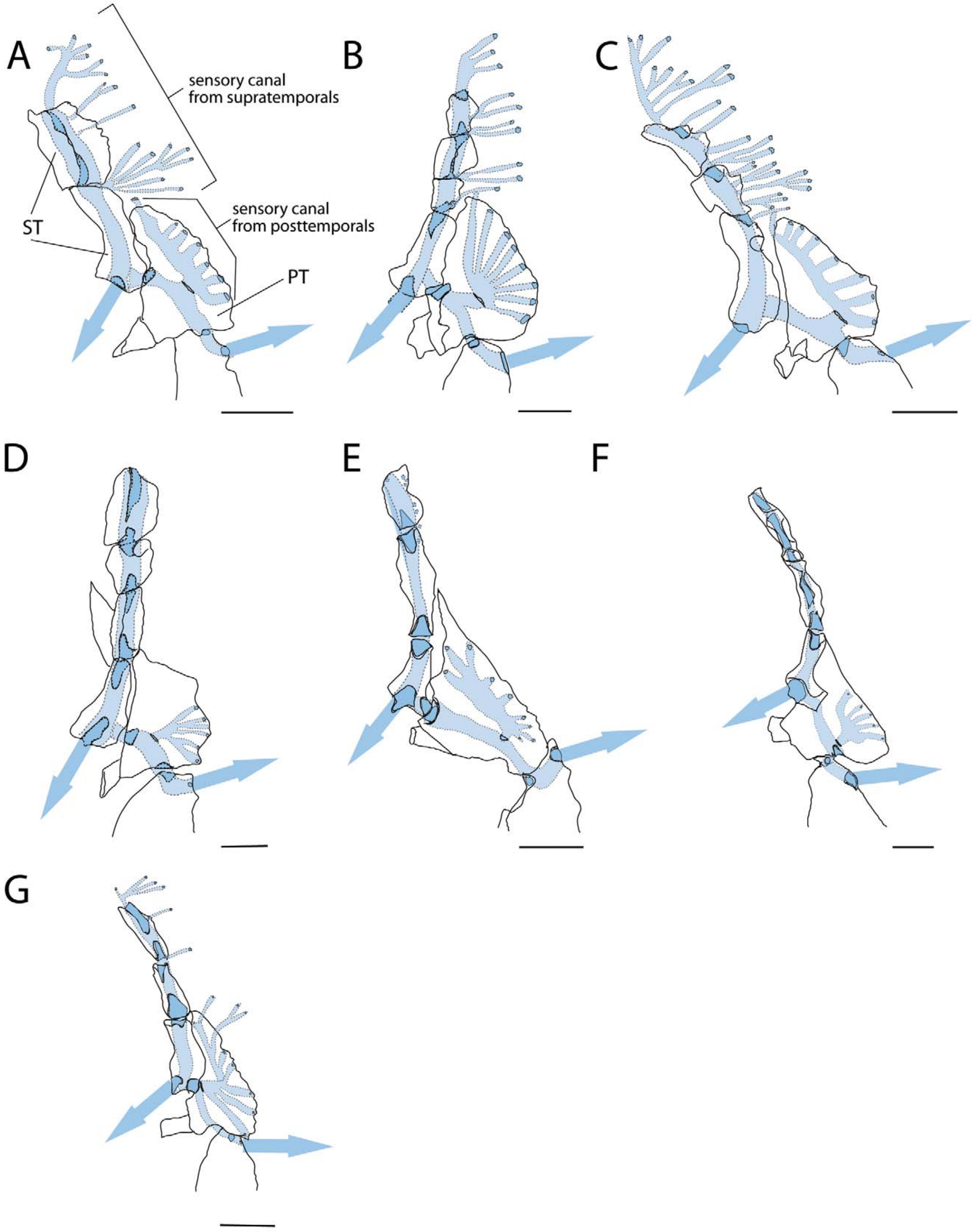

FIGURE 33. Supratemporals and posttemporal, showing the sensory canal (dotted areas). A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*; G, *Pentaceropsis recurvirostris*. B, E, and G are shown as mirror images. Scale bar = 5 mm.

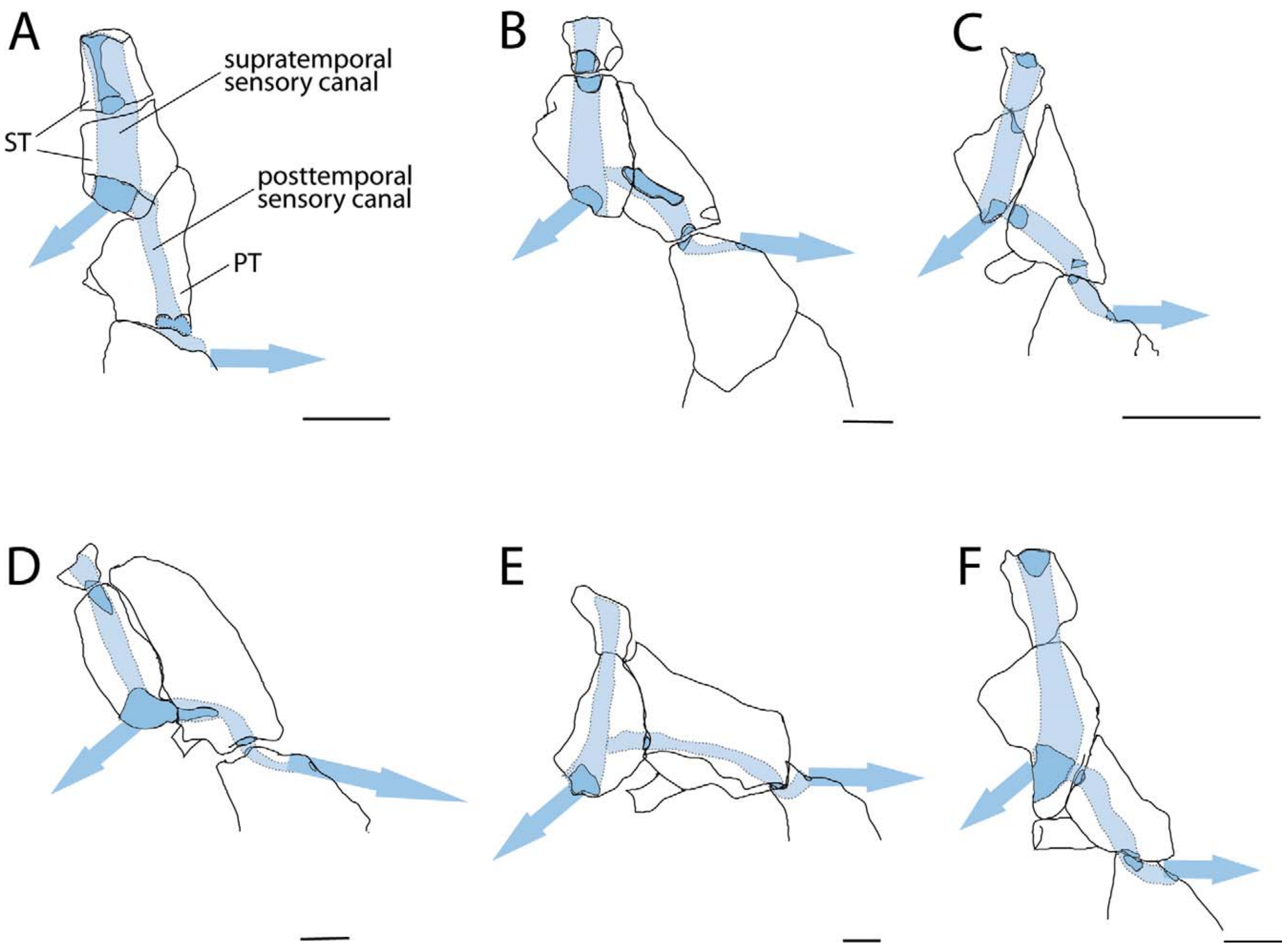

FIGURE 34. Supratemporals and posttemporal, showing the sensory canal (dotted areas). A, *Pentaceros capensis*; B, *P. decacanthus*; C, *P. japonicus*; D, *P. quinquespinis*; E, *Pseudopentaceros richardsoni*; F, *P. wheeleri*. A, B, and E are shown as mirror images. Scale bar = 5 mm.]

Synapomorphies of Pentacerotidae

None.

Character recognition

TS 21. Connection between the supratemporal and neurocranium. (0: loosely attached; 1: firmly attached)

Ingroup. The supratemporal is loosely attached to the neurocranium in many pentacerotids (character 21-0), while it is firmly attached to the neurocranium in *Pentaceros* and *Pseudopentaceros* (character 21-1).

Outgroup. The supratemporal is loosely attached to the neurocranium in typical percoids (character 21-0) (e.g., Sasaki, 1989; Imamura, 1996; pers. obs.).

TS 22. Exposed tubercles on the supratemporal. (0: absent; 1: present)

Ingroup. Many exposed tubercles are present on the lateral surface of the supratemporal in all pentacerotids (character 22-1), except for *Parazanclistius*, *Paristiopterus*, and *Pentaceropsis* (character 22-0).

Outgroup. The exposed tubercles on the supratemporal are typically absent in percoids (character 22-0) (e.g., Gregory, 1933; Fraser, 1972; Imamura, 1996; pers. obs.).

TS 23. Shape of the supratemporal. (0: narrow and tubular; 1: wide and disk like)

Ingroup. The supratemporal is narrow and tubular in *Histiopterus*, *Zanclistius*, *Evistias*, *Parazanclistius*, *Paristiopterus*, and *Pentaceropsis* (character 23-0), while it is wide and disk-like in *Pentaceros* and *Pseudopentaceros* (character 23-1).

Outgroup. The supratemporal is narrow and tubular in typical percoids (character 23-0) (e.g., Tyler et al., 1989; pers. obs.).

TS 24. Position of the connection of the supratemporals with the pterotic. (0: lateral; 1: ventral)

Ingroup. The supratemporals are connected with the pterotic laterally in *Pentaceros* and *Pseudopentaceros* (character 24-0), while it is connected with the bone ventrally in *Histiopterus*, *Zanclistius*, *Evistias*, *Parazanclistius*, *Paristiopterus*, and *Pentaceropsis* (character 24-1).

Outgroup. The supratemporals are typically connected with the pterotic laterally in the percoids (character 24-0) (e.g., Sasaki, 1989; Kim, 2002; pers. obs.).

TS 25. Sensory canal supported by the upper supratemporal(s). (0: not branched; 1: branched to form subcanals)

Ingroup. The sensory canal is supported by the upper supratemporal(s) and is branched to form many subcanals and their openings in *Histiopterus*, *Zanclistius*, *Evistias*, and *Pentaceropsis* (character 25-1), whereas it is not branched in *Parazanclistius*, *Paristiopterus*, *Pentaceros*, or *Pseudopentaceros* (character 25-0).

Outgroup. The sensory canal is not branched in typical percoids (character 25-0) (e.g., Harrington, 1955; Branson and Moore, 1962; Yabe, 1985; pers. obs.).

TS 26. Exposed tubercles on the posttemporal. (0: absent; 1: present)

Ingroup. Many exposed tubercles are present on the lateral surface of the posttemporal in all pentacerotids (character 26-1), except for *Parazanclistius*, *Paristiopterus gallipavo*, and *Pentaceropsis* (character 26-0).

Outgroup. The tubercles on the posttemporal are typically absent in the percoids (character 26-0) (e.g., Gregory, 1933; Imamura, 1996; pers. obs.).

TS 27. Sensory canal supported by the posttemporal. (0: not branched; 1: branched)

Ingroup. The sensory canal is supported by the posttemporal and branched to form subcanals and their openings in *Histiopterus*, *Zanclistius*, *Evistias*, *Parazanclistius*, *Paristiopterus*, and *Pentaceropsis* (character 27-1), whereas it is not branched in *Pentaceros* and *Pseudopentaceros* (character 27-0).

Outgroup. The sensory canal is not branched in typical percoids (character 27-0) (e.g., Harrington, 1955; Branson and Moore, 1962; pers. obs.).

Other variations

Number of supratemporals. The number of supratemporals varies from two to four in the pentacerotids, whereas there are only two in typical percoids (e.g., Branson and Moore, 1962; Yabe, 1985; pers. obs.). Therefore, conditions of three and four supratemporals are regarded to be derived. Intraspecific variation is observed, however in the number in *Histiopterus* (two and three); and therefore the variation is not used in this study.

1-8. Pelvic girdle

(Figs. 35–39)

Description

The pelvic girdle comprises a pair of elongated triangular pelvic bones, and is situated below the pectoral girdle. The pelvic bone articulates with the anteroventral part of the cleithrum ventrally. It bears the pelvic fin comprised of one spine and five soft rays posteriorly. This bone has a cartilaginous cap on its anterior tip, and a cartilaginous margin for articulation with the pelvic fin rays posteriorly. The pelvic spine has two well developed processes at its basal portion for articulation with the pelvic bone. The two processes are separated distally in most pentacerotids, whereas the processes are attached to each other and form a ring-like structure in *Pentaceros* and *Pseudopentaceros*. A deep facet for articulation with the pelvic spine is present on the mid-lateral on posterolateral corner of the pelvic bone in most pentacerotids, while a small penetrated pore, interlocked with the ring-like structure of the pelvic spine, is present there in *Pentaceros* and *Pseudopentaceros*. This bone has three processes ventrally; a process from the accessory subpelvic keel, a subpelvic process, and a postpelvic process. The accessory subpelvic keel is well developed and extends anteroventrally in most pentacerotids, while it is weakly developed in *Pentaceros* and *Pseudopentaceros*. The subpelvic process is V-shaped and is situated on the anteromedial portion of the pelvic bone. The subpelvic process is well developed and long in most pentacerotids, whereas it is short in *Pentaceros* and *Pseudopentaceros*. The postpelvic process is situated on the posterior end of this bone and the processes on both sides are separated from each other posteriorly. This process is well developed and extends backward.

Synapomorphies of Pentacerotidae

None.

Character recognition

TS 28. Articulation between the pelvic bone and pelvic spine. (0: articulating; 1: interlocked)

Ingroup. The mid-lateral corner of the pelvic bone has a deep facet for articulation with the pelvic spine in most pentacerotids (character 28-0), while it possesses a small penetrated pore that is interlocked with the ring-like structure of the pelvic spine in *Pentaceros* and *Pseudopentaceros* (character 28-1).

Outgroup. The pelvic bone has a deep facet for articulation with the pelvic spine in typical percoids (character 28-0) (e.g., Katayama, 1959; Tominaga, 1968; Mok and Shen, 1983; Imamura, 1996; pers. obs.).

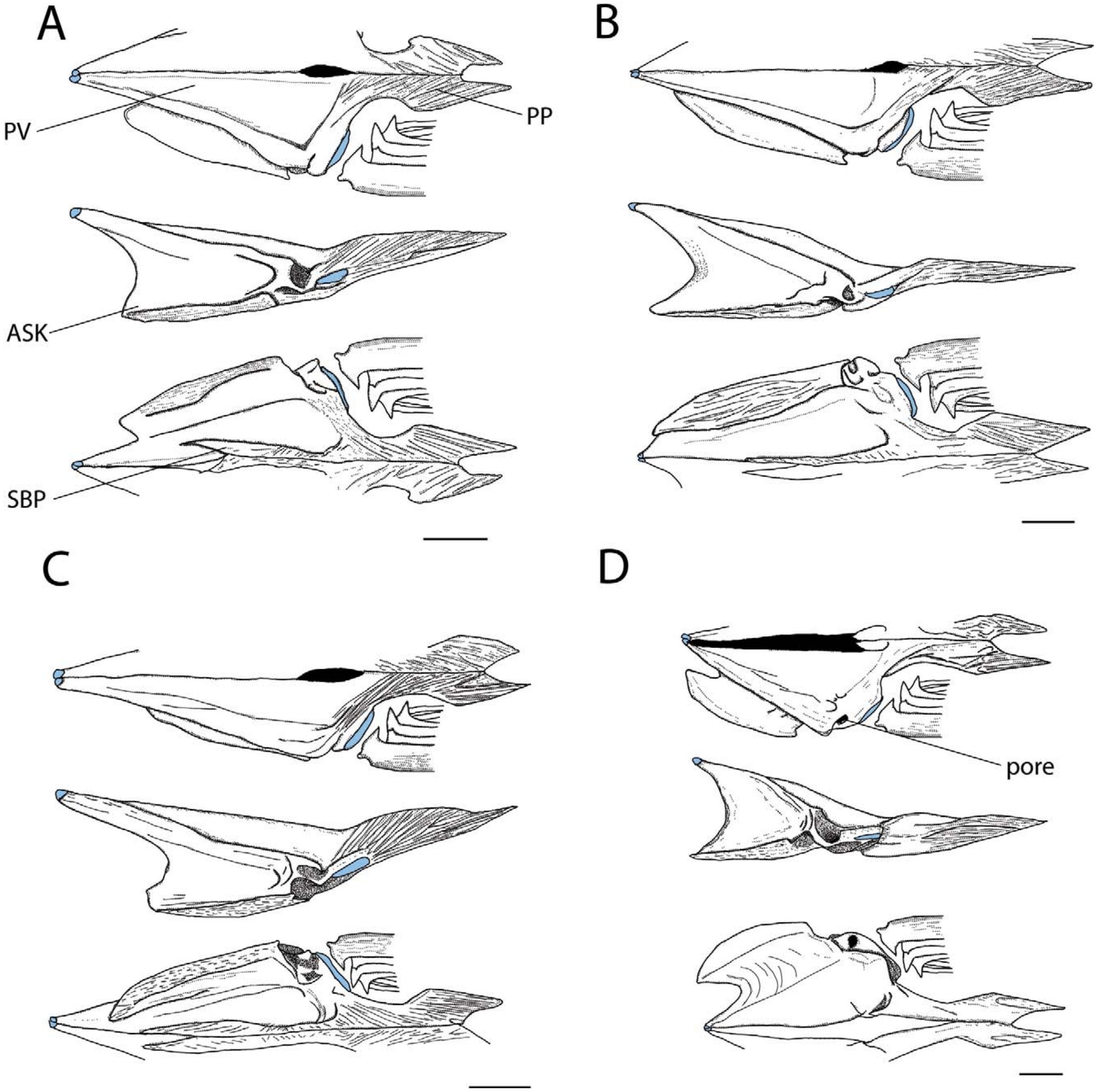

FIGURE 35. Dorsal (above), lateral (middle) and ventral (below) aspects of the pelvic girdle. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*. B is shown as mirror images. Scale bar = 5 mm.

TS 29. Accessory subpelvic keel. (0: weakly developed; 1: well developed and extending anteroventrally)

Ingroup. The accessory subpelvic keel is well developed and extends anteroventrally in most pentacerotids (character 29-1), while it is weakly developed in *Pentaceros* and *Pseudopentaceros* (character 29-0).

Outgroup. The accessory subpelvic keel is typically weakly developed in percoids (e.g., Tominaga, 1968; Sasaki, 1989; Kim, 2002; pers. obs.).

TS 30. Subpelvic process. (0: short; 1: long)

Ingroup. The subpelvic process is well developed and long in most pentacerotids (character 30-1), whereas it is short in *Pentaceros* and *Pseudopentaceros* (character 30-0).

Outgroup. The subpelvic process is typically short in percoids (character 30-0) (e.g., Tominaga, 1968; Sasaki, 1989; Prokofiev, 2007a; pers. obs.).

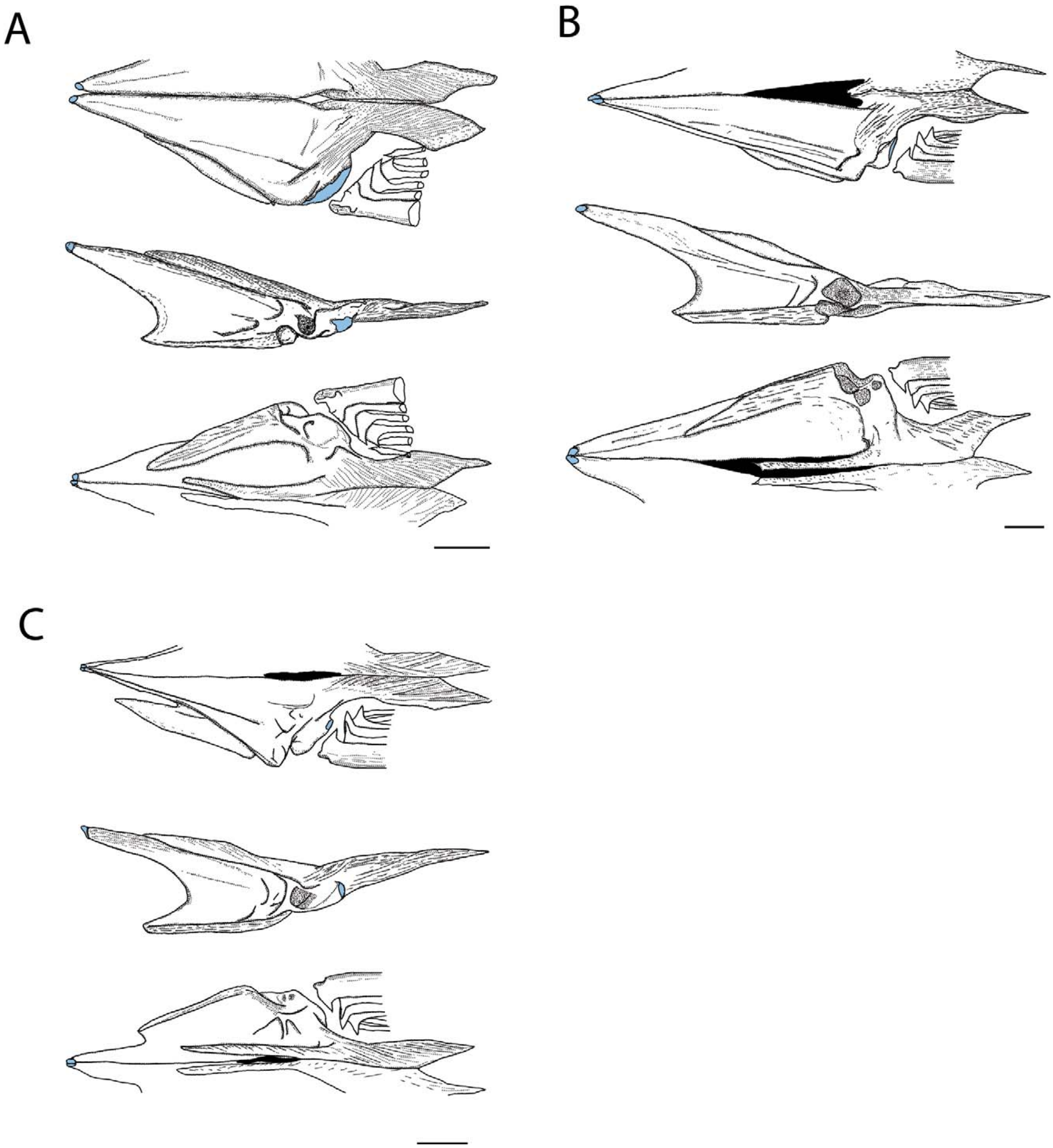

FIGURE 36. Dorsal (above), lateral (middle), and ventral (below) aspects of the pelvic girdle. A, *Paristiopterus labiosus*; B, *P. gallipavo*; C, *Pentaceropsis recurvirostris*. A and C are shown as mirror images. Scale bar = 5 mm.

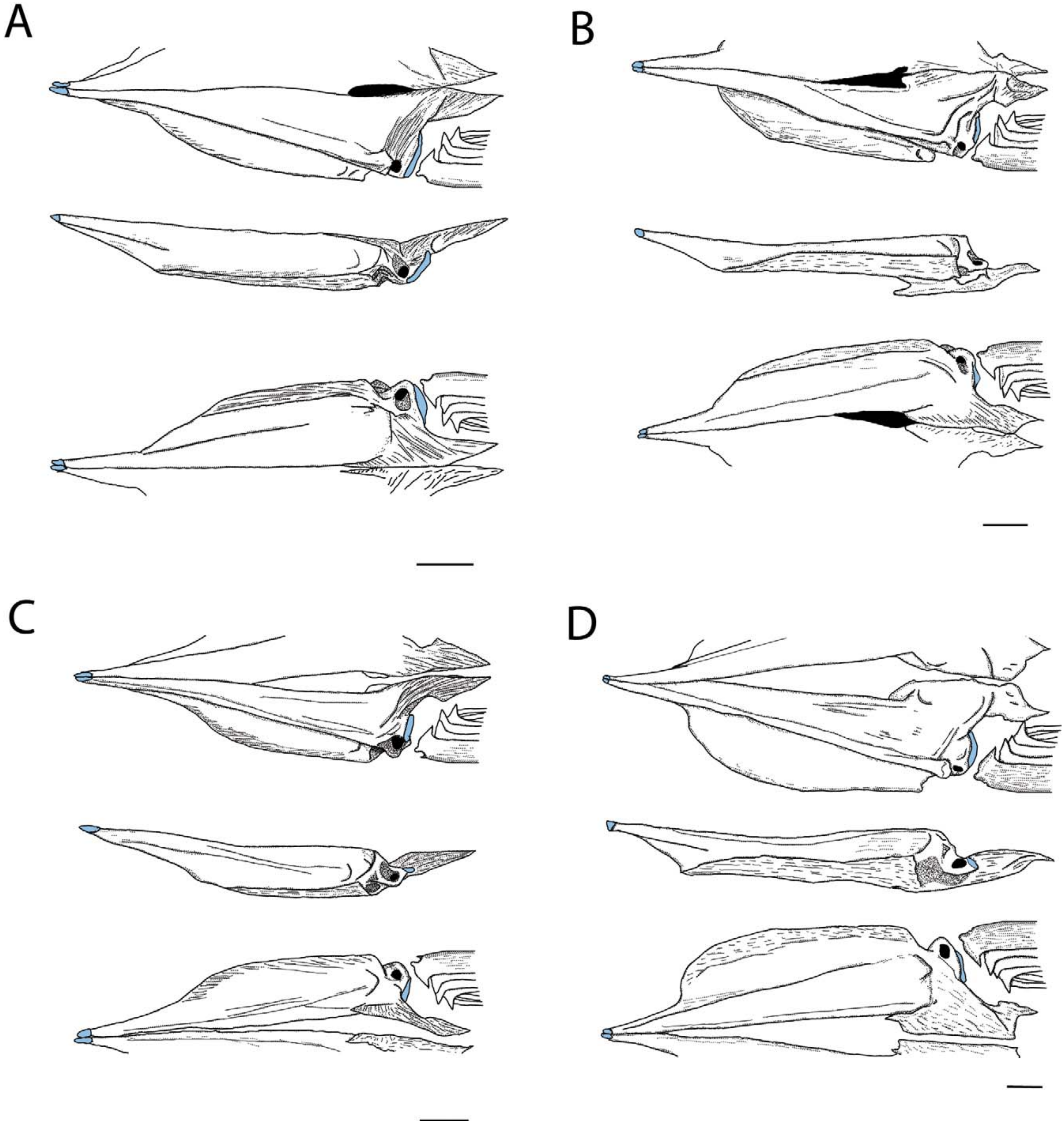

FIGURE 37. Dorsal (above), lateral (middle) and ventral (below) aspects of the pelvic girdle. A, *Pentaceros capensis*; B, *P. decacanthus*; C, *P. japonicus*; D, *P. quinquespinis*. A and B are shown as mirror images. Scale bar = 5 mm.

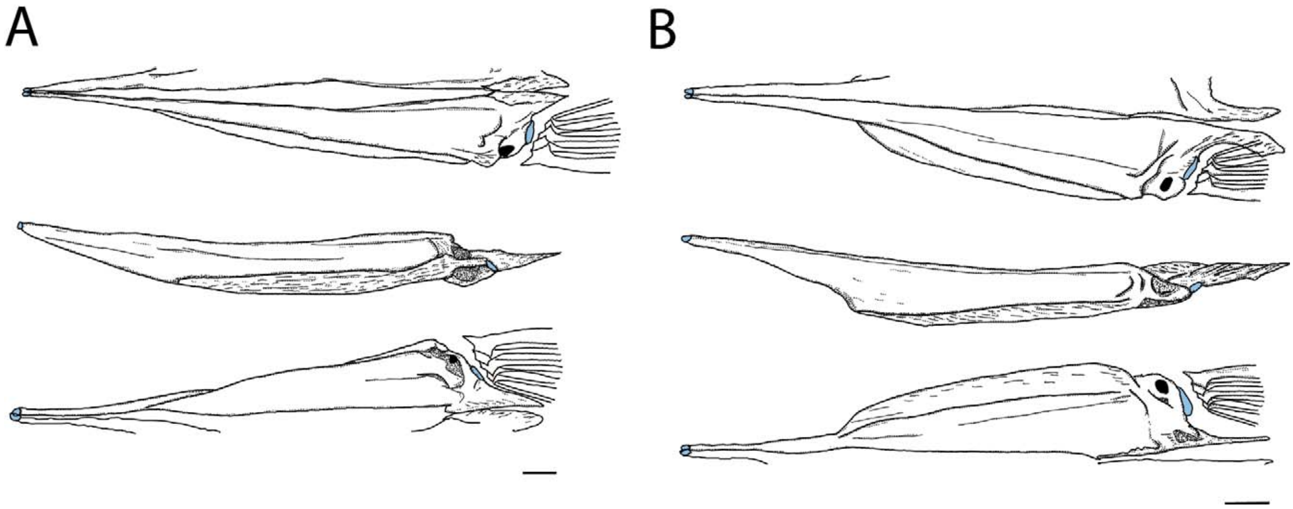

FIGURE 38. Dorsal (above), lateral (middle), and ventral (below) aspects of the pelvic girdle. A, *Pseudopentaceros richardsoni*; B, *P. wheeleri*. A is shown as mirror images. Scale bar = 5mm.

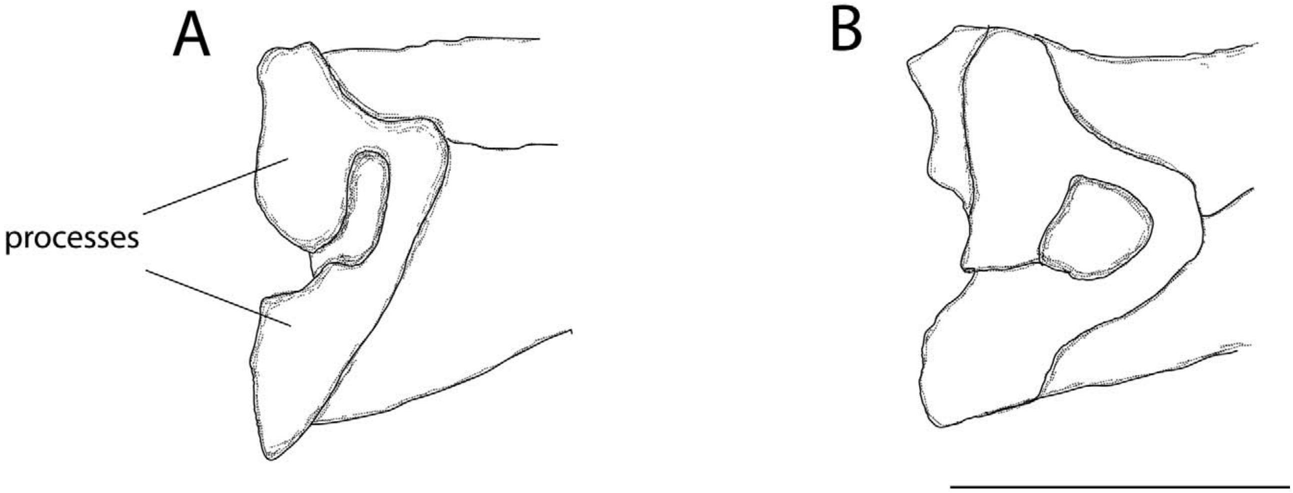

FIGURE 39. Lateral aspect of the basal portion of the pelvic spine. A, *Parazanclistius hutchinisi*; B, *Pentaceros japonicus*. Scale bar = 5 mm.

1-9. Axial skeleton and median fin supports

(Figs. 40–42)

Description

The axial skeleton is comprised of the vertebrae, epineurals (*sensu* Patterson and Johnson, 1995), and pleural ribs. The median fin supports consist of the proximal and distal pterygiophores, and stays. The supraneural is also described here.

Axial skeleton. The vertebrae are comprised of two (abdominal and caudal) elements. The abdominal vertebrae possess the neural prezygapophyses anterodorsally, the neural postzygapophyses posterodorsally, and the neural arches and neural spines dorsally. The first abdominal vertebra has a long neural spine and articulates with the exoccipitals of both sides anterodorsally and with the basioccipital anteroventrally. This bone possesses the epineurals and pleurals. The number of the abdominal vertebrae is 12 in *Histiopterus*, *Zanclistius*, *Parazanclistius*, *Paristiopterus*, *Pentaceros*, and *Pseudopentaceros*, whereas it is 13 in *Evistias* and *Pentaceropsis*. The caudal vertebrae possess the hemal prezygapophyses anteroventrally, the hemal postzygapophyses posteroventrally, and the hemal arches and hemal spines in addition to structures of the abdominal vertebrae. The number of the caudal vertebrae is 11 in *Pentaceropsis recurvirostris*; 12 in *Zanclistius elevatus, Paristiopterus labiosus, P. gallipavo*, and

Pentaceros capensis; 13 in *Histiopterus typus*, *Parazanclistius hutchinsi*, *Pentaceros decacanthus*, *P. japonicus*, *P. quinquespinis*, and *Pseudopentaceros wheeleri*; and 14 in *Evistias acutirostris* and *Pseudopentaceros richardsoni*.

The epineurals are rod-like slender bones, attached with the lateral surface of the first and second abdominal vertebrae, and with the lateral surface of the pleural ribs of other abdominal vertebrae.

The pleural ribs are well developed rod-like bones, attached with the lateral surface of the abdominal vertebrae.

Medial fin supports. The proximal pterygiophores are leaf-like bones supporting the dorsal and anal rays. These bones are inserted between the neural spines (dorsal fin proximal pterygiophores) and between the hemal spines (anal fin proximal pterygiophores) of the vertebrae. The first dorsal proximal pterygiophore bears two spines dorsally in all pentacerotids, except for *Histiopterus* and *Evistias* having one spine on the bone. The first dorsal proximal pterygiophore is inserted into the space between the first and second neural spines in most pentacerotids, whereas it is inserted into that between the second and third neural spines in *Pentaceros* and *Pseudopentaceros*. The base of the anterior edge of the anterior dorsal spines, except for the first spine is serrated in *Pentaceros* and *Pseudopentaceros*, whereas it is smooth in the others. Most of the anal proximal pterygiophores are inserted into the space between the hemal spines, while the first anal proximal pterygiophore is situated anterior to the first hemal spine. The first anal proximal pterygiophore bears two spines ventrally.

The distal pterygiophores are small bony and cartilaginous elements, located on the posterior tip of each proximal pterygiophore, except the last dorsal and anal proximal pterygiophores. The distal pterygiophores supporting spines are unpaired bones, while those supporting soft rays are paired bones.

The stay is a small, plate-like bone situated on the posterior tip of the last dorsal and anal proximal pterygiophores.

The two supraneurals are rod-like bones. The first supraneural is inserted into the space between the neurocranium posterior tip of and the first neural spine, and its anterior tip is attached to the posterior tip of supraoccipital. The second supraneural is inserted into the space between the first and second neural spines along with the first dorsal fin proximal pterygiophore.

Synapomorphies of Pentacerotidae

None.

Character recognition

TS 31. Number of abdominal vertebra. (0: 10; 1: 12; 2: 13) (ordered)

Ingroup. The number of the abdominal vertebrae is 12 in *Histiopterus*, *Zanclistius*, *Parazanclistius*, *Paristiopterus*, *Pentaceros*, and *Pseudopentaceros* (character 31-1), whereas it is 13 in *Evistias* and *Pentaceropsis* (character 31-2).

Outgroup. The number of the abdominal vertebrae is 10 in typical percoids (character 31-0) (e.g., Tominaga, 1968; Sasaki, 1989; Kim, 2002; pers. obs.).

TS 32. Number of spines on first dorsal proximal pterygiophore. (0: two; 1: one)

Ingroup. The first dorsal proximal pterygiophore bears two spines dorsally in all pentacerotids (character 32-0), except for *Histiopterus* and *Evistias* having spine on the bone (character 32-1).

Outgroup. The first dorsal proximal pterygiophore bears two spines in typical percoids (character 32-0) (e.g., Smith and Bailey, 1962; Gosline, 1966; Johnson, 1983; pers. obs.).

TS 33. Insertion of first dorsal proximal pterygiophore. (0: between second and third neural spines; 1: between first and second neural spines)

Ingroup. The first dorsal proximal pterygiophore is inserted into the space between the first and second neural spines in most pentacerotids (character 33-1), whereas it is inserted into that between the second and third neural spines in *Pentaceros* and *Pseudopentaceros* (character 33-0).

Outgroup. The first dorsal proximal pterygiophore is inserted into the space between the second and third neural spines in typical percoids (character 33-0) (e.g., Yabe, 1985; Sasaki, 1989; Kim, 2002; Prokofiev, 2007a; pers. obs.).

TS 34. Base of anterior edge of anterior dorsal spines. (0: smooth; 1: serrated)

Ingroup. The base of the anterior edge of the anterior dorsal spines, except for the first spine, is serrated in *Pentaceros* and *Pseudopentaceros* (character 34-1), whereas it is smooth in the others (character 34-0).

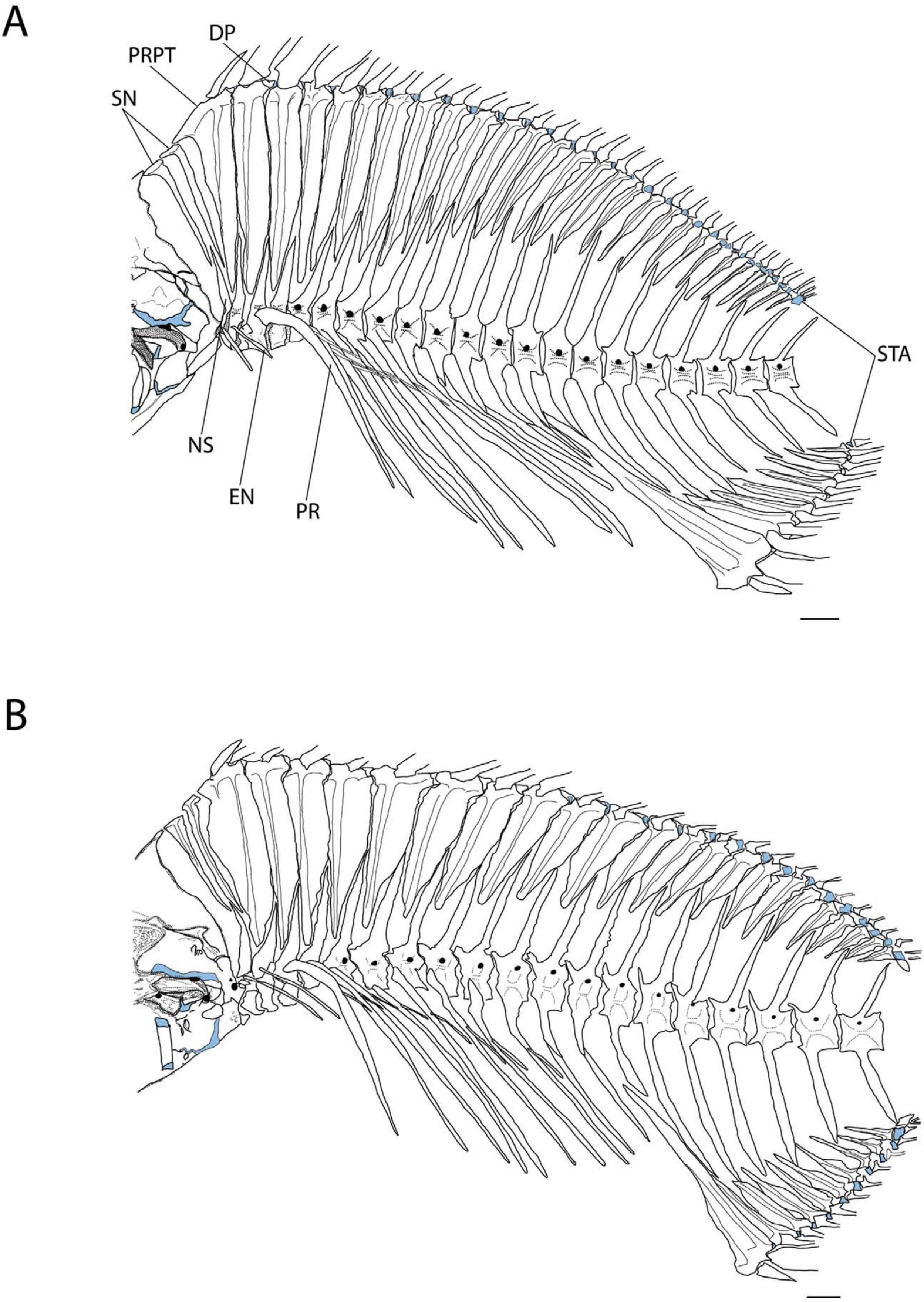

FIGURE 40. Lateral aspects of the axial skeleton and median fin supports. A, *Histiopterus typus*; B, *Paristiopterus labiosus*. B is shown as mirror image. Scale bar = 5 mm.

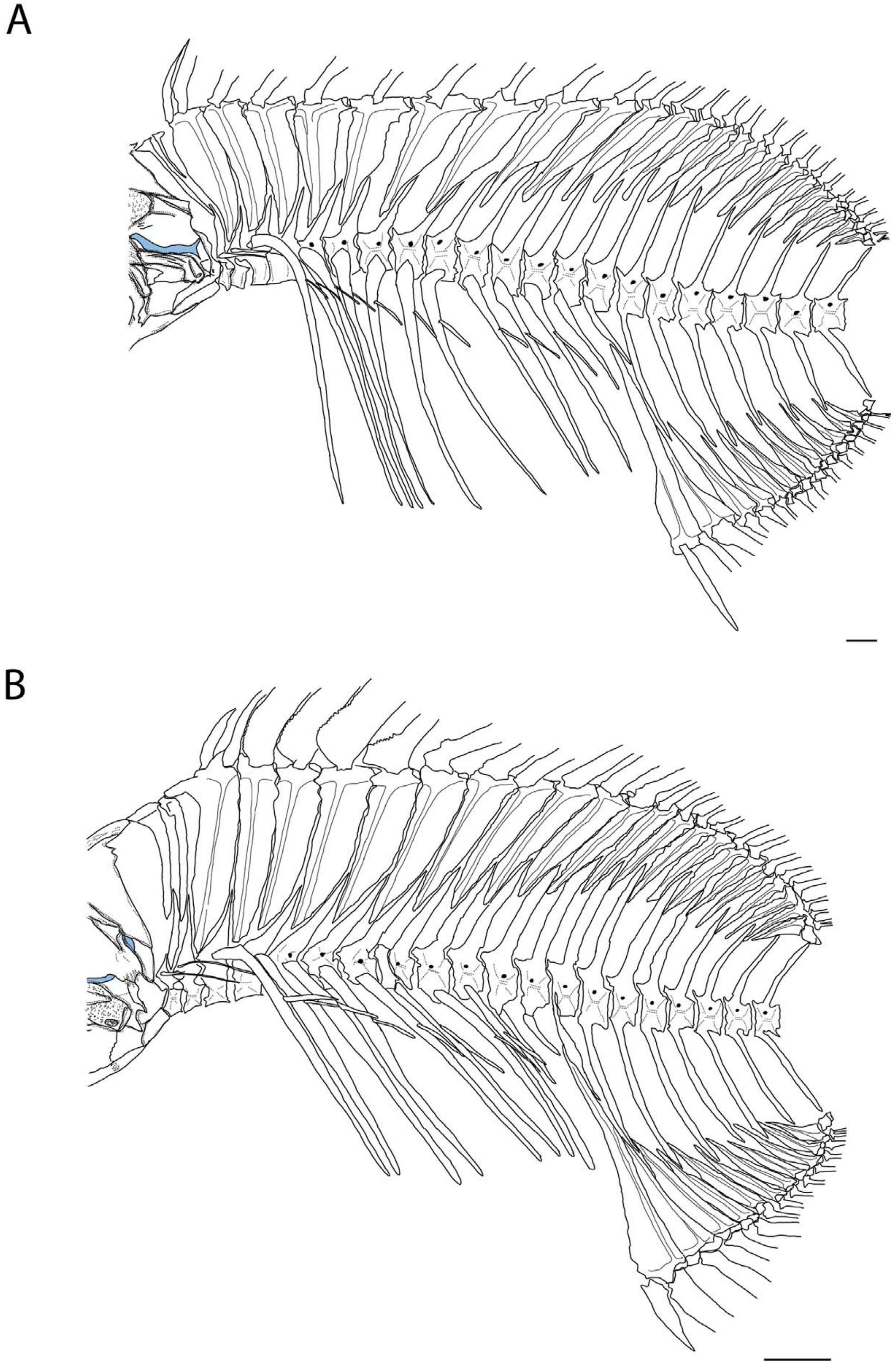

FIGURE 41. Lateral aspects of the axial skeleton and median fin supports. A, *Pentaceropsis recurvirostris*; B, *Pentaceros capensis*. A and B are shown as mirror images. Scale bar = 5 mm.

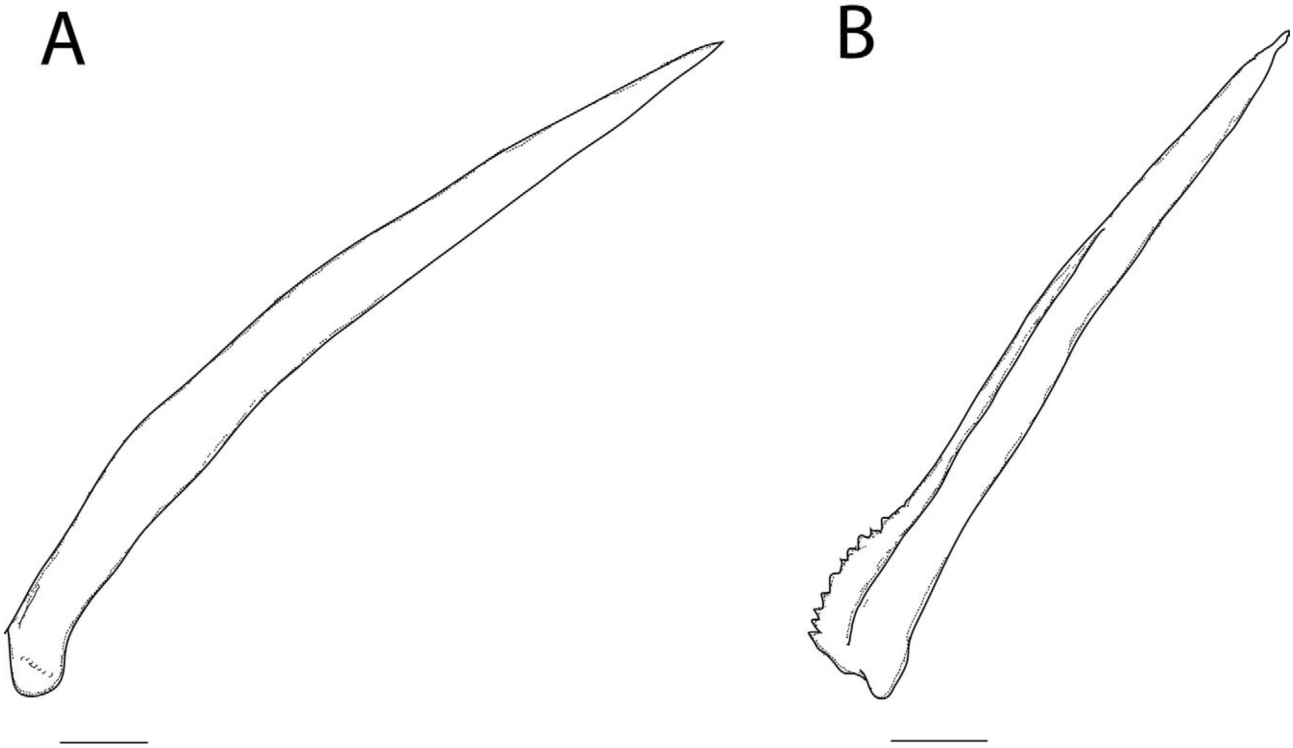

FIGURE 42. Lateral aspects of the third dorsal spine. A, *Histiopterus typus*; B, *Pentaceros capensis*. Scale bar = 5 mm.

Outgroup. The base of the anterior edge of the anterior dorsal spines is smooth in typical percoids (character 34-0) (e.g., Tominaga, 1968; Tyler et al., 1989; pers. obs.).

1-10. Caudal skeleton

(Figs. 43–45)

Description

The caudal skeleton consists of the hypurals, parhypural, uroneural, epurals, and urostyle, plus hemal spines on the second and third preural centra. The upper caudal lobe supports eight branched fin rays in *Parazanclistius hutchinsi* and *Pentaceros capensis*, nine in *Histiopterus typus*, *Paristiopterus labiosus*, *P. gallipavo*, *Pentaceros decacanthus*, *P. japonicus*, *P. quinquespinis*, *Pseudopentaceros richardsoni*, and *P. wheeleri*, and 10 in *Zanclistius elevatus*, *Evistias acutirostris*, and *Pentaceropsis recurvirostris*. The lower caudal lobe supports seven branched fin rays in most pentacerotids, whereas it supports eight branched rays in *Zanclistius elevatus* and *Pentaceropsis recurvirostris*.

The hypurals consists of five plate-like bones situated on the posterior portion of the urostyle, and supports the caudal fin rays posteriorly. Three elements occur in the upper caudal lobe and two in the lower lobe. These bones are separated from each other in most pentacerotids, while the third and fourth are fused in *Paristiopterus labiosus*.

The parhypural is a plate-like bone located under the lowermost hypural. This bone has well developed parhypurapophysis dorsally. The parhypurapophysis is sharp in most pentacerotids, whereas it is robust in *Pentaceros* and *Pseudopentaceros*.

The uroneurals are comprised of two long rod-like bones and are situated anterior to the upper hypurals. There are two of these bones in most pentacerotids, whereas there is only one in *Pentaceros capensis*. The first uroneural is attached with the ventral surface of the urostyle and the second uroneural is situated between the posterior-most epural and the uppermost hypural.

The epurals are three rod-like bones, located above the uroneural. The anterior epural is longer than the other two epurals, and its ventral tip lies over the neural spine of the second preural centrum. The epurals are becoming progressively shorter posteriorly.

The urostyle a wedge-like bone, free from other caudal skeleton elements. It articulates with the second preural centrum anteriorly. The posterior portion of the urostyle has a long spine in *Histiopterus*, *Pentaceropsis*, *Pentaceros capensis*, *P. decacanthus*, and *Pseudopentaceros wheeleri*, while it lacks a spine in *Zanclistius*, *Evistias*, *Parazanclistius*, *Paristiopterus*, *Pentaceros japonicus*, *P. quinquespinis*, and *Pseudopentaceros richardsoni*.

The second preural centrum is located anterior to the urostyle. It bears a short neural spine dorsally in most pentacerotids, whereas it has a long neural spine in *Pentaceropsis recurvirostris*. The third preural centrum is situated anterior to the second preural centrum and bears a long neural spine dorsally. The hemal spines on the second and third preural centra are free from the centra.

The caudal skeleton has the following six distal cartilaginous: inter-neural spine 4 cartilage of preural centra (CINPU4); post-epural 2 and/or 3 cartilage (CPEP2, 3); post-hypural 5 cartilage (CPHY 5); post-hemal spine 2 cartilage of preural centra (CPHPU 2); interhemal spine 3 cartilage of preural centra (CPHPU 3); and interhemal spine 4 cartilage of preural centra (CIHPU 4) (*sensu* Fujita, 1990).

Synapomorphies of Pentacerotidae

None.

Character recognition

TS 35. Number of branched caudal fin rays supported by the upper caudal lobe. (0: 8; 1: 9; 2: 10) (ordered)

Ingroup. The upper caudal lobe supports eight branched fin rays in *Parazanclistius hutchinsi* and *Pentaceros capensis* (character 35-0), nine in *Histiopterus typus*, *Paristiopterus labiosus*, *P. gallipavo*, *Pentaceros decacanthus*, *P. japonicus*, *P. quinquespinis*, *Pseudopentaceros richardsoni*, and *P. wheeleri* (character 35-1), and 10 in *Zanclistius elevatus*, *Evistias acutirostris*, and *Pentaceropsis recurvirostris* (character 35-2).

Outgroup. The upper caudal lobe supports eight branched fin rays in typical percoids (character 35-0) (e.g., Johnson, 1984; Yabe, 1985; Fujita, 1990; pers. obs.).

TS 36. Number of branched caudal fin rays supported by the lower caudal lobe. (0: 7; 1: 8)

Ingroup. The lower caudal lobe supports seven branched fin rays in most pentacerotids (character 36-0), whereas it supports eight branched rays in *Zanclistius elevatus* and *Pentaceropsis recurvirostris* (character 36-1).

Outgroup. The lower caudal lobe supports seven branched fin rays in typical percoids (character 36-0) (e.g., Katayama, 1959; Patterson, 1968; Yabe, 1985; pers. obs.).

TS 37. Parhypurapophysis. (0: sharp; 1: robust)

Ingroup. The parhypurapophysis is sharp in most pentacerotids (character 37-0), whereas it is robust in *Pentaceros* and *Pseudopentaceros* (character 37-1).

Outgroup. The parhypurapophysis is sharp in typical percoids (character 37-0) (e.g., Fujita, 1990; Hilton and Johnson, 2007; pers. obs.).

TS 38. Posterior portion of the urostyle. (0: having spine; 1: lacking spine)

Ingroup. The posterior portion of the urostyle has a long spine in *Histiopterus*, *Pentaceropsis*, *Pentaceros capensis*, *P. decacanthus*, and *Pseudopentaceros wheeleri* (character 38-0), while it lacks the spine in *Zanclistius*, *Evistias*, *Parazanclistius*, *Paristiopterus*, *Pentaceros japonicus*, *P. quinquespinis*, and *Pseudopentaceros richardsoni* (character 38-1).

Outgroup. The urostyle has a long spine in typical percoids (character 38-0) (e.g., Sasaki, 1989; Fujita, 1990; pers. obs.).

Other variations

Fusion of hypural. Five hypurals are usually separated from each other in most pentacerotids, as well as in typical percoids (e.g., Tominaga 1968; Sasaki, 1989; pers. obs.), while the third and fourth hypurals are fused in *Paristiopterus labiosus*. Therefore, the latter condition can be treated as an autapomorphy of this species and is not used for the phylogenetic analysis.

Number of uroneurals. There are two of the uroneurals in most pentacerotids, whereas there is only one in *Pentaceros capensis*. The character in *Pentaceros capensis* is regarded as an autapomorphy of this species, because one uroneural is not a typical condition in percoids (e.g., Sasaki, 1989; Fujita, 1990; pers. obs.). Therefore, this feature is excluded from the analysis.

Long neural spine of second preural centrum. The second preural centrum bears a long neural spine dorsally in *Pentaceropsis recurvirostris*. In contrast, the neural spine is short in other pentacerotids. The former condition is regarded as an apomorphy, because it is not found in typical percoids (e.g., Sasaki, 1989; Fujita, 1990; pers. obs.).

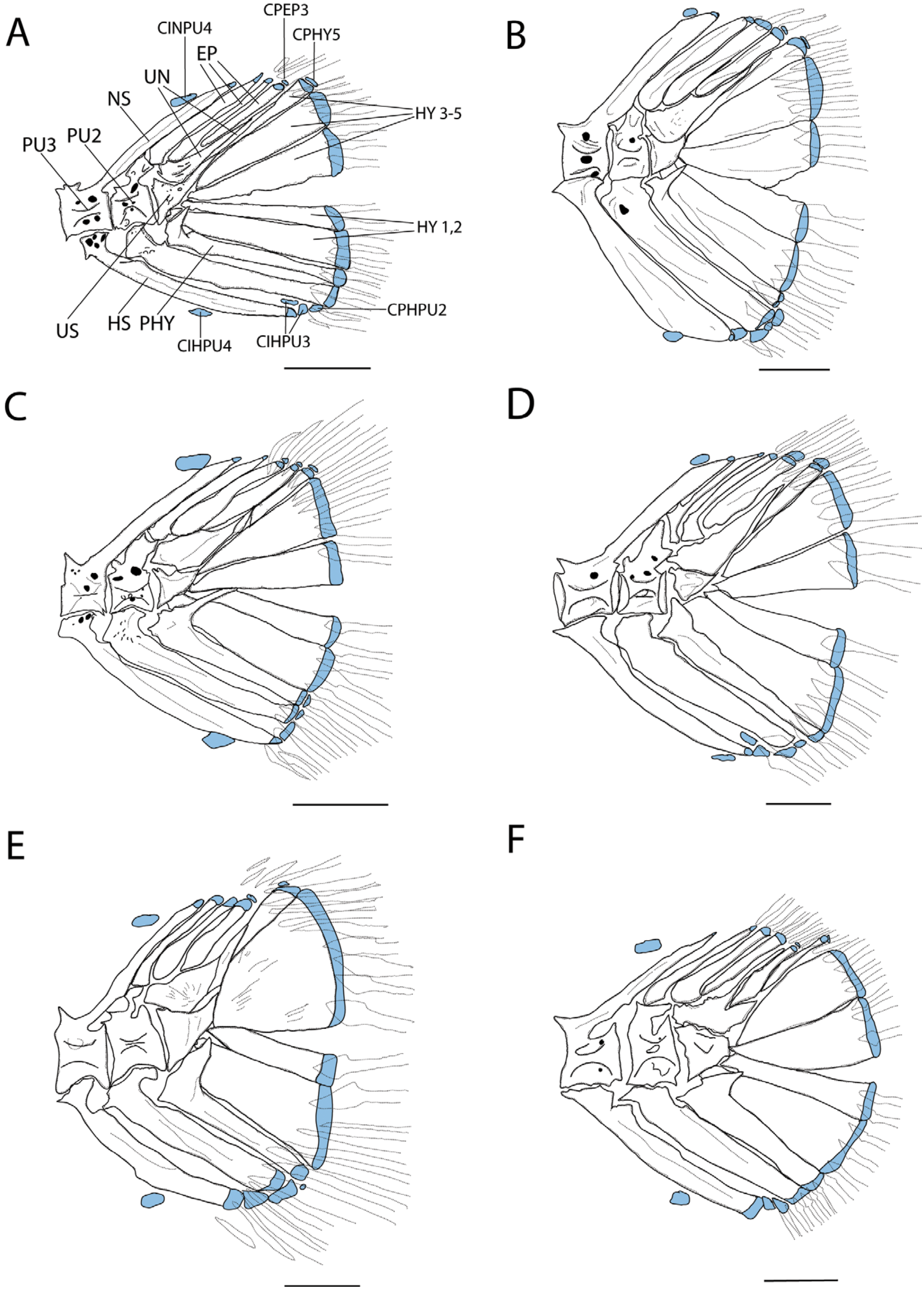

FIGURE 43. Lateral aspects of the caudal skeleton. A, *Histiopterus typus*; B, *Zanclistius elevatus*; C, *Evistias acutirostris*; D, *Parazanclistius hutchinsi*; E, *Paristiopterus labiosus*; F, *P. gallipavo*. B is shown as mirror image. Scale bar = 5 mm.

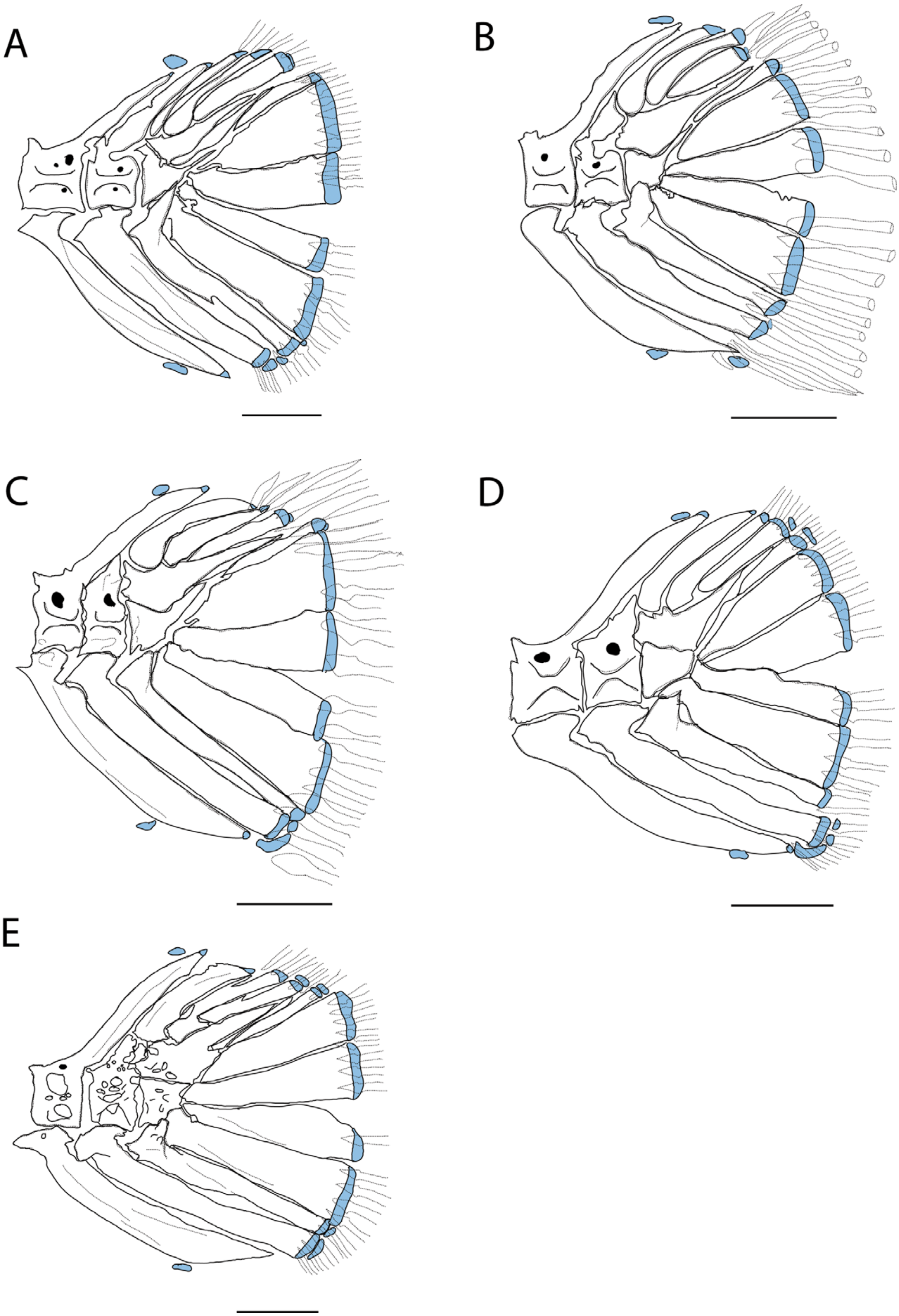

FIGURE 44. Lateral aspects of the caudal skeleton. A, *Pentaceropsis recurvirostris*; B, *Pentaceros capensis*; C, *P. decacanthus*; D, *P. japonicus*; E, *P. quinquespinis*. A to C are shown as mirror images. Scale bar = 5 mm.

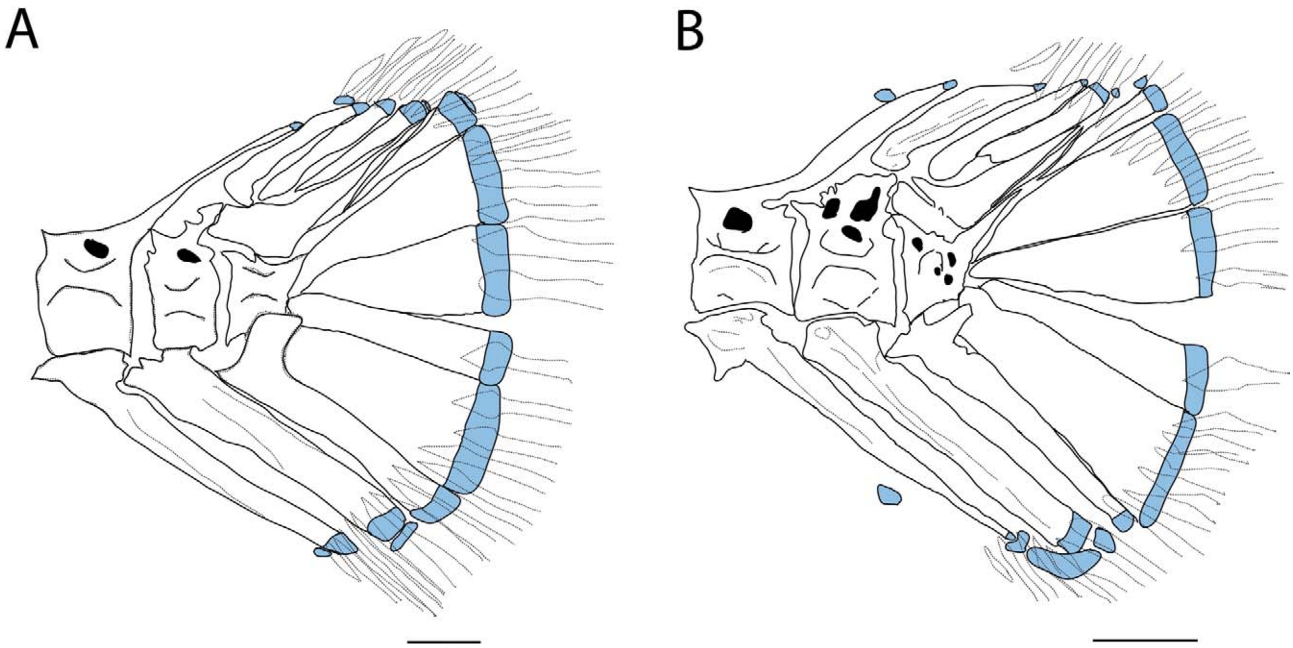

FIGURE 45. Lateral aspects of the caudal skeleton. A, *Pseudopentaceros richardsoni*; B, *P. wheeleri*. A is shown as a mirror image. Scale bar = 5 mm.

It is an autapomorphy of *Pentaceropsis recurvirostris*, however, and is therefore excluded from the phylogenetic analysis.

2. Myology

2-1. Cheek muscle

(Figs. 46–48)

Description

The cheek muscle consists only of the adductor mandibulae, a large muscle comprising four sections: A1, A2, A3, and Aw.

Section A1 overlies the dorsolateral part of the sections A2 and A3. It originates from the hyomandibula and anterodorsal surface of the preopercle, and inserts onto the ventromedial surface of the maxilla by a strong tendon. This section also inserts onto the ligamentum primordium ventrally. The anterodorsal portion of this section is medially connected with the sections A2 and A3 by a strong tendon.

Section A2 is located on the ventrolateral part of the cheek region. It originates from the ventrolateral part of the preopercle and is usually fused with section A3 anteromedially. This section is inserted onto the lateral surface of the coronomeckelian.

Section A3 is not well separated from section A2. It originates from the lateral surface of the metapterygoid, symplectic, quadrate, and hyomandibular, and inserts onto the posteroventral surface of the Meckelian cartilage.

The section Aw is located on the medial surface of the lower jaw. The Aw is quite expanded dorsally and fused by a tendon with section A3 posterodorsally in most pentacerotids, whereas it is separated from section A3 in *Histiopterus*, *Zanclistius*, *Evistias*, *Parazanclistius*, *Paristiopterus*, and *Pentaceropsis*. Section Aw originates from the medial surface of the dentary and anguloarticular, and inserts onto the medial surface of the quadrate by a strong tendon.

Synapomorphies of Pentacerotidae

None.

Character recognition

TS 39. Relationship between sections Aw and A3. (0: fused; 1: separated)

Ingroup. Section Aw is quite expanded dorsally and fused by a tendon with section A3 posterodorsally in most pentacerotids (character 39-0), whereas it is separated from section A3 in *Histiopterus*, *Zanclistius*, *Evistias*, *Parazanclistius*, *Paristiopterus*, and *Pentaceropsis* (character 39-1).

Outgroup. The Aw is fused with A3 or a muscle formed by A2 and A3 in typical percoids (character 39-0) (e.g., Johnson, 1980; Yabe, 1985; Gosline, 1989; Kim, 2002; pers. obs.).

Other variations

None.

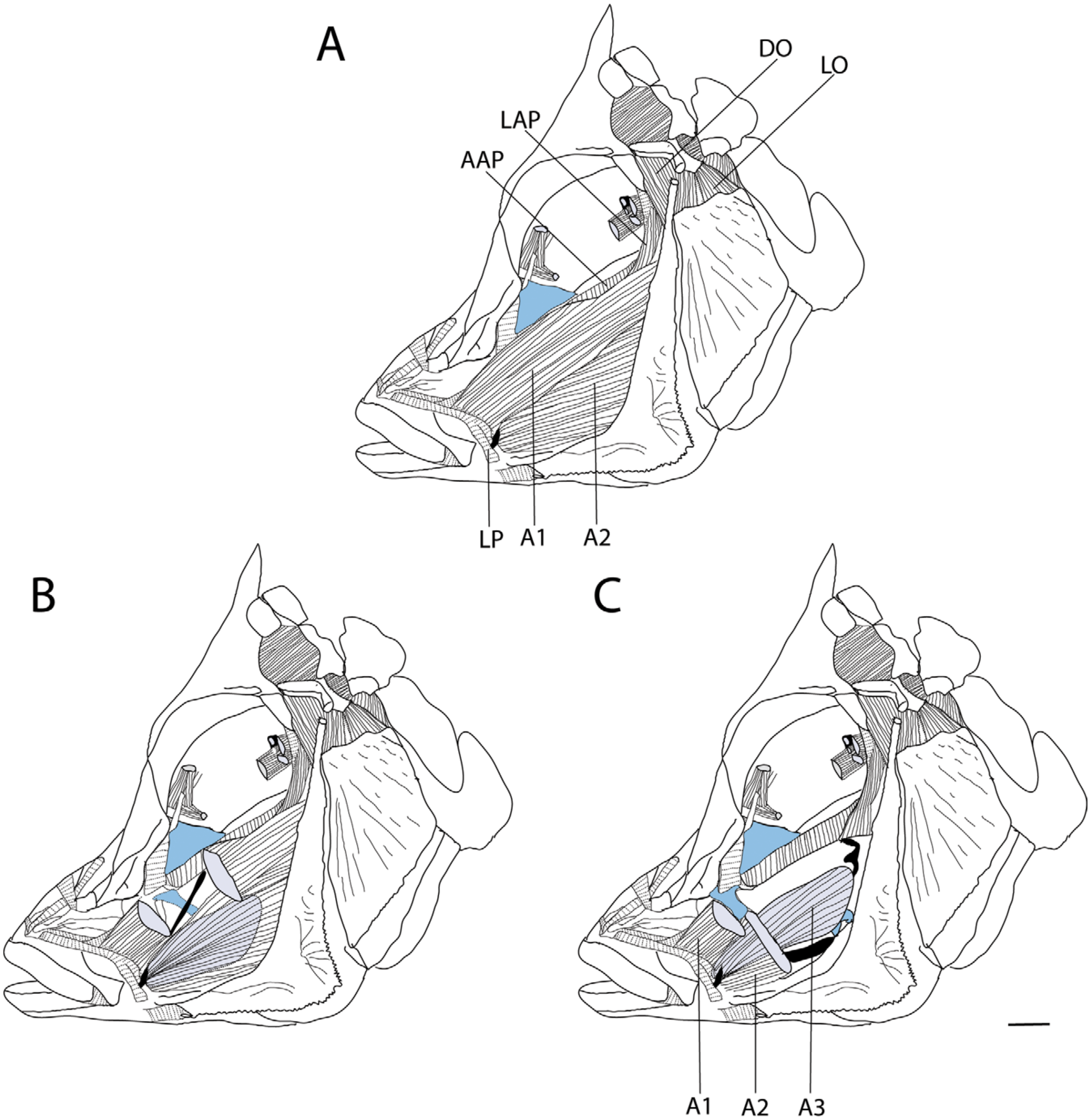

FIGURE 46. Lateral aspect of the cheek and other cephalic muscles in *Histiopterus typus*. A, superficial aspect; B, lateral aspect after the removal of A1; B, lateral aspect after the removal of A1 and A2. Scale bar = 5 mm.

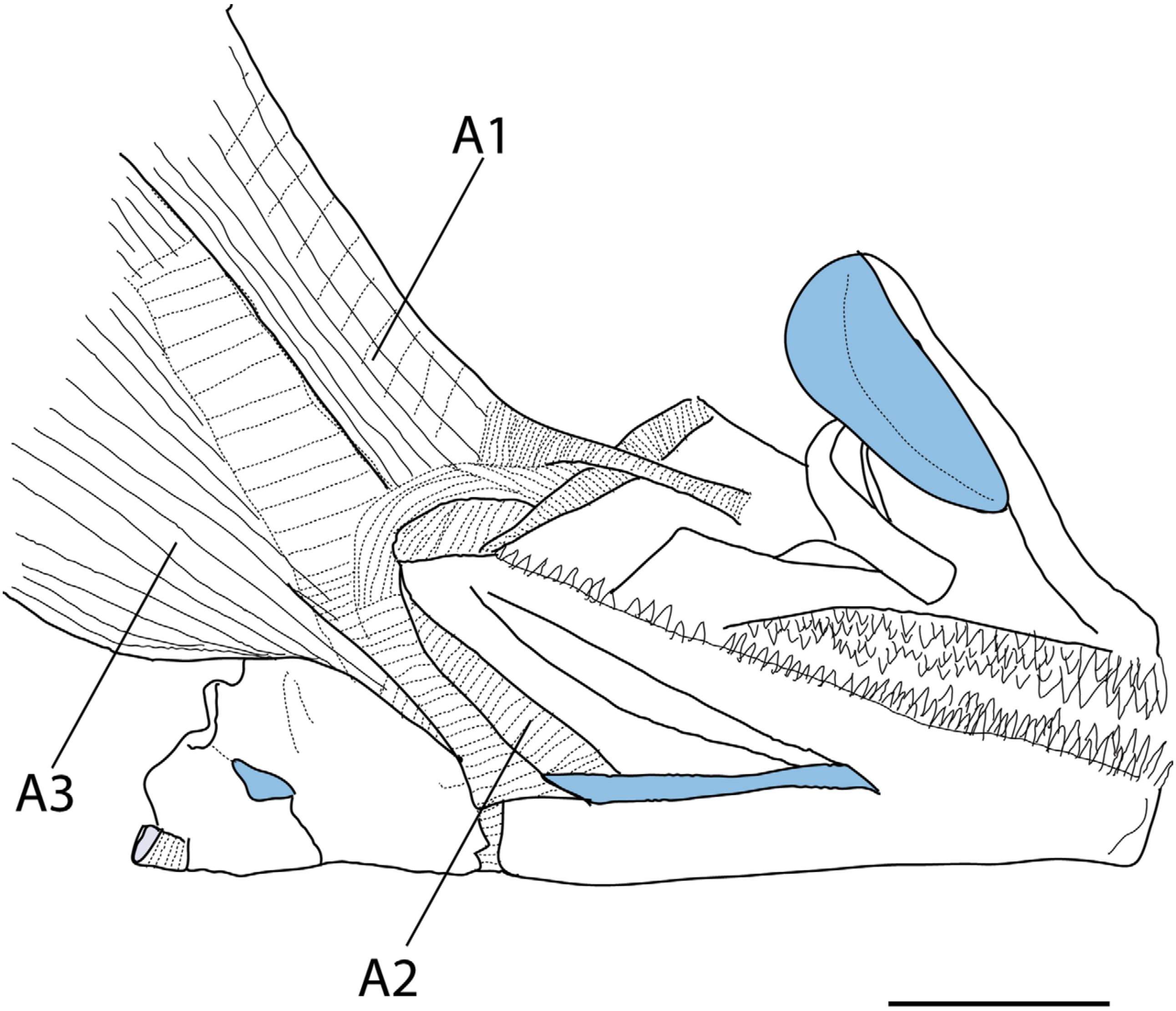

FIGURE 47. Medial aspect of the adductor mandibulae in *Zanclistius elevatus* (after removal of Aw, IM, and PH). Shown as a mirror image. Scale bar = 5 mm.

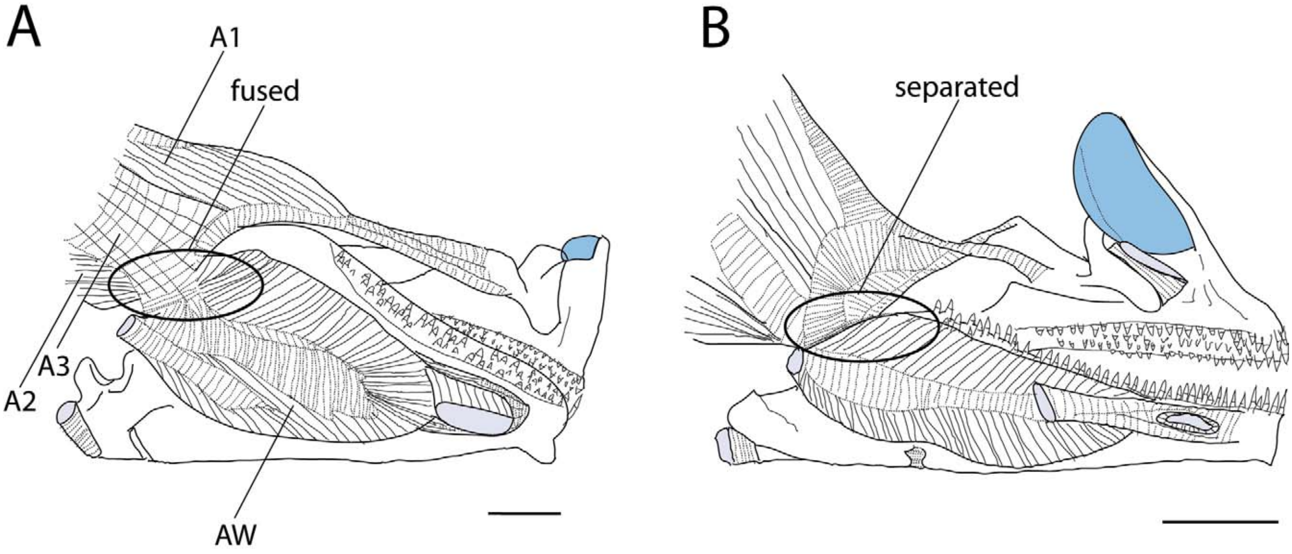

FIGURE 48. Medial aspects of the adductor mandibulae section w. A, *Pseudopentaceros wheeleri*; B, *Zanclistius elevatus*. B is shown as a mirror image. Scale bar = 5 mm.

2-2. Cephalic muscles between neurocranium and suspensorium-operculum
(Figs. 49, 50)

Description
The cephalic muscles between the neurocranium and suspensorium-operculum consist of the levator arcus palatini, adductor arcus palatini, dilatator operculi, adductor operculi, adductor hyomandibulae, and levator operculi.

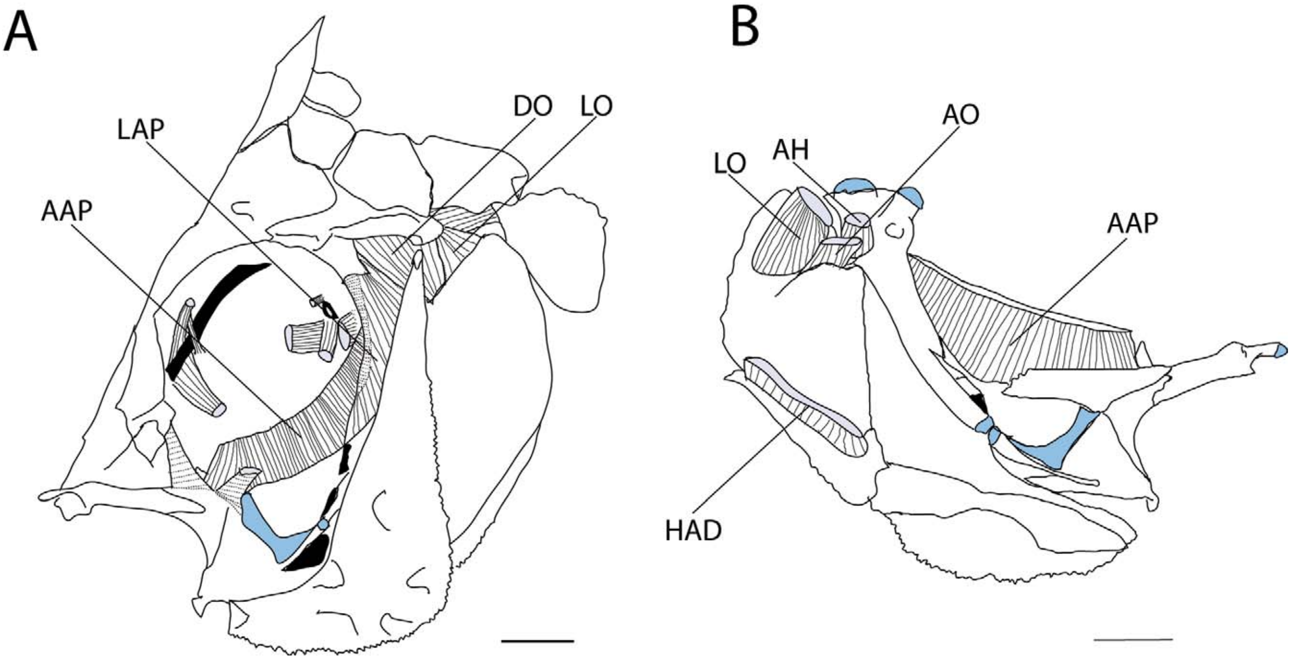

FIGURE 49. Lateral aspect of the cephalic muscles (A) and medial aspect of the suspensorium and related muscles (B) of *Pentaceros japonicus*. Scale bar = 5 mm.

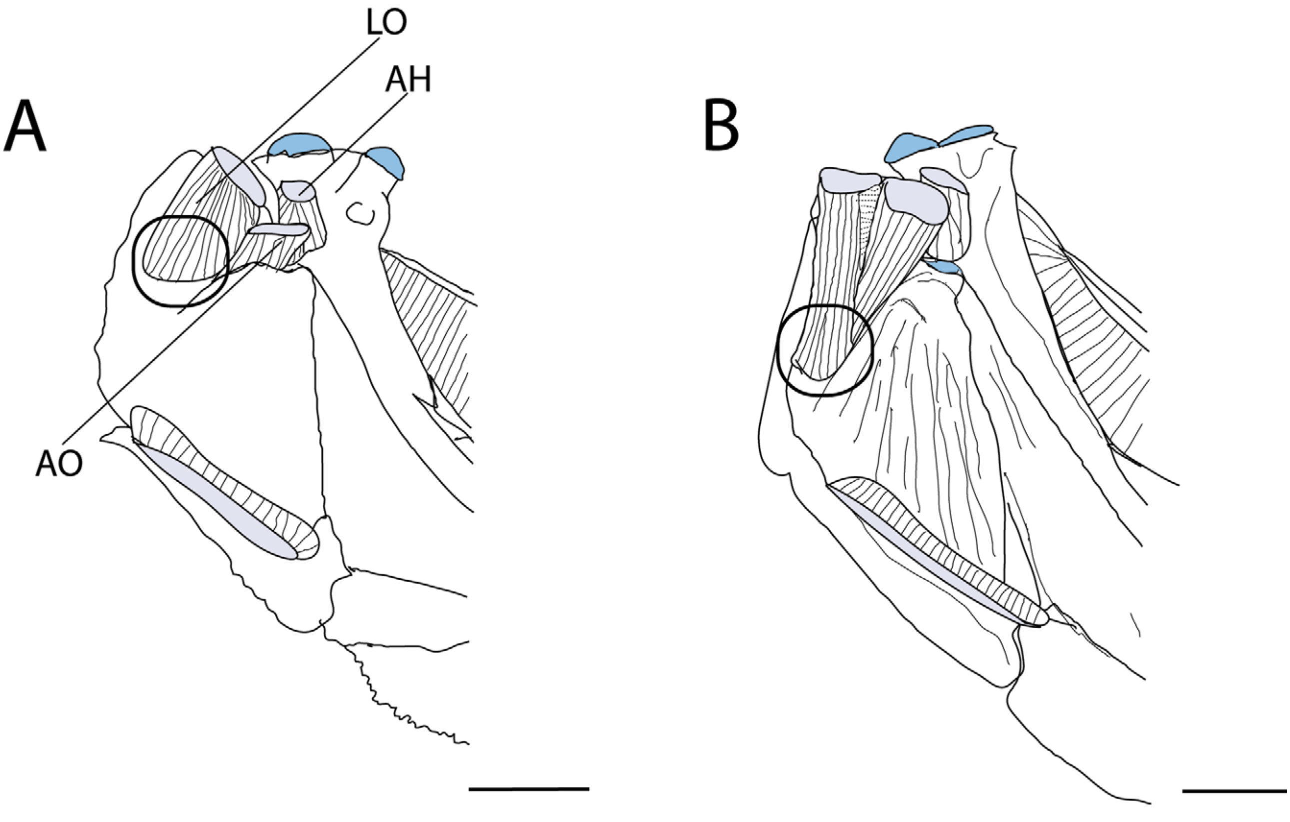

FIGURE 50. Medial aspect of the opercular muscles. A, *Pentaceros japonicus*; B, *Evistias acutirostris*. Scale bar = 5 mm.

The levator arcus palatini is situated on the posterodorsal region of the suspensorium. It originates from the sphenotic and inserts onto the lateral surface of the preopercle, hyomandibular, and metapterygoid.

The adductor arcus palatini is located below the posteroventral region of the orbit and extends to the anterior portion of the endopterygoid. This muscle connects the parasphenoid with the hyomandibular, endopterygoid, and metapterygoid.

The dilatator operculi originates from the sphenotic and pterotic, and inserts onto the anterior corner of the opercle.

The adductor operculi connects the posteroventral surface of the pterotic to the medial surface of the anterodorsal part of the opercle.

The adductor hyomandibulae, connecting with the adductor operculi posteriorly, originates from the lateral surface of the prootic and inserts onto the medial surface of posterodorsal part of the hyomandibular.

The levator operculi originates from the posterolateral margin of the pterotic and inserts onto the dorsomedial part of the opercle in most pentacerotids, whereas it inserts onto the posteromedial part of the opercle in *Histiopterus*, *Zanclistius*, and *Evistias*.

Synapomorphies of Pentacerotidae

None.

Character recognition

TS 40. Insertion of the levator operculi onto the opercle. (0: dorsomedial part; 1: posteromedial part)

Ingroup. The levator operculi inserts onto the dorsomedial part of the opercle in most pentacerotids (character 40-0), whereas it inserts onto the posteromedial part of the opercle in *Histiopterus*, *Zanclistius*, and *Evistias* (character 40-1).

Outgroup. The levator operculi inserts onto the dorsomedial part of the opercle in typical percoids (character 40-0) (e.g., Winterbottom, 1974; Johnson, 1980; Yabe, 1985; pers. obs.).

Other variations

None.

2-3. Ventral muscles of head

(Figs. 51–53)

Description

The ventral muscles of head comprise the intermandibularis, protractor hyoidei, hyohyoidei abductors, and hyohyoidei adductores.

The intermandibularis is a membranous muscle that connects the anteromedial portions of both dentaries.

The protractor hyoidei is an elongated muscle. It is separated into two layers anteriorly, which originate from the anteromedial portion of dentary via a short tendon and sandwich the intermandibularis. This muscle inserts the posterolateral surface of the ceratohyal, and third and fourth branchiostegal rays posteriorly.

The hyohyoidei abductores consist of two sections. Muscular masses of section 1 originate from the anteroventral part of the ceratohyal and insert onto the proximal parts of the branchiostegal rays. The muscular masses of section 2 interconnect the ventral hypohyal with the first branchiostegal ray of the opposite side. Bundles of section 2 on both sides cross each other.

The hyohyoidei adductores are sheet-like muscles, and connect the branchiostegal rays with the posteroventromedial aspect of the opercle and subopercle.

Synapomorphies of Pentacerotidae

None.

Character recognition

No variations were recognized that were useful for the phylogenetic analysis.

Other variations

None.

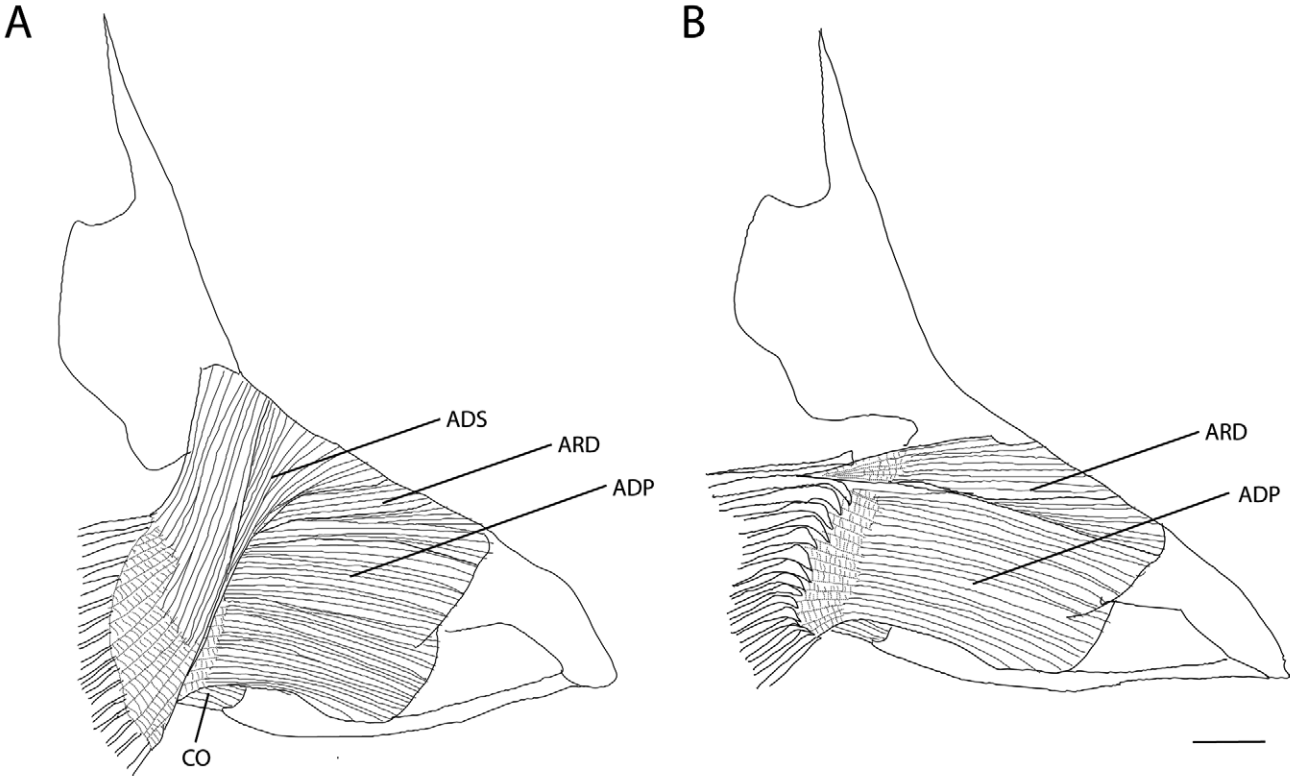

FIGURE 51. Ventral aspect of the ventral muscles in the head in *Evistias acutirostris*. Scale bar = 5 mm.

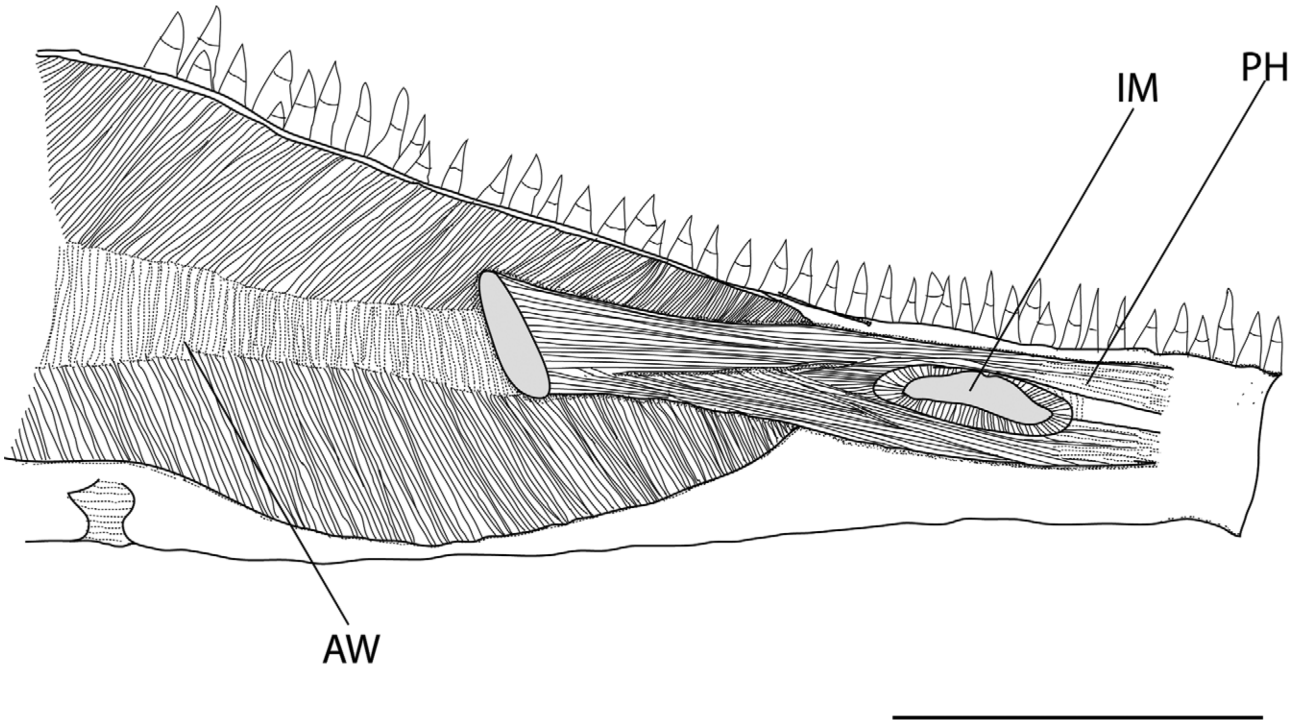

FIGURE 52. Medial aspect of the lower jaw; showing anterior ventral muscles of the head in *Zanclistius elevatus*. Shown as a mirror image. Scale bar = 5 mm.

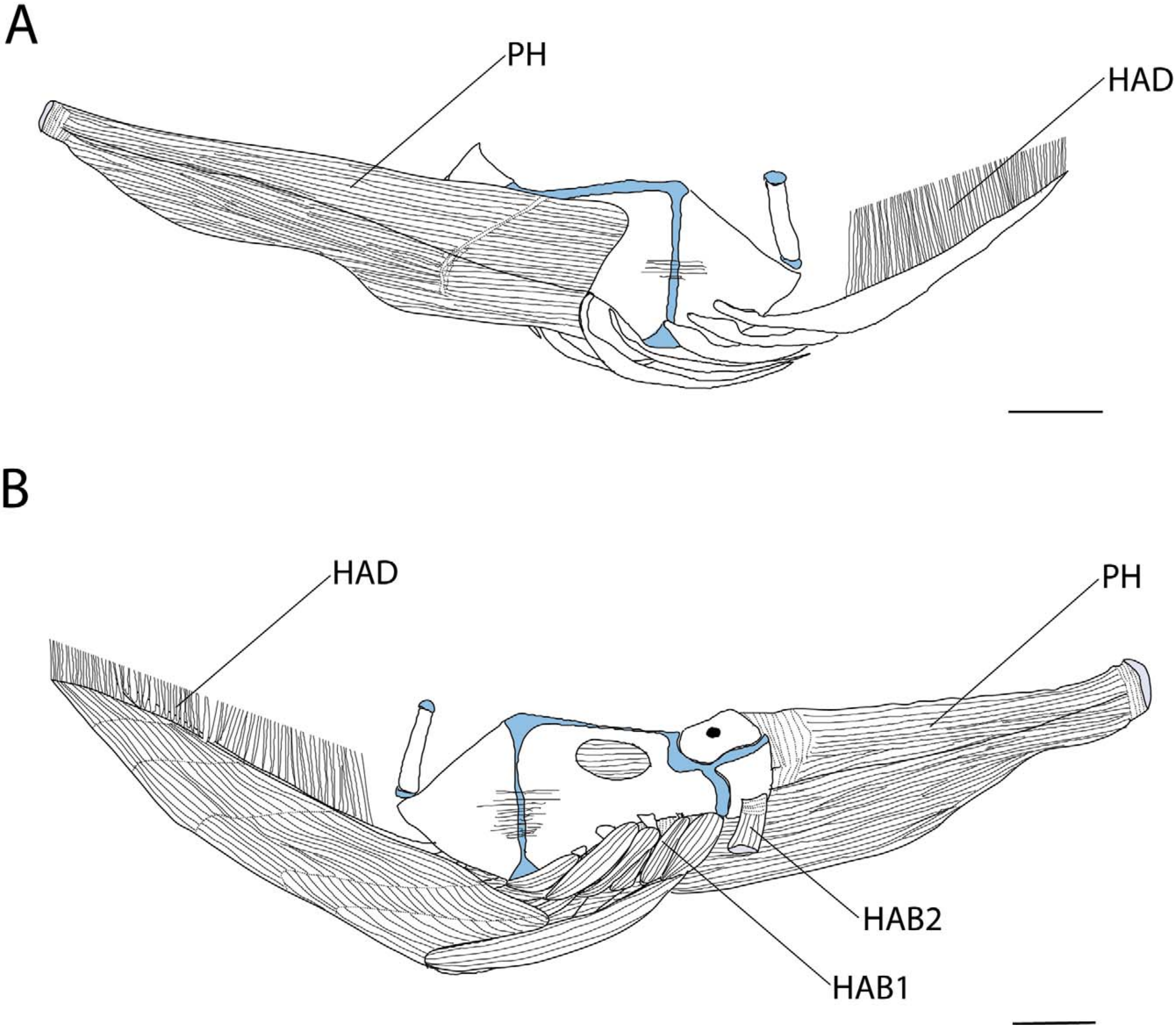

FIGURE 53. Lateral (A) and medial (B) aspects of the hyoid arch; showing ventral muscles of the head in *Evistias acutirostris*. Scale bar = 5 mm.

2-4. Branchial muscles

(Figs. 54–57)

Description

The branchial muscles consist of the levatores externi, levatores interni, levator posterior, transversus dorsalis, obliqui dorsales, retractor dorsalis, rectus communis, rectus ventralis, obliquus ventralis, transversus ventralis, sphincter esophagi, obliquus posterior, pharyngoclaviculares, and adductor.

The levatores externi comprise four elements. These elements commonly originate from the prootic and pterotic, and insert onto the dorsal aspect of each epibrancial.

The levatores interni are comprised of anterior and posterior elements. They originate from the prootic and pterotic, just medial to the origin of the levatores externi. The anterior element inserts onto the dorsal surface of the second pharyngobranchial, and the posterior element onto the third pharyngobranchial.

The levator posterior is a slender muscle bundle. It originates from the lateral surface of the intercalar, and inserts onto the posterodorsal surface of the fourth epibranchial.

The transversi dorsales consist of two elements, the transversus dorsalis anterior and posterior. The transversus dorsalis anterior is a pad-like muscle. The medial portion of this element is replaced by a tendon, and connects with the midline of the parasphenoid and basioccipital. It is laterally divided into the two branches, the transversus pharyngobranchialis 2 and the transversus epibranchialis 2 (*sensu* Springer and Johnson, 2004). Transversus pharyngobranchialis 2 lies onto the dorsal surface of the second epibranchials and second pharyngobranchials, and the transversus epibranchials 2 is circular. The transversus dorsalis posterior lies under the obliqui dorsales, connecting the third epibranchial and third pharyngobranchial of each side.

The obliqui dorsalis connects the posterodorsal surface of the third pharyngobranchial, and the dorsal surface of the third and fourth epibranchials. The anterior portion of this muscle is covered with the transversus dorsalis anterior.

The retractor dorsalis originates from the posteromedial surface of the third and fourth pharyngobranchials, and inserts onto the ventrolateral part of the first and/or second abdominal vertebrae in most pentacerotids, while it inserts onto the ventrolateral part of the first to third abdominal vertebra in *Paristiopterus gallipavo* and *Pentaceropsis recurvirostris.*

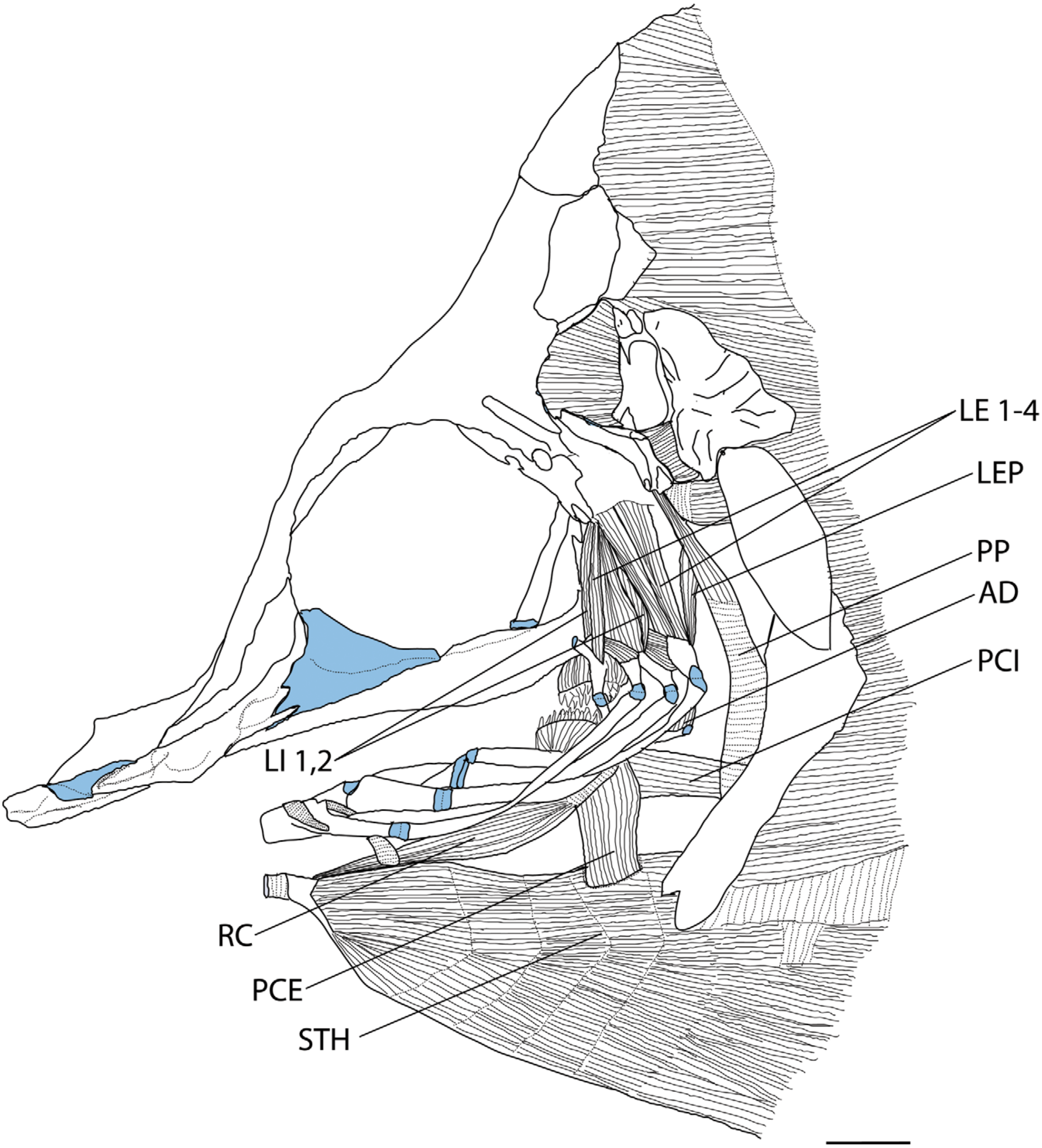

FIGURE 54. Lateral aspect of the branchial muscles in *Zanclistius elevatus*. Shown as a mirror image. Scale bar = 5 mm.

The rectus communis originates form the dorsal process of the urohyal, and inserts onto the fifth ceratobranchial via a tendon.

The rectus ventralis originates from the ventral surface of the fourth ceratobranchial, and inserts onto the ventral process of the third hypobranchial.

The obliqui ventrales comprises three elements. The three elements interconnect ventral surfaces of the first to third hypobranchials with the first to third ceratobranchials, respectively.

The transversi ventrales comprises two elements, the transversus ventralis anterior and posterior. The transversus ventralis anterior lies between the fourth ceratobranchials, and the transversus ventralis posterior between the fifth ceratobranchials.

The sphincter esophagi encircles the esophagus in the posterior region of the branchial arch.

The obliquus posterior connects the posterior surface of the fourth epibranchial with the posteromedial surface of the fifth ceratobranchial.

The pharyngoclaviculares, comprising the pharyngoclavicularis externus and internus, connect the cleithrum and fifth ceratobranchial. The externus element originates from the anteroventral surface of the cleithrum and inserts onto the ventral surface of the fifth ceratobranchial. The externus origin is sandwiched by the posterior portion of the sternohyoideus. The internus element originates from the anteromedial surface of cleithrum, and inserts onto the ventral surface of the fifth ceratobranchial.

The adductores comprise two elements. Adductor 4 interconnects the fourth epibranchial and the fourth ceratobranchial, and adductor 5 interconnects the fourth and fifth ceratobranchials.

Synapomorphies of Pentacerotidae

SA. 9. Pad-like bundle of transversus dorsalis anterior.

The transversus dorsalis anterior is a pad-like branch of muscle in pentacerotids. These conditions are considered a synapomorphy of pentacerotids, because the transversus dorsalis anterior is a bar-like unbranched muscle in typical percoids (e.g., Yabe, 1985; Sasaki, 1989; Imamura, 2004; Springer and Johnson, 2004; pers. obs.).

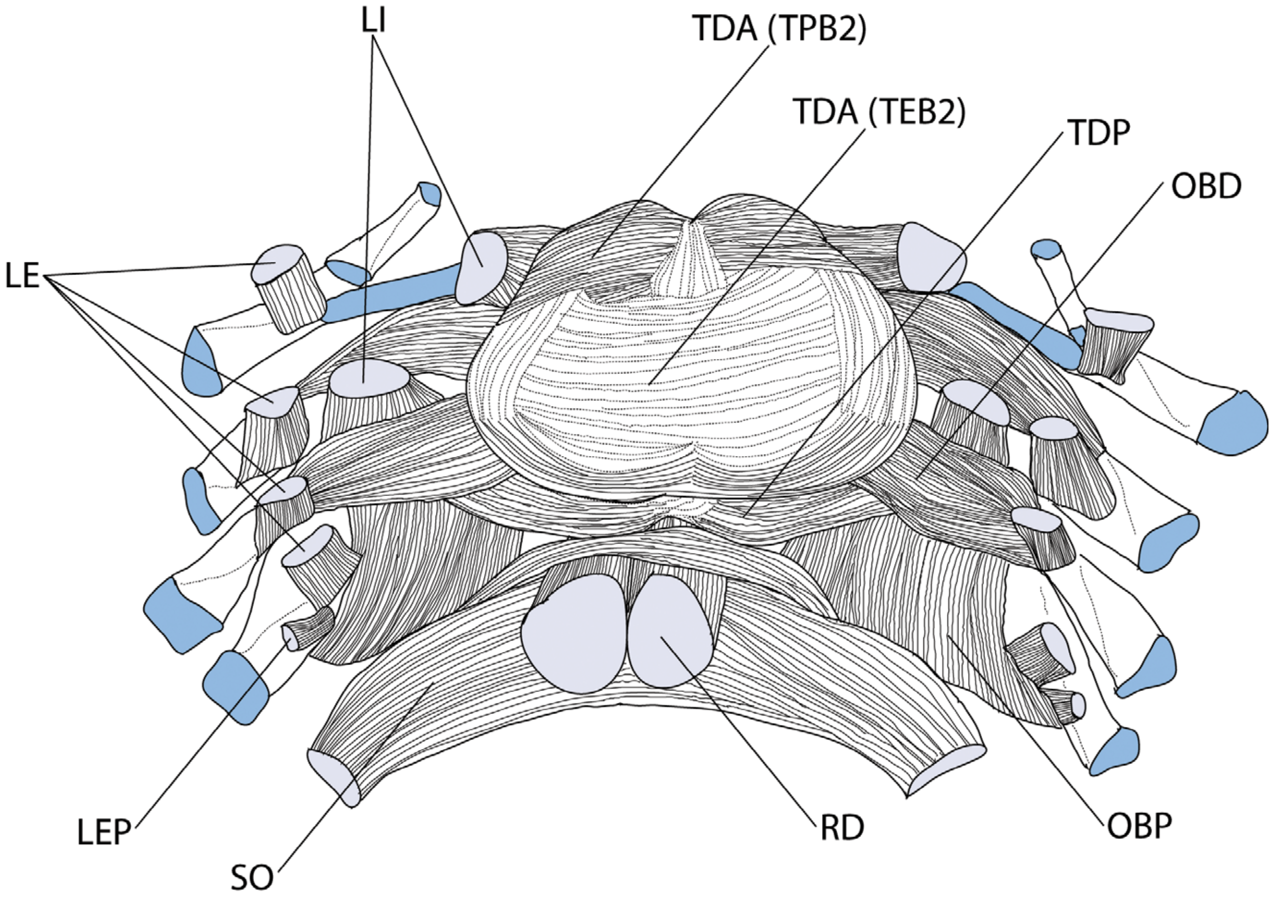

FIGURE 55. Dorsal aspect of muscles serving the upper branchial arches of *Zanclistius elevatus.* Scale bar = 5 mm.

Character recognition

TS 41. Insertion of the retractor dorsalis. (0: first and/or second vertebrae; 1: first to third vertebrae)

Ingroup. The retractor dorsalis inserts onto the ventrolateral part of the first and/or second abdominal vertebrae in most pentacerotids (character 41-0), while it inserts onto the ventrolateral part of the first to third abdominal vertebra in *Paristiopterus gallipavo* and *Pentaceropsis recurvirostris* (character 41-1).

Outgroup. The retractor dorsalis inserts onto the ventrolateral part of the first and/or second abdominal vertebrae and is not attached to the third abdominal vertebra in typical percoids (character 41-0) (e.g., Winterbottom, 1974; Gobalet, 1989; Sasaki, 1989; pers. obs.).

Other variations

None.

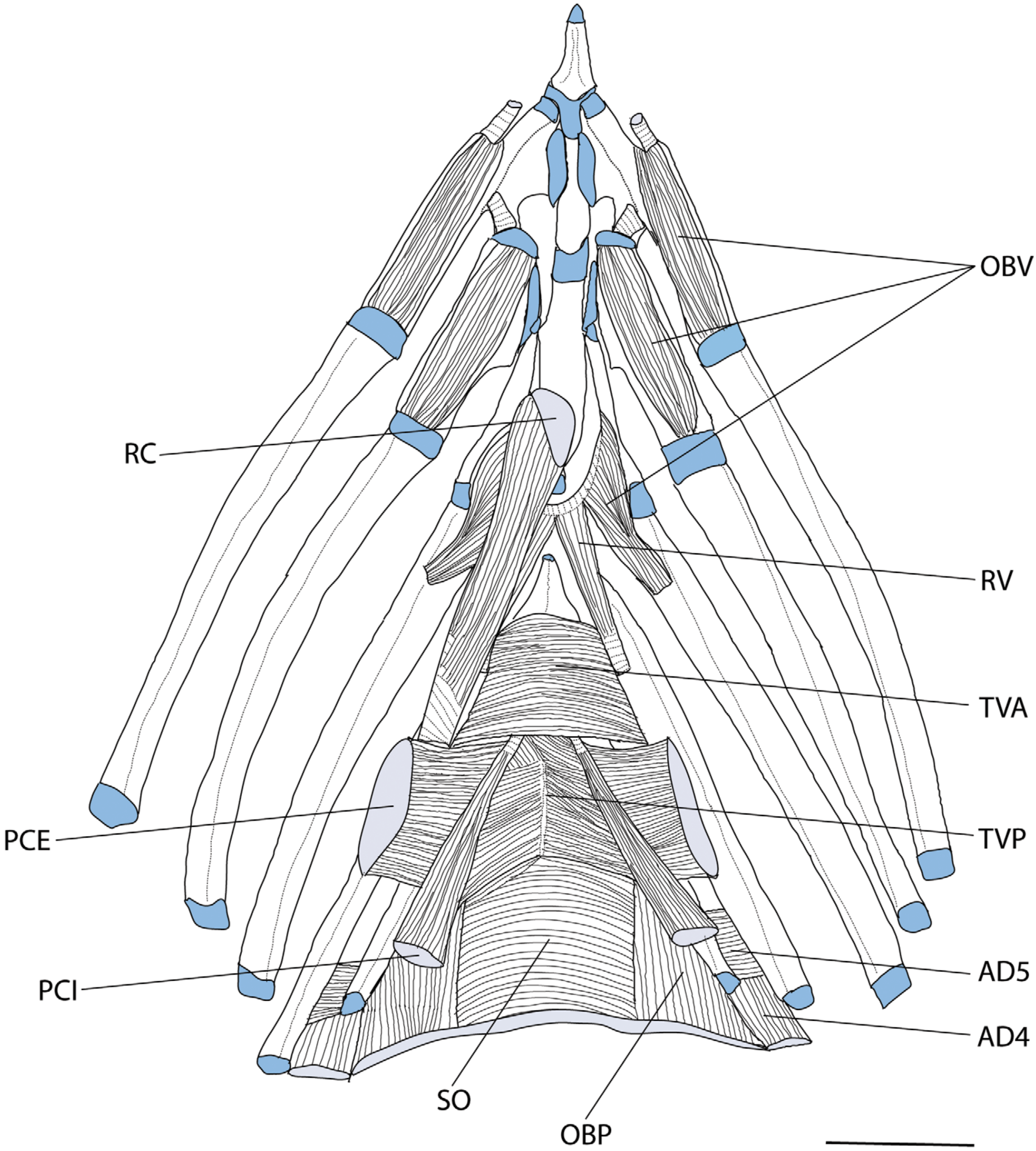

FIGURE 56. Ventral aspect of muscles serving the lower branchial arches of *Zanclistius elevatus.* Scale bar = 5 mm.

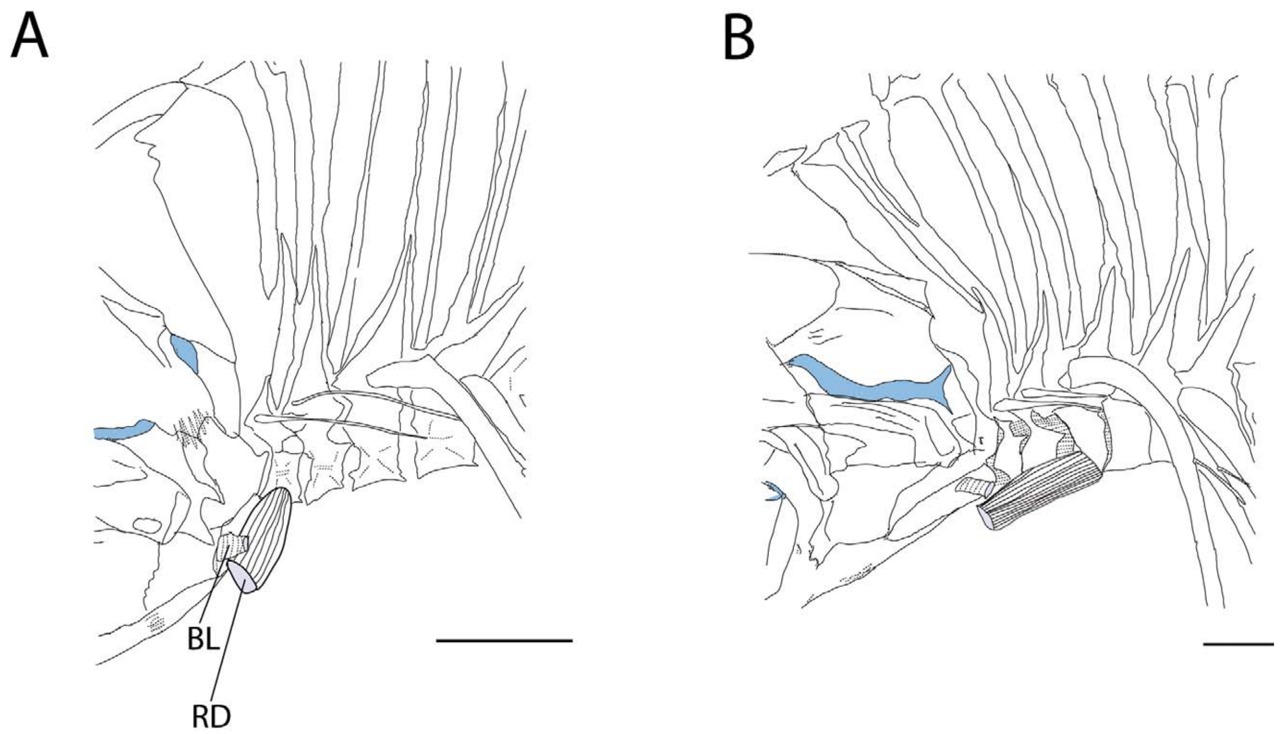

FIGURE 57. Posterior neurocranium and anterior vertebrae. A, *Pentaceros capensis*; B, *Pentaceropsis recurvirostris*. Shown as a mirror image. Scale bar = 5 mm.

2-5. Pectoral fin muscles

(Figs. 58–61)

Description

The pectoral fin muscles comprise the abductor superficialis, abductor profundus, arrector ventralis, adductor superficialis, adductor profundus, arrector dorsalis, adductor radialis, and coracoradialis. The protractor pectoralis and sternohyoideus are also described here.

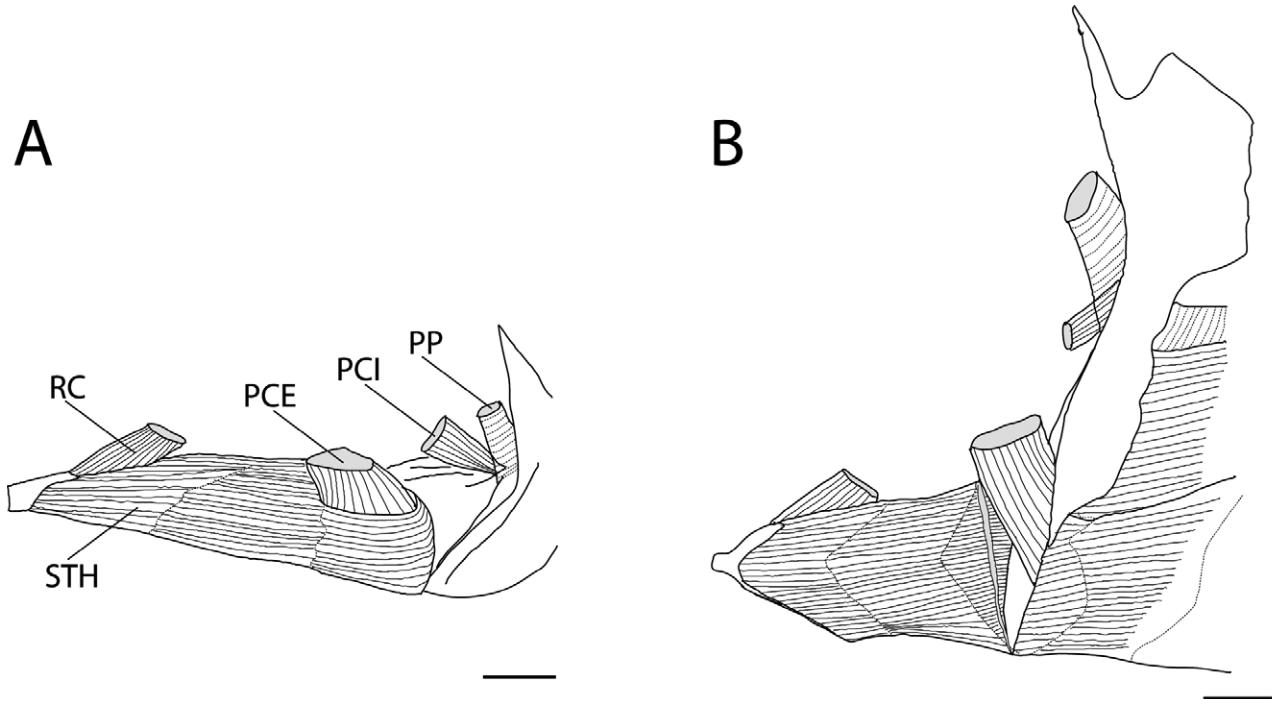

FIGURE 58. Dorsolateral (A) and lateral (B) aspects of muscles associated with pectoral girdle in *Histiopterus typus*. Scale bar = 5 mm.

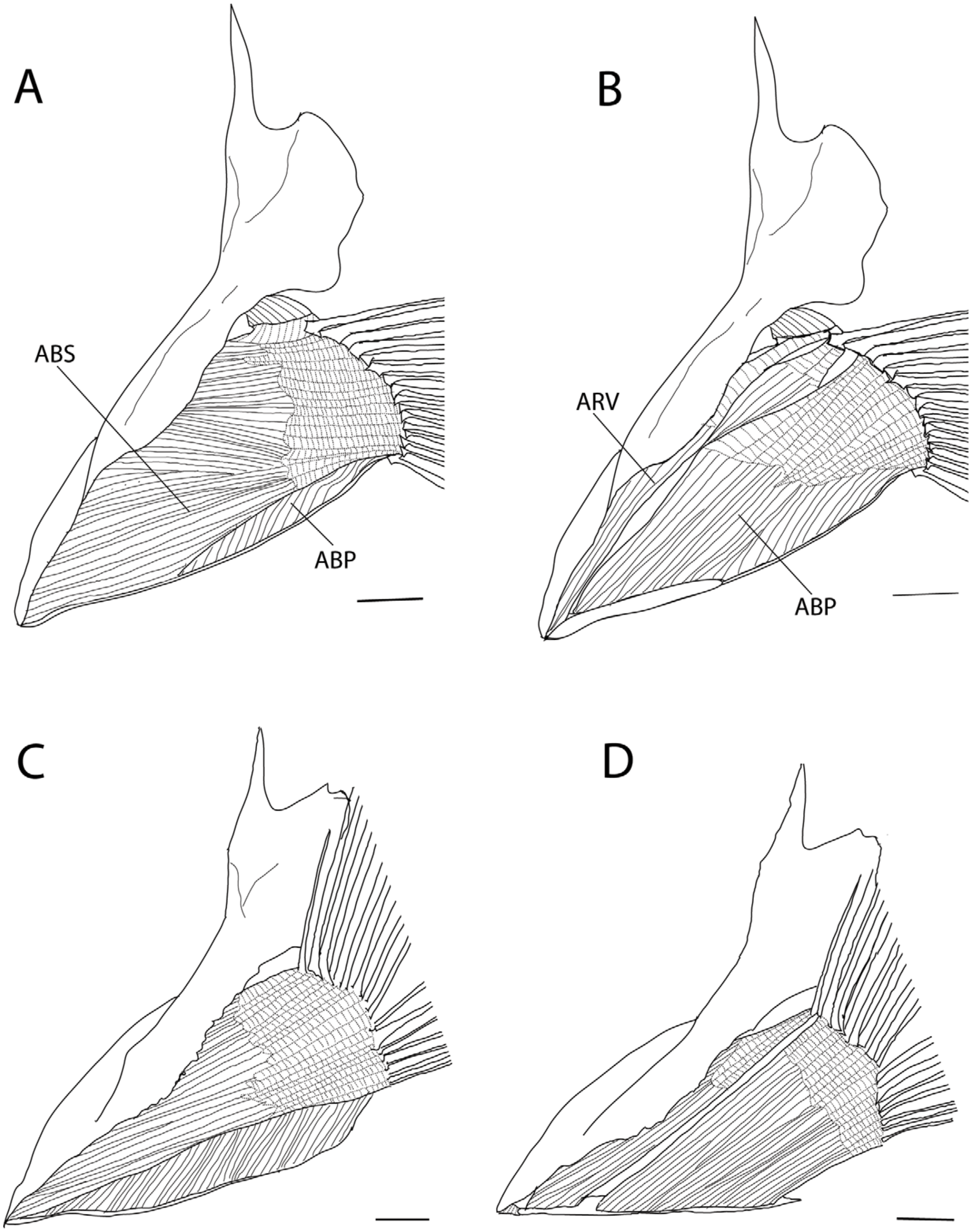

FIGURE 59. Lateral aspects of pectoral girdle. A and B, *Histiopterus typus*; C and D, *Zanclistius elevatus*. B and D, after removal of ABS. C and D shown as mirror images. Scale bar = 5 mm.

The abductor superficialis is a superficial muscle on the lateral surface of the pectoral girdle. It originates from the posterolateral surface of the cleithrum in most pentacerotids, whereas it originates from the posterolateral surface of the cleithrum and anterior region of the coracoid in *Histiopterus*, *Evistias*, *Paristiopterus*, and *Pentaceros japonicus*. This muscle inserts onto the base of each pectoral fin ray, except for the uppermost one, via a strong tendon.

The abductor profundus is situated under the abductor superficialis. It originates from the lateral aspect of the coracoid, and inserts onto the basal portion of each ray by a strong tendon.

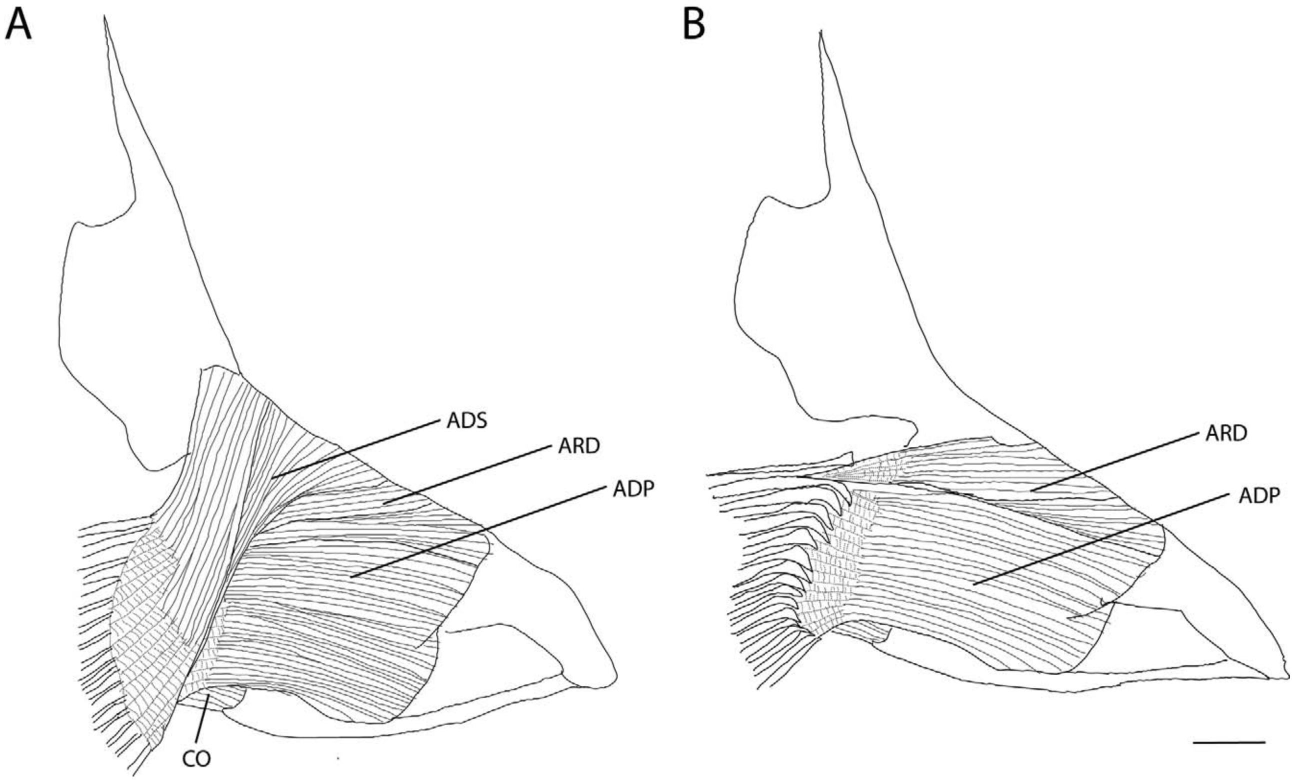

FIGURE 60. Medial aspects of pectoral girdle in *Histiopterus typus*. B, after removal of ADS. Scale bar = 5 mm.

The arrector ventralis is located on the medial aspect of the abductor superficialis and the dorsal aspect of the abductor profundus. It originates from the posterolateral surface of the cleithrum in most pentacerotids, while it originates from the posterolateral surface of the cleithrum and anterolateral surface of coracoid in *Zanclistius elevatus*, *Parazanclistius hutchinsi*, *Pentaceros japonicus*, *P. quinquespinis*, *Pseudopentaceros richardsoni*, and *P. wheeleri*. This muscle inserts onto the base of the uppermost ray.

The adductor superficialis is situated on the medial surface of the pectoral girdle. It originates from the dorsomedial surface of the cleithrum and inserts via tendons onto the medial surface of each pectoral fin ray, but not the uppermost one.

The adductor profundus is located on the lateral aspect of the adductor superficialis. This muscle originates from the medial aspect of the cleithrum and coracoid, and inserts onto each ray, but not the uppermost one.

The arrector dorsalis is situated on the dorsomedial surface of the cleithrum, and covered with the adductor superficialis. It originates from the medial surface of the cleithrum and scapula, and inserts onto the basal portion of the uppermost ray.

The adductor radialis is a small muscle situated on the medial surface of the actinosts. It originates from the medial surface of the third actinost, and inserts onto the basal portions of the lower two pectoral fin rays.

The coracoradialis is a sheet-like muscle and connects the posterior border of the coracoid and the lowermost actinost.

The protractor pectoralis, lying between the neurocranium and cleithrum, originates from the posterior process of the pterotic and inserts onto the anterodorsal margin of the cleithrum.

The sternohyoideus, a robust muscle, originates from the anteroventral portions of the cleithrum and coracoid, and inserts onto the both the lateral and ventral aspects of the urohyal.

Synapomorphies of Pentacerotidae

SA 10. Adductor radialis.

The adductor radialis originates from the medial surface of the third actinost in pentacerotids. It originates from the medial surface of all actinosts, except for the first actinost, in typical percoids (e.g., Winterbottom, 1974;

Sasaki, 1989; Kim, 2002; pers. obs.). Thus, the former condition can be regarded as a synapomorphy of the family for phylogenetic analysis.

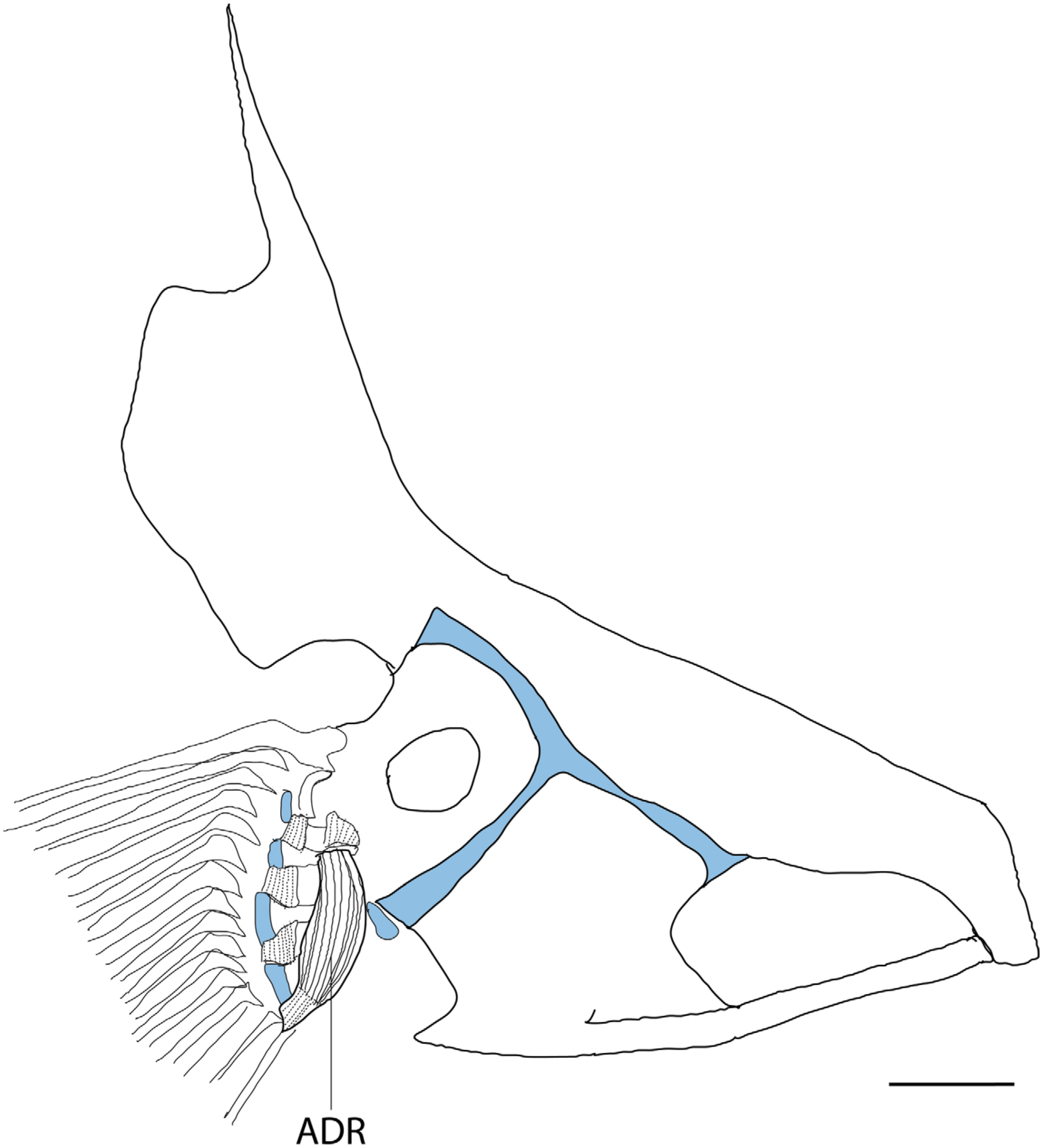

FIGURE 61. Medial aspects of pectoral girdle in *Histiopterus typus*. Scale bar = 5 mm.

Character recognition

TS 42. Origin of abductor superficialis. (0: cleithrum; 1: cleithrum and coracoid)

Ingroup. The abductor superficialis originates from the posterolateral portion of the cleithrum in most pentacerotids (character 42-0), whereas it originates from the cleithrum and coracoid in *Histiopterus*, *Evistias*, *Paristiopterus*, and *Pentaceros japonicus* (character 42-1).

Outgroup. The abductor superficialis typically originates from the cleithrum in percoids (character 42-0) (e.g., Winterbottom, 1974; Yabe, 1985; Sasaki, 1989; pers. obs.).

TS 43. Origin of arrector ventralis. (0: cleithrum; 1: cleithrum and coracoid)

Ingroup. The arrector ventralis originates from the posterolateral portion of the cleithrum in most pentacerotids (character 43-0), while it originates from the cleithrum and coracoid in *Zanclistius*, *Parazanclistius*, *Pentaceros japonicus*, *P. quinquespinis*, *Pseudopentaceros richardsoni*, and *P. wheeleri* (character 43-1).

Outgroup. The abductor superficialis typically originates from the cleithrum in percoids (character 42-0) (e.g., Winterbottom, 1974; Sasaki, 1989; Kim, 2002; pers. obs.).

Other variations

None.

2-6. Pelvic fin muscles

(Fig. 62)

Description

The pelvic fin muscles, supporting the pelvic fin rays, comprise both dorsal and ventral elements. The dorsal elements include the adductor superficialis pelvicus, adductor profundus pelvicus, arrector dorsalis pelvicus, and extensor proprius, and the ventral elements contain the abductor superficialis pelvicus, abductor profundus pelvicus, and arrector ventralis pelvicus.

The adductor superficialis pelvicus lies between the extensor proprius and the adductor profundus pelvicus, and is connected with the outer three soft rays and spine via long and strong tendons.

The adductor profundus pelvicus originates from the dorsal surface of the pelvis, and inserts onto all the soft fin ray bases.

The arrector dorsalis pelvicus originates from the lateral surface of the pelvis and inserts onto the base of the spine laterally.

The extensor proprius overlies the adductor superficialis pelvicus and adductor profundus pelvicus. This muscle inserts onto the two innermost soft fin rays.

The abductor superficialis pelvicus originates from the ventral surface of the pelvis, and inserts onto the bases of the soft fin rays by a strong tendon.

The abductor profundus pelvicus originates from the ventral surface of the pelvis, and inserts via tendons onto the bases of the first to three soft fin rays.

The arrector ventralis pelvicus, which is covered with the abductor superficialis pelvicus, originates from the lateral margin of the ventral surface of the pelvis and inserts onto the base of the spine by a strong tendon.

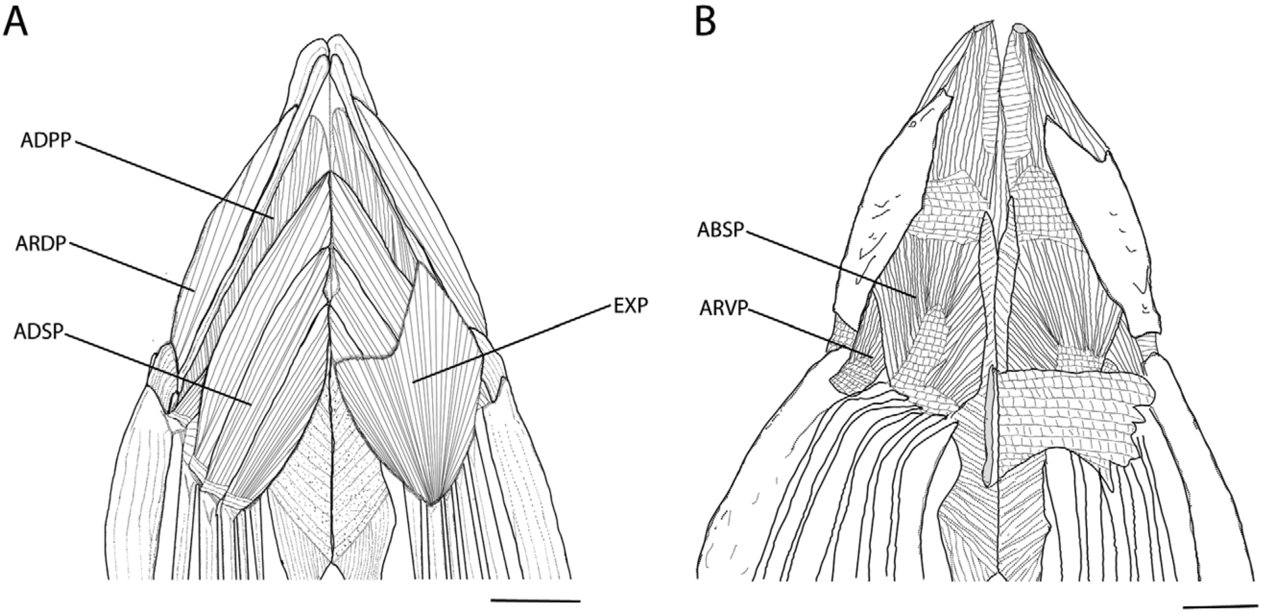

FIGURE 62. Dorsal (A) and ventral (B) aspects of the pelvic fin muscles in *Zanclistius elevatis*. A left side, after removal of the EXP. Scale bar = 5 mm.

Synapomorphies of Pentacerotidae

None.

Character recognition

No variations were recognized that were useful for the phylogenetic analysis.

Other variations

None.

2-7. Caudal fin muscles

(Fig. 63)

Description

The caudal fin muscles, supporting the caudal fin rays, comprise the interradialis, hypochordal longitudinalis, flexor dorsalis superior, flexor dorsalis, flexor ventralis, flexor ventralis externus, and flexor ventralis inferior. The adductor dorsalis is absent in all pentacerotids.

The interradialis are a series of small angled muscles interconnecting each of the fin rays. They split into dorsal and ventral elements associated with the dorsal and ventral lobes of the caudal fin, respectively.

The hypochordal longitudinalis is a triangular muscle. It originates from the anteroventral portion of hypurals, parhypural, and urostyle, and inserts onto several upper caudal fin rays via long and strong tendons. The anterolateral fibers of this muscle attach to the parhypurapophysis.

The flexor dorsalis superior originates from the epurals and neural spine of the third preural centrum, and inserts via tendons onto the posterodorsal corner of the caudal fin.

The flexor dorsalis originates from the second to fourth preural centra, hemal spines, uroneural, urostyle and the lower portion of two posterior epurals. This muscle inserts onto the bases of caudal fin rays on the upper lobe.

The flexor ventralis originates from the second and third preural centra, urostyle, lower hypurals, and parhypural, and inserts onto the bases of the caudal fin rays on the lower lobe.

The flexor ventralis externus originates from the hemal spines, and inserts onto the bases of some upper caudal fin rays on the lower lobe via a long tendon.

The flexor ventralis inferior originates from the hemal spines of the second and third preural centra, and inserts onto the caudal fin rays at the posteroventral corner of the caudal skeleton.

Synapomorphies of Pentacerotidae

None.

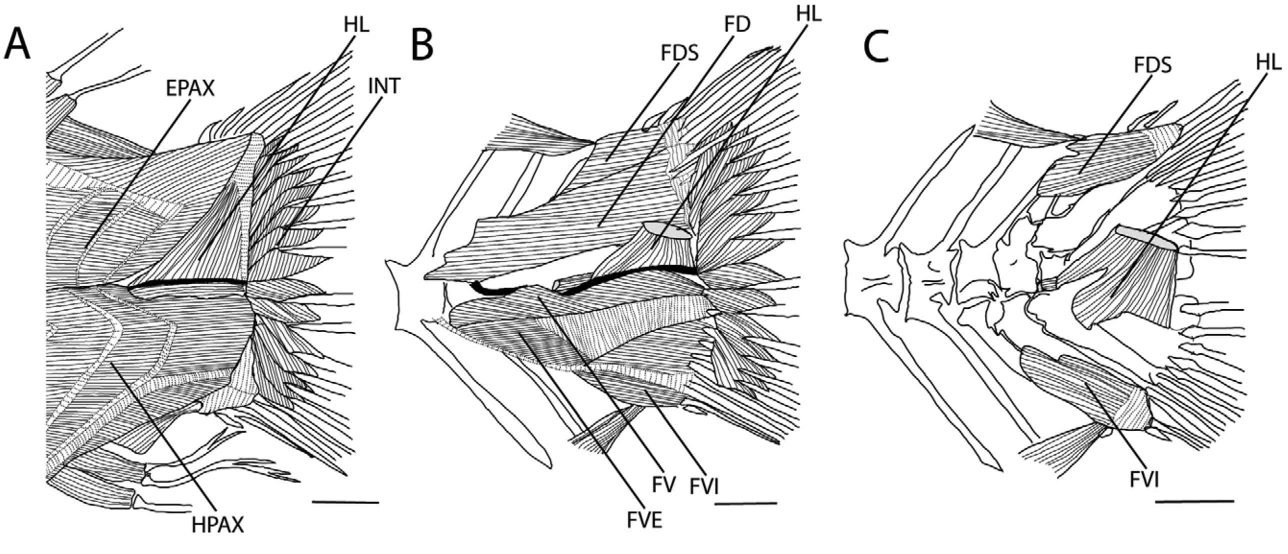

FIGURE 63. Lateral aspects of the caudal fin muscles in *Evistias acutirostris*. A, superficial view; B, after removal of EPAX and HPAX; C, after removal of the FD, FVE, and FV. Scale bar = 5 mm.

Character recognition

No variations were recognized that were useful for the phylogenetic analysis.

Other variations

None.

2-8. Muscles of median fins and their supportive elements

(Fig. 64)

Description

Muscles of median fins consist of three categories, the erector, depressor, and inclinator. These muscles attach to the fin bases of the dorsal and anal fins.

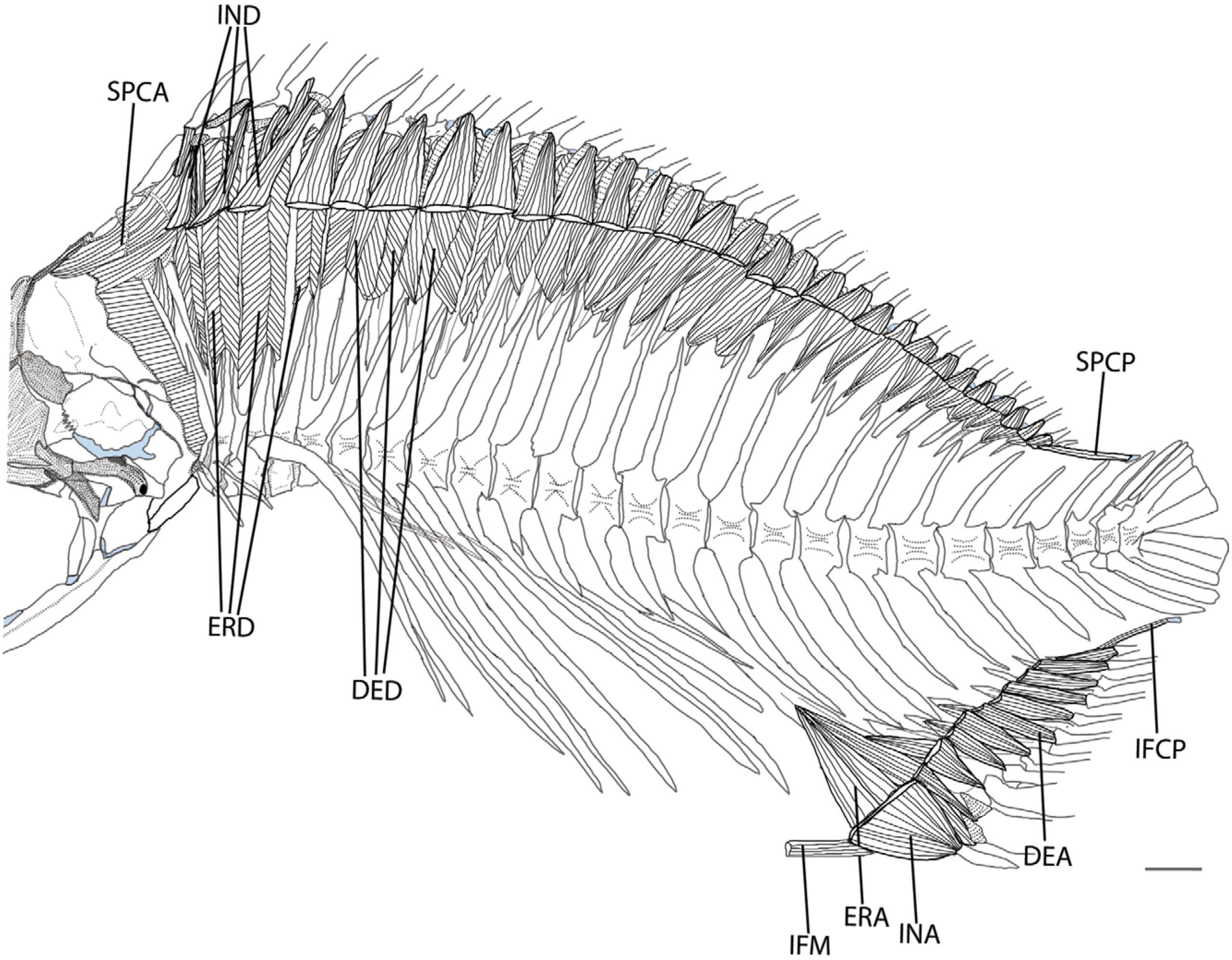

FIGURE 64. Lateral aspects of the median fin muscles and their supporting in *Histiopterus typus*. The anterior portion of the infracarinalis medius is removed. Scale bar = 5 mm.

Muscles of dorsal fin. The dorsal fin muscles include the erectores dorsales, depressores dorsales, and inclinatores dorsales.

The erectores dorsales originate from the anterolateral surfaces of the proximal pterygiophores of the dorsal fin and inserts via tendons onto the anterolateral bases of the fin rays.

The depressores dorsales originate from the posterolateral region of the proximal pterygiophores of the dorsal fin and inserts via tendons onto the posterolateral bases of the fin rays.

The inclinatores dorsales originate from the fascia between the skin and epaxialis, and inserts onto the lateral bases of the spines or fin rays.

Muscles of the anal fin. The anal fin comprise the erectores anales, depressores anales and inclinatores anales.

The erectores anales originate from the lateral surfaces of the proximal pterygiophores of the anal fin and insert onto the anterolateral bases of the fin rays.

The depressores anales originate from the lateral surface of the proximal pterygiophores and insert on the posterolateral bases of the anal fin rays.

The inclinatores anales originate from the fascia between the skin and the hypaxial, and insert onto the lateral regions of the anal fin ray bases.

Carinal muscles. The carinal muscles consist of the supracarinalis anterior, supracarinalis posterior, infracarinalis anterior, infracarinalis medius and infracarinalis posterior.

The supracarinalis anterior lies on the dorsal midline and connects the neurocranium and the anterior margin of the first proximal pterygiophore of the dorsal fin.

The supracarinalis posterior connects the stay of the dorsal fin support and the anterior-most procurrent ray of the upper lobe of the caudal fin.

The infracarinalis anterinalis connects the posteroventral surface of the cleithrum tip of the pectoral fin and the anteroventral surface of the pelvic fin.

The infracarinalis medius connects the posterodorsal surface of the postpelvic process of the pelvic fin and the ventrolateral surface of the first proximal pterygiophore of the anal fin.

The infracarinalis posterior connects the stay of the anal fin and supports to the anterior-most procurrent ray of lower lobe of the caudal fin.

Synapomorphies of Pentacerotidae

None.

Character recognition

No variations were recognized that were useful for the phylogenetic analysis.

Other variations

None.

2-9. Body muscles

(Figs. 65, 66)

Description

The body muscles comprise the main musculature of the body, and are formed by segmently arranged myomeres separated by myocommata. They are separated into three divisions: the epaxialis, lateralis superficialis, and hypaxialis. A swimbladder is present all pentacerotids, although both intrinsic and extrinsic muscles of the swimbladder muscles are absent.

The epaxialis is a large, dorsal component of the body musculature that lies above the lateral septum. This muscle is attached to the posterior surface of the neurocranium and to the anterior surface dorsal elements of the pectoral girdle. The posterior part of this muscle inserts onto the lateral bases of the caudal fin rays on the upper lobe.

The lateral superficialis consists of a sheet of fibers on both sides of the lateral midline.

The hypaxialis occupies the ventral component of the body musculature lying below the lateral septum, and comprises two elements, the obliquus superioris and obliquus inferioris. The obliquus superioris, lying just below the horizontal septum, originates from the posterolateral region of the neurocranium (including the exoccipital and basioccipital), cleithrum, and supracleithrum. The obliquus superioris is penetrated by the Baudelot’s ligament anteriorly. The obliquus inferioris originates from the posterior surface of the cleithrum and coracoid, and is usually fused with the sternohyoideus anterolaterally and also attaches to the obliquus superior ventrolaterally.

Synapomorphies of Pentacerotidae

None.

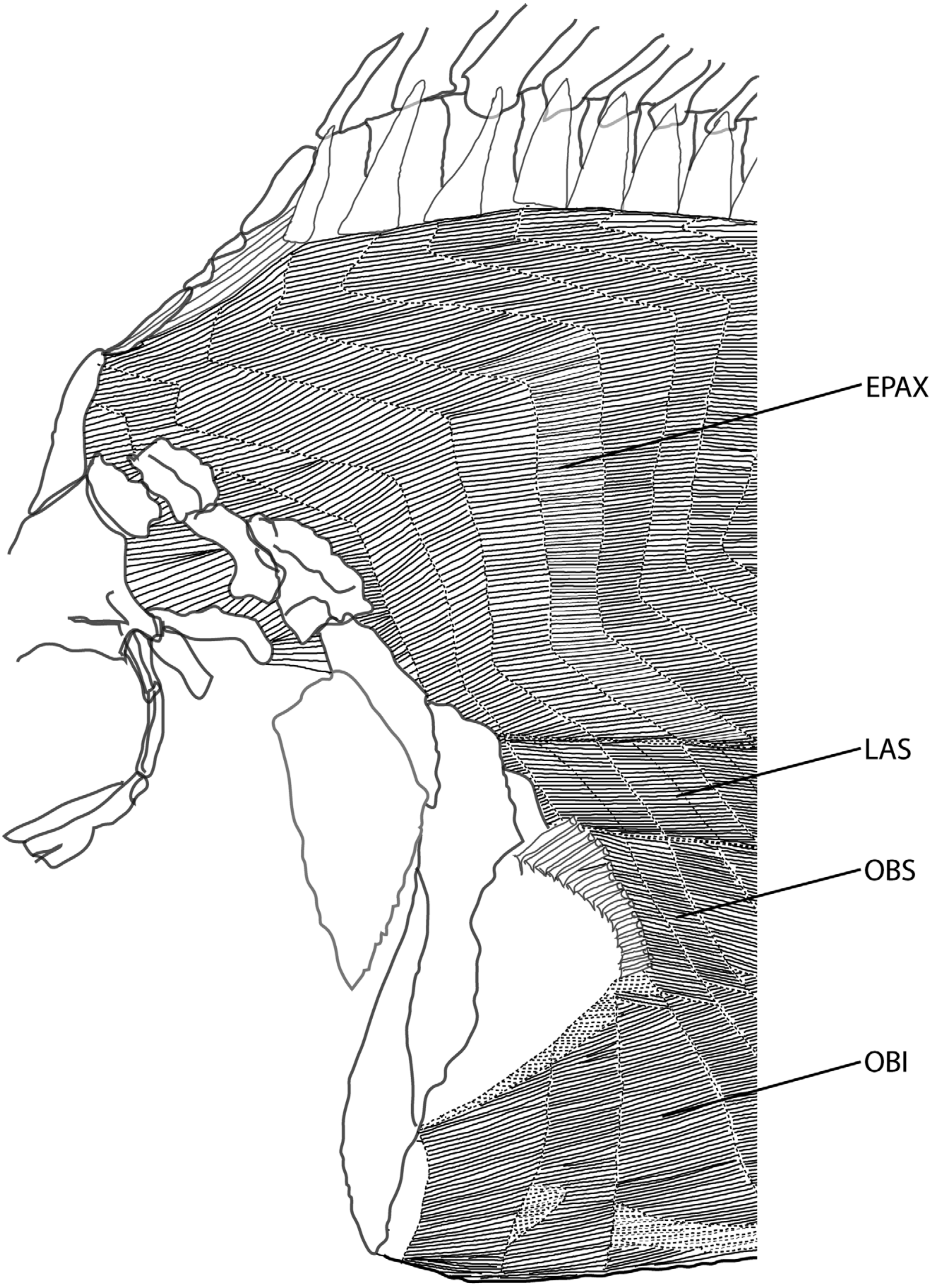

FIGURE 65. Lateral aspect of the body muscles in *Histiopterus typus*. Scale bar = 5 mm.

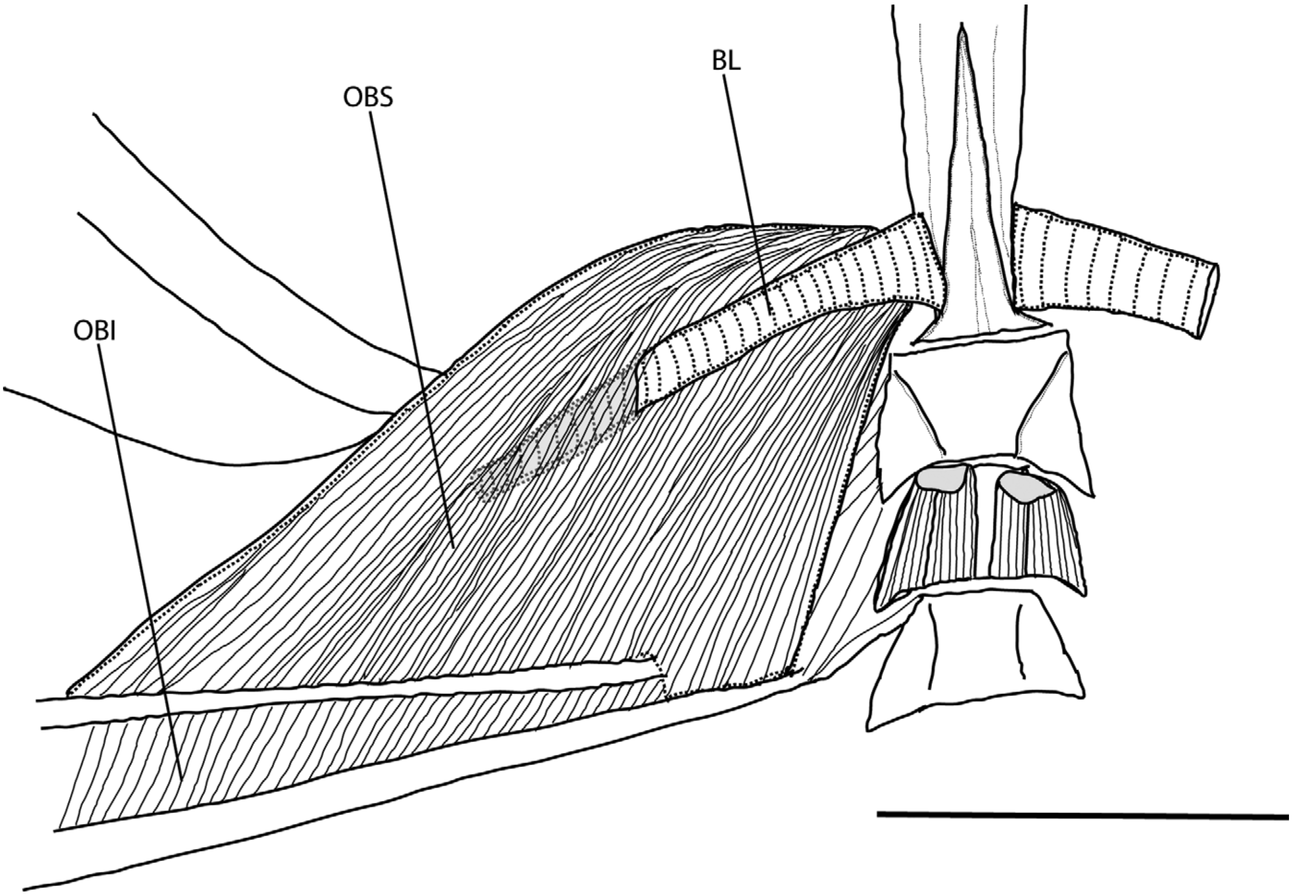

FIGURE 66. Ventral aspect of the body muscles in *Histiopterus typus*. Scale bar = 5 mm.

Character recognition

No variations were recognized that were useful for the phylogenetic analysis.

Other variations

None.

3. External morphology

(Fig. 67)

Description

The body is strongly compressed. The body profile has moderate on deep (1.3–3.2 in SL). The infraorbital ridge is prominent, nearly extending backward vertically from the anterior margin of the preopercle. The mouth is small; the supramaxilla is absent. Teeth are small, villiform and cylindrical, in broad bands on both jaws, and slightly enlarged on the outer jaw series. The lateral line is complete, rising in a strongly curved anteriorly running body posteriorly. The scales are ctenoid and small in size. Small scales cover the cheek region and are loosely attached to the cheeks in most pentacerotids, whereas they are scute-like and firmly attached to the skin in *Pentaceros* and *Pseudopentaceros*. The scales are absent on the dorsal surface of the head. Body scales situated along the mesial-lateral line anterior part of the body are loosely attached to the skin in most pentacerotids, whereas they are scute-like and firmly attached to the skin in *Pentaceros* and *Pseudopentaceros*. The dorsal fin originates anterior to the base of the pelvic fins. The anal fin is inserted posterior to the vent. The pectoral fin length is almost the same as the head length. The pelvic fin is inserted onto the region anterior to the base of the pectoral fin in *Histiopterus*, *Evistias*, *Zanclistius*, and *Pentaceropsis*, whereas it is inserted onto the region posterior to the base of the pectoral fin in *Paristiopterus*, *Pentaceros*, and *Pseudopentaceros*.

Synapomorphies of Pentacerotidae

None.

Character recognition

TS 44. Attachment of cheek scales to skin. (0: loose; 1: firm)

Ingroup. The cheek scales are ctenoid and loosely attached to the skin in most pentacerotids (character 44-0), whereas they are scute-like and firmly attached to the skin in *Pentaceros* and *Pseudopentaceros* (character 44-1).

Outgroup. The scales are loosely attached to the skin in typical percoids (character 44-0) (e.g., Roberts, 1993; Govoni et al., 2004; pers. obs.).

Other variations

Body deep and strongly compressed. All pentacerotids have a deep and strongly compressed body. Body profile high (body depth 1.3–1.8 in SL) in *Histiopterus typus*, *Evistias acutirostris*, *Zanclistius elevatus*, and *Parazanclistius hutchinsi*, while the body profile is moderately high (body depth 1.8–3.2 in SL) in *Paristiopterus labiosus*, *P. gallipavo*, *Pentaceros capensis*, *P. decacanthus*, *P. japonicus*, *P. quinquespinis*, *Pseudopentaceros richardsoni*, and *P. wheeleri*. Therefore, body shape could not be used in the analysis.

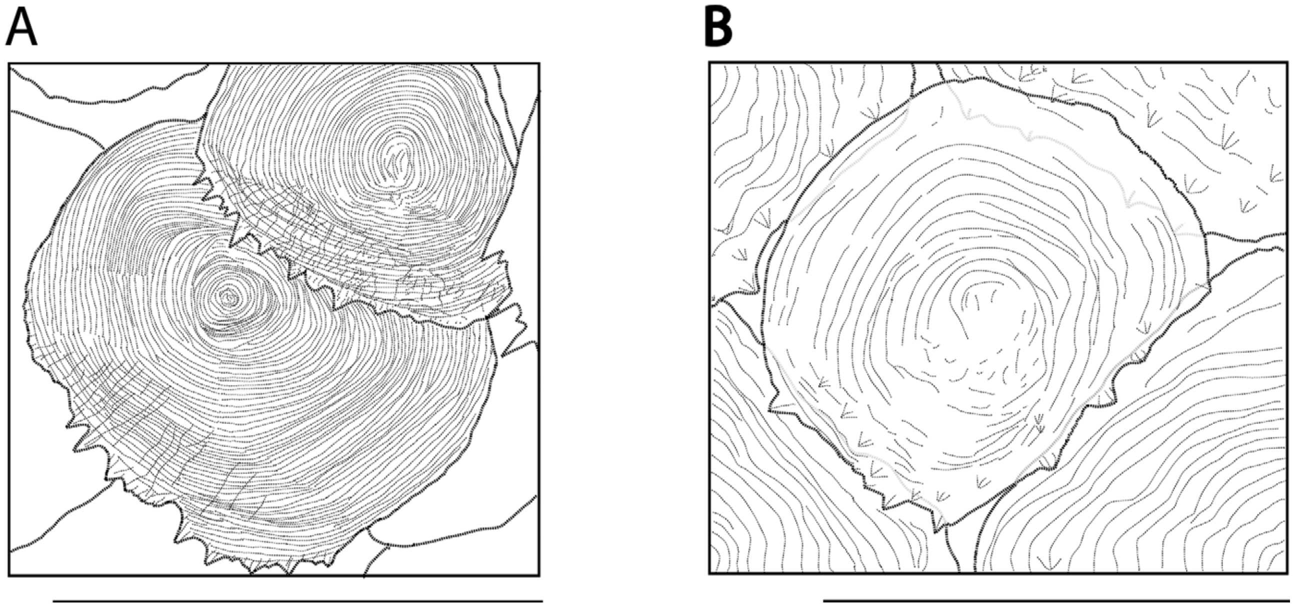

FIGURE 67. Lateral aspect of mid-cheek scales. A, *Histiopterus typus*; B, *Pentaceros japonicus*. Scale bar = 1 mm.

V. Monophyly of Pentacerotidae

Based on the detailed examination of the pentacerotids, the following 11 derived characters are commonly recognized in all members of the family: 1) the second infraorbital articulates with the lateral ethmoid anteromedially; 2) many exposed tubercles are present on the dorsal and lateral surfaces of the head (including frontal, supraoccipital, and pterotic); 3) the supraoccipital crest is high and stout; 4) the ascending and articular processes of the premaxillaries are continuous; 5) the supramaxilla is absent; 6) the distal ends of the premaxilla and maxilla articulate; 7) the palatine teeth are absent; 8) the endopterygoid articulates with the lateral ethmoid; 9) a tooth plate on the third epibranchial is absent; 10) pad-like bundle of the transversus dorsalis anterior is present, and 11) the adductor radialis originating from the medial surface of the third actinost. Accordingly, the monophyly of the family Pentacerotidae is supported by these 11 synapomorphies. Among the percoids, other families having this combination of synapomorphies have not been reported. Of the 11 synapomorphies, 1) and 8) are rare conditions in the percoids; and thus, these two synapomorphies strongly support the monophyly of the family. This is the first evaluation of the monophyly of this family base on synapomorphies.

VI. Phylogenetic Relationships within the Family Pentacerotidae

Characters in 44 transformation series (TS) were accepted for the phylogenetic analysis for the Pentacerotidae (Table 2). Primitive characters are expressed by "0", and derived characters by "1" and "2". The outgroup condition in TS 2 is expressed by "?", because the condition cannot be specified. As a result of the analysis, four equally mostly parsimonious trees were obtained. The consistency index was 0.66, the rescaled consistency index 0.57, and tree length 74. In this study, a strict consensus tree was constructed on the basis of these parsimonious trees and this consensus tree was adopted as the relationships of the Pentacerotidae (Fig. 68).

TABLE 2. Matrix of characters in 44 transformation series for examined pentacerotids. "?" indicates that the outgroup conditions are unspecified.

SPECIES	TRANSFORMATION SERIES AND CHARACTERS								
	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–44
1. OUTGROUP	0 ? 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0
2. *Histiopterus typus*	1 1 0 0 0	0 0 0 1 1	0 0 0 0 0	0 1 0 0 1	0 1 0 1 1	1 1 0 1 1	1 1 1 0 1	0 0 0 1 1	0 1 0 0
3. *Zanclistius elevatus*	1 1 0 0 0	0 0 0 1 1	0 0 0 0 0	0 1 0 0 1	0 1 0 1 1	1 1 0 1 1	1 0 1 0 2	1 0 1 1 1	0 0 1 0
4. *Evistias acutirostris*	1 1 0 0 0	0 0 0 1 1	0 0 0 0 0	0 1 0 0 1	0 1 0 1 1	1 1 0 1 1	2 1 1 0 2	0 0 1 1 1	0 1 0 0
5. *Parazanclistius hutchinsi*	1 1 0 0 0	0 0 0 1 1	0 0 0 0 0	0 0 0 0 1	0 0 0 1 0	0 1 0 1 1	1 0 1 0 0	0 0 1 1 0	0 0 1 0
6. *Paristiopterus labiosus*	1 2 0 0 0	0 0 0 0 1	0 0 0 1 1	0 1 0 0 1	0 0 0 1 0	1 1 0 1 1	1 0 1 0 1	0 0 1 1 0	0 1 0 0
7. *P. gallipavo*	0 2 0 0 0	0 0 0 0 1	0 0 0 1 1	0 0 0 0 1	0 0 0 1 0	0 1 0 1 1	1 0 1 0 1	0 0 1 1 0	1 1 0 0
8. *Pentaceropsis recurvirostris*	0 3 0 1 0	0 0 0 0 1	1 0 0 0 0	0 1 0 0 1	0 0 0 1 1	0 1 0 1 1	2 0 1 0 2	1 0 0 1 0	1 0 0 0
9. *Pentaceros capensis*	1 4 1 1 1	1 1 1 1 0	1 1 1 0 0	1 1 1 1 0	1 1 1 0 0	1 0 1 0 0	1 0 0 1 0	0 1 0 0 0	0 0 0 1
10. *P. decacanthus*	1 4 1 1 1	1 1 1 1 0	1 1 1 0 0	1 1 1 1 0	1 1 1 0 0	1 0 1 0 0	1 0 0 1 1	0 1 0 0 0	0 0 0 1
11. *P. japonicus*	1 4 1 1 1	1 1 1 1 0	1 1 1 0 0	1 1 1 1 0	1 1 1 0 0	1 0 1 0 0	1 0 0 1 1	0 1 1 0 0	0 1 1 1
12. *P. quinquespinis*	1 4 1 1 1	1 1 1 1 0	1 1 1 0 0	1 1 1 1 1	1 1 1 0 0	1 0 1 0 0	1 0 0 1 1	0 1 1 0 0	0 0 1 1
13. *Pseudopentaceros richardsoni*	1 5 1 1 1	1 1 1 1 0	1 1 1 0 0	1 1 1 1 0	1 1 1 0 0	1 0 1 0 0	1 0 0 1 1	0 1 1 0 0	0 0 1 1
14. *P. wheeleri*	1 5 1 1 1	1 1 1 1 0	1 1 1 0 0	1 1 1 1 0	1 1 1 0 0	1 0 1 0 0	1 0 0 1 1	0 1 0 0 0	0 0 1 1

The monophyly of the Pentacerotidae is supported by 11 synapomorphies, as shown previously, and two derived characters, 1-1 (many exposed tubercles are present on the lateral surface of the infraorbitals) and 31-1 (the number of abdominal vertebra is 12), were recognized to support the monophyly based on phylogenetic analysis. In addition, characters 9-1 (many exposed tubercles are present on the lateral or dorsal surface of the nasal, lateral ethmoid, and parietal) and 17-1 (many exposed tubercles are present on the lateral surface of the opercle) support the monophyly of this family according to ACCTRAN.

The Pentacerotidae is divided into clades A1 and A2. Each clade among the Pentacerotidae is described below. Asterisk and "r" indicate autapomorphic character and reversal, respectively.

Clade A1. Includes *Histiopterus*, *Evistias*, *Zanclistius*, *Pentaceropsis*, *Paristiopterus*, and *Parazanclistius.* This clade is supported by 10 synapomorphies, 2-1* (the first infraorbital is L-shape), 10-1* (teeth are absent on the vomer), 20-1 (autogenous tooth plate on the second pharyngobranchial is absent), 24-1* (the supratemporals are connected to the pterotic ventrally), 27-1* (sensory canal supported by the posttemporal is branched), 29-1* (the accessory subpelvic keel is well developed and extends anteroventrally), 30-1* (the subpelvic process is long), 33-1* (the first dorsal proximal pterygiophore is inserted into the space between the first and second neural spines), 38-1 (the posterior portion of the urostyle lacks spine) and 39-1* (adductor mandibulae section Aw is separated from section A3). Clade A1 is divided into clades B1 and B2.

Clade B1. Includes *Histiopterus*, *Evistias*, *Zanclistius*, *Pentaceropsis*, and *Paristiopterus*. This clade is supported by synapomorphy 35-1 (the upper caudal lobe supports nine or ten branched rays). It is also supported by character 9-0r (exposed tubercles are absent on the lateral or dorsal surface of the nasal, lateral ethmoid and parietal) according to ACCTRAN. This clade is divided into C1 and C2.

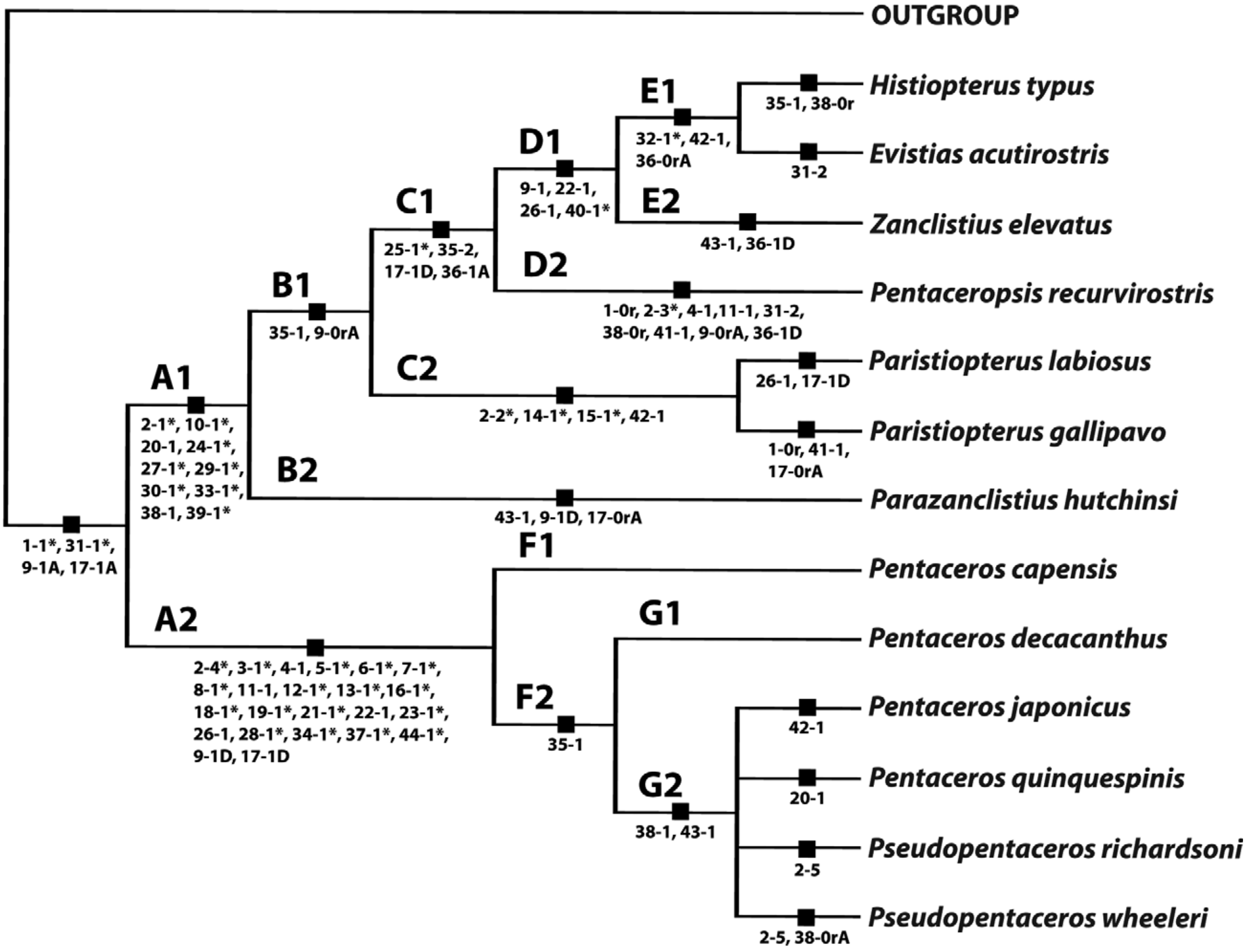

FIGURE 68. Phylogenetic relationships of Pentacerotidae with characters supporting clades. Numbers of characters series correspond to those of Table 1. Characters labeled “A” and “D” indicate apomorphies when ACCTRAN or DELTRAN was employed, respectively. Asterisk and “r” indicate an autapomorphy and reversal, respectively.

Clade B2. Includes only *Parazanclistius hutchinsi*. This clade has a single derived character 43-1 (the arrector ventralis originates from the cleithrum and coracoid). This clade also possesses character 9-1 (many exposed tubercles are present on the lateral or dorsal surface of the nasal, lateral ethmoid, and parietal) according to DELTRAN and character 17-0r (exposed tubercles are absent on the lateral surface of the opercle) according to ACCTRAN.

Clade C1. Includes *Histiopterus*, *Evistias*, *Zanclistius*, and *Pentaceropsis*. This clade is supported by two unambiguous synapomorphies, 25-1* (sensory canal supported by the upper supratemporal(s) is branched) and 35-2 (the upper caudal lobe supports 10 branched rays). This clade is also supported by character 17-1 (many exposed tubercles are present on the lateral surface of the opercle) according to DELTRAN and by character 36-1 (the lower caudal lobe supports eight branched rays) according to ACCTRAN. This clade is divided into clades D1 and D2.

Clade C2. Includes *Paristiopterus labiosus* and *P. gallipavo*. This clade is supported by four synapomorphies, 2-2* (the first infraorbital is robust and triangular shape), 14-1* (villiform and enlarged cylindrical teeth are present in both jaws), 15-1* (a facet is present on the middle part on the palatine) and 42-1 (the abductor superficialis originates from the cleithrum and coracoid).

Paristiopterus labiosus has a single derived character 26-1 (many exposed tubercles are present on the lateral surface of the posttemporal). This species also possesses character 17-1 (many exposed tubercles are present on the lateral surface of the opercle) according to DELTRAN. In addition *P. labiosus* has a single autapomorphy, the third and fourth hypurals are fused, although this character was not used for the analysis.

Paristiopterus gallipavo has two derived characters, 1-0r (exposed tubercles on the infraorbitals are absent) and 41-1 (the retractor dorsalis inserts onto the ventrolateral part of the first to third abdominal vertebra). It also has character 17-0r (exposed tubercles are absent on lateral surface of the opercle) according to ACCTRAN.

Clade D1. Includes *Histiopterus*, *Evistias*, and *Zanclistius*. This clade is supported by four synapomorphies, 9-1 (many exposed tubercles are present on the lateral or dorsal surface of the nasal, lateral ethmoid, and parietal), 22-1 (many exposed tubercles are present on the lateral surface of the supratemporal), 26-1 (many exposed tubercles are present on the lateral surface of the posttemporal) and 40-1* (the levator operculi inserts onto the posteromedial part of the opercle). Clade D1 is divided into clade E1 and E2.

Clade D2. Included only *Pentaceropsis recurvirostris*. This clade has seven derived characters, 1-0r (exposed tubercles on the infraorbitals are absent), 2-3* (the first infraorbital is rod like), 4-1 (the subocular shelf is present on the fourth infraorbital), 11-1 (the ethmoid projection is blunt), 31-2 (the number of the abdominal vertebrae is 13), 38-0r (the posterior portion of the urostyle has a long spine) and 41-1 (the retractor dorsalis inserts onto the ventrolateral part of the first to third abdominal vertebra). It also possesses character 9-0r (exposed tubercles are absent on the lateral or dorsal surface of the nasal, lateral ethmoid, and parietal) according to ACCTRAN, and characters 36-1 (the lower caudal lobe supports eight branched rays) according to DELTRAN. In addition, this clade has two autapomorphies, the subocular shelf lacking on the third infraorbital and the second preural centrum with a long neural spine dorsally.

Clade E1. Includes *Histiopterus typus* and *Evistias acutirostris.* This clade is supported by two synapomorphies, 32-1* (one spine is present on first dorsal proximal pterygiophore) and 42-1 (the abductor superficialis originates from the cleithrum and coracoid). It is also supported by character 36-0r (the lower caudal lobe supports seven branched fin rays) according to ACCTRAN.

Histiopterus typus has two derived characters, 35-1 (the upper caudal lobe supports nine branched rays) and 38-0r (the posterior portion of the urostyle has a long spine), and *Evistias acutirostris* possesses one derived character 31-2 (with 13 abdominal vertebrae).

Clade E2. Includes only *Zanclistius elevatus.* This clade has a single derived character 43-1 (the arrector ventralis originates from the cleithrum and coracoid). It also has character 36-1 (the lower caudal lobe supports eight branched fin rays) according to DELTRAN.

Clade A2. Includes *Pentaceros* and *Peseudopentaceros*. This clade is supported by the following 21 synapomorphies: 2-4* (the first infraorbital is square-shaped), 3-1* (the subocular shelf is present on the second infraorbital), 4-1 (the subocular shelf is present on the fourth infraorbital), 5-1* (the posteroventral margin of the fourth infraorbital is sutured with the preopercle), 6-1* (the subocular shelf is present on the fifth infraorbital), 7-1* (the fifth infraorbital is firmly attached to the sphenotic), 8-1* (the nasal bone is firmly attached to the ethmoid posteromedially), 11-1 (the ethmoid projection is blunt), 12-1* (the ethmoid-maxillary ligament is connected with the ventral surface of the nasal), 13-1* (many exposed tubercles are present on the lateral surface of the dentary and anguloarticular), 16-1* (the preopercular sensory canal runs along a series of grooves partly covered by a tubular structure of the preopercle), 18-1* (the interopercle is thin), 19-1* (the ventral margin of the interopercle is concave), 21-1* (the supratemporal is firmly attached to the neurocranium), 22-1 (many exposed tubercles are present on the lateral surface of the supratemporal), 23-1* (the supratemporal is wide and disk-like), 26-1 (many exposed tubercles are present on the lateral surface of the posttemporal), 28-1* (articulation between pelvic bone and pelvic spine is interlocked with the ring-like structure), 34-1* (the base of the anterior edge of the anterior dorsal spines, except for the first spine, is serrated), 37-1* (the parhypurapophysis is robust) and 44-1* (the cheek scales are scute-like and firmly attached to the skin). This clade is also supported by characters 9-1 (many exposed tubercles are present on the lateral or dorsal surface of the nasal, lateral ethmoid, and parietal bones) and 17-1 (many exposed tubercles are present on the lateral surface of the opercle) according to DELTRAN. This clade is divided into clade F1 and F2.

Clade F1. Includes only *Pentaceros capensis*, having no derived characters after the analysis. This clade has two autapomorphies, which were not used for the analysis; those with exposed tubercles present on the ethmoid dorsally and those with a number of tubercles located uroneurally.

Clade F2. Includes *Pentaceros decacanthus*, *P. japonicus*, *P. quinquespinis*, *Pseudopentaceros richardsoni*, and *P. wheeleri*. This clade is supported by a single synapomorphy 35-1 (the upper caudal lobe supports nine branched rays). It is divided into clades G1 and G2.

Clade G1. Includes only *Pentaceros decacanthus*. This clade lacks derived characters.

Clade G2. Includes *Pentaceros japonicus*, *P. quinquespinis*, *Pseudopentaceros richardsoni*, and *P. wheeleri*. This clade is supported by two synapomorphies, 38-1 (the posterior portion of the urostyle has a long spine) and 43-1 (the arrector ventralis originates from the cleithrum and coracoid). Relationships of the four species are unresolved. *Pentaceros japonicus* is characterized by a single derived character 42-1 (the abductor superficialis originates from the cleithrum and coracoid), *Pentaceros quinquespinis* by a single derived character 20-1 (autogenous tooth plate on the second pharyngobranchial is absent), *Pseudopentaceros richardsoni* by a single derived character 2-5 (the first infraorbital is sharp and triangular shape) and *Pseudopentaceros wheeleri* by a single derived character 2-5 (the first infraorbital is sharp and triangular shape). *Pseudopentaceros wheeleri* also has a derived character 38-0r (the posterior portion of the urostyle has a long spine) according to ACCTRAN. Additionally, *P. quinquespinis* possesses a single autapomorphy, which was not used for the analysis; those with a small canine tooth row present on the ceratobranchial posteriorly.

VII. Classification

After the phylogenetic analysis, all members of the family Pentacerotidae are recognized to belong to a monophyletic group. Therefore, the family is redefined by 11 synapomorphies commonly found in the members and two additional synapomorphies recognized after the analysis and thus, the Pentacerotidae can be strongly defined by 13 synapomorphies in total.

Of the family, two monophyletic groups, clades A1 and A2, are recognized. Smith (1964) separated this family into the subfamilies Histiopterinae (including *Histiopterus*, *Zanclistius*, and *Paristiopterus*) and Pentacerotinae (*Pentaceropsis* and *Pentaceros*). My findings do not support the two subfamilies of Smith because they are not monophyletic, compared with the phylogenetic relationships reconstructed in this study (Fig. 69). Hardy (1983a, b)

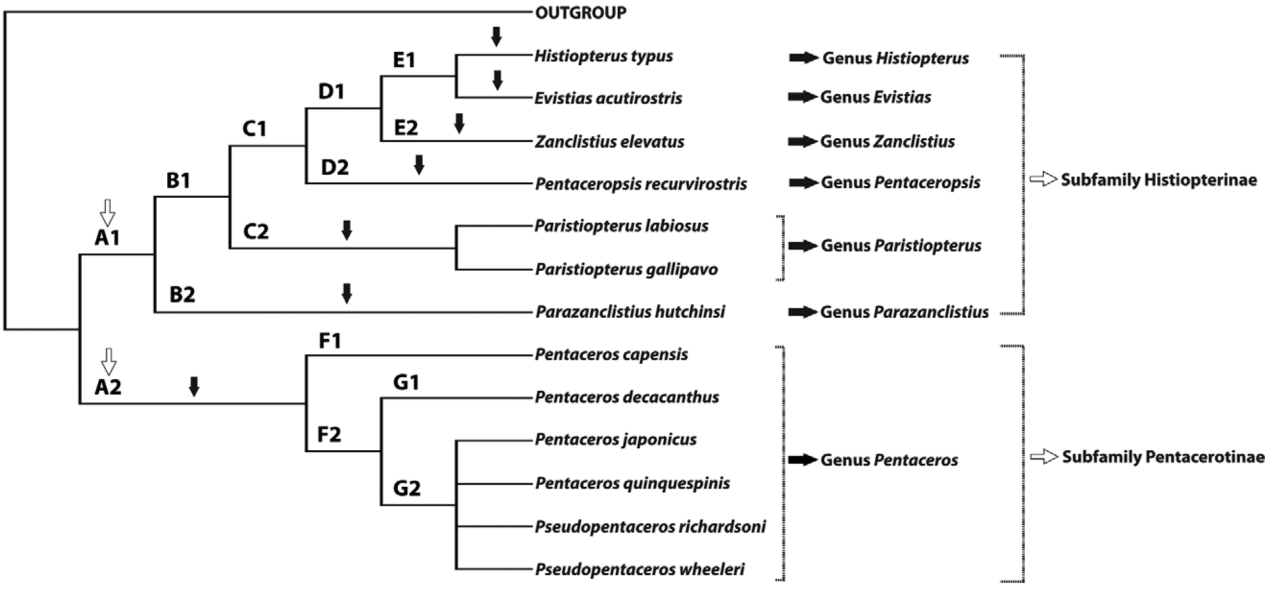

FIGURE 69. Phylogenetic relationships within Pentacerotidae and ranking at subfamilial (shown by open arrow) and generic (show by solid arrow) levels.

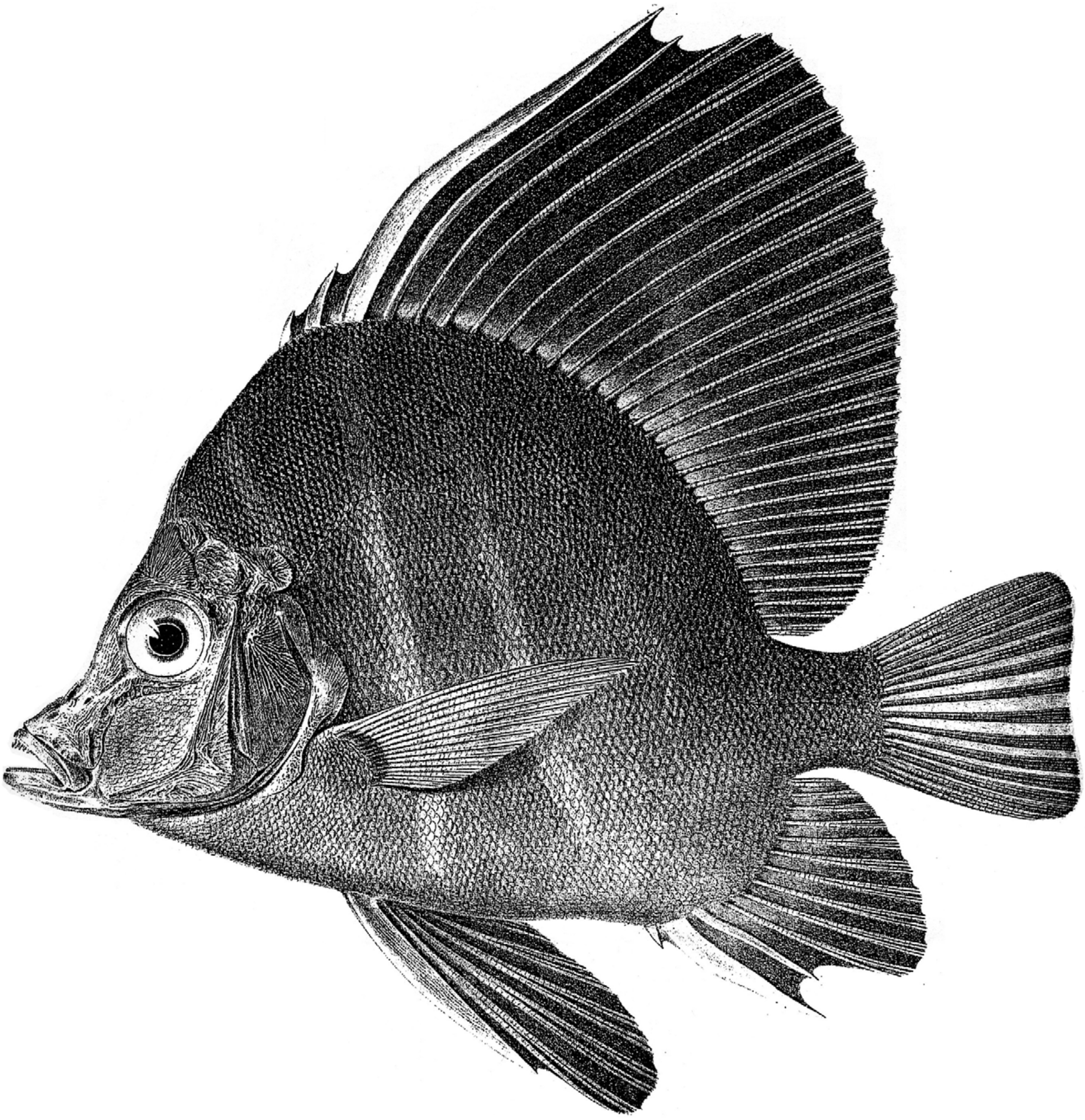

FIGURE 70. *Histiopterus typus*, type species of the genus (from Steindachner and Döderlein, 1883).

divided the family Pentacerotidae into three subfamilies: Histiopterinae (including *Histiopterus*, *Zanclistius*, *Evistias*, and *Parazanclistius*), Paristiopterinae (including *Paristiopterus* and *Pentaceropsis*) and Pentacerotinae (including *Pentaceros* and *Pseudopentaceros*). Although Hardy's (1983a, b) Pentacerotinae is monophyletic, because *Pentaceros* and *Pseudopentaceros* are included into clade A2, his Histiopterinae and Paristiopterinae are also not monophyletic groups. Therefore, the latter two subfamilies by Hardy (1983a, b) are unacceptable in this study. Clade A1, containing the genera *Histiopterus*, *Evistias*, *Zanclistius*, *Pentaceropsis*, *Paristiopterus*, and *Parazanclistius*, is monophyletic, supported by 10 synapomorphies, and clade A2 by 21 synapomorphies. In this study, the names of Histiopterinae and Pentacerotinae are applied to clades A1 and A2, respectively, because the Histiopterinae is the oldest available family group name applicable for clade A1. Histiopterinae was established by Jordan (1907) and the other name Paristiopterinae by Hardy (1983a). Pentacerotinae is the only subfamily name applicable for clade A2.

When considering the generic ranking the Pentacerotidae, all the genera (*Histiopterus* Temminck and Schlegel, 1844, *Evistias* Jordan, 1907, *Zanclistius* Jordan, 1907, *Pentaceropsis* Steindachner and Döderlein, 1883, *Paristiopterus* Bleeker, 1876, *Parazanclistius* Hardy, 1983, *Pentaceros* Cuvier, 1829, and *Pseudopentaceros* Smith, 1844) included into the subfamily Histiopterinae (clade A1) can be retained, because each of them is monophyletic or monotypic. In contrast, *Pentaceros*, belonging to clade A2, is a non-monophyletic group, because *Pseudopentaceros* is nested within the members of *Pentaceros*. Therefore, the two genera should be united into a single genus cladistically. Because *Pentaceros* has priority over *Pseudopentaceros* on the basis of the International Code of Zoological Nomenclature (ICZN, 1999), *Pentaceros* should be used as the genus name for this clade.

As a result, the following classification of the Pentacerotidae based on the phylogenetic relationships is proposed:

Family Pentacerotidae
- **Subfamily Histiopterinae**
    - **Genus *Histiopterus* Temminck and Schlegel, 1844**
    - **Genus *Evistias* Jordan, 1907**
    - **Genus *Zanclistius* Jordan, 1907**
    - **Genus *Pentaceropsis* Steindachner and Döderlein, 1883**
    - **Genus *Paristiopterus* Bleeker, 1876**
    - **Genus *Parazanclistius* Hardy, 1983**
- **Subfamily Pentacerotinae**
    - **Genus *Pentaceros* Cuvier, 1829**

Family Pentacerotidae

Diagnosis. Second infraorbital articulating with lateral ethmoid anteromedially; many exposed tubercles present on infraorbital and head (including frontal, supraoccipital and pterotic); supraoccipital crest high and stout; ascending and articular processes of premaxilla continuous; supramaxilla absent; distal ends of premaxilla and maxilla articulating; palatine teeth absent; endopterygoid articulating with lateral ethmoid; pad-like bundle of transversus dorsalis anterior present; adductor radialis originating from medial surface of third actinost; number of abdominal vertebrae 12.

Remarks. This family is redefined by the 12 synapomorphies listed above. No percoid families have this combination of characters. This family includes two subfamilies, 7 genera and 13 species.

Subfamily Histiopterinae

Diagnosis. Vomer toothless; supratemporals connected with pterotic ventrally; branched sensory canal extended from posttemporal present; accessory subpelvic keel well developed and extending anteroventrally; subpelvic process well developed and long; first dorsal fin proximal pterygiophore inserted into space between first and second neural spines; adductor mandibulae section Aw quite expanded dorsally and fused by a tendon separated from section A3 posterodorsally.

Remarks. The subfamily Histiopterinae includes 6 genera, *Histiopterus*, *Evistias*, *Zanclistius*, *Pentaceropsis*, *Paristiopterus*, and *Parazanclistius*, and seven species. This subfamily differs from the Pentacerotinae in having the vomer toothless and the supratemporals connected with the pterotic ventrally (vs. vomer with teeth and supratemporals connected with pterotic laterally).

Genus *Histiopterus* Temminck and Schlegel, 1844

(Fig. 70)

Histiopterus Temminck and Schlegel, 1844: 86 (type species: *Histiopterus typus* Temminck and Schlegel, 1844).

Diagnosis. Number of abdominal vertebrae 12; upper caudal lobe supporting eight branched caudal fin rays; posterior portion of urostyle having long spine; third and forth dorsal spines long; second anal fin spine longest.

Remarks. The genus is monotypic, containing only *Histiopterus typus* Temminck and Schlegel, 1844.
In addition to derived characters recognized in *Histiopterus* based on the phylogenetic analysis (see section VI), two external characters, the third and fourth dorsal spines long and second anal-fin spine longest, are useful distinguishing this genus from other pentacerotid genera (vs. spines short in others).

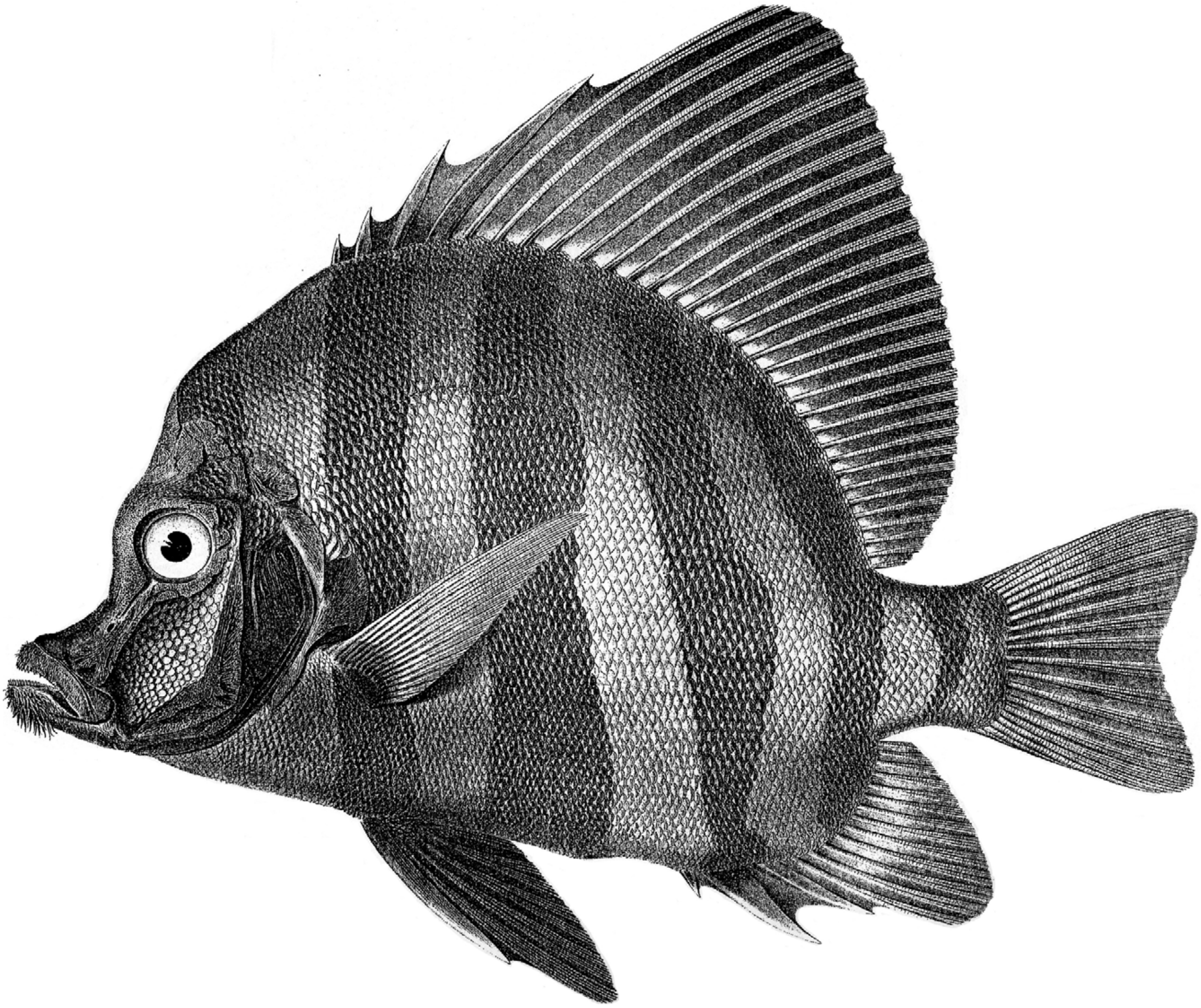

FIGURE 71. *Evistias acutirostris*, type species of the genus (from Steindachner and Döderlein, 1883).

Genus *Evistias* Jordan, 1907

(Fig. 71)

Evistias Jordan, 1907: 236 (type species: *Histiopterus acutirostris* Temminck and Schlegel, 1844).
Evistiopterus Whitley, 1932: 334 (type species: *Histiopterus acutirostris*Temminck and Schlegel, 1844).

Diagnosis. Number of abdominal vertebrae 13; upper caudal lobe supporting 10 branched caudal fin rays; posterior portion of urostyle lacking spine; dorsal and anal fin spines short.

Remark. The genus *Evistias* is monotypic, including only *Evistias acutirostris* Jordan, 1907.
This genus is similar to the genus *Histiopterus* in having higher and striped body. *Evistias* is distinguished from the *Histiopterus* by its short dorsal and anal spines (vs. third and fourth dorsal, and third anal spines are long in *Histiopterus*).

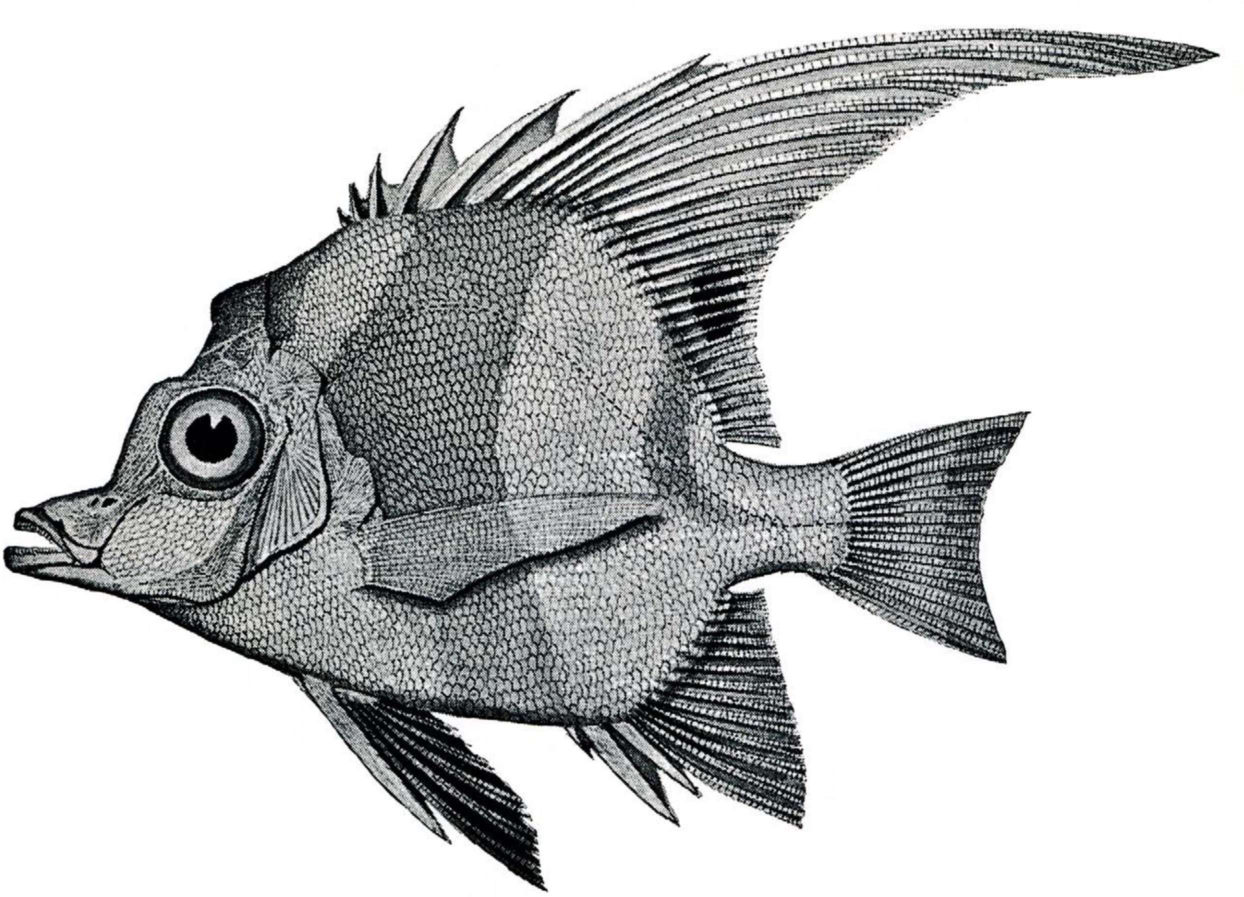

FIGURE 72. *Zanclistius elevatus*, type species of the genus (from Scott et al., 1974).

Genus *Zanclistius* Jordan, 1907

(Fig. 72)

Zanclistius Jordan, 1907: 236 (type species: *Histiopterus elevatus* Ramsay and Ogilby, 1888).

Diagnosis. Arrector ventralis originating from posterolateral portion of cleithrum and coracoid; lower caudal lobe supporting eight branched fin rays; dark spot posteriorly on dorsal fin; number of lateral line pores 55-65.

Remark. The genus *Zanclistius* is monotypic, containing only *Zanclistius elevatus* (Ramsay and Ogilby 1888). This genus is separable from other members of the pentacerotids from the Australian and New Zealand waters (e.g., *Pentaceropsis, Paristiopterus*, and *Parazanclistius*) by having falcate-shaped body and extremely long dorsal fin (vs. a crescent body and dorsal fin not extremely long in others).

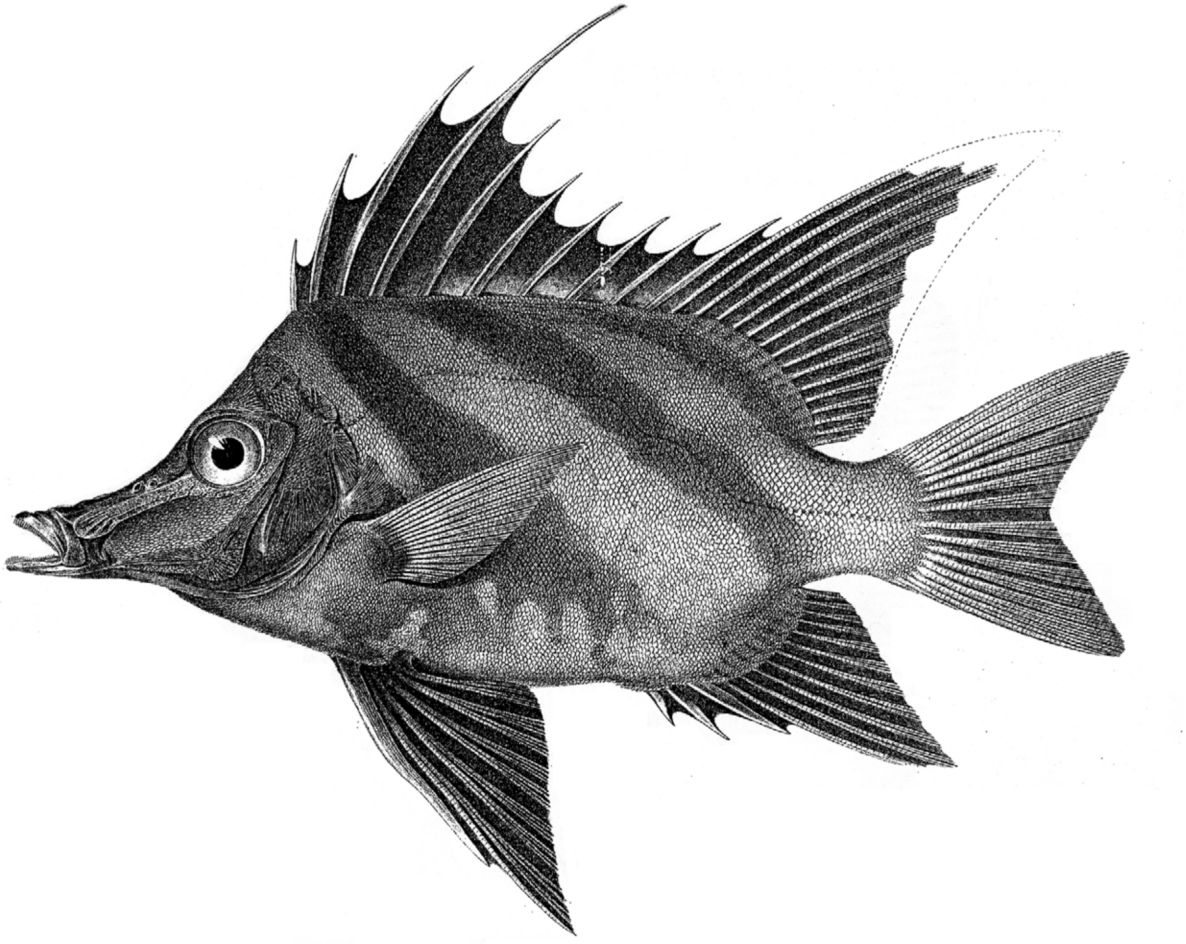

FIGURE 73. *Pentaceropsis recurvirostris*, type species of the genus (from Steindachner and Döderlein, 1883).

Genus *Pentaceropsis* Steindachner and Döderlein, 1883

(Fig. 73)

Pentaceropsis Steindachner and Döderlein, 1883: 13 (type species: *Histiopterus recurvirostris* Richardson, 1845).
Prosoplismus Waite, 1903: 59 (type species: *Histiopterus recurvirostris* Richardson, 1845).

Diagnosis. Exposed tubercles absent on infraorbitals, nasal, lateral ethmoid, and parietal; first infraorbital rod like; subocular shelf present on fourth infraorbital; ethmoid projection blunt; number of abdominal vertebrae 13; posterior portion of urostyle having long spine; retractor dorsalis inserted onto ventrolateral part of first to third abdominal vertebra; lower caudal lobe supporting eight branched fin rays; snout deeply concave and extensively elongating.

Remark. The genus *Pentaceropsis* is monotypic, containing only *Pentaceropsis recurvirostris* Steindachner and Döderlein, 1883.

This genus is similar to the genera *Histiopterus*, *Evistias*, and *Zanclistius* in having a high body profile. *Pentaceropsis* differs from *Histiopterus*, *Evistias*, and *Zanclistius* in that it has a deeply concave and extensively elongated snout (*Histiopterus*, *Evistias*, and *Zanclistius* have a moderately cancave and somewhat elongated snout).

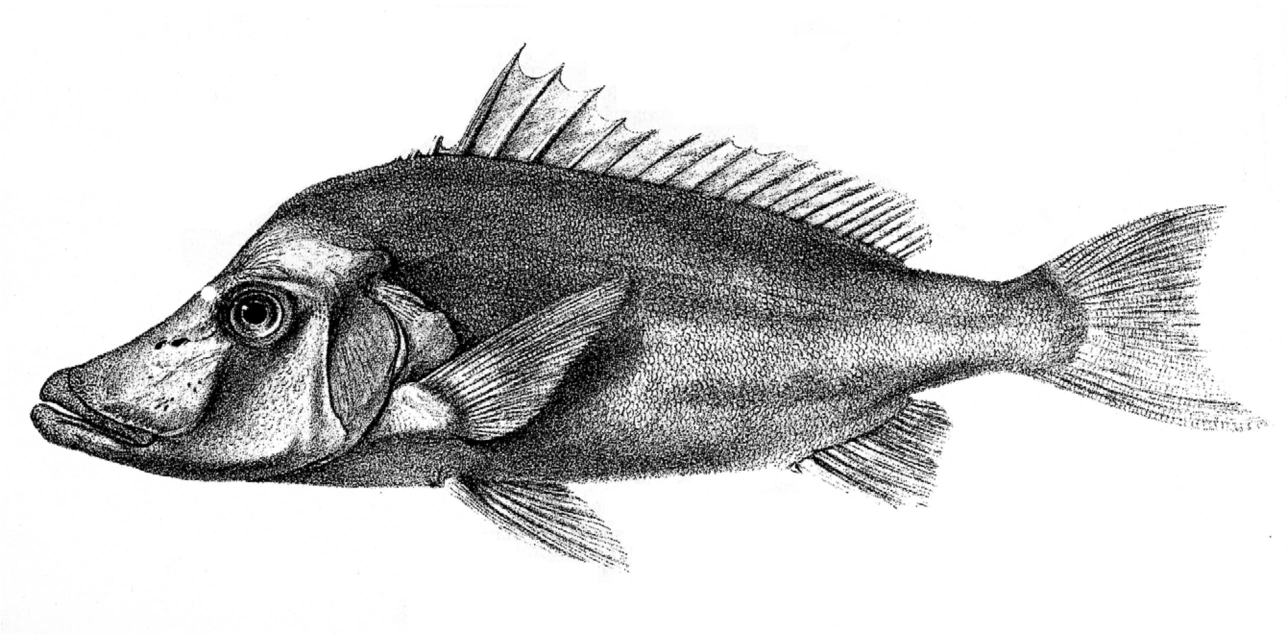

FIGURE 74. *Paristiopterus labiosus*, type species of the genus (from Günther, 1872).

Genus *Paristiopterus* Bleeker, 1876

(Fig. 74)

Paristiopterus Bleeker, 1876: 268 [type species: *Richardsonia insignis* Castelnau, 1872: (junior synonym of *Paristiopterus labiosus* Günther, 1872)].

Diagnosis. First infraorbital robust and triangular; villiform and enlarged cylindrical teeth present on both jaws; large facet for articulation with head of lateral ethmoid present on middle part of palatine; abductor superficialis originating from posterolateral portion of cleithrum and coracoid; number of lateral line pores 78–85.

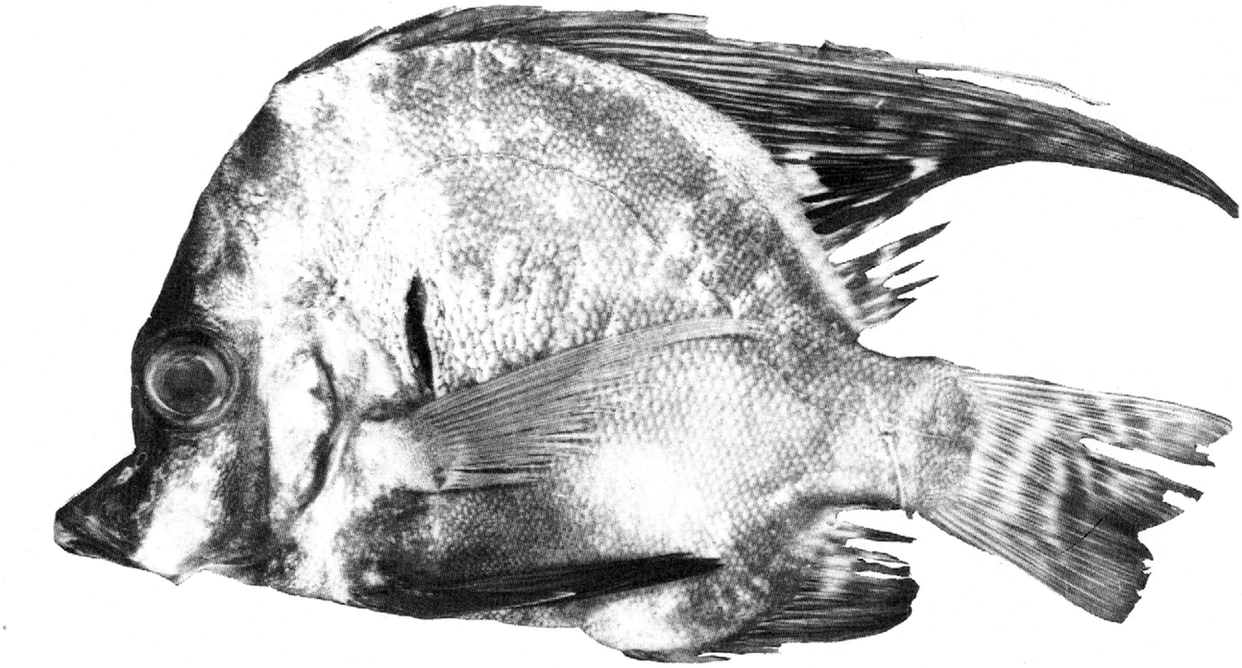

FIGURE 75. *Parazanclistius hutchinsi*, type species of the genus (from Hardy, 1983b).

Remark. Two species, *Paristiopterus labiosus* (Günther, 1872) (=type species), and *P. gallipavo* (Whitley, 1944), are included in this genus.

The genus *Paristiopterus* can be distinguished from other members of the family by having enlarged and cylindrical teeth on the inner margin of both jaws (vs. enlarged cylindrical teeth absent in others).

Genus *Parazanclistius* Hardy, 1983

(Fig. 75)

Parazanclistius Hardy, 1983: 373 (type species: *Parazanclistius hutchinsi* Hardy, 1983).

Diagnosis. Arrector ventralis originating from posterolateral portion of cleithrum and coracoid; many exposed tubercles present on lateral or dorsal surface of nasal, lateral ethmoid and parietal; exposed tubercles absent on opercle; dark spot posteriorly on dorsal fin; number of lateral line pores 66–72.

Remark. The genus *Parazanclistius* is monotypic, containing only *Parazanclistius hutchinsi* Hardy, 1983.

This genus is similar to the genus *Zanclistius* in having a prominent dark spot on the dorsal fin posteriorly. *Parazanclistius* has a greater number of lateral line pores (66–72) than *Zanclistius* (55–65).

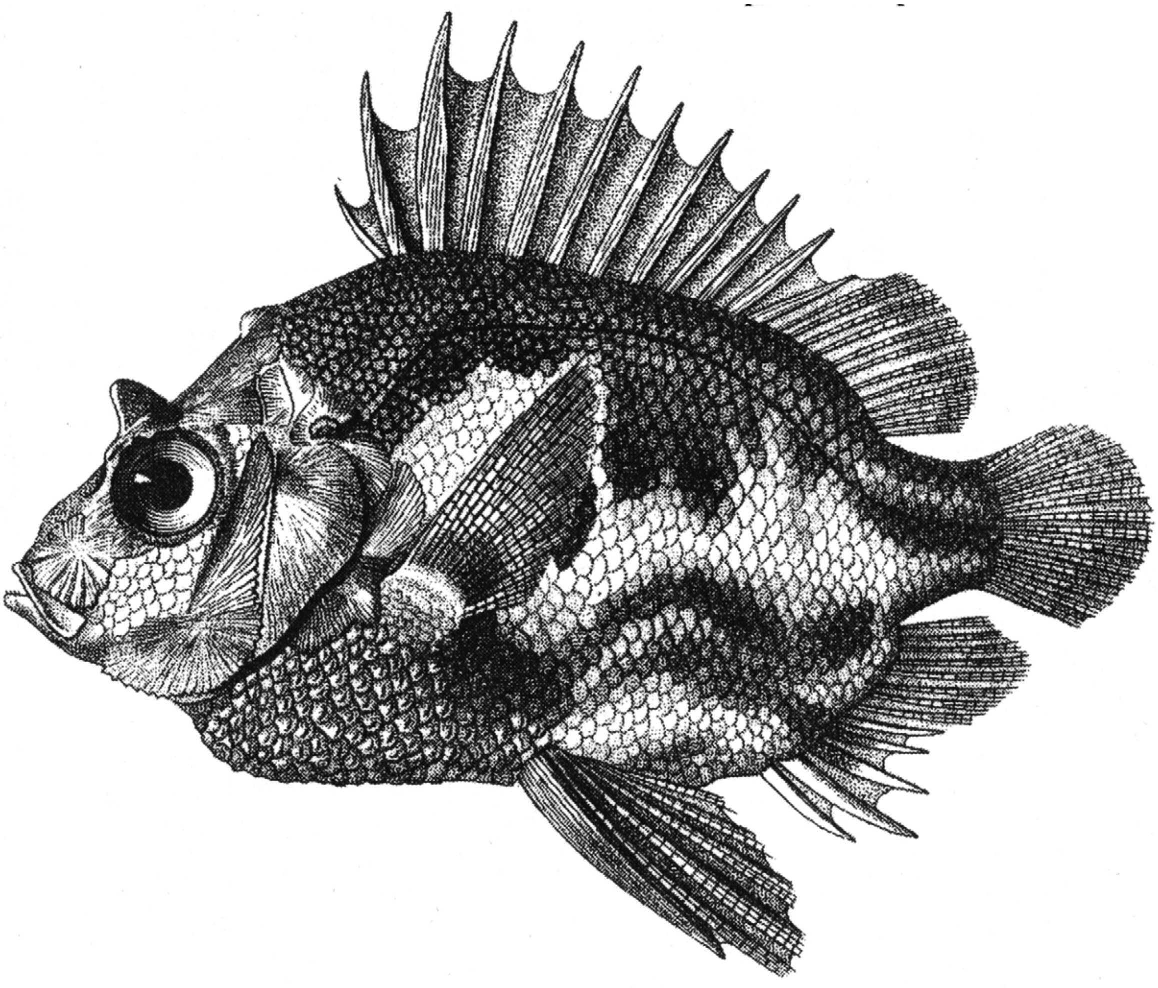

FIGURE 76. *Pentaceros capensis,* type species of the genus (from Cuvier, 1829).

Subfamily Pentacerotinae

Diagnosis. Vomer toothed; supratemporals connected with pterotic laterally; branched sensory canal from posttemporal absent; accessory subpelvic keel undeveloped; subpelvic process short; first dorsal fin proximal pterygiophore inserted into space between second and third neural spines; adductor mandibulae section Aw quite expanded dorsally and tendinously fused with section A3 posterodorsally.

Remarks. The subfamily Pentacerotinae includes a single genus *Pentaceros* and six species. This subfamily is distinguished from Histiopterinae by a toothed vomer and supratemporals connected with the pterotic laterally (vs. vomer toothless and supratemporals connected with pterotic ventrally in Histiopterinae).

Genus *Pentaceros* Cuvier, 1829

(Fig. 76)

Pentaceros Cuvier in Cuvier and Valenciennes, 1829: 30 (type species: *Pentaceros capensis* Cuvier, 1829).
Pseudopentaceros Smith, 1844: unnumbered (type species: *Pentaceros richardsoni* Smith, 1844) [junior synonym of *Pentaceros* Cuvier, 1829].

Diagnosis. Subocular shelf present on second infraorbital; subocular shelf present on fourth infraorbital; posteroventral margin of fourth infraorbital sutured with preopercle; subocular shelf present on fifth infraorbital; fifth infraorbital firmly attached to sphenotic; nasal bone firmly attached to ethmoid posteromedially; ethmoid projection blunt; ethmoid-maxillary ligament connected with ventral surface of nasal; preopercular sensory canal mostly covered by wide bridges; interopercle thin; ventral margin of interopercle concave; supratemporal firmly attached to neurocranium; supratemporal wide and disk like; mid-lateral corner of pelvic bone having processes connected, forming a small penetrated pore interlocked with ring-like structure of pelvic spine; base of anterior edge of anterior dorsal spines, except for first spine, serrated; parhypurapophysis robust; cheek scales scute-like and is firmly attached to skin; many exposed tubercles present on dentary, anguloarticular, nasal, lateral ethmoid, parietal, posttemporal, and opercle.

Remarks. *Pentaceros* contains six species, *Pentaceros capensis* (Cuvier 1829) (= type species), *P. decacanthus* (Günther, 1859), *P. japonicus* (Döderlein in Steindachner and Döderlein, 1883), *P. quinquespinis* (Parin and Kotlyar, 1988), *P. richardsoni* (Smith, 1844) and *P. wheeleri* (Hardy, 1983). Among them, *P. richardsoni* and *P. wheeleri* have been previously included in the genus *Pseudopentaceros*, which is synonymous with *Pentaceros* in this study. This genus is easily separable from other genera due to their lack of the vomerine tooth.

Key to the genera of the family Pentacerotidae

1a. Vomerine tooth absent	2
1b. Vomerine tooth present	*Pentaceros*
2a. First dorsal fin proximal pterygiophore supporting two spines	4
2b. First dorsal fin proximal pterygiophore supporting one spine	3
3a. Number of the abdominal vertebrae 12	*Histiopterus*
3b. Number of the abdominal vertebrae 13	*Evistias*
4a. Lower caudal lobe supporting 8 branched caudal fin rays	5
4b. Lower caudal lobe supporting 7 branched caudal fin rays	6
5a. Number of lateral line pores 55–65	*Zanclistius*
5b. Number of lateral line pores 78–85	*Pentaceropsis*
6a. Upper caudal lobe supporting 8 branched caudal fin rays	*Parazanclistius*
6b. Upper caudal lobe supporting 9 branched caudal fin rays	*Paristiopterus*

VIII. General Considerations

1. Zoogeography

The pentacerotids widely occur in the temperate subantarctic to temperate waters of the Indo-Pacific and southwestern Atlantic (e.g., Hardy, 1983a; Hoese et al., 2006; Nelson, 2006). This family is a relatively small group and is of a moderate size (13 species and 15–50 cm SL). The geographic ranges differ for each genus (Figs. 77–83). The origin of the pentacerotids and their dispersions are inferred and discussed here to elucidate the zoogeographic characteristics of the family.

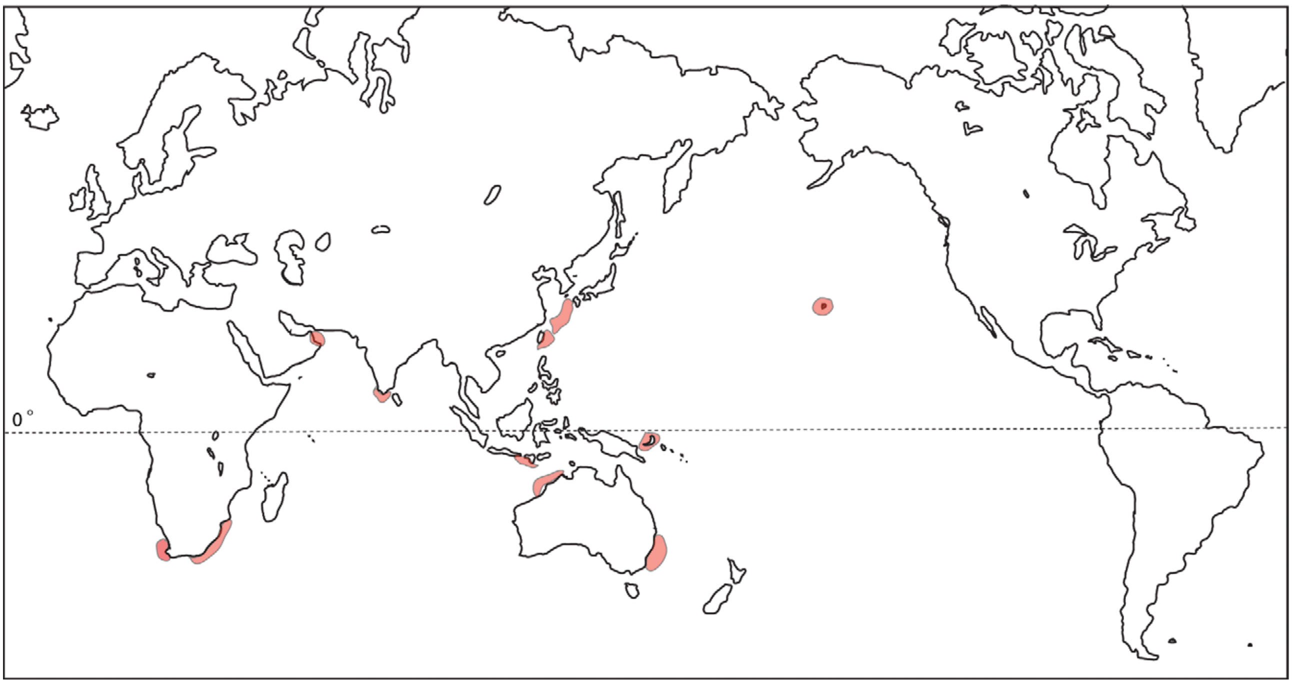

FIGURE 77. Geographic distributions of the genus *Histiopterus*.

1-1. Distribution of pentacerotids

Histiopterus typus is distributed in southern Japan, Korea, the South China Sea, southern India, the Red Sea, southern Africa, Bali, New Britain, northern and southern Australia, and Hawaii (Hardy, 1983a; Okamura et al., 1985; Kailola, 1987; Randall, 1995; Kim et al., 2005; Hoese et al., 2006) (Fig. 77).

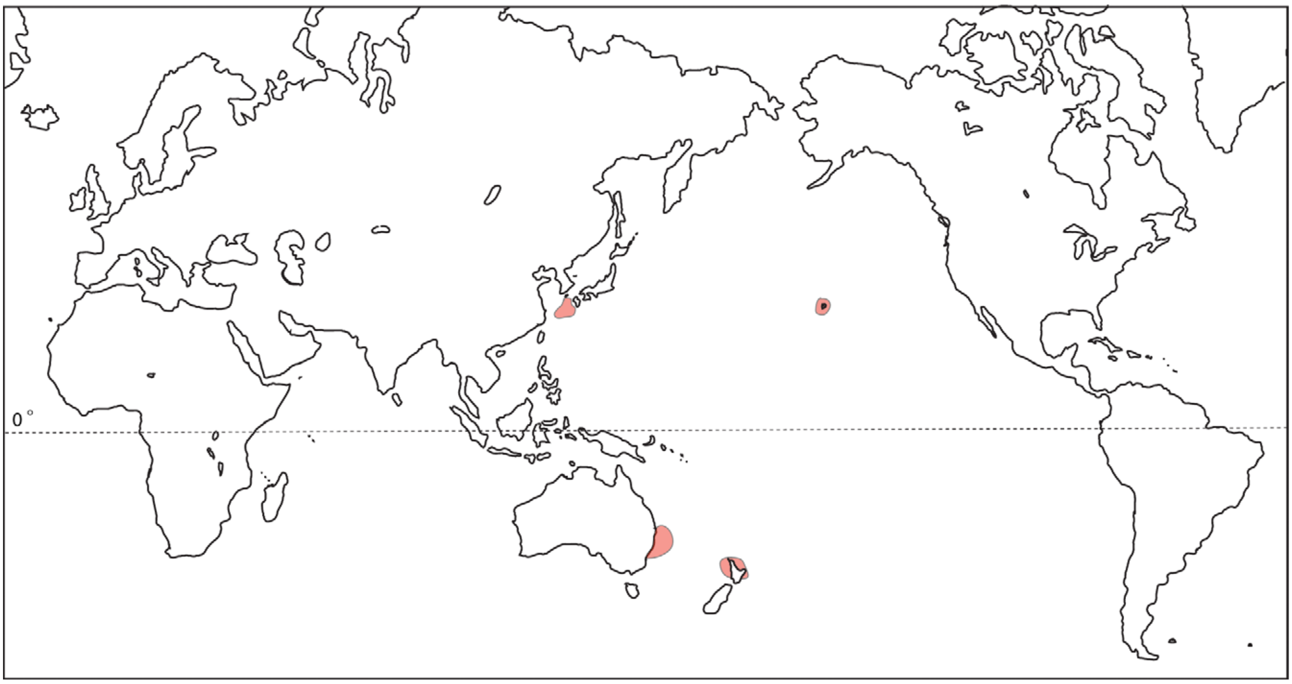

FIGURE 78. Geographic distributions of the genus *Evistias*.

Evistias acutirostris is known from southern Japan, Korea, southern Australia, and New Zealand, Hawaii (Coleman, 1980; Hardy, 1983a; Kuiter, 1993; Kim et al., 2005) (Fig. 78).

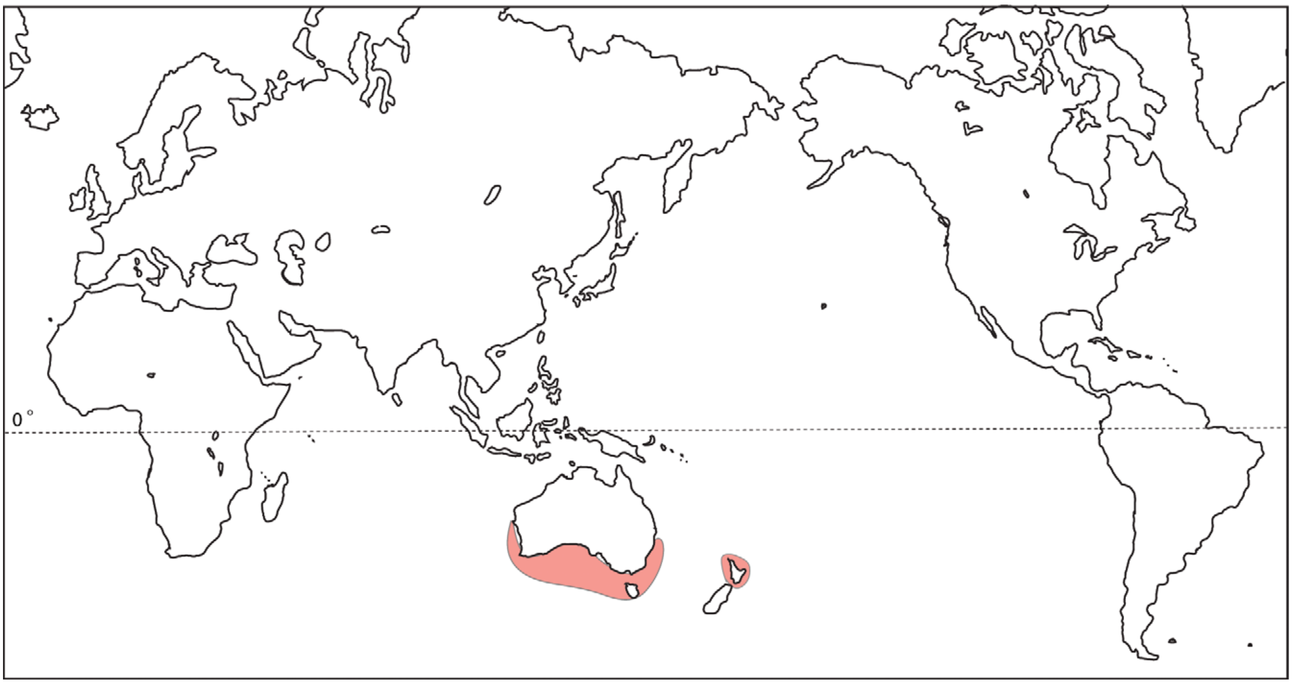

FIGURE 79. Geographic distributions of the genus *Zanclistius*.

Zanclistius elevatus is distributed from southern Australia, northeastern Tasmania, and New Zealand (Hardy, 1983a; Last et al., 1983; Gomon et al., 2008) (Fig. 79).

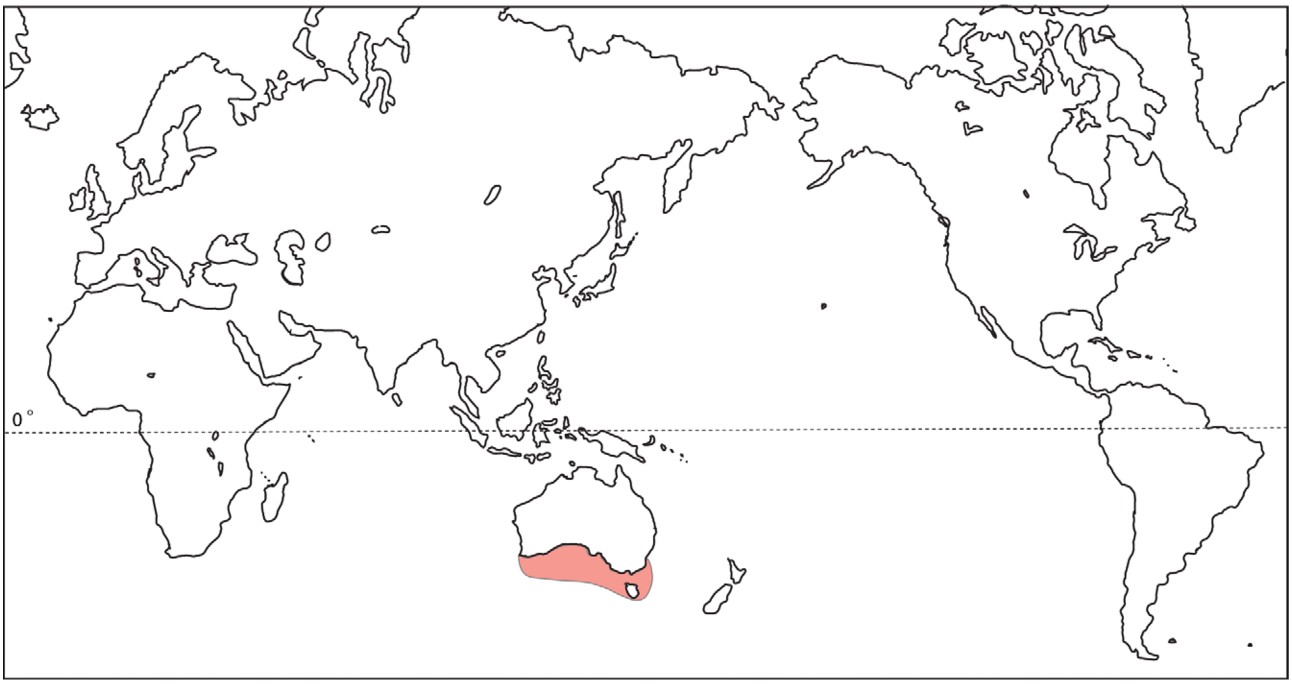

FIGURE 80. Geographic distributions of the genus *Pentaceropsis*.

Pentaceropsis recurvirostris is reported from southern Australia and Tasmania (Hardy, 1983a; Last et al., 1983; Gomon et al., 2008) (Fig. 80).

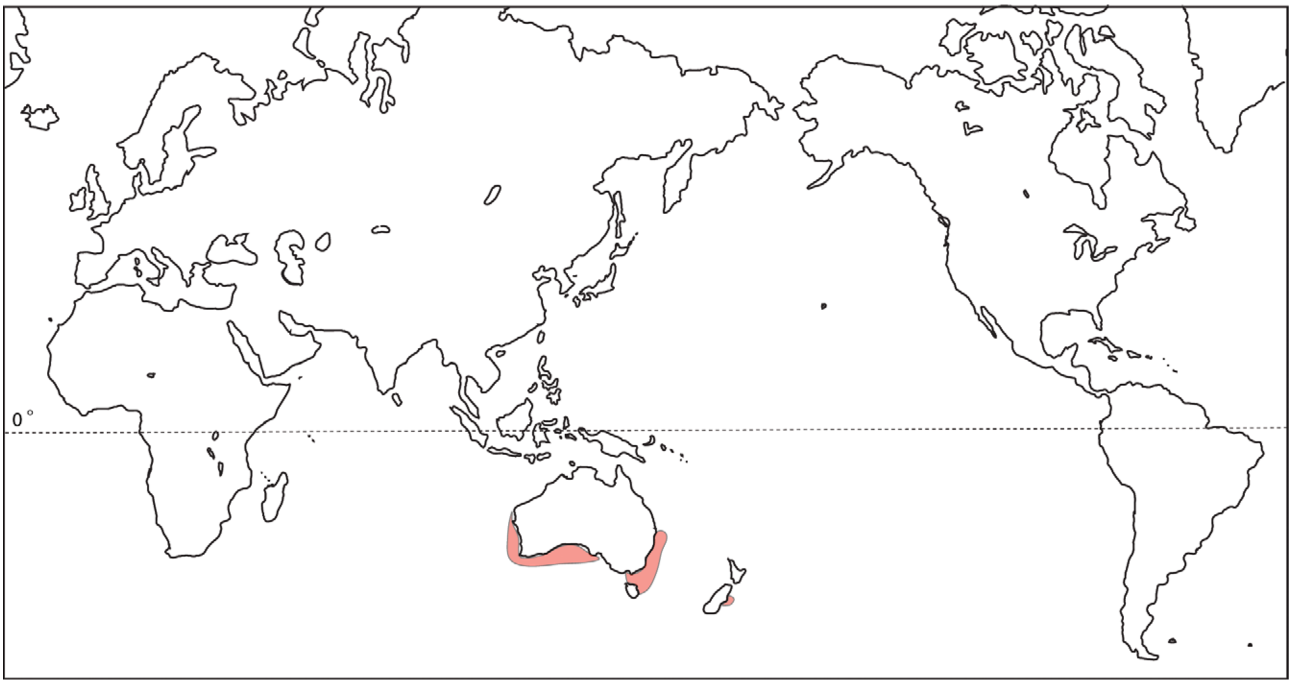

FIGURE 81. Geographic distributions of the genus *Paristiopterus*.

Paristiopterus labiosus is known from southwestern Australia, northeastern Tasmania, and New Zealand (Hardy, 1983a; Last et al., 1983; Hoese et al., 2006; Gomon et al., 2008), and *P. gallipavo* from southeastern Australia (Hardy, 1983a; Last et al., 1983; Hoese et al., 2006; Gomon et al., 2008) (Fig. 81).

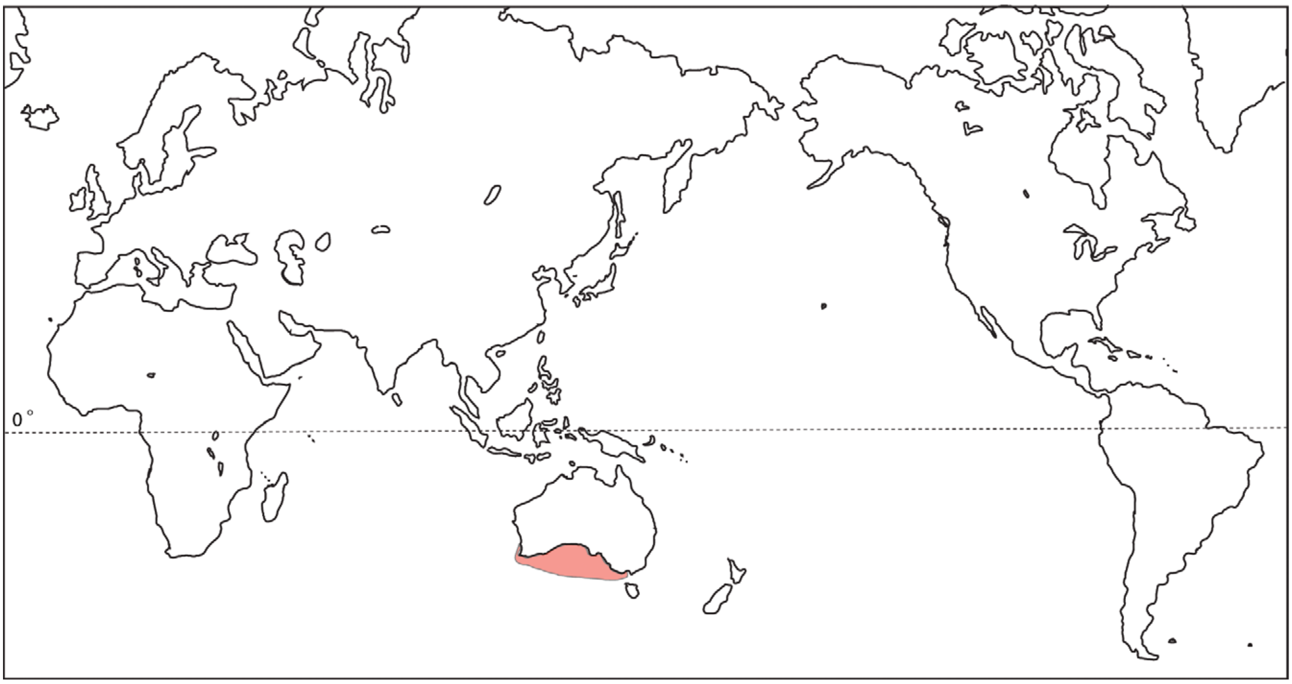

FIGURE 82. Geographic distributions of the genus *Parazanclistius*.

Parazanclistius hutchinsi is distributed only in southern Australia (Hardy, 1983b; May and Maxwell, 1986; Kuiter, 1993; Gomon et al., 2008) (Fig. 82).

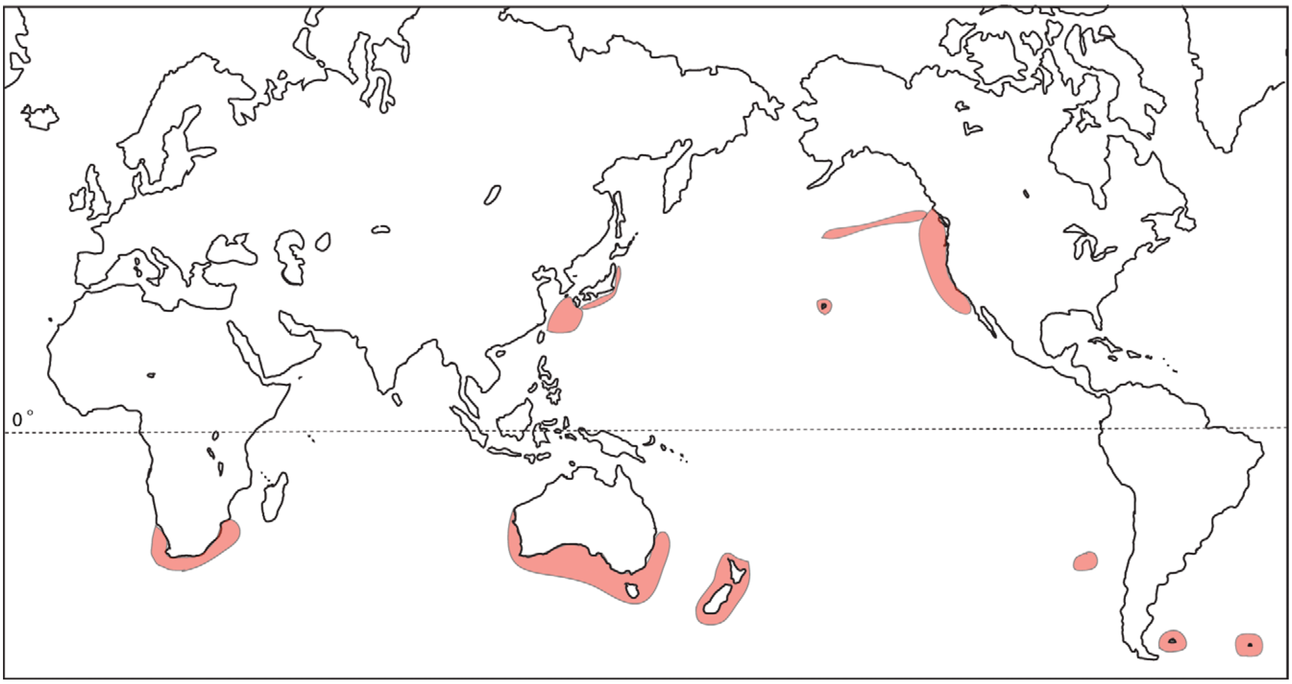

FIGURE 83. Geographic distributions of the genus *Pentaceros*.

Pentaceros capensis is distributed only in southern Africa (Smith, 1964; Hardy, 1983a; Smith and Heemstra, 1986; Hoese et al., 2006), *P. decacanthus* from southern and southeastern Australia, and New Zealand (Smith, 1964; Hardy, 1983a; Hoese et al., 2006), *P. japonicus* from southern Japan and Korea (Hardy, 1983a, Okamura et al., 1985; Kim et al., 2005), *P. quinquespinis* from the eastern Pacific (Parin and Kotlyar, 1988; Pequeño, 1997), *P. richardsoni* in southern Africa, southern Australia, New Zealand, Cape Horn and Chile (Smith, 1964; Hardy, 1983a; Amaoka et al., 1990; Gomon et al., 2008), and *P. wheeleri* in northern Japan, Hawaii, and the western coast of Alaska to southern California (Hardy, 1983a; Mecklenburg et al., 2002; Nelson et al., 2004) (Fig. 83).

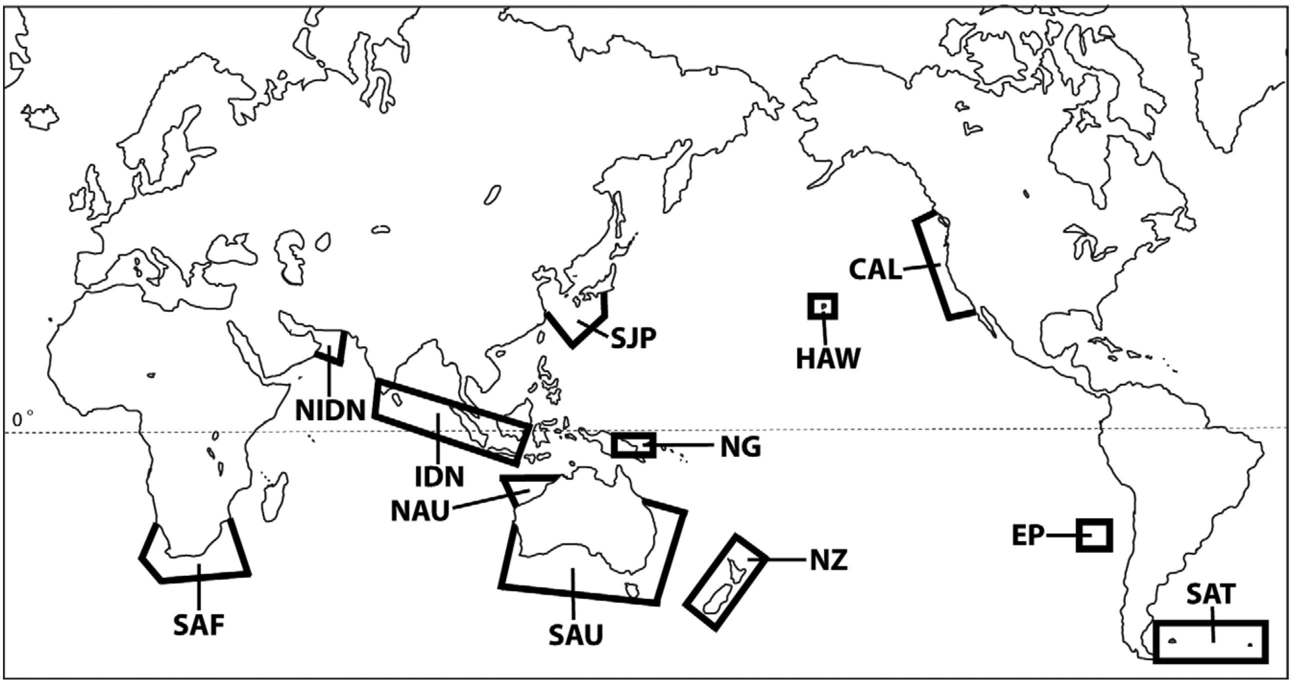

FIGURE 84. Conceptual diagram of 12 regions characterized by geographic distributions of pentacerotids.

1-2. Geographic origin of pentacerotid fish

Geographic regions are categorized into 12 areas on the basis distributional patterns of pentacerotids and Briggs's (1974) marine biogeographic provinces (Fig. 84). The 12 areas are California region (CAL), Eastern Pacific region (EP), Hawaiian region (HAW), Indian region (IDN), Northern Australia region (NAU), Northern Indian region (NIDN), New Guinea region (NG), New Zealand region (NZ), Southern Africa region (SAF), Southern Atlantic region (SAT), Southern Australian region (SAU) and Southern Japan region (SJP). The center of origin of pentacerotids are inferred following the method of Sawada (1982) based on the phylogenetic relationships reconstructed in this study and the above 12 regions (Fig. 85).

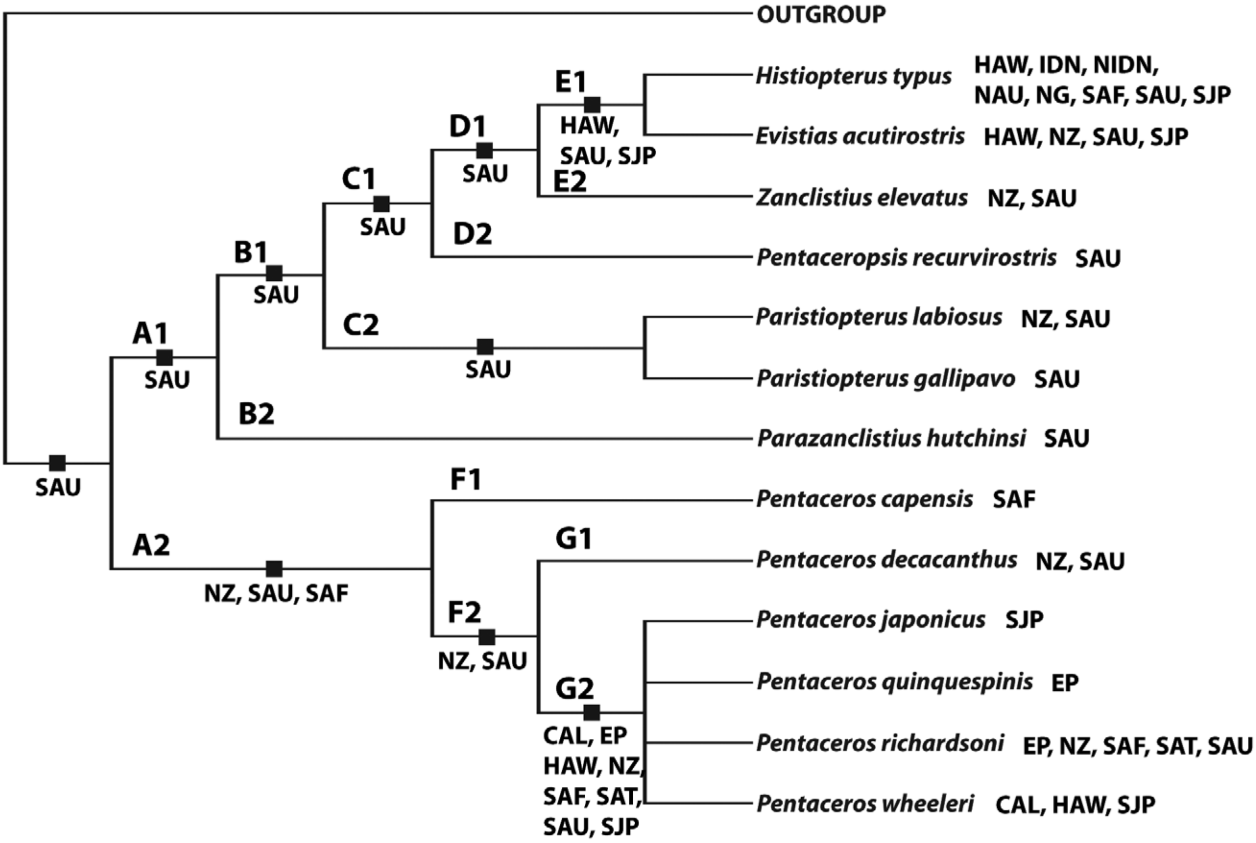

FIGURE 85. Relationships between branching pattern and distribution of each pentacerotid species.

The distribution of the common ancestor of *Histiopterus typus* and *Evistias acutirostris* (shown as node of clad E1) was inferred in HAW, SAU and/or SJP, and that of above two species and *Zanclistius elevates* (node of clade D1) in SAU. The distribution of the common ancestor of the above three species and *Pentaceropsis recurvirostris* (node of clade C1) was inferred to be in SAU. *Paristiopterus labiosus* and *P. gallipavo* had the common ancestor (node of clade C2) distributed in SAU. Thus, the ancestor of clades C1 and C2 (node of clade B1) was also distributed in SAU. The ancestor above six species plus *Parazanclistius hutchinsi* (node of clade A1) was placed in SAU.

The ancestor of *Pentaceros japonicus*, *P. quinquespinis*, *P. richardsoni* and *P. wheeleri* (node of clade G2) was presumed to be distributed in CAL, EP, HAW, NZ, SAF, SAT, SAU and/or SJP, and these four species plus *P. decacanthus* had the common ancestor (node of clade F2) in NZ and SAU. The ancestor of above five species of *Pentaceros* plus *P. capensis* (node of clade A2) was ranged in NZ, SAU and/or SAF.

As the result, clade A1 including seven species has the common ancestor in SAU, and clade A2 consisted of six species has the common ancestor in NZ, SAU and/or SAF.

Finally, on the basis of the analyses of two major clades A1 and A2, it is inferred that the common ancestor of all pentacerotids originated in SAU, that is South Australia region.

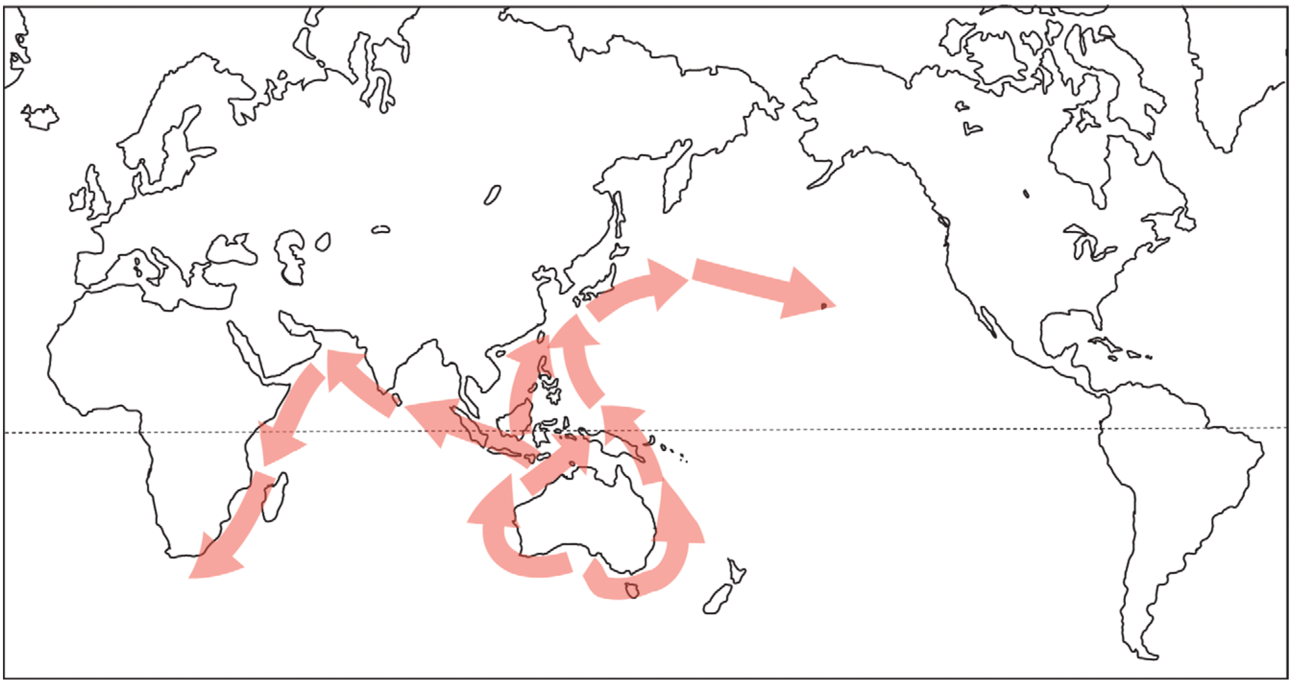

FIGURE 86. Geographic dispersal pattern of the genus *Histiopterus*.

1-3. Dispersal patterns of pentacerotids

The dispersal pattern of pentacerotids is estimated and discussed on the basis of center of their origin considered in the previous subsection and the phylogenetic relationships reconstructed in this study.

As the result, it is presumed that the Pentacerotidae has its center of origin in Southern Australian region, and dispersal patterns of each genus are categorized into five types as follows. The genus *Histiopterus* was dispersed from the western and eastern parts of Southern Australian region northward (Northern Australia, Indian, New Guinea and Southern Japan regions), then further dispersed in two ways, eastward (Hawaiian region) and southwestward (Northern India and Southern Africa regions) dispersions, (Type A, Fig. 86).

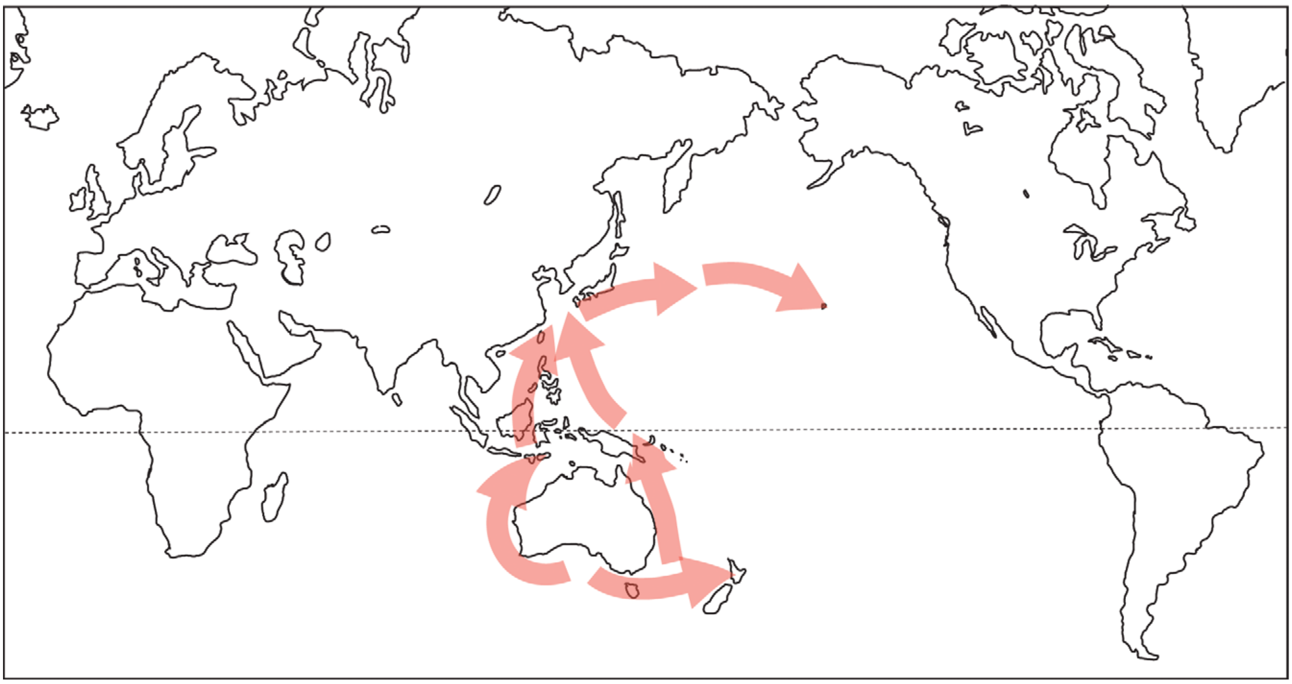

FIGURE 87. Geographic dispersal pattern of the genus *Evistias*.

The genus *Evistias* has spread eastward (New Zealand region) and northward (Southern Japan region) over the Southern Australian region from the western and eastern parts of the region, respectively, and next to eastward (Hawaiian region) (Type B, Fig. 87). The genera *Zanclistius* and *Paristiopterus* dispersed eastward from the southern Australian region (New Zealand region) (Type C, Fig. 88). The distributions of the genera *Pentaceropsis* and *Parazanclistius* are limited in Southern Australian region and not dispersed beyond the region (Type D, Fig. 89).

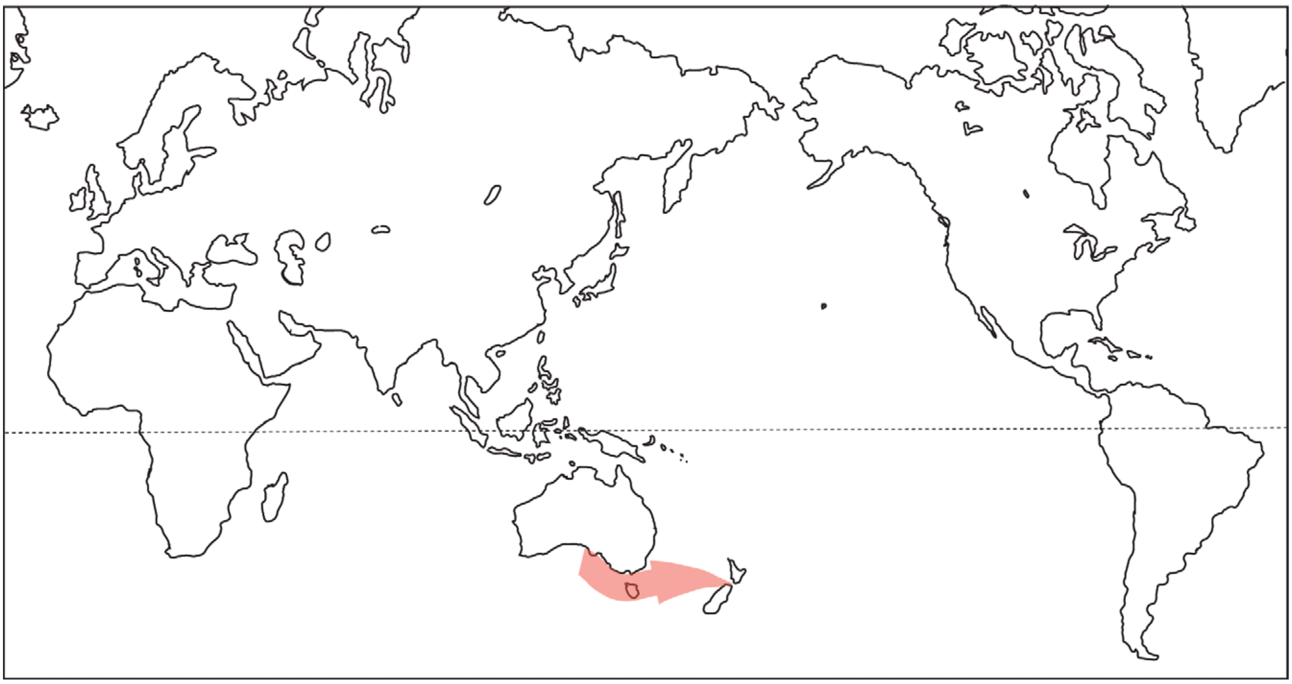

FIGURE 88. Geographic dispersal pattern of the genera *Zanclistius* and *Paristiopterus*.

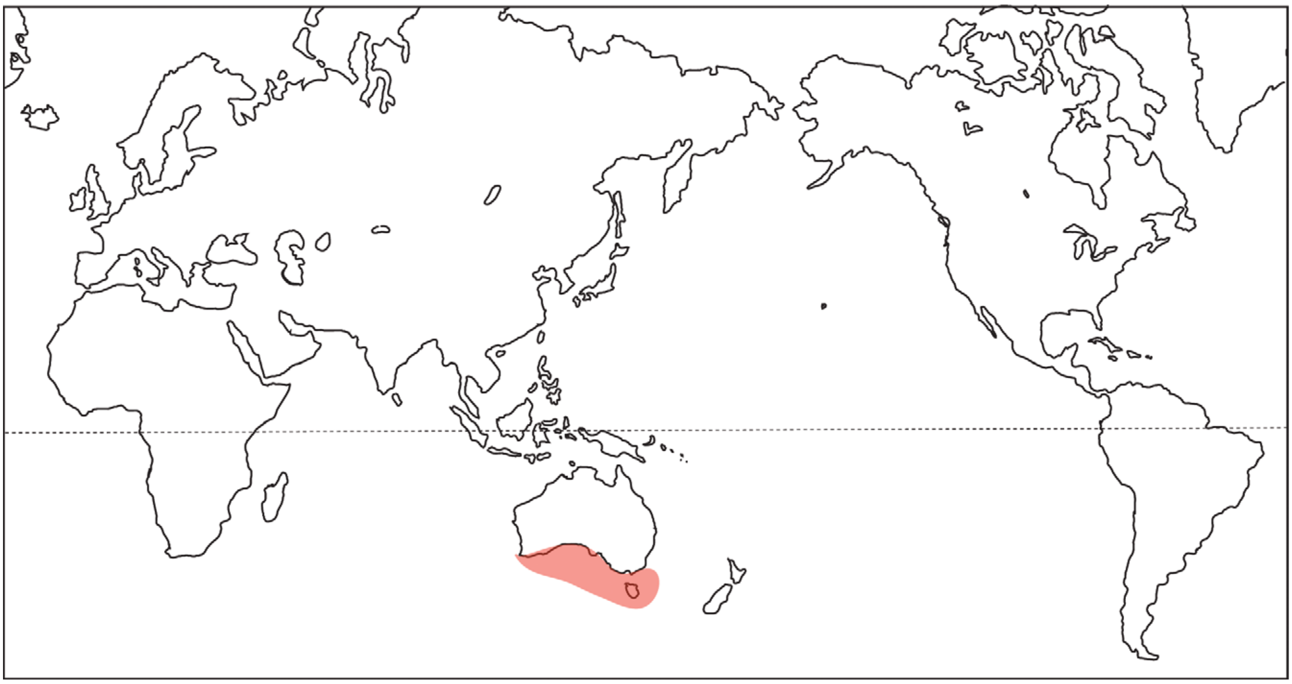

FIGURE 89. Geographic dispersal pattern of the genera *Pentaceropsis* and *Parazanclistius*.

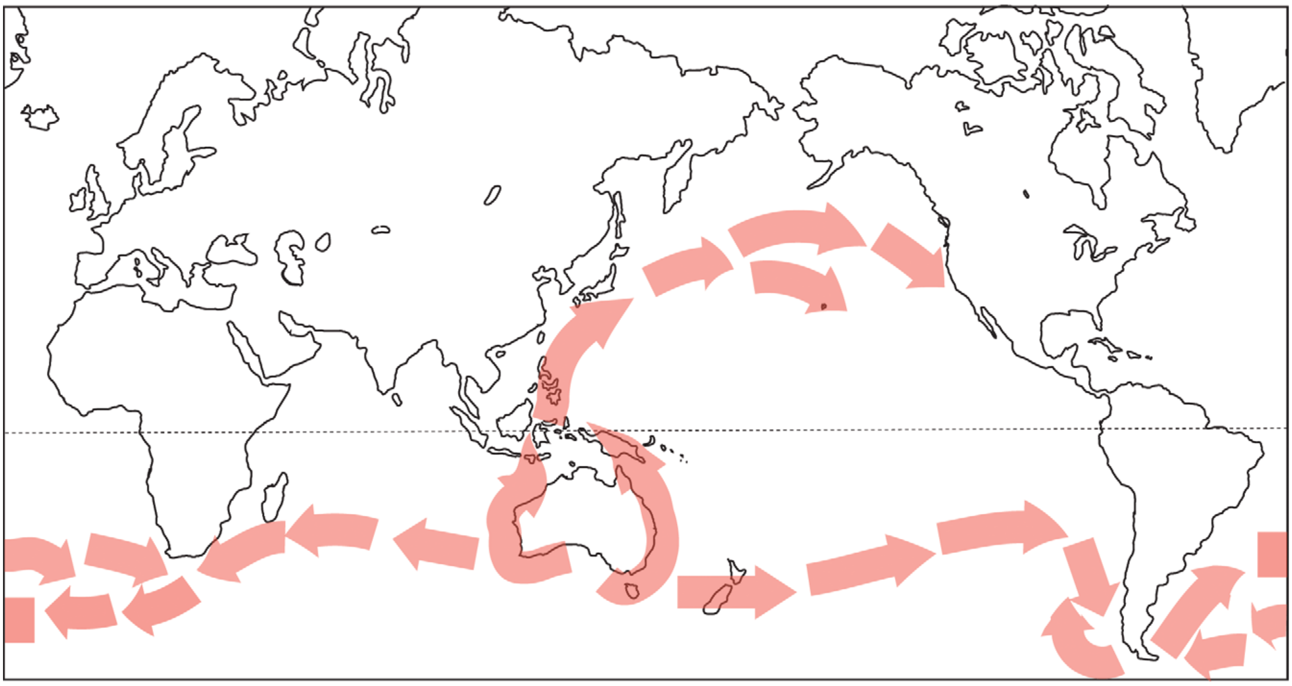

FIGURE 90. Geographic dispersal pattern of the genus *Pentaceros*.

The genus *Pentaceros* is broadened from the western and eastern parts of Southern Australian region to northward (Southern Japan region). Judging from the distribution of *P. wheeleri*, it can be inferred that the species eastwardly dispersed from Southern Japan region to Hawaiian region and to California region. It is possible that this genus was dispersed Southern Australian region to eastward (New Zealand region) and finally arrived in Southern Africa region through Eastern Pacific region and Southern Atlantic region, judging from recent distribution of *P. richardsoni*, which is the sole species of this family known from Eastern Pacific region and Southern Atlantic region, and is also known from Southern Africa region with *Histiopterus typus* and *Pentaceros capensis*. However, when considering on *Pentaceros capensis*, which is presumed to be branched off from clade A2 initially and recently known only from South Africa region, it is also parsimonious to infer that the species dispersed from Southern Australia region to Southern Africa region directly (Type E, Fig. 90).

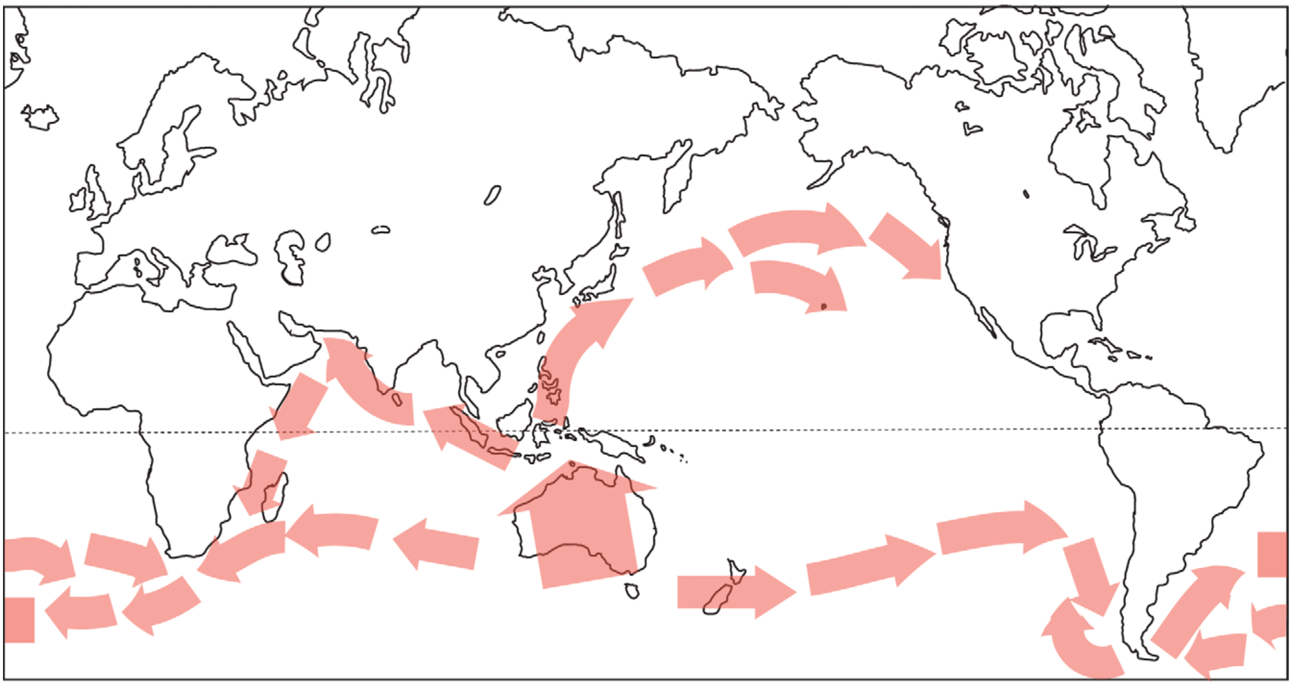

FIGURE 91. Geographic dispersal of the pentacerotids from Southern Australian region.

In conclusion, based on the above five patterns of pentacerotids and the dispersion of this family, it is inferred that they dispersed from the Southern Australian region in three major directions, New Zealand eastwardly, Northern Australian region and New Guinea region northwardly, and Southern African region westwardly (Fig. 91). After the northward dispersion, they dispersed again in two directions; i.e., westward and northward. The ancient pentacerotids dispersed westwardly from the Northern Australian region to the Southern African region through the Indian region and Northern Indian region. The ancient pentacerotids also dispersed northwardly to the Southern Japan region, and then eastwardly to the Hawaiian and Californian regions. The ancient pentacerotids also dispersed eastwardly from the New Zealand region to the Southern African region through the Eastern Pacific and the Southern Atlantic regions. Therefore, it can be inferred that the pentacerotids in the Southern African region originated independently from the Indian Ocean (including two possibilities) and South Atlantic Ocean.

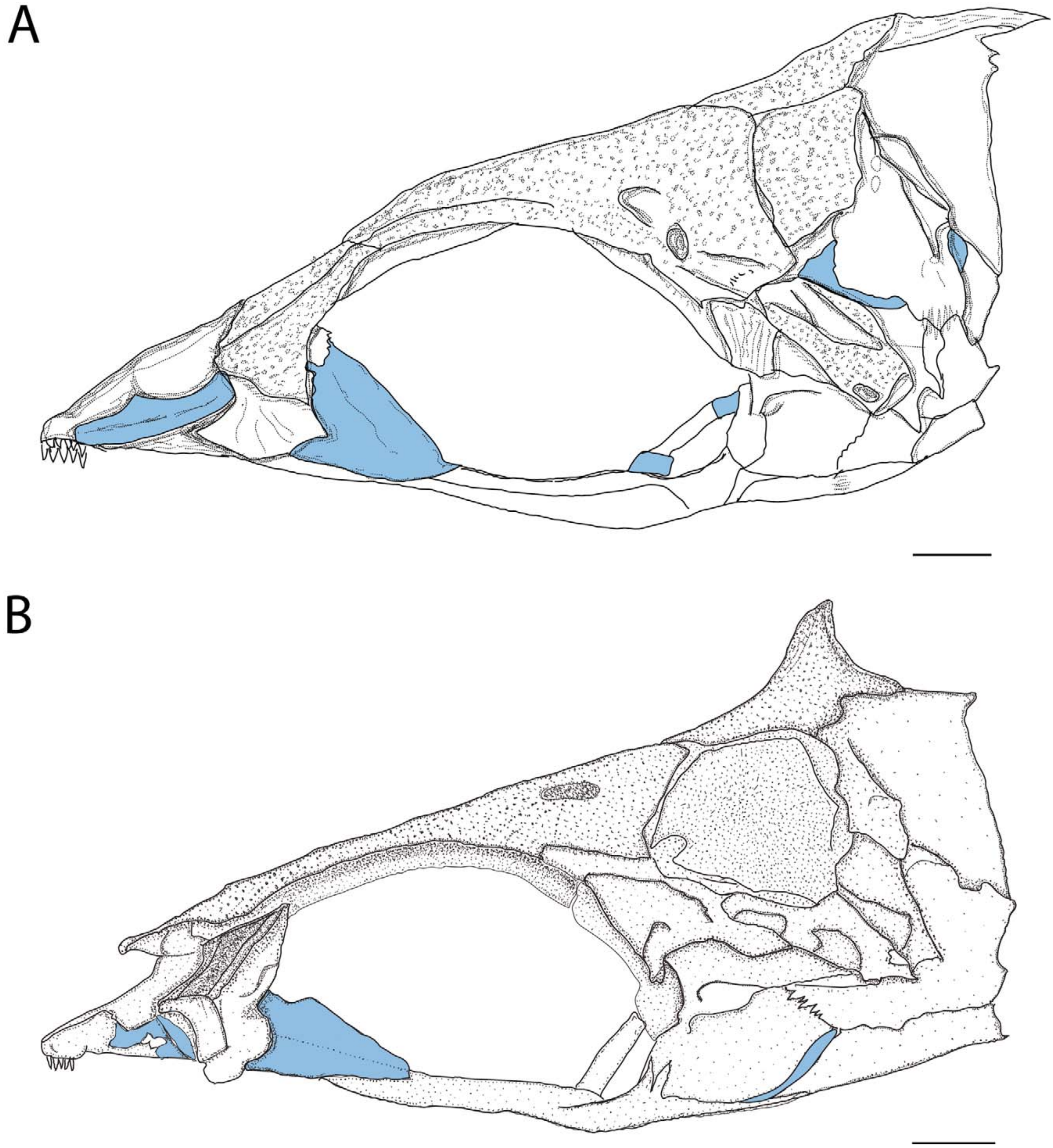

FIGURE 92. Lateral aspects of neurocranium. A, *Pentaceros capensis* (Pentacerotidae); B, *Ostracoberyx dorygenys* (Ostracoberycidae). Scale bar = 5 mm.

At present, no fossils of the family Pentacerotidae have been recorded. To discuss on the ages of origin and dispersions of the family, the data of fossils is required. Further study is needed to solve the question, based on the fossil records.

2. Search for closely related taxa with Pentacerotidae

In this section, I search for candidates of taxa closely related with the family Pentacerotidae, from comparison of characters in perciformes and the following synapomorphies recognized in the family: the second infraorbital articulates with the lateral ethmoid anteromedially (SA 1); many exposed tubercles present on the dorsal and lateral surfaces of the head (including frontal, supraoccipital, and pterotic) (SA 2); the supraoccipital crest high and stout (SA 3); the ascending and articular processes continuous (SA 4); the supramaxilla absent (SA 5); the distal ends of premaxilla and maxilla articulate (SA 6); the palatine teeth absent (SA 7); the endopterygoid articulating with the lateral ethmoid (SA 8); absence of a tooth plate on the third epibranchial (SA 9); pad-like bundle of the transversus dorsalis anterior present (SA 10); and the adductor radialis originating from the medial surface or the third actinost (SA 11). In this study, I compare the Pentacerotidae and many perciformes based on data examined in this study and also those from literature.

All Pentacerotidae have many exposed tubercles present on the dorsal and lateral surfaces of the head (SA 2). This character is quite rare in the Percoidei, because it is usually absent in the suborder, except for the Ostracoberycidae, in which the exposed tubercles are also recognized. In addition, the Ostracoberycidae also possesses two derived characters, being consistent with SA 3 (Fig. 92) and SA 10 (Fig. 93).

Mok and Shen (1983) considered that the Pentacerotidae and a monophyletic group including the Chaetodontidae, Pomacanthidae, Scatophagidae, Siganidae, Acanthuridae, Zanclidae, and Tetraodontiformes have a sister relationship. Tyler et al. (1989) did not accept the hypothesis by Mok and Shen (1983), because the relationship is supported by only one derived character, the pelvic bone interlocks with the spine. In the present study, it was revealed that the interlocked pelvic bone and spine occured only in *Pentaceros* in the Pentacerotidae, and this character does not support Mok and Shen’s (1983) hypothesis. Among the sister group for Pentacerotidae proposed by Mok and Shen (1983), the Chaetodontidae larvae have an exposed and rugose head bone (e.g., Johnson, 1984), which is quite similar to head bones with exposed tubercles in the Pentacerotidae. In addition to this character, the Chaetodontidae has derived characters consistent with four synapomorphies of the Pentacerotidae; i.e., the supraoccipital crest is high and stout (SA 3), the ascending and articular processes are continuous (SA 4) (Fig. 94), the supramaxilla is absent (SA 5) (Fig. 95), and the palatine teeth are absent (SA 7) (Fig. 96), although these derived characters are also recognized in some percoids (for example, SA 3 in Banjosidae, Gerreidae, and Sparidae; SA 4 in Banjosidae and Mullidae; SA 5 in Pempheridae, Banjosidae, and Sciaenidae, and SA 7 in Banjosidae and Sciaenidae) (e.g., Gregory, 1933; Katayama, 1959; Fraser, 1968; Tominaga, 1968; Vari, 1978; Johnson, 1980; Yabe, 1985; Sasaki, 1989; Imamura, 1996). In addition, although one character, the stongly compressed body, is not recognized as a synapomorphy of the Pentacerotidae in this study; the Chaetodontidae also possesses this character.

In this study, as pointed out above, when considering head morphology, the Pentacerotidae has derived similarity with the Ostracoberycidae and Chaetodontidae. Of the two families, the Chaetodontidae has several derived characters more similar to synapomorphies of the Pentacerotidae than the Ostracoberycidae. Because four characters (SA 3, 4, 5 and 7) are not unique to the Pentacerotidae and Chaetodontidae, the four characters do not strongly support the monophyly of the two families. Accordingly, I equally propose two families, the Ostracoberycidae and Chaetodontidae, as candidate taxa closely related with the Pentacerotidae in this study.

IX. Summary

The present study was made to describe the comparative anatomy of the family Pentacerotidae (*sensu* Nelson, 2006) in detail, to infer the phylogenetic relationships of the family and related taxa based on recognized characters, to verify the monophyly of the family Pentacerotidae, and to propose a new classification system on the basis of the inferred relationships of the family.

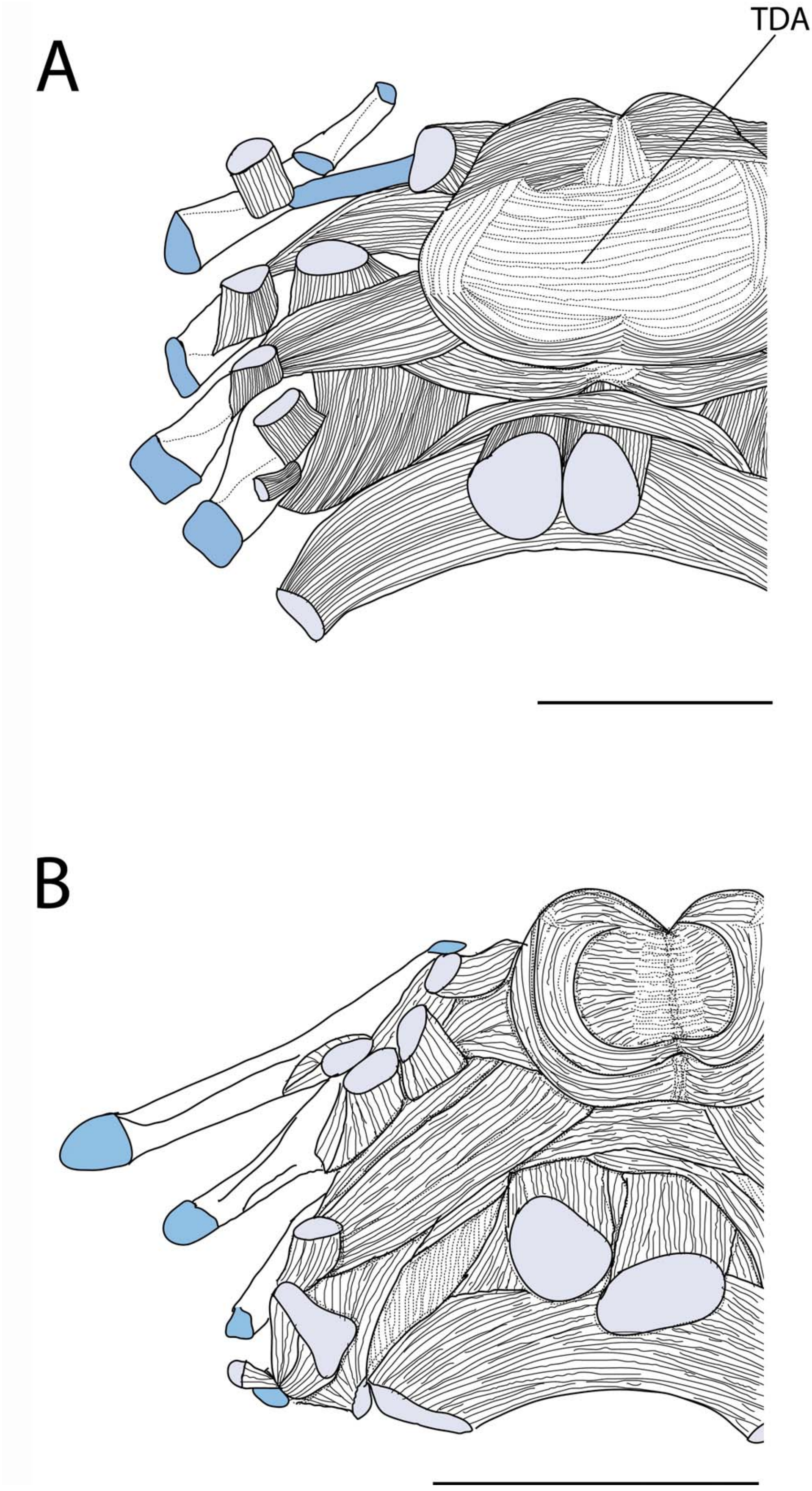

FIGURE 93. Dorsal aspect of upper gill arch muscles of *Zanclistius elevatus* (Pentacerotidae) (A) and *Ostracoberyx dorygenys* (Ostracoberycidae) (B). Scale bar = 5 mm.

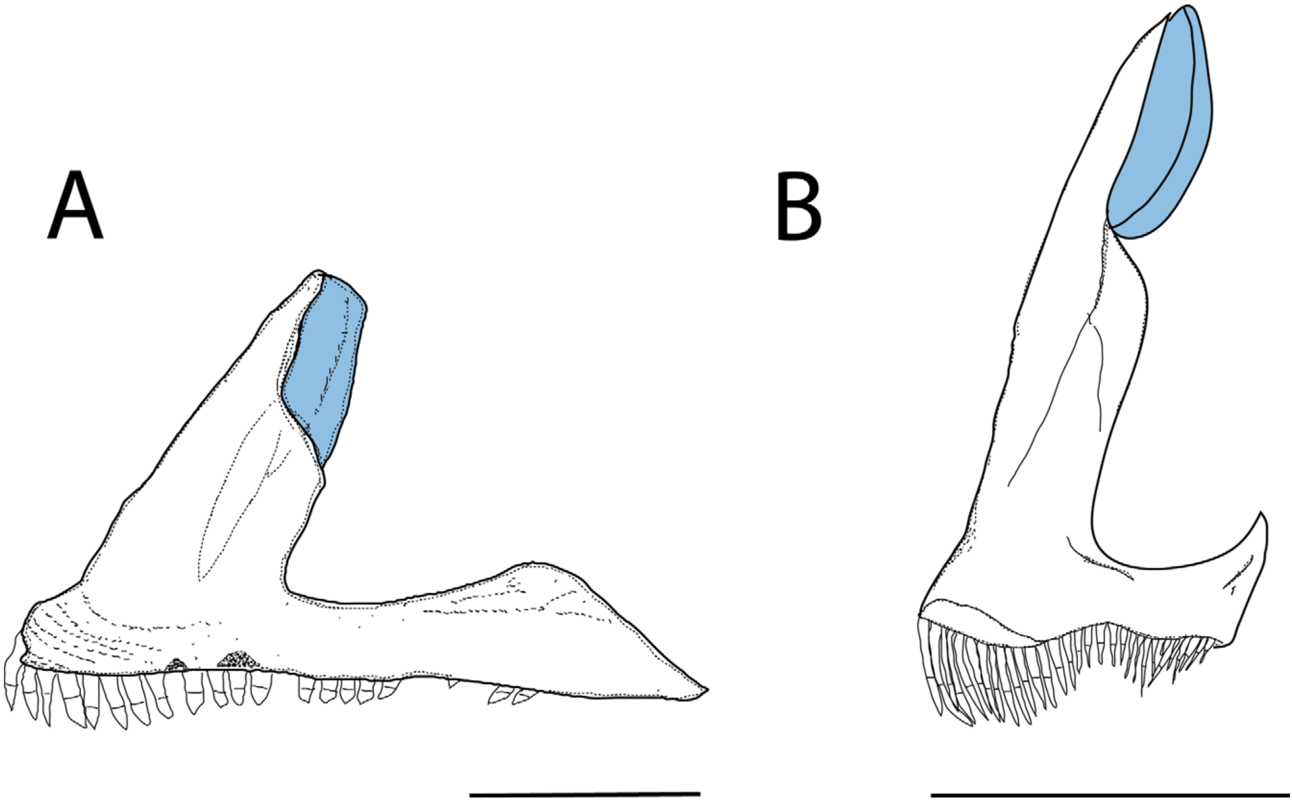

FIGURE 94. Lateral aspects of premaxilla of *Evistias acutirostris* (A) and *Chaetodon modestus* (B). Scale bar = 5 mm.

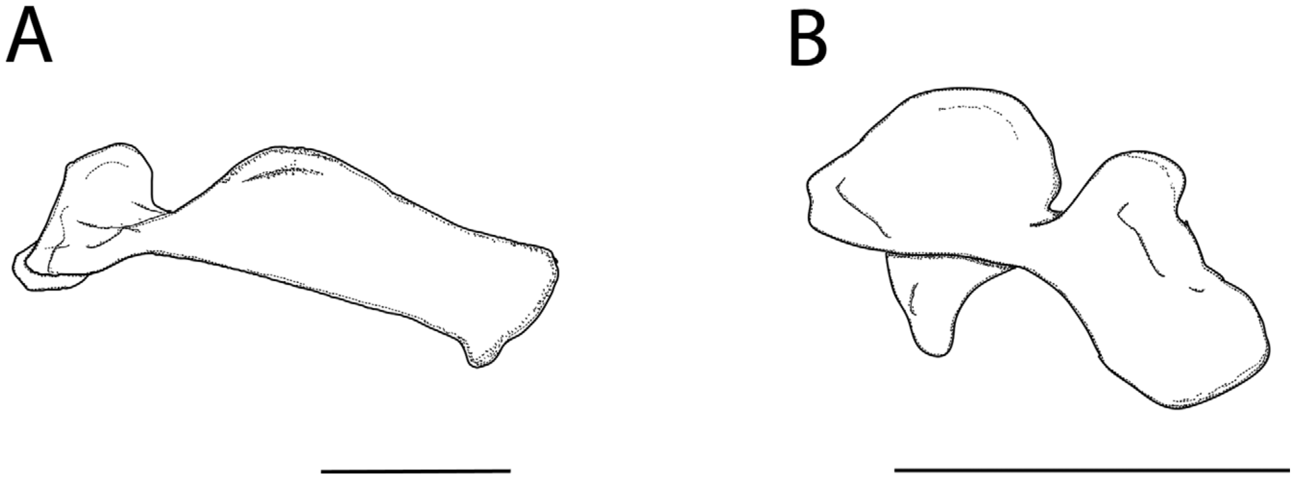

FIGURE 95. Lateral aspects of maxilla of *Evistias acutirostris* (Pentacerotidae) (A) and *Chaetodon modestus* (Chaetodontidae) (B). Scale bar = 5 mm.

The conclusions of present study are summarized as below.

1. The osteologic and myologic characteristics of the family Pentacerotidae were described in detail, and variations of the morphology were demonstrated.
2. The family Pentacerotidae is a monophyletic group supported by 11 synapomorphies found in all members of the family. Of their synapomorphies, two characters (the second infraorbital articulating with the lateral ethmoid anteromedially, and the endopterygoid articulating with the lateral ethmoid) are considerably rare in the percoids and the monophyly of the family was strongly supported.
3. After the phylogenetic analysis using the morphologic characters recognized in 44 transformation series, four equally parsimonious trees were obtained, and a strict consensus tree of these trees was adopted. It was inferred that the family Pentacerotidae was divided into two major clades, initially.
4. On the basis of the inferred phylogenetic relationships of the Pentacerotidae, this family was cladistically classified into two

subfamilies and seven genera. The genus *Pseudopentaceros* was regarded as a junior synonym of *Pentaceros*. The newly proposed classification of the family is shown as below:

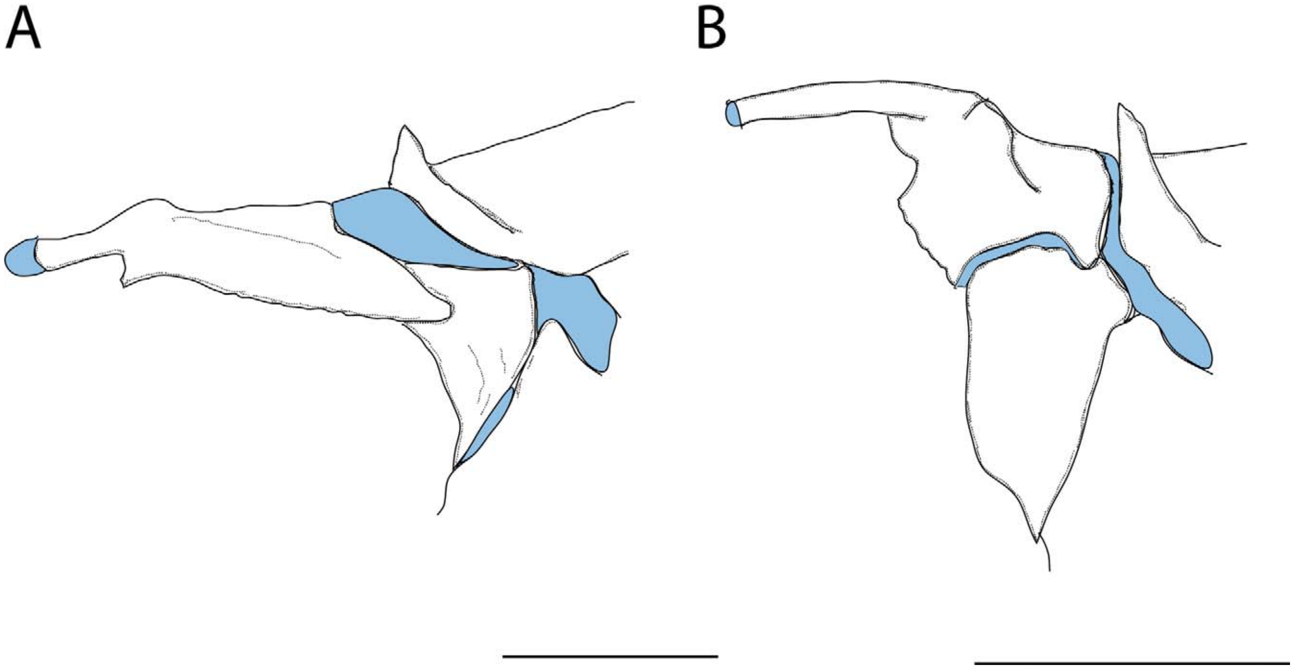

FIGURE 96. Lateral aspects of palatine of *Pentaceros japonicus* (Pentacerotidae) (A) and *Chaetodon modestus* (Chaetodontidae) (B). Scale bar = 5 mm.

Family Pentacerotidae
    Subfamily Histiopterinae
        Genus *Histiopterus* Temminck and Schlegel, 1844
        Genus *Evistias* Jordan, 1907
        Genus *Zanclistius* Jordan, 1907
        Genus *Pentaceropsis* Steindachner and Döderlein, 1883
        Genus *Paristiopterus* Bleeker, 1876
        Genus *Parazanclistius* Hardy, 1983
    Subfamily Pentacerotinae
        Genus *Pentaceros* Cuvier, 1829

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XI. Literature cited

Amaoka, K., Matsuura, K., Inada, T., Takeda, M., Hatanaka, H & Okada, K. (1990) Pentacerotidae. *In*: Hardy, G.S. (Ed), *Fishes collected by the R/V Shinkai Maru around New Zealand*. Japan Marine Fishery Resource Research Center, Tokyo, pp. 285.

Baldwin, C.C. & Johnson, G.D. (1993) Phylogeny of the Epinephelinae (Teleostei: Serranidae). *Bulletin of Marine Science*, 52, 240–283.

Bleeker, P. (1876) Systema Percarum revisum. Pars Ia. Percae. *Archives Neerlandais de Sciences Naturelles, Haarlem*, 11(1), 247–288.

Boehlert, G.W. & Sasaki, T. (1988) Pelagic biogeography of the armorhead, *Pseudopentaceros wheeleri*, and recruitment to isolated seamounts in the North Pacific Ocean. *Fishery Bulletin*, 86, 453–465.

Branson, B.A. & Moore, G.A. (1962) The lateralis components of the acoustico-lateralis system in the sunfish family Centrarchidae. *Copeia*, 1962, 1–108.

Briggs, J.C. (1974) *Marine Zoogeography*. McGraw-Hill, New York, 475 pp.

Carnevale, G. (2006) Morphology and biology of the Miocene butterflyfish *Chaetodon ficheuri* (Teleostei: Chaetodontidae). *Zoological Journal of the Linnean Society*, 146, 251–267.

Carpenter, K.E. & Johnson, G.D. (2002) A phylogeny of sparoid fishes (Perciformes, Percoidei) based on morphology. *Ichthyological Research*, 49, 114–127.

Castelnau, F. de (1872) Contributions to the ichthyology of Australia. *Proceedings of the Zoological and Acclimatisation Society of Victoria*, 1, 29–242.

Coleman, N. (1980) *Australia Sea fishes South of 30°S*. Doubleday Australia. Sydney, 309 pp.

Cuvier, G.L.C.F.D & Valenciennes, A. (1829) *Histoire naturelle des poissons. Tome troisième. Suite du Livre troisième. Des percoïdes à dorsale unique à sept rayons branchiaux et à dents en velours ou en cardes*. 3. Paris & Strasbourg (Levrault), 500 pp.

Eschmeyer, W.N. (1998) *Catalog of fishes*. 1–3 vols. California Academy of Sciences, San Francisco, 2905 pp.

Farris, J.A. (1970) Method for computing Wagner trees. *Systematic Zoology*, 19, 83–92.

Fitch, W.M. (1971) Toward defining the course of evolution: minimal change for a specific tree topology. *Systematic Zoology*, 20, 406–416.

Fraser, T.H. (1968) Comparative osteology of the Atlantic snooks (Pisces: *Centropomus*). *Copeia*, 1968, 433–460.

Fraser, T.H. (1972) Comparative osteology of the shallow water cardinal fishes [Perciformes: Apogonidae] with reference to the systematics and evolution of the family. *Ichthyological bulletin of the J.L.B. Smith Institute of Ichthyology*, 34, 1–105.

Fujita, K. (1990) *The caudal skeleton of teleostean fishes*. Tokai University Press, Tokyo. 897 pp. (in Japanese with English summary).

Gill, A.C. & Mooi, R.D. (1993) Monophyly of the Grammatidae and of the notograptidae, with evidence for their phylogenetic positions among perciforms. *Bulletin of Marine Science*, 52, 327–350.

Gobalet, K.W. (1989) Morphology of the parrotfish pharyngeal jaw apparatus. *Integrative and Comparative Biology*, 29, 319–331.

Gomon, M.F., Bray,D. & Kuiter, R.H. (2008) *The Fishes of Australia's South Coast*. State Printer. New Holland Publishers, Sydney, pp. 611–617.

Gosline, W.A. (1966) The limits of the fishes family Serranidae, with notes on other percoids. *Proceedings of the California Academy of Sciences*, (4), 33, 91–112.

Gosline, W.A. (1968) The suborders of perciform fishes. *Proceedings of the United States National Museum*, 124, 1–78.

Gosline, W.A. (1984) Structure, function, and ecology of the goatfishes (family Mullidae). *Pacific Science*, 38, 312–323.

Gosline, W.A. (1985) Relationships among some relatively deep-bodied percoid fish group. *Japanese Journal of Ichthyology*, 31, 351–357.

Gosline, W.A. (1989) Two patterns of differentiation in the jaw musculature of teleostean fishes. *Journal of Zoology*, 218, 649–661.

Govoni, J.J., West, M.A., Zivotofsky, D., Bowser, P.R., & Collette, B.B. (2004) Ontogeny of squamation in swordfish, *Xiphias gladius*. *Copeia*, 2004, 391–396.

Gregory, W.K. (1933) *Fish skulls: a study of the evolution of natural mechanisms*. Transactions of the American Philosophical Society, 23, 75–481 pp.

Günther, A. (1859) *Catalogue of the acanthopterygian fishes in the collection of the British Museum. Gasterosteidae, Berycidae, Percidae, Aphredoderidae, Pristipomatidae, Mullidae, Sparidae*. Catalogue of the fishes in the British

Museum, London, 524 pp.

Günther, A. (1872) Report on several collections of fishes recently obtained for the British Museum. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London*, 1871, 652–675.

Hardy, G.S. (1983a) A revision of the fishes of the family Pentacerotidae (Perciformes). *New Zealand Journal of Zoology*, 10, 177–220.

Hardy, G.S. (1983b) A new genus and species of boarfish (Perciformes: Pentacerotidae) from Western Australia. *Records of the Western Australian Museum*, 10, 373–380.

Harrington, R.W. (1955) The osteocranium of the American cyprinid fish, *Notropis bifrenatus*, with an annotated synonymy of teleost skull bones. *Copeia*, 1955, 267–290.

Hennig, W. (1966) *Phylogenetic systematics*. University of Illinois Press, Urbana, 263 pp.

Hilton, E.J. & Johnson, G.D. (2007) When two equals three; developmental osteology and homology of the caudal skeleton in carangid fishes (Perciformes: Carangidae). *Evolution & Development*, 9, 178–189.

Hoese, D.F., Bray, D.J., Allen, G.R., Paxton, J.R., Wells, A. & Beesley, P.L. (2006) Pentacerotidae. *In*: Bray, D.J., Hoese, D.F. & Paxton, J.R. (Eds.), *Zoological Catalogue of Australia. Vol.35.2* ABRS & CSIRO Publishing, Australia, pp. 1312–1316.

Hubbs, C.L. & Lagler, K.F. (1958) *Fishes of the Great Lakes region*. Cranbrook Institute of Science Bulletin, 26, 1–213.

ICZN. (1999) *International code of zoological nomenclature. 4th ed*. The International Trust for Zoological Nomenclature, London, 306 pp.

Imamura, H. (1996) Phylogeny of the family Platycephalidae and related taxa (Pisces: Scorpaeniformes). *Species Diversity*, 1, 123–233.

Imamura, H. (2000) An alternative hypothesis on the phylogenetic position of the family Dactylopteridae (Pisces: Teleostei), with a proposed new classification. *Ichthyological Research*, 47, 203–222.

Imamura, H. (2004) Phylogenetic relationships and new classification of the superfamily Scorpaenoidea (Actinopterygii: Perciformes). *Species Diversity*, 9, 1–36.

Imamura, H. & Yabe, M. (2002) Demise of the Scorpaeniformes (Actinopterygii: Percomorpha): an alternative phylogenetic hypothesis. *Bulletin of Fisheries Sciences Hokkaido University*, 53, 107–128.

Ishida, M. (1994) Phylogeny of the suborder Scorpaenoidei (Pisces: Scorpaeniformes). *Bulletin of the Nansei National Fisheries Research Institute*, 27, 1–112.

Johnson, G.D. (1980) The limits and relationships of the Lutjanidae and associated families. *Bulletin of the Scripps Institution of Oceanography*, 24, 1–114.

Johnson, G.D. (1983) *Niphon spinosus*: a primitive Epinepheline Serranid, with comments on the monophyly and intrarelationships of the Serranidae. *Copeia*, 1983, 777–787.

Johnson, G.D. (1984) Percoidei: development and relationships. *In*: Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall, A.W.Jr., & Richardson, S.L. (Eds.). Ontogeny and Systematics of Fishes. *American Society of Ichthyologists and Herpetologists*, *Special Publication*, 1, 464–498.

Johnson, G.D. (1993) Percomorph phylogeny: progress and problems. *Bulletin of Marine Science*, 52, 3–28.

Johnson, G.D. & Patterson, C. (1993) Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science*, 52, 554–626.

Jordan, D.S. (1907) A review of the fishes of the family Histiopteridae, found in the waters of Japan; with a note on *Tephritis* Günther. *Proceedings of the United States National Museum*, 32 (1523), 235–239.

Kailola, P.J. (1987) *The fishes of Papua New Guinea*: *a revised and annotated checklist. Vol. II Scopaenidae to Callionymidae*. Research Bulletin No. 41, Research Section, Dept. of Fisheries and Marine Resources, Papua New Guinea. pp. 344.

Katayama, M. (1959) Studies on the serranid fishes of Japan (I). *Bulletin of the Faculty of Education, Yamaguchi University*, 8, 103–180.

Kim, B.-J. (2002) Comparative Anatomy and Phylogeny of the Family Mullidae (Teleostei; Perciformes). *Memoirs of the Graduate School of Fisheries Sciences, Hokkaido University*, 49, 1–74.

Kim, I.-S., Choi, Y., Lee, C.-L., Lee, Y.-J., Kim, B.-J. & Kim, J.-H. (2005) *Illustrated book of Korean fishes*. Kyo-Hak Publishing Seoul, Korea, pp. 353. (in Korean).

Kuiter, R.H. (1993) *Coastal fishes of south-eastern Australia*. University of Hawaii Press, Honolulu, pp. 249-250.

Last, P.R., Scott, E.O.G. & Talbot, F.H. (1983) *Fishes of Tasmania*. Hobart: Tasmanian fisheries Development Authority, Tasmania, 563 pp.

Matsubara, K. (1943) Studies on the scorpaenoid fishes of Japan. Anatomy, phylogeny and taxonomy (I). *Transactions Sigenkagaku Kenkyusho*, 1, 1–170.

May, J.L. & Maxwell, J.G.H. (1986) *Field Guide to Trawl Fish from Temperate Waters of Australia*. Hobart. CSIRO Division of Marine Research Revised Edn, Sydney, 492 pp.

McAllister, D.E. (1968) The evolution of branchiostegals and associated opercular, gular, and hyoid bones and the classification of teleostome fishes, living and fossil. *National Museum of Canada, Bulletin*, 221, 1–239.

Mecklenburg, C.W., Mecklenburg, T. A. & Thorsteinson, L. K. (2002) *Fishes of Alaska*. American Fisheries Society, Bethesda, Maryland, 1037 pp.

Mok, H.-K. & Shen, S.-C. (1983) Osteology and phylogeny of squamipinnes. *Taiwan Museum Special Publication Series Zoology*, 1, 1–87.

Mooi, R.D. (1993) Phylogeny of the Plesiopidae (Pisces: Perciformes) with evidence for the inclusion of the Acanthoclinidae. *Bulletin of Marine Science*, 52, 284–326.

Nelson, J.S., Crossman, E.J., Espinosa–Pérez, H., Findley, L.T., Gilbert, C.R., Lea, R. N. & Williams, J.D. (2004) *Common and scientific names of fishes from the United States, Canada, and Mexico*. *6th ed*. American Fisheries Society, Special Publication, 29, Bethesda, Maryland, 386 pp.

Nelson, J.S. (2006) *Fishes of the world*. *4th ed*. John Wiley & Sons, Inc, Hoboken, New Jersey, 601 pp.

Okamura, O., Machida, Y., Yamakawa, T., Matsuura K. & Yatou, T. (1985) *Fishes of the Okinawa Trough and the adjacent waters*. *Vol. 2*. *The intensive research of unexploited fishery resources on continental slopes*. Japan Fisheries Resource Conservation Association, Tokyo, 2, pp. 520–521, 694. (in Japanese, English summary).

Otero, O. (2004) Anatomy, systematics and phylogeny of both recent and fossil latid fishes (Teleostei, Perciformes, Latidae). *Zoological Journal of the Linnean Society*, 141, 81–133.

Parin, N.V. & Kotlyar, A.N. (1988) A new armorhead species, *Pentaceros quinquespinis* (Pentacerotidae), from the southeast Pacific. *Voprosy Ikhtiologii*, 28, 355–360. (in Russian. English translation in *Journal of Ichthyology*, 28, 79–84.).

Patterson, C. (1968) The caudal skeleton in Mesozoic acanthopterygian fishes. *Bulletin of the British Museum (Natural History) Geology*, 17, 49–102.

Patterson, C. & Johnson, G.D. (1995) The intermuscular bones and ligaments of teleostean fishes. *Smithsonian Contributions Zoology*, 559, 1–85.

Pequeño, G. (1997) Peces de Chile. Lista sistemática revisada y comentada: addendum. *Revista de Biología Marina y Oceanografica*, 32, 77–94.

Prokofiev, A.M. (2007a) Osteology and some other morphological characters of *Howella sherborni*, with a discussion of the systematic position of the genus (Perciformes, Percoidei). *Journal of Ichthyology*, 47, 412–426.

Prokofiev, A.M. (2007b) Osteology of *Florenciella lugubris* (Percoidei: Epigonidae). *Journal of Ichthyology*, 47, 715–725.

Ramsay, E.P. & Ogilby, J.D. (1888) Descriptions of two new Australian fishes. *Proceedings of the Linnean Society of New South Wales (2nd series)*, 3, 1310–1312.

Randall, J.E. (1995) *Coastal fishes of Oman*. Crawford House Publishing, Bathurst, Australia, pp. 256.

Richardson, J. (1845) Ichthyology of the voyage of H. M. S. Erebus & Terror, under the command of Captain Sir J. C. Ross. *In*: Richardson, J. & Gray, J. E. (Eds.), *The zoology of the voyage of H. H. S. "Erebus & Terror," under the command of Captain Sir J. C. Ross.* Edward Newman, London, 17–52.

Roberts, C.D. (1993) Comparative morphology of spined scales and their phylogenetic significance in the Teleostei. *Bulletin of Marine Science*, 52, 60–113.

Sasaki, K. (1989) Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). *Memoirs of the Faculty Fisheries, Hokkaido University*, 36, 1–137.

Sawada, Y. (1982) Phylogeny and zoogeography of the superfamily Cobitoidea (Cyprinoidei, Cypriniformes). *Memoirs of the Faculty Fisheries, Hokkaido University*, 28, 65–223.

Scott, T.D., Glover, C.J.M. & Southcott, R.V. (1974) *The marine and freshwater fishes of South Australia*. *2nd ed.* Government Printer, South Australia, 392 pp.

Seki, M.P. & Somerton, D.A. (1994) Feeding ecology and daily ration of the pelagic armorhead, *Pseudopentaceros wheeleri* at Southeast Hancock Seamount. *Environmental Biology Fishes*, 39, 73–84.

Shinohara, G. (1994) Comparative morphology and phylogeny of the suborder Hexagrammoidei and related taxa (Pisces: Scorpaeniformes). *Memoirs of the Faculty of Fisheries, Hokkaido University*, 41, 1–97.

Smith, A. (1838–1849) Pisces. *In: Illustrations of the zoology of South Africa; Consisting Chiefly of Figures and Descriptions of the Objects of Natural History Collected During an Expedition into the Interior of South Africa in 1834, 1835, and 1836, Fitted Out by the Cape of Good Hope Association for Exploring Central Africa, Vol. 4,* Smith, Elder, London, pp. 1-77, 31 pl.

Smith, J.L.B. (1964) Fishes of the family Pentacerotidae. *Ichthyological Bulletin of the Department of Ichthyology, Rhodes University, Grahamstown, South Africa*, 29, 567–578.

Smith, C.L. & Bailey, R.M. (1962) The subocular shelf of fishes. *Journal of Morphology*, 110, 1–18.

Smith, M.M. & Heemstra, P.C. (1986) Pentacerotidae. *In*: Heemstra, P.C. (Ed), *Smiths'Sea Fishes*. *1st ed*. Springer-Verlag, Berlin, pp. 622-623.

Springer, V.G. & Johnson, G.D. (2004) Study of the dorsal gill-arch musculature of teleostome fishes, with special reference to the Actinopterygii. *Bulletin of the Biological Society of Washington*, 11, 1–260.

Stiassny, M.L.J. (1991) Phylogenetic intrarelationships of the family Cichlidae: an overview. *In*: Keenleyside, M.H.A. (Ed.), *Cichlid Fishes*: *Behaviour, Ecology and Evolution*. Chapman & Hall, London, pp. 1–35.

Steindachner, F. & Döderlein, L. (1883) Beiträge zur Kenntniss der Fische Japan's (II). *Denkschriften der Kaiserlichen Akademie der Wissenschaften*, 48, 1–40.

Swofford, D.L. (2002) PAUP*: *Phylogenetic analysis using parsimony, version 4.0b10*. Sinauer Associates, Sunderland, Massachusetts.

Temminck, C.J. & Schlegel, H. (1844) Pisces, parts 5–6. *In*: von Siebold, P.F (Ed.), *Fauna Japonica, sive descriptio animalium quae in itinere per Japonium suscepto annis 1823–1830 collegit, notis observationibus et adumbrationibus illustravit P.F. de Siebold*. Lugdunum Batavorum, Amsterdam, pp. 73–112.

Tominaga, Y. (1968) Internal morphology, mutual relationships and systematic position of the fishes belonging to the family

Pempheridae. *Japanese Journal of Ichthyology*, 15, 43–95.

Tyler, J.C., Johnson, G.D, Nakamura, I. & Collette, B.B. (1989) Morphology of *Luvarus imperialis* (Luvaridae), with a phylogenetic analysis of the Acanthuroidei (Pisces). *Smithsonian Contributions to Zoology*, 485, 1–78.

Vari, R.P. (1978) The terapon perches (Percoidei, Teraponidae). A cladistic analysis and taxonomic revision. *Bulletin of the American Museum Natural History*, 159, 175–340.

Waite, E.R. (1903) New records or recurrences of rare fishes from eastern Australia. *Records of the Australian Museum*, 5, 56–61.

Watrous, L.E. & Wheeler, Q. D. (1981) The out-group comparison method of character analysis. *Systematic Zoology*, 30, 1–11.

Westneat, M.W. (1993) Phylogenetic relationships of the tribe cheilinini (Labridae: Perciformes). *Bulletin of Marine Science*, 52, 351–394.

Whitley, G.P. (1932) Studies in ichthyology. *Records of the Australian Museum*, 18, 321–348.

Whitley, G.P. (1944) Illustrations of some Western Australian fishes. *Proceedings of the Royal Society of New South Wales*, 1943–44, 25–29.

Wiley, E.O. (1981) *Phylogenetics*: *the theory and practice of phylogenetic systematics*. Wiley Interscience, New York, 439 pp.

Winterbottom, R. (1974) A descriptive synonymy of the striated muscles of the Teleostei. *Proceedings of the Academy Natural Sciences of Philadelphia*, 125, 225–317.

Yabe, M. (1985) Comparative osteology and myology of the superfamily Cottoidea (Pisces: Scorpaeniformes), and its phylogenetic classification. *Memoirs of Faculty of Fisheries, Hokkaido University*, 32, 1–130.