



# HOKKAIDO UNIVERSITY

Title	Comparative morphology and phylogenetic relationships of the family Polynemidae (Pisces: Perciformes)
Author(s)	亢, 世华
Degree Grantor	北海道大学
Degree Name	博士(水産科学)
Dissertation Number	甲第12945号
Issue Date	2017-12-25
DOI	<a href="https://doi.org/10.14943/doctoral.k12945">https://doi.org/10.14943/doctoral.k12945</a>
Doc URL	<a href="https://hdl.handle.net/2115/88262">https://hdl.handle.net/2115/88262</a>
Type	doctoral thesis
File Information	Shihua_Kang.pdf



Comparative morphology and phylogenetic  
relationships of the family Polynemidae  
(Pisces: Perciformes)

( ツバメコノシロ科魚類の比較形態学および系統類縁関係  
に関する研究 )

**Shi-Hua KANG**

**2017**

**Doctoral Thesis**

Laboratory of Marine Biology and Biodiversity

(Systematic Ichthyology)

Graduate School of Fisheries Sciences

Hokkaido University

# Contents

I. Introduction .....	1
II. Materials and Methods.....	4
III. Systematic Methodology .....	10
IV. Monophyly of Polynemidae .....	12
V. Sister relationship of Polynemidae and Sciaenidae .....	15
VI. Comparative Anatomy .....	17
1. Osteology .....	17
1-1. Circumorbital bones .....	17
1-2. Neurocranium .....	29
1-3. Jaws .....	43
1-4. Suspensorium and opercular bones .....	50
1-5. Hyoid arch .....	60
1-6. Branchial arch .....	67
1-7. Pectoral girdle .....	79
1-8. Pelvic girdle .....	91
1-9. Axial skeleton and median fin supports .....	95
1-10. Caudal skeleton .....	108
2. Myology .....	116
2-1. Cheek muscle .....	116
2-2. Cephalic muscles between cranium and suspensorium-opercular	

bones .....	124
2-3. Ventral muscles of head .....	127
2-4. Branchial muscles .....	130
2-5. Pectoral fin muscles .....	139
2-6. Pelvic fin muscles .....	145
2-7. Muscles associated with median fins .....	147
2-8. Caudal fin muscles .....	152
3. Others .....	155
3-1. Swimbladder .....	155
3-2. External morphology .....	157
VII. Phylogenetic Relationships of Polynemidae .....	164
VIII. Classification .....	181
IX. Summary .....	200
X. Acknowledgments .....	202
XI. Literature cited .....	203

## I. Introduction

The family Polynemidae (sensu Nelson, 2006), known as threadfins, is classified into the perciform suborder Percoidei, and comprises eight valid genera and about 50 species (e.g., Feltes 2003; Motomura, 2004; Nelson et al. 2016). Most polynemids are epibenthic fishes found from coastal waters and estuaries in the tropical and subtropical waters of all oceans, although some live entirely in fresh-water rivers (Motomura, 2004). This family is easily identified by the following diagnostic features: the adipose eyelid covering the eye; the body elongated to deep and compressed; the snout obtusely conical and overhanging; the pectoral fins divided into an upper part with 12 to 19 rays joined by membrane and a lower part with three to 16 separate filament-like rays; and two widely separated dorsal fins (see Motomura, 2004; Nelson, 2006). The pectoral filaments, their most distinctive feature, have been considered as a sense organ, enabling polynemids to search for food in sandy and muddy waters (Motomura et al., 2002a). Polynemids are important in commercial fisheries in tropical and subtropical seas worldwide (Motomura et al., 2002a). A few species are used in aquaculture, while the fresh-water polynemids are sometimes used as aquarium fishes (Motomura, 2004). Most polynemids exhibit protandry, having a normal bisexual reproductive cycle from male to female with fish growth (e.g., Longhurst, 1965; Motomura, 2004).

Polynemidae has been variously classified by many ichthyologists. The oldest genus of the family Polynemidae, *Polynemus*, was originally described by Linnaeus (1758). The largest genus *Polydactylus*, including 20 species at present

(Motomura, 2004), was described by Lacepède (1803). Günther (1860) originally described two African genera, *Galeoides* and *Pentanemus*, and Gill (1861) the genus *Polistonemus*. The genera *Eleutheronema* and *Filimanus* were described by Bleeker (1862) and Myers (1936), respectively. Nelson (1984) recognized that Polynemidae includes seven genera, *Eleutheronema*, *Filimanus*, *Galeoides*, *Polistonemus*, *Pentanemus*, *Polydactylus* and *Polynemus*. Feltes (1993) described a new genus *Parapolynemus*, and redefined the family Polynemidae including seven genera with synonym of *Polistonemus* under *Polynemus*. The newest genus, *Leptomelanosoma*, was described by Motomura and Iwatsuki (2001f). Now the classification of the Polynemidae defined by Motomura (2004) with eight genera, *Eleutheronema*, *Filimanus*, *Galeoides*, *Leptomelanosoma*, *Parapolynemus*, *Pentanemus*, *Polydactylus* and *Polynemus*, is adopted by several ichthyologists, such as Nelson (2006), Nakabo (2013) and Nelson et al. (2016). However, the phylogenetic relationships providing the basis of the classification have not been reconstructed in Polynemidae. Although four genera, *Galeoides*, *Leptomelanosoma*, *Parapolynemus* and *Pentanemus*, are monotypic, the other four genera include several species. Accordingly, the phylogenetic relationships of the family should be reconstructed to evaluate the monophyly of these four genera, and to show stable classification of the family.

Johnson (1993) showed morphological evidences supporting a sister-group hypothesis of Polynemidae and Sciaenidae, suggesting that they might be included in a superfamily Polynemoidea, while otolith evidence does not support such a hypothesis (Grove and Lavenberg, 1997). Many authors showed various

candidates of the sister group of Polynemidae; Mugilidae and Sphyraenidae (e.g., Rosen, 1964; Gosline, 1968, 1971), Pleuronectiformes plus Carangiformes (Near et al., 2013), Menidae (Betancur-R et al., 2013, 2014), Menidae plus Lactariidae (Sanciango et al., 2015). More recently, the author (SK) and co-authors confirmed the monophyly of the family Polynemidae by 19 synapomorphies, and showed the evidences to support the sister relationship of Polynemidae and Sciaenidae (Kang et al., 2017).

The goals of the present study are: (1) to show the monophyly of this family and the sister relationship of Polynemidae and Sciaenidae; (2) to describe its osteological and myological characters; (3) to reconstruct its phylogenetic relationships based on morphological characters; and (4) to discuss the classification of Polynemidae.

## II. Materials and Methods

Materials examined in this study are listed below. Institutional abbreviations follow Eschmeyer (1998), except for the Hokkaido University Museum, Hakodate, Japan (HUMZ), Kagoshima University Museum, Kagoshima, Japan (KAUM), and Faculty of Agriculture, University of Miyazaki, Miyazaki, Japan (MUFS). Specimen sizes are expressed as standard length (SL). Examinations were made on specimens stained in alcian blue and alizarin Red-S. “O” and “M” after catalogue numbers indicate materials used for osteological and myological examination, respectively. “S” indicates materials used for examination of the sensory canal on the nasal region. The specimens were dissected under stereo-microscope utilized in the preparation of drawings. The craniums of several materials were cleared and stained. Counts and measurement (eye diameter) follow Motomura (2004). Terminology of osteology generally follows Sasaki (1989), and for myology, Winterbottom (1974). The present study uses classification shown by Nelson (2006) fundamentally.

**Polynemidae.** *Eleutheronema tetradactylum*, HUMZ 47088, 219 mm SL (O) and HUMZ 47084, 222 mm SL (M); *Eleutheronema rhadinum*, HUMZ 216342, 214 mm SL (O) and HUMZ 216344, 20.5 mm SL (M & S); *Polydactylus approximans*, CAS 234425, 192 mm SL (O) and SU 6960, 189 mm SL (M); *Polydactylus macrochir*, NTM 15924-001, 204 mm SL (O & M & S); *Polydactylus microstomus*, SU 38934, 116 mm SL (O & M & S); *Polydactylus multiradiatus*, FRLM 23416, 145 mm SL (O & M); *Polydactylus nigripinnis*, FRLM 23470, 163 mm SL (O & M & S); *Polydactylus octonemus*, USNM

427563, 107 mm SL (O & M & S); *Polydactylus oligodon*, USNM 307236, 109 mm SL (O & M & S); *Polydactylus opercularis*, SU 6649, 181 mm SL (O & M & S); *Polydactylus plebeius*, HUMZ 119215, 163 mm SL (O) and HUMZ 48686, 147 mm SL (M & S); *Polydactylus sexfilis*, CAS 50923, 117 mm SL (O & M & S); *Polydactylus sextarius*, HUMZ 33443, 121 mm SL (O) and USNM 278227, 101 mm SL (M & S); *Polydactylus virginicus*, SU 4888, 222 mm SL (O) and SU 22102, 142 mm SL (M & S); *Galeoides decadactylus*, USNM 408037, 102 mm SL (M & S) and USNM 408037, 149 mm SL (O); *Pentanemus quinquarius*, USNM 289627, 138 mm SL (O) and USNM 289627, 133 mm SL (M & S); *Parapolynemus verekeri*, NTM 14652-001, 97 mm SL (O) and NTM 14653-001, 98 mm SL (M & S); *Leptomelanosoma indicum*, KAUM 39445, 98 mm SL (O) and KAUM 36426, 111 mm SL (M & S); *Filimanus sealei*, KAUM 43957, 103 mm SL (O & M & S); *Filimanus similis*, MUFS 16809, 104 mm SL (O) and MUFS 16813, 106 mm SL (M); *Filimanus xanthonema*, USNM 278199, 106 mm SL (O & M & S); *Polynemus aquilonaris*, KAUM 23381, 96 mm SL (O & M & S); *Polynemus melanochir melanochir*, KAUM 59910, 127 mm SL (O & M & S); *Polynemus multifilis*, KAUM 44962, 86 mm SL (O & M & S); *Polynemus paradiseus*, USNM 363716, 166 mm SL (O & M).

**Comparative materials.** Order Polymixiiformes. Family Polymixiidae: *Polymixia japonica*, HUMZ 79394, 146 mm SL (O & M). Order Mugiliformes. Family Mugilidae: *Mugil cephalus cephalus*, HUMZ 107570, 101 mm SL (O & M). Order Atheriniformes. Family Atherinidae: *Atherinomorus lacunosus*, HUMZ 124892, 81 mm SL (O & M). Order Beryciformes. Family Berycidae:

*Beryx splendens*, HUMZ 79840, 122 mm SL (O & M); *Centroberyx affinis*, HUMZ 49793, 170 mm SL (O). Order Zeiformes. Family Zeidae: *Zeus faber*, HUMZ 107038, 147 mm SL (O & M). Order Scorpaeniformes. Suborder Dactylopteroidei. Family Dactylopteridae: *Dactylopterus orientalis*, HUMZ 105801, 128 mm SL (O & M). Suborder Scorpaenoidei. Family Scorpaenidae: *Helicolenus hilgendorfi*, HUMZ 39743, 136 mm SL (O & M). Order Perciformes. Suborder Percoidei. Family Acropomatidae: *Malakichthys wakiyae*, HUMZ 110763 SL, 145 mm SL (O & M); *Acropoma japonicum*, HUMZ 39772, 106 mm SL (O). Family Apogonidae: *Ostorhinchus doederleini*, HUMZ 175508, 132 mm SL (O). Family Bramidae: *Brama dussumieri*, HUMZ 129210, 166 mm SL (O & M). Family Carangidae: *Trachurus japonicus*, HUMZ 124654, 94 mm SL (O & M). Family Centrarchidae: *Lepomis macrochirus*, HUMZ 123931, 101 mm SL (O & M). Family Cepolidae: *Cepola schlegeli*, HUMZ 15163, unmeasured (O & M). Family Chaetodontidae: *Chaetodon auripes*, HUMZ 35103, 96 mm SL (O & M); *Chaetodontoplus septentrionalis*, HUMZ 48679, 102 mm SL (O & M). Family Cirrhitidae: *Cirrhitichthys aprinus*, HUMZ 101188, 60 mm SL (O & M). Family Coryphaenidae: *Coryphaena hippurus*, HUMZ 64757, 163 mm SL (O & M). Family Drepanidae: *Drepane longimana*, HUMZ 50142, 126 mm SL (O & M). Family Emmelichthyidae: *Emmelichthys struhsakeri*, HUMZ 208856, 63 mm SL (O, M & S). Family Gerreidae: *Gerres oyena*, HUMZ 106117, 117.9 mm SL (O & M). Family Kyphosidae: *Microcanthus strigatus*, HUMZ 157938, 126 mm SL (O & M). Family Lactariidae: *Lactarius lactarius*, HUMZ 227762, 163 mm SL (O, M & S).

Family Lateolabracidae: *Lateolabrax japonicus*, HUMZ 46767, 142 mm SL (O & M). Family Leiognathidae: *Eubleekeria splendens*, HUMZ 217049, 85 mm SL (O & M). Family Lutjanidae: *Lutjanus ehrenbergii*, HUMZ 166120, 147 mm SL (O & M). Family Menidae: *Mene maculata*, HUMZ 12333, 117 mm SL (O, M & S). Family Monodactylidae: *Monodactylus argentus*, HUMZ 165513, 126 mm SL (O, M & S). Family Moronidae: *Morone americana*, USNM 359266, 147 mm SL (O, M & S). Family Mullidae: *Mulloidichthys martinicus*, HUMZ 32262, 137 mm SL (O & M). Family Oplegnathidae: *Oplegnathus fasciatus*, HUMZ 109944, 99 mm SL (O & M). Family Pempheridae: *Pempheris xanthoptera*, HUMZ 101191, 91 mm SL (O); *Pempheris schwenkii*, HUMZ 195702, 129 mm SL (O). Family Pentacerotidae: *Pentaceros japonicus*, HUMZ 90278, 117 mm SL (O & M). Family Percidae: *Perca flavescens*, HUMZ 17389, 108 mm SL (O & M); *Perca fluviatilis*, HUMZ 74637, 90 mm SL (O). Family Percichthyidae: *Howella zina*, HUMZ 130513, 75 mm SL (O). Family Plesiopidae: *Plesiops coeruleolineatus*, HUMZ 119731, 53 mm SL (O & M). Family Priacanthidae: *Priacanthus macracanthus*, HUMZ 97044, 143 mm SL (O). Family Sparidae: *Evygnis cardinalis*, HUMZ 110547, 114 mm SL (O & M). Family Sillaginidae: *Sillago japonica*, HUMZ 55598, 165 mm SL (O & M). Family Sciaenidae: *Argyrosomus japonicus*, HUMZ 106580, 161 mm SL (O & M); *Argyrosomus regius*, HUMZ 111136, 217 mm SL (S); *Atrubucca nibe*, HUMZ 110192, 215 mm SL (O & M); *Collichthys lucidus*, HUMZ 106569, 111 mm SL (S); *Ctenosciaena gracilicirrhus*, HUMZ 30856, 133 mm SL (O & M); *Cynoscion squamipinnis*, HUMZ 34607, 236 mm SL (O & M); *Kathala axillaris*, HUMZ

112119, 95 mm SL (S); *Larimichthys crocea*, HUMZ 106568, 179 mm SL (O & M); *Larimichthys polyactis*, HUMZ 108710, 137 mm SL (O & M); *Leiostomus xanthurus*, HUMZ 109630, 67 mm SL (S); *Macrodon ancylodon*, HUMZ 32362, 206 mm SL (O & M) and HUMZ 30752, 99 mm SL (S); *Pennahia argentata*, HUMZ 48531, 118 mm SL (O & M); *Pennahia macrocephalus*, HUMZ 107208, 137 mm SL (S); *Pentheroscion mbizi*, HUMZ 106567, 150 mm SL (O & M); *Protonibea diacantha*, HUMZ 110966, 188 mm SL (O & M); *Sciaenops ocellata*, HUMZ 104920, 294 mm SL (O); *Stellifer microps*, HUMZ 31090, 117 mm SL (S); *Umbrina coroides*, HUMZ 104918, 114 mm SL (S). Family Serranidae: *Epinephelus latifasciatus*, HUMZ 36511, 113 mm SL (O). Suborder Zoarcoidei. Family Bathymasteridae: *Bathymaster signatus*, HUMZ 46589, 205 mm SL (O & M). Family Pholidae: *Pholis nebulosa*, HUMZ 92281, 201 mm SL (O & M). Family Stichaeidae: *Lumpenella longirostris*, HUMZ uncatalogued, 244 mm SL (O & M). Family Zoarcidae: *Lycodes microporus*, HUMZ 76006, 154 mm SL (O). Suborder Notothenioidei. Family Bovichtidae: *Cottoperca gobio*, HUMZ 82217, 174 mm SL (O & M). Family Channichthyidae: *Champscephalus gunneri*, HUMZ 69281, 237 mm SL (O & M). Family Nototheniidae: *Patagonotothen ramsayi*, HUMZ 30575, 211 mm SL (O & M). Suborder Trachinoidei. Family Champsodontidae: *Champsodon snyderi*, HUMZ 109313, 88 mm SL (O); Family Trichodontidae: *Arctoscopus japonicus*, HUMZ 45194, 142 mm SL (O & M); Family Uranoscopidae: *Uranoscopus japonicus*, HUMZ 131759, 91 mm SL (O & M). Suborder Blennioidei. Family Chaenopsidae: *Neoclinus bryope*, NMT-P 32728, 65 mm SL (O & M). Family Tripterygiidae:

*Enneapterygius etheostomus*, NSMT-P 45532, 37 mm SL (O & M). Suborder Gobioidae. Family Gobiidae: *Suruga fundicola*, HUMZ uncatalogued, 66 mm SL (O & M). Suborder Acanthuroidei. Family Acanthuridae: *Acanthurus triostegus*, HUMZ 48479, 85 mm SL (O & M). Suborder Scombroidei. Family Scombridae: *Scombrus heterolepis*, HUMZ 148196, 207 mm SL (O). Suborder Scombroidei. Family Sphyraenidae: *Sphyraena obtusata*, HUMZ 39257, 116 mm SL (O & M). Suborder Stromateoidei. Family Nomeidae: *Cubiceps whiteleggii*, HUMZ 117446, unmeasured (O & M). Family Stromateidae: *Stromsteus brasiliensis*, HUMZ 91730, 227 mm SL (O & M). Suborder Channoidei. Family Channidae: *Channa argus*, HUMZ 44272, 118 mm SL (O & M). Order Pleuronectiformes. Family Paralichthyidae: *Citharichthys spilopterus*, USNM 159569, 114 mm SL (O & M). Family Pleuronectidae: *Poecilopsetta plinthus*, HUMZ 48094, 83 mm SL (O & M). Family Psettodidae: *Psettodes erumei*, HUMZ 109145, 180 mm SL (O & M). Family Scophthalmidae: *Scophthalmus aquosus*, HUMZ 101744, 167 mm SL (O). Order Tetraodontiformes. Family Aracanidae: *Kentrocapros aculeatus*, HUMZ 110594, SL unmeasured (O).

### **III. Systematic Methodology**

In order to reconstruct phylogenetic relationships of Polynemidae, the cladistic approach formulated by Hennig (1966) is adopted. The outgroup comparison was used to determine the character polarity (Watrous and Wheeler, 1981; Wiley, 1981).

To evaluate the monophyly of this family and find the sister taxa of Polynemidae, all the comparative materials (86 acanthomorph species in 8 orders and 63 families) were considered as subjects to be filtrated. Polynemidae has been taxonomically placed into the perciform suborder Percoidei by many researches (e.g., Johnson, 1993; Nelson, 2006; Nakabo, 2013). The suborder Percoidei, considered to retain primitive perciform characters, was selected as an outgroup for character polarity determination among polynemids. Typical or primitive percoid characters were assessed from literature descriptions (e.g., Yabe 1985; Sasaki 1989; Imamura 1996; Kim 2012) and percoid taxa examined in this study.

To reconstruct polynemid phylogenetic relationships based on morphological characters in this study, the family Sciaenidae, which is considered to be the sister group of Polynemidae (see chapter Sister relationship of Polynemidae and Sciaenidae), is selected as the outgroup to determine character polarity among polynemids, and sciaenid characters were assessed from the sciaenid species examined in this study and literatures including sciaenid descriptions (e.g., Green, 1941; Kim and Kim, 1965; Topp and Cole, 1968; Taniguchi, 1969; Sasaki, 1989).

The data were analyzed using PAUP\*4.0b10 (Swofford, 2002), including ACCTRAN and DELTRAN optimizations, and the heuristic algorithms. Character evolution was assumed as “ordered” (wagner parsimony: Farris, 1970) when character order was decidable, or as “unordered” (Fitch parsimony: Fitch, 1971) when some modifications have an affect on character order. When the character conditions of outgroup are not specified, question mark was coded. Data matrix was made by using MacClade version 4.0 (Maddison and Maddison, 2000).

## IV. Monophyly of Polynemidae

Johnson (1993) noted that polynemids shared five potential synapomorphies identified by Sasaki (1989) with Sciaenidae, including (1) absence of trisegmental pterygiophores, (2) absence of supramaxilla, (3) insertion of single branchiostegal ray on posterior ceratohyal (=epihyal in this study), (4) medial interdigitation of metapterygoid and quadrate, and (5) extension of epaxial musculature onto frontals. Motomura (2004) described the species catalogue of the family Polynemidae and listed some diagnostic features, such as adipose eyelid covering the eye, the supramaxilla absent, pectoral fins divided into an upper part with 12–19 rays joined by the membrane and a lower part with 3–16 separated filament-like rays.

More recently, the author (SK) and two co-authors showed the following 19 synapomorphies of Polynemidae (Kang et al., 2017): (1) intercalar and epiotic connected; (2) supramaxilla absent; (3) tooth plate present on ectopterygoid; (4) ectopterygoid strongly elongated; (5) metapterygoid and quadrate interdigitated medially; (6) a single branchiostegal ray suspended by epihyal; (7) an unnamed bone present on cephalic sensory canal extending from supratemporal; (8) ventral process of cleithrum present; (9) third actinost not supporting pectoral-fin rays; (10) rod-like process extending from the ventral margin of the coracoid; (11) pelvis and pelvic spine interlocked; (12) posterior portions of pelvic bones on both sides interdigitated; (13) median pterygiophores absent in the dorsal and anal fins; (14) third and fourth hypurals fused anteriorly; (15) adductor mandibulae section 1 comprised the lateral and medial elements; (16) abductor

superficialis, abductor profundus, adductor superficialis and adductor profundus all separated into dorsal and ventral subdivisions; (17) coracoradialis absent; (18) division of obliquus inferioris present between lower postcleithrum and rod-like process on coracoid; and (19) anterior extension of nasal canal present. Of them, Kang et al. (2017) considered that although characters 2, 13 and 14 occur in many perciform taxa (thus regarded to be common derived characters), characters 3, 5, 8, 10, 16 and 19, and 1, 4, 6, 11, 12 and 17 are regarded as rare and rather rare characters recognized in a few and some percoids, respectively, and characters 7, 9, 15 and 18 are unique characters recognized only in Polynemidae, and finally concluded that the monophyly of the family Polynemidae was strongly supported [See Kang et al. (2017) and Descriptions shown below for detailed descriptions of these characters].

In addition to the 19 synapomorphies, a single new synapomorphy was found here: levator arcus palatini divided into two subsections, anterior and posterior subsections. In polynemids, this muscle is completely or incompletely separated into the anterior and posterior subsections. The anterior subsection originates from the ventral surfaces of the frontal and sphenotic, and is inserted onto the anterior edge of the hyomandibula or the lateral surfaces of the endopterygoid and metapterygoid. The posterior subsection originates from the sphenotic and pterotic, and is inserted onto the hyomandibula and metapterygoid. The levator arcus palatini is subdivided into two separate or almost separate sections in a few fish taxa, such as aulopiform *Harpodon*, perciform *Ammodytes* and siluriform *Lctalurus* (Winterbottom, 1974). Because such division is rare in

percoids (e.g., Winterbottom 1974; this study), it was regarded as a derived character. Thus, this study recognizes 20 synapomorphies supporting the monophyly of Polynemidae.

## **V. Sister relationship of Polynemidae and Sciaenidae**

Johnson (1993) firstly suggested that Polynemidae had a sister relationship with Sciaenidae, sharing five putative synapomorphies. However, many authors showed different viewpoints on the sister group of Polynemidae. Polynemidae has long been considered to be related to Mugilidae and Sphyraenidae, but there is no convincing evidence to support that relationship (Johnson, 1993). Near et al. (2013) showed that Polynemidae had a close relation with Pleuronectiformes plus Carangiformes. Betancur-R et al. (2013, 2014) indicated that Polynemidae was a part of Carangimorphariae (one subseries of series Carangimorpharia), which includes fishes such as Sphyraenidae, Xiphiidae and Pleuronectiformes, and suggested that Polynemidae had a close relationship with Menidae. Sanciangco et al. (2015) suggested that Polynemidae was the sister group of Menidae plus Lactariidae.

The author (SK) and two co-authors proposed the sister relationship of Polynemidae and Sciaenidae supported by six synapomorphies (Kang et al., 2017): (1) supramaxilla absent; (2) metapterygoid and quadrate interdigitated medially; (3) a single branchiostegal ray suspended by epihyal; (4) posterior portions of pelvic bones on both sides interdigitated; (5) median pterygiophores absent in the dorsal and anal fins; (6) anterior extension of nasal canal present. Of them, (1) and (5) are common derived characters occurring in many perciform taxa, (3) and (4) are rather rare derived characters recognized in some percoids, and (2) and (6) are rare derived characters recognized in few percoids. This study sustains this conclusion, and use the sister group, Sciaenidae, as the outgroup in

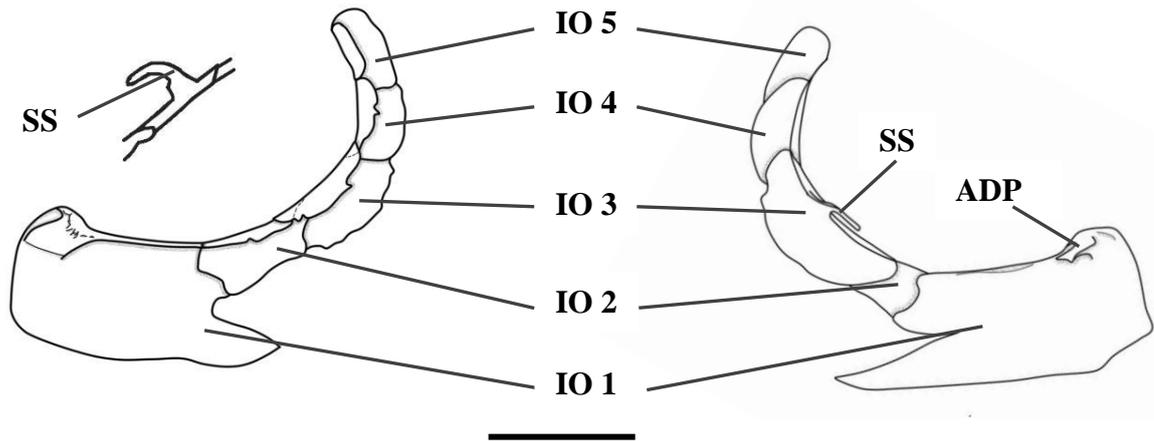
the following phylogenetic analysis.

## VI. Comparative Anatomy

### 1. Osteology

#### 1-1 Circumorbital bones (Figs. 1–2)

**Description.** The circumorbital bones consist of six infraorbitals in polynemids, except for *Parapolyneumus verekeri* having five elements including the fused third and fourth infraorbitals with three or four bridges for the sensory canal. They are thin, weak and plate-like, surrounding the ventral and posterior parts of the orbit. The infraorbitals support tubular structure for the sensory canal continuous with those on the frontal and pterotic. These bones are arranged in semi-circular in polynemids, except for *Polynemus melanochir melanochir*, *Polynemus paradiseus* and *Parapolyneumus verekeri*, in which they are arranged in V-shape deeply. The first to fifth infraorbitals expand posteriorly behind the bridged structure in most polynemids, and the degree of the expansions are varied among them (e.g., expansion of fifth infraorbital absent in *Polynemus*, *Filimanus*, *Parapolyneumus verekeri* and *Pentanemus quinquarius*; those of third and fourth infraorbitals weakly developed in *Polynemus*, *Filimanus*, *Parapolyneumus verekeri*, *Pentanemus quinquarius* and *Galeoides decadactylus*; those of third and fourth infraorbitals well developed in *Eleutheronema* and *Polydactylus opercularis*).



**Fig. 1.** Lateral (lower left) and medial (right) views of infraorbitals, and dorsal (upper left) view of third infraorbital in *Polydactylus sextarius*. IO 1–5, first to fifth infraorbitals; SS, subocular shelf; ADP, process on anteriordorsal margin of first infraorbital medially. The sixth infraorbital is shown in Figs. 3–10 with the cranium. Bar indicates 5 mm.

The first infraorbital (= lachrymal), the anteriormost and largest trapezoid element of the infraorbitals, well elongates posteroventrally and forms the ventral portion of the orbit. The bone overlaps with the dorsal portion of the maxilla ventrally. The anterodorsal portion of the first infraorbital medially possesses a process having a glenoid cavity anteriorly and posteroventrally for the articulation with the lateral ethmoid and palatine, respectively. The anterodorsal portion of the first infraorbital has a bridged structure for the sensory canal laterally. The posterior part of this bone is laterally attached with the anteromedial part of the second infraorbital in polynemids, except for *Pentanemus quinquarius* and *Polydactylus nigripinnis*, in which the posterodorsal part of the first infraorbital is situated lateral to the second infraorbital and the posteroventral part of this bone medial to the second.

The second infraorbital, forming the ventral part of the orbit, is a small bone. Its shape is variable in polynemids: trapezoid in *Polydactylus sextarius*,

*Polydactylus microstomus* and *Galeoides decadactylus*; ellipse in *Filimanus similis* and *Leptomelanosoma indicum*; and triangular in the others. The anterior part of the second infraorbital covers the posterior portion of the first infraorbital laterally in polynemids, except for *Pentanemus quinquarius* and *Polydactylus nigripinnis* (see above description on the first infraorbital in detail for the condition in the two species). The posterodorsal part of the second infraorbital covers the ventral part of the third infraorbital medially.

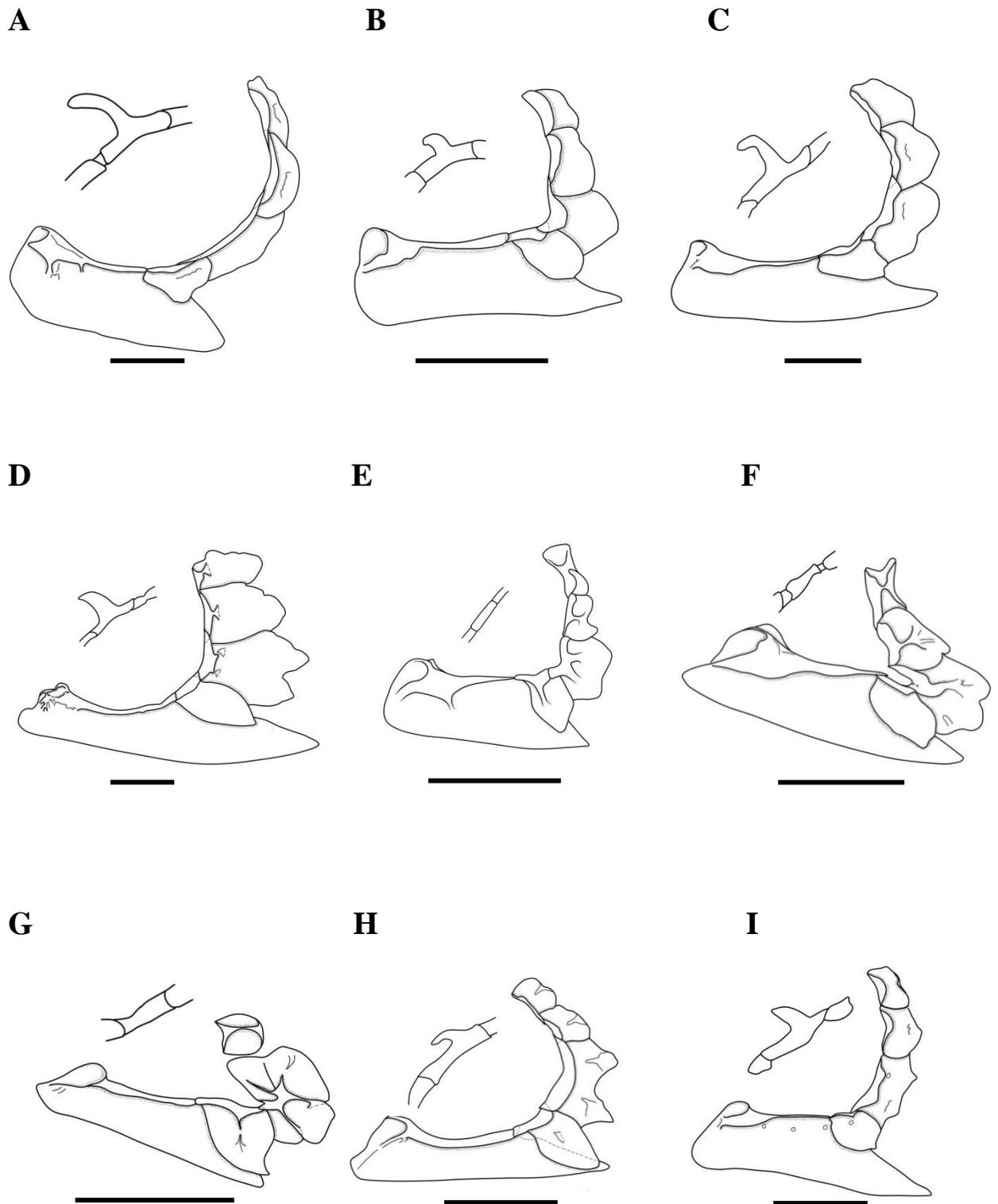
The third infraorbital is well developed and broad, situated posteroventral to the orbit. This bone bears the subocular shelf on its anterior margin in polynemids, except for *Parapolyneumus verekeri* and *Polynemus* lacking it. The third infraorbital bears one or two complete bridges laterally in *Parapolyneumus verekeri* and *Polynemus*, whereas it laterally bears one or two incomplete bridges, or lacks bridges in other polynemids. The anterior margin of the third infraorbital is deeply concaved in *Polynemus melanochir melanochir*, *Polynemus paradiseus* and *Parapolyneumus verekeri*, and it is shallowly concaved in *Polynemus aquilonaris*, *Polynemus multifilis* and *Leptomelanosoma indicum*, while it is slightly curved in the others. The anteroventral and posterodorsal portions of this bone laterally cover the second and fourth infraorbitals, respectively.

The fourth infraorbital is smaller than the third infraorbital and forms the posterior portion of the orbit. This bone covers the dorsal portion of the third infraorbital medially. Its dorsal portion covers the ventral portion of the fifth infraorbital medially in polynemids, except for *Polydactylus sextarius*, *Polydactylus microstomus*, *Filimanus*, *Parapolyneumus verekeri* and *Polydactylus*

*oligodon*. In *Polydactylus sextarius*, *Polydactylus microstomus* and *Filimanus*, the dorsal portion of the fourth infraorbital covers the ventral portion of the fifth infraorbital laterally. In *Parapolyneumus verekeri*, the fourth infraorbital is tightly attached with or is narrowly separated from the fifth infraorbital (thus not overlapped with it). In *Polydactylus oligodon*, the anterodorsal portion of the fourth infraorbital is situated lateral to the anteroventral portion of the fifth infraorbital, while the posterodorsal portion of the former is situated medial to the posteroventral portion of the latter. The fourth infraorbital bears a single complete bridge in *Polynemus*, while it bears an incomplete bridge or lacks it in other polynemids.

The fifth infraorbital is a small bone situated posterior to the orbit. Its dorsal margin is attached with the sixth infraorbital by a strong connective tissue. The fifth infraorbital bears a single complete bridge in *Parapolyneumus verekeri*, *Polynemus paradiseus*, *Polynemus melanochir melanochir*, *Polynemus aquilonaris* and *Polydactylus multiradiatus*, while it lacks bridges in the others.

The sixth infraorbital (= dermosphenotic) is a small bone, tightly attached with the dorsolateral face of the sphenotic medially. The sensory canal supported by this bone is continuous with those on the pterotic and frontal.



**Fig. 2.** Lateral (lower right) view of infraorbitals and dorsal (upper left) view of third infraorbital. A, *Galeoides decadactylus*; B, *Leptomelanosoma indicum*; C, *Polydactylus approximans*; D, *Eleutheronema tetradactylum*; E, *Polynemus aquilonaris*; F, *Polynemus paradiseus*; G, *Parapolynemus verekeri*; H, *Pentanemus quinquarius*; I, *Filimanus similis*. Bars indicate 5 mm.

## Character recognition

**TS 1. Arrangement of infraorbitals.** 0: semi-circular; 1: deeply V-shape.

The infraorbitals are arranged in semi-circular in many polynemids (character 1-0), while they are arranged in V-shape deeply in *Polynemus melanochir melanochir*, *Polynemus paradiseus* and *Parapolynemus verekeri* (Fig. 2F, G) (character 1-1). The infraorbitals are arranged in semi-circular in sciaenids (character 1-0) (Sasaki, 1989; this study).

**Remarks.** The anterior margin of the third infraorbital is slightly curved or shallowly concaved in the species having the semi-circular arrangement of the infraorbitals in many polynemids, while it is deeply concaved in *Polynemus melanochir melanochir*, *Polynemus paradiseus* and *Parapolynemus verekeri*, in which they are arranged in V-shape deeply. Therefore it can be assumed that the difference of the arrangement of infraorbitals is well associated with the configuration of the third infraorbital. Many polynemid species, having a slightly curved anterior margin of the third infraorbital, possess larger eyes (4.8-8.2% SL). In contrast, *Polynemus aquilonaris*, *Polynemus multifilis* and *Leptomelanosoma indicum*, which possess a shallow concavity on the third infraorbital, has smaller eyes (3.5-3.9% SL), and *Polynemus melanochir melanochir*, *Polynemus paradiseus* and *Parapolynemus verekeri*, with the third infraorbital having a deep concavity, have much smaller eyes than other species (1-2.5% SL). Accordingly, it is considered that the arrangement of infraorbitals and the configuration of the anterior margin of the third infraorbital are associated with the eye size. Therefore, characters on the configuration of the

bone and the eye size are not separately used for the phylogenetic analysis in this study. Eye diameters in examined polynemids are listed in Table 1.

Table 1. Eye diameters in polynemid species examined in this study

Species	Eye diameter (%SL)	
	Present study	Data from literature (modes in parentheses)
<i>Polydactylus plebeius</i>	7	8 <sup>a</sup>
<i>Polydactylus approximans</i>	6	6–7 (6) <sup>b</sup>
<i>Polydactylus sextarius</i>	8	7–9 (8) <sup>c</sup>
<i>Polydactylus virginicus</i>	6	No data
<i>Polydactylus multiradiatus</i>	6.4	5–7 (7) <sup>d</sup>
<i>Polydactylus nigripinnis</i>	5.5	No data
<i>Polydactylus opercularis</i>	4.8	5–7 (6) <sup>b</sup>
<i>Polydactylus microstomus</i>	6.3	7–10 (8) <sup>c</sup>
<i>Polydactylus sexfilis</i>	6.8	6–9 (8) <sup>e</sup>
<i>Polydactylus octonemus</i>	7.1	No data
<i>Polydactylus oligodon</i>	6.6	No data
<i>Polydactylus macrochir</i>	4.8	4–7 (5) <sup>f</sup>
<i>Galeoides decadactylus</i>	7.5	7–10 (8) <sup>g</sup>
<i>Filimanus similis</i>	6.6	7.6 <sup>h</sup>
<i>Filimanus sealei</i>	7.1	No data
<i>Filimanus xanthonema</i>	7	6.5–9 (7.9) <sup>i</sup>
<i>Eleutheronema tetradactylum</i>	5.5	4–6 (5) <sup>j</sup>
<i>Eleutheronema rhadinum</i>	5.2	5–6 (6) <sup>j</sup>
<i>Pentanemus quinquarius</i>	8.2	No data
<i>Leptomelanosoma indicum</i>	3.5	3–5 (4) <sup>k</sup>
<i>Polynemus paradiseus</i>	1	1–2 (2) <sup>l</sup>
<i>Polynemus aquilonaris</i>	3.5	3–4 (3) <sup>m</sup>
<i>Polynemus melanochir melanochir</i>	2.3	2 <sup>n</sup>
<i>Polynemus multifilis</i>	3.9	No data
<i>Parapolyneumus verekeri</i>	2.5	No data

a, Motomura et al. (2001a); b, Motomura et al. (2002b); c, Motomura et al. (2001b); d, Motomura et al. (2002c); e, Motomura et al. (2001c); f, Motomura et al. (2000); g, Motomura et al. (2001d); h, Feltes (1991); i, Motomura et al. (2001e); j, Motomura et al. (2002d); k, Motomura, (2001f); l, Motomura (2004); m, Motomura, (2003); n, Motomura, (2002e).

**TS 2. Subocular shelf on third infraorbital.** 0: present; 1: absent.

The subocular shelf is present on the third infraorbital in most polynemids (character 2-0), while it is absent in *Polynemus* and *Parapolynemus verekeri* (Fig. 2E, F, G) (character 2-1). This shelf is primitively present in sciaenids (Sasaki, 1989; this study) (character 2-0), while it is absent in some sciaenids (character 2-1) (e.g., Smith and Baily, 1962; Topp and Cole, 1968; Sasaki, 1989).

**TS 3. First and second infraorbitals.** 0: first covering second medially; 1: posterodorsal part of first lateral to second and posteroventral part of first medial to second.

In most polynemids, the posterior portion of the first infraorbital covers the anterior portion of the second infraorbital medially (character 3-0). While the posterodorsal part of the first infraorbital is situated lateral to the second infraorbital and the posteroventral part of this bone medial to the second infraorbital in *Pentanemus quinquarius* (Fig. 2H) and *Polydactylus nigripinnis* (character 3-1). The former condition is present in most sciaenids (e.g., Smith and Baily, 1962; Sasaki, 1989) (character 3-0), while the latter condition is present in the other sciaenids (character 3-1) (this study, e.g., *Pennahia argentata*, *Argyrosomus japonicus* and *Ctenosciaena gracilicirrhus*).

**TS 4. Fourth and fifth infraorbitals.** 0: not overlapped; 1: fourth covering fifth laterally; 2: fourth covering fifth medially; 3: anterodorsal portion of fourth lateral to anteroventral portion of fifth and posterodorsal portion of former medial to posteroventral portion of latter. (unordered)

In most polynemids, the dorsal portion of the fourth infraorbital covers the

ventral portion of the fifth infraorbital laterally (character 4-1). In contrast, it is tightly attached with or is narrowly separated from the fifth infraorbital (thus not overlapped with it) in *Parapolyneumus verekeri* (Fig. 2G) (character 4-0), the former covers the latter medially in *Polydactylus sextarius* (Fig. 1), *Polydactylus microstomus* and *Filimanus* (Fig. 2I) (character 4-2), and the anterodorsal portion of the fourth infraorbital is situated lateral to the anteroventral portion of the fifth infraorbital and the posterodorsal portion of the former is situated medial to the posteroventral portion of the latter in *Polydactylus oligodon* (character 4-3). In sciaenids, the fourth infraorbital is tightly attached with or is narrowly separated from the fifth infraorbital (character 4-0) (e.g., Sasaki, 1989; this study).

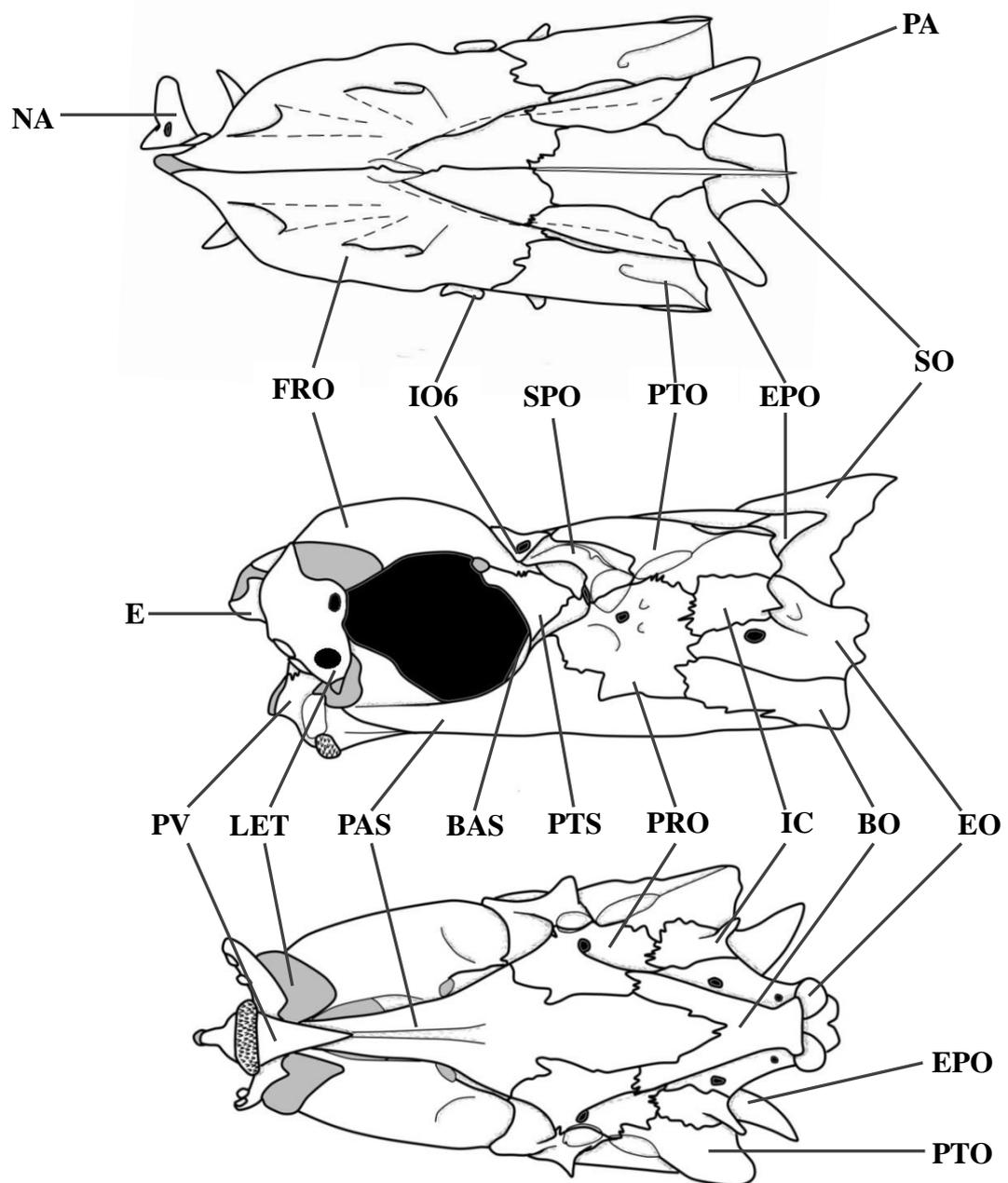
## **Other variations**

**Fusion of third and fourth infraorbitals.** The number of infraorbitals is six in most polynemids, while it is five in *Parapolyneumus verekeri* (Fig. 2G). “The third infraorbital” in *Parapolyneumus verekeri* is larger and bears three or four bridges. In contrast, in species having bridged structures, the third and fourth infraorbitals have one or two bridges, respectively. Therefore it is assumed that the condition of five-infraorbitals in *Parapolyneumus verekeri* is caused by the fusion of the third and fourth infraorbitals. The fusion of the third and fourth infraorbitals is an autapomorphy for *Parapolyneumus verekeri* because they are usually autogenous in sciaenids (e.g., Smith and Baily, 1962: figs. 1–3; Sasaki, 1989; this study).

**Second to fifth infraorbitals expanded posteriorly.** The second to fifth infraorbitals expand posteriorly behind the bridged structure in most polynemids. For example, the expansion is well developed in *Eleutheronema tetradactylum* and *Eleutheronema rhadinum*, while it is weakly developed in *Pentanemus quinquarius* and *Galeoides decadactylus*. However, degree of the expansions is serially changed in polynemids and it is difficult to separate the variation into any distinct morphotypes. In consequence, this variation is eliminated from the phylogenetic analysis.

## 1-2 Neurocranium (Figs. 3–8)

**Description.** The neurocranium is comprised of eleven paired elements, the nasal, lateral ethmoid, frontal, pterosphenoid, sphenotic, prootic, parietal, pterotic, epiotic, intercalar and exoccipital, and six unpaired elements, the prevomer, ethmoid, parasphenoid, basisphenoid, supraoccipital and basioccipital.



**Fig. 3.** Dorsal (upper), lateral (middle) and ventral (lower) views of neurocranium in *Polydactylus approximans*. BAS, basisphenoid; BO, basioccipital; E, ethmoid; EO, exoccipital; EPO, epiotic; FRO, frontal; IC, intercalar; IO6, sixth infraorbital; LET, lateral ethmoid; NA, nasal; PA, parietal; PAS, parasphenoid; PRO, prootic; PTO, pterotic; PTS, pterosphenoid; PV, prevomer; SO, supraoccipital; SPO, sphenotic. Bar indicates 10 mm.

The nasal is a flat tubular bone, connected with the frontal posteriorly and the ethmoid medially. It has a sensory canal continuous with that of the frontal.

The prevomer is a broad triangular bone, situated on the anteroventral portion of the neurocranium. It possesses a cartilaginous ridge for the articulation with the rostral cartilage on its anterior margin. It is connected with the ethmoid dorsally, the lateral ethmoid posterodorsally and laterally, and the parasphenoid posteriorly. The prevomer possesses a tooth plate anteroventrally in many polynemids, whereas it is absent in *Galeoides decadactylus*, *Polydactylus microstomus*, *Polydactylus sextarius*, *Polydactylus nigripinnis*, *Pentanemus quinquarius*, *Filimanus xanthonema*, *Parapolynemus verekeri*, *Polynemus melanochir melanochir* and *Polynemus paradiseus*.

The ethmoid is a thick, L-shaped bone, situated on the anterior region of the neurocranium. It is connected with the lateral ethmoid laterally, the prevomer ventrally and the frontal posteriorly. The lateral portion of the ethmoid is broad in polynemids, except for *Polydactylus sextarius*, *Polydactylus multiradiatus*, *Polydactylus sexfilis* and *Galeoides decadactylus*, in which it is narrow.

The lateral ethmoid is a pair of broad thin bones, situated on the anterolateral portion of the neurocranium. This bone is connected with the prevomer anteroventrally, the ethmoid medially, the frontal posterodorsally and the parasphenoid posteroventrally. The lateral expansion of the lateral ethmoid has two condyles for the articulation with the first infraorbital dorsolaterally and palatine ventrolaterally. A foramen, in which the head of the maxilla inlays, is present on the lateral ethmoid in polynemids, except for *Parapolynemus verekeri*,

*Polydactylus nigripinnis* and *Polynemus*, lacking this foramen. The lateral ethmoid is separated from the pterosphenoid by the frontal posterodorsally in polynemids, except for *Parapolynemus verekeri* and *Polynemus*, in which the lateral ethmoid is connected with the pterosphenoid.

The frontal is a large bone, forming the anterior portion of the dorsal neurocranium roof. It is connected with the ethmoid and lateral ethmoid ventroanteriorly, the sphenotic and pterosphenoid posteroventrally, and the supraoccipital, parietal and pterotic posteriorly. The frontal is penetrated by the supraorbital sensory canal continuous with that of the nasal anteriorly, and those of the sixth infraorbital and pterotic laterally. The canal on the frontal is roofed in most polynemids, whereas it has only a few complete and incomplete bridges in *Polydactylus sextarius*, *Pentanemus quinquarius*, *Parapolynemus verekeri* and *Polynemus*.

The parietal is a long elliptical bone with a dorsal embossment, forming the posterior portion of the dorsal neurocranium roof. It is connected with the frontal anteriorly, the pterotic laterally, the supraoccipital medially and the epiotic posteriorly.

The sphenotic is a stout bone, situated on the lateral surface of the neurocranium. It is connected with the frontal anteromedially, the pterotic posteriorly, the pterosphenoid anteroventrally and the prootic ventrally. The sphenotic is firmly attached with the sixth infraorbital dorsally and contacted with the fifth infraorbital laterally. A protuberant process, which provides the origin of the levator arcus palatini, is present on the posterolateral surface of the

sphenotic. The sphenotic does not form the dorsal surface of the neurocranium in most polynemids, whereas it is surrounded by the pterotic, parietal and frontal, and occupies its dorsal surface in *Leptomelanosoma indicum*.

The pterosphenoid is situated on the posterior wall of the orbit. It is connected with the frontal anterodorsally, the sphenotic posterodorsally, the prootic posteriorly and the basisphenoid ventrally (if it is Y-shaped). It is also attached to the parasphenoid in *Leptomelanosoma indicum*, *Eleutheronema*, *Polydactylus nigripinnis*, *Polydactylus opercularis*, *Parapolynemus verekeri* and *Polynemus*, while they are separated from each other in other polynemids.

The parasphenoid, situated on the ventral portion of the neurocranium, is long and shaft-like. It is connected with the prevomer and lateral ethmoid anteriorly, the prootic dorsally, and the basioccipital posteriorly.

The basisphenoid is a small and Y-shaped bone (except for that of *Filimanus*), situated on the posteroventral margin of the orbit, and attached with the parasphenoid in the midline ventrally. The basisphenoid is present in polynemids, except for *Polydactylus macrochir* and *Polynemus*, in which it is absent. When it is present, the dorsal margin of the basisphenoid is attached with the pterosphenoid and prootic dorsolaterally in most polynemids, with the pterosphenoid and parasphenoid in *Polydactylus nigripinnis* and *Polydactylus opercularis*, with the parasphenoid in *Eleutheronema rhadinum*, and with the pterosphenoid in *Leptomelanosoma indicum* and *Eleutheronema tetradactylum*. The basisphenoid is stick-like, and its dorsal margin is separated from other bones in *Filimanus*.

The prootic is a plate-like bone, forming most of the posteroventral region of the orbit and anteroventral region of the auditory bulla. It is connected with the pterosphenoid anteriorly, the intercalar, basioccipital and exoccipital posteriorly, the sphenotic and pterotic dorsally, and the parasphenoid ventrally. The prootic possesses the trigeminofacialis chamber and forms a glenoid cavity with the sphenotic dorsally for the articulation with the anterior condyle of the hyomandibula.

The pterotic forms the dorsolateral portion of the neurocranium posteriorly. It is connected with the frontal and sphenotic anteriorly, the prootic, exoccipital and intercalar ventrally, the parietal medially, and the epiotic posteromedially. The lateral and dorsal surfaces of the pterotic have a glenoid cavity for the articulation with the posterodorsal condyle of the hyomandibula and the sensory canal, respectively.

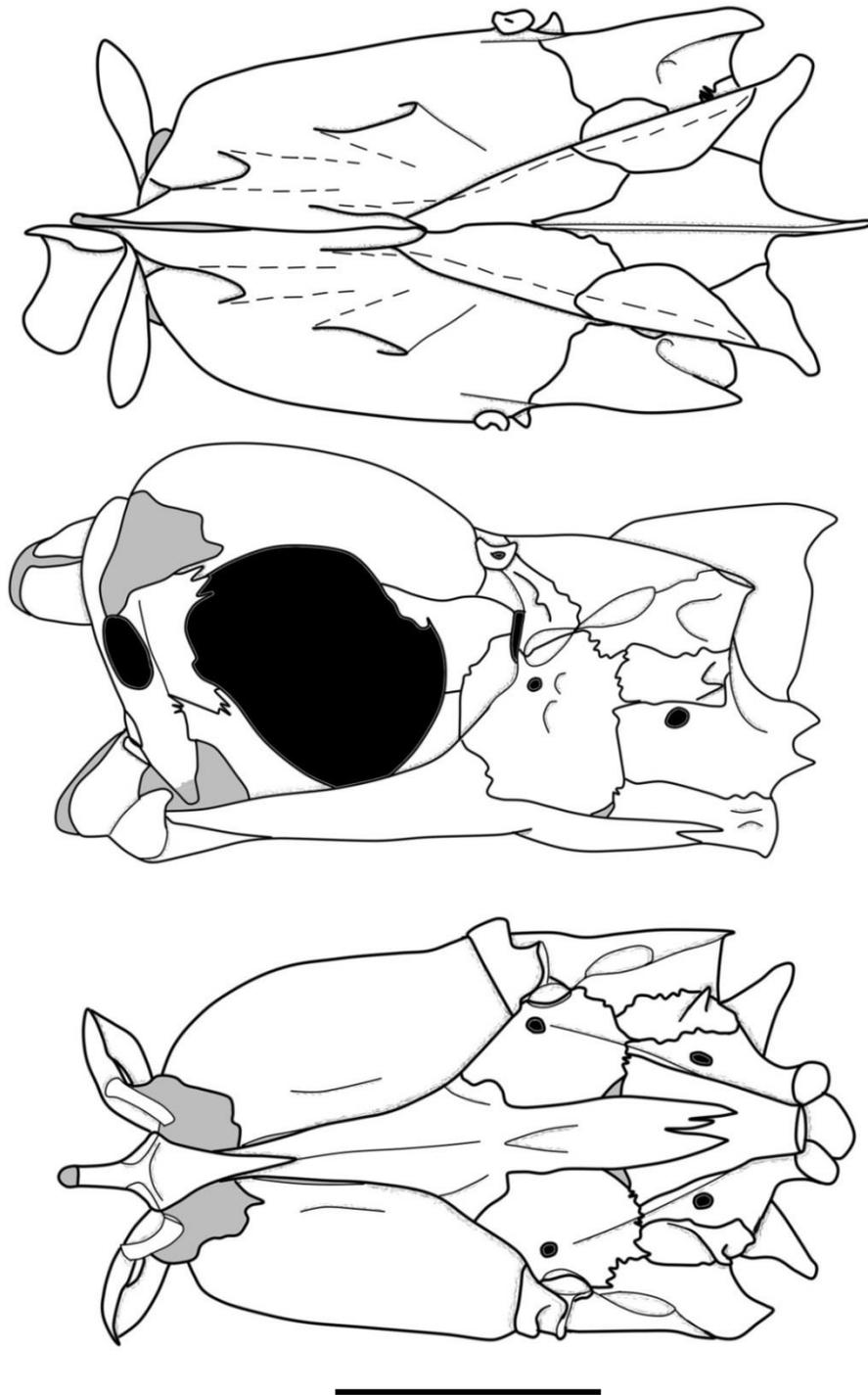
The epiotic is situated on the posterior part of the neurocranium. It is connected with the parietal anteriorly, the supraoccipital medially, the pterotic laterally, the intercalar ventrolaterally and the exoccipital posteroventrally. The epiotic bears a posterior arm connected with the upper limb of the posttemporal.

The intercalar is a small bone, situated on the posterolateral portion of the neurocranium. It is connected with the prootic anteriorly, the pterotic dorsally, the epiotic dorsomedially and the exoccipital ventromedially. The intercalar posteriorly possesses a process attached with the lower limb of the posttemporal by a short ligament. A foramen for the nervus glossopharyngeus (sensu Freihofer, 1978) is present on the intercalar in *Parapolyneumus verekeri*.

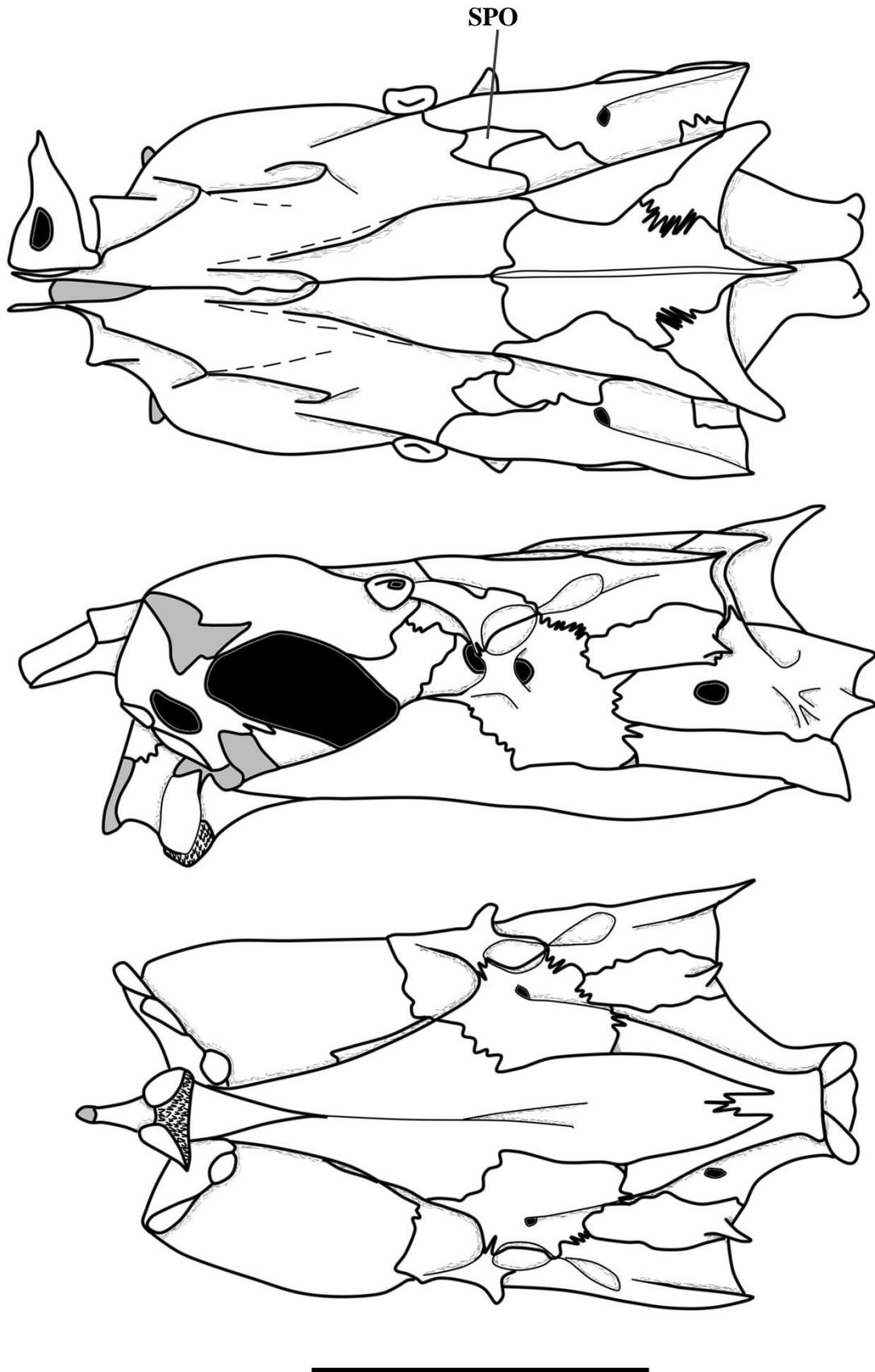
The supraoccipital occupies the posteromedial roof of the neurocranium. It is connected with the frontal anteriorly, the parietal and epiotic laterally, and the exoccipital posteriorly. The supraoccipital crest is well developed dorsally and formed on the posterior portion of this bone.

The exoccipital is situated on the posterior portion of the neurocranium and surrounds the posterior region of the auditory bulla. It is connected with the supraoccipital dorsomedially, the prootic anteriorly, the intercalar and pterotic dorsally, and the basioccipital ventrally. The exoccipital posteriorly possesses a condyle; those on both sides are connected with each other above the basioccipital. The condyles firmly articulate with the first vertebra. A foramen for the nervus glossopharyngeus is present on the lateral surface of the exoccipital in polynemids, except for *Parapolyneumus verekeri*, in which it is present on the intercalar.

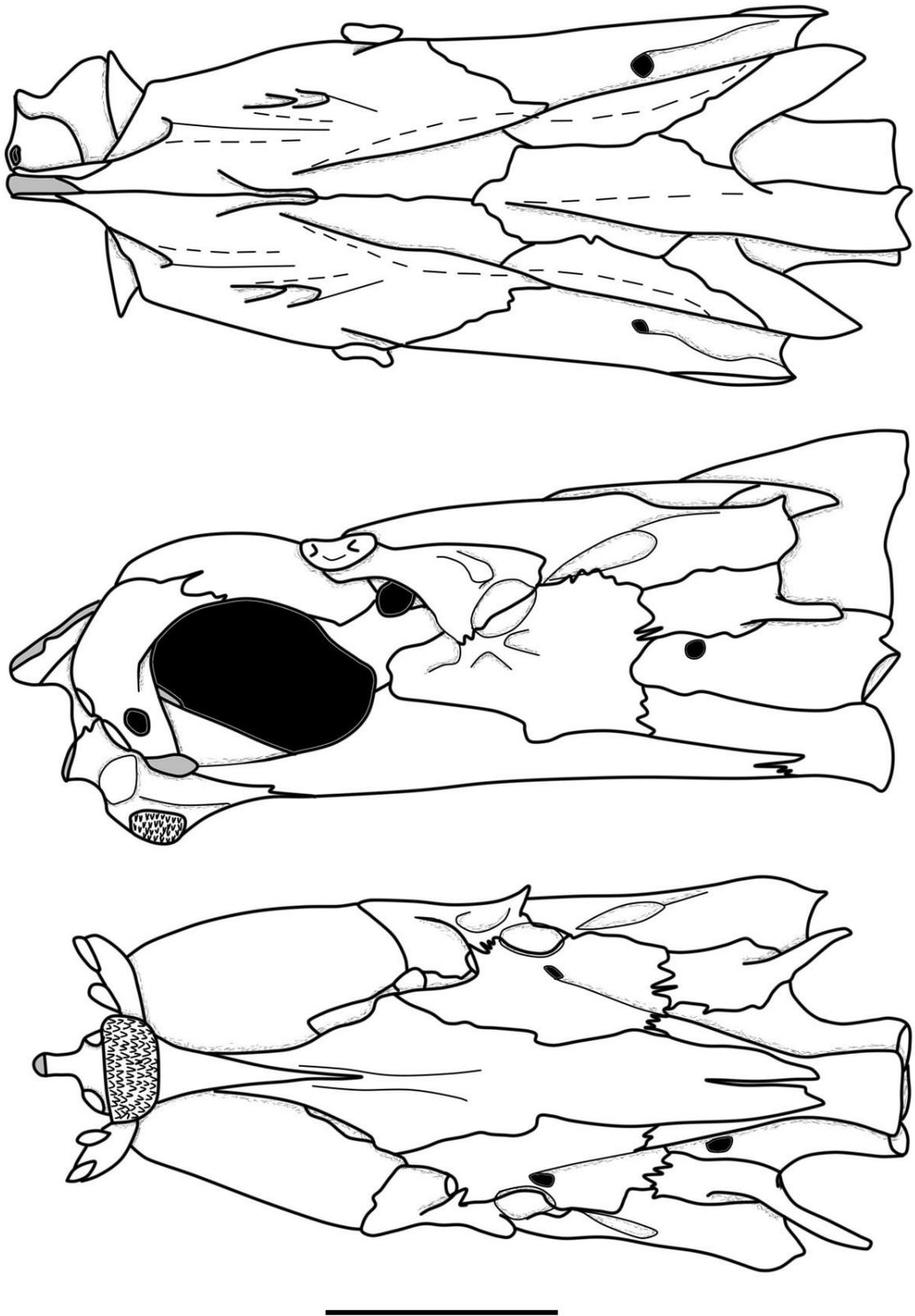
The basioccipital is situated on the posteroventral portion of the neurocranium and possesses a condyle for the articulation with the first vertebra. It is connected with the exoccipital dorsally, the prootic dorsolaterally and the parasphenoid anteroventrally.



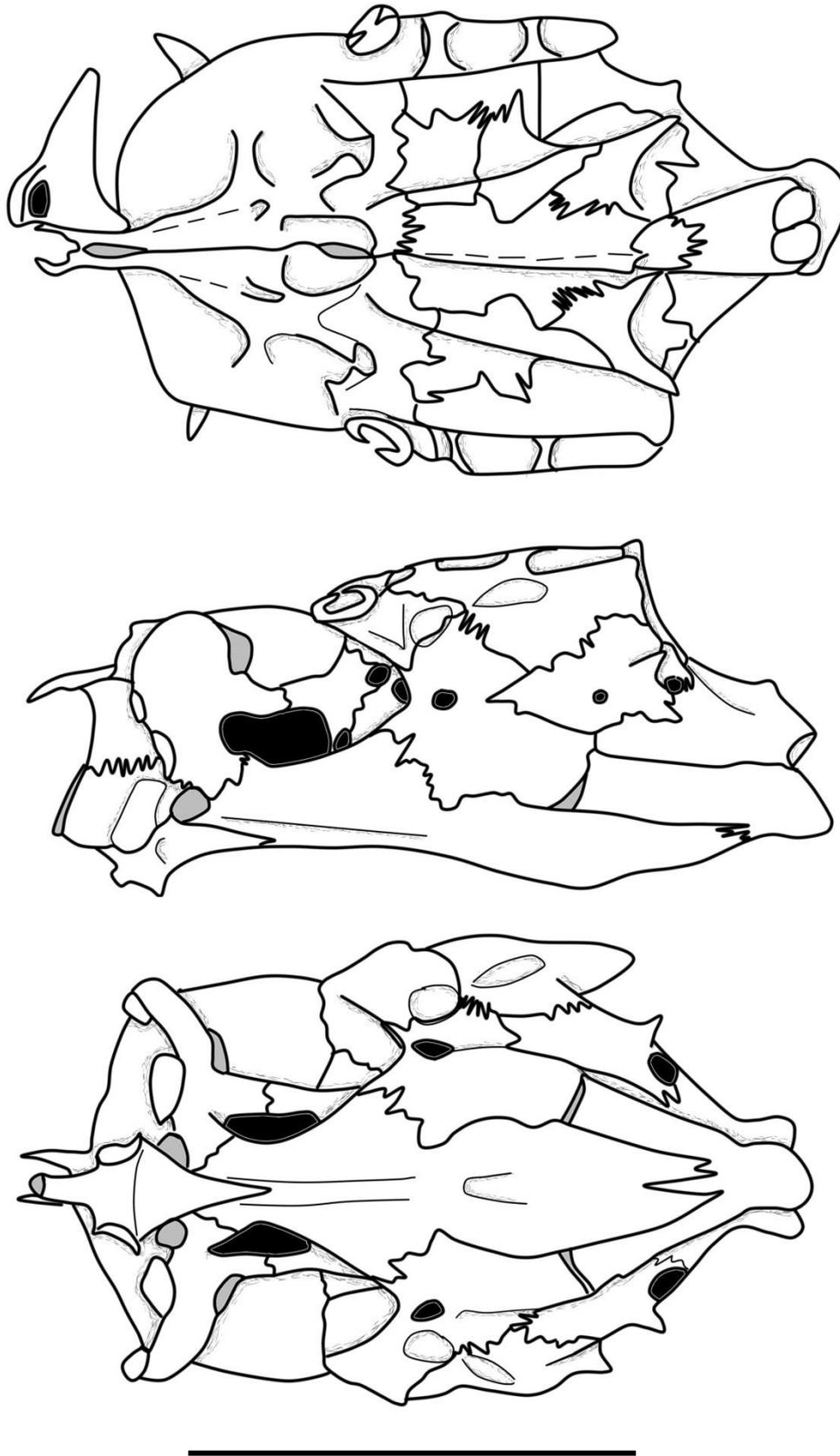
**Fig. 4.** Dorsal (upper), lateral (middle) and ventral (lower) views of neurocranium in *Galeoides decadactylus*. Bar indicates 10 mm.



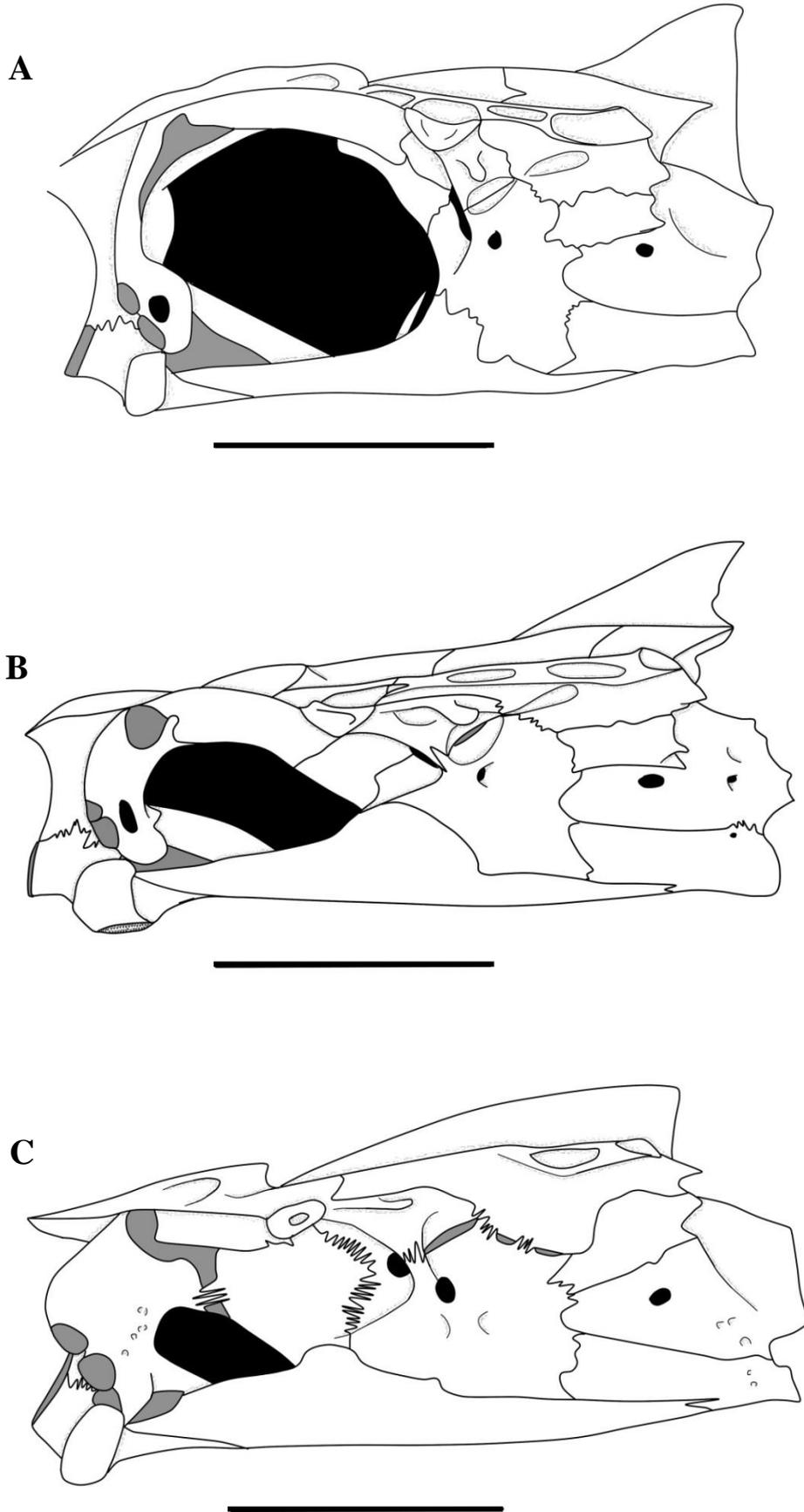
**Fig. 5.** Dorsal (upper), lateral (middle) and ventral (lower) views of neurocranium in *Leptomelanosoma indicum*. SPO, sphenotic. Bar indicates 10 mm.



**Fig. 6.** Dorsal (upper), lateral (middle) and ventral (lower) views of neurocranium in *Eleutheronema rhadinum*. Bar indicates 10 mm.



**Fig. 7.** Dorsal (upper), lateral (middle) and ventral (lower) views of neurocranium in *Parapolyneumus verekeri*. Bar indicates 10 mm.



**Fig. 8.** Lateral views of neurocraniums. A, *Filimanus sealei*; B, *Polydactylus macrochir*; C, *Polynemus aquilonaris*. Bars indicate 10 mm.

## Character recognition

**TS 5. Tooth plate on prevomer.** 0: absent; 1: present.

The prevomer possesses a tooth plate anteroventrally in most polynemids (Figs. 3, 5, 6) (character 5-1), whereas it is absent in *Galeoides decadactylus*, *Polydactylus microstomus*, *Polydactylus sextarius*, *Polydactylus nigripinnis*, *Pentanemus quinquarius*, *Filimanus xanthonema*, *Parapolynemus verekeri*, *Polynemus melanochir melanochir* and *Polynemus paradiseus* (Figs. 4, 7) (character 5-0). The tooth plate on the prevomer is absent in sciaenids (character 5-0) (e.g., Taniguchi, 1969; Sasaki, 1989; this study).

**TS 6. Lateral portion of ethmoid.** 0: broad; 1: narrow.

The lateral portion of the ethmoid is broad in polynemids (character 6-0), except for *Polydactylus sextarius*, *Polydactylus multiradiatus*, *Polydactylus sexfilis* and *Galeoides decadactylus*, in which it is narrow (Fig. 4) (character 6-1). Both conditions are found in Sciaenidae; for example, it is broad in *Stellifer rastrifer*, *Macrodon ancylodon* and *Pteroscion peli* (character 6-0), and it is narrow in *Sciaena trewavasae*, *Panna microdon* and *Johnius* (character 6-1) (e.g., Sasaki, 1989; this study).

**TS 7. Lateral ethmoid and pterosphenoid.** 0: separated; 1: connected.

The lateral ethmoid is separated from the pterosphenoid by the frontal posterodorsally in polynemids (Figs. 3–6, 8A, B) (character 7-0), except for *Polynemus* and *Parapolynemus verekeri*, in which the lateral ethmoid is connected with the pterosphenoid (Figs. 7, 8C) (character 7-1). Both conditions are recognized in sciaenids. For example, character 7-1 is found in

*Paralonchurus brasiliensis*, *P. elegans*, *Lonchurus lanceolatus* and *Collichthys lucidus*, and character 7-0 in other sciaenids (Sasaki, 1989).

**TS 8. Sensory canal on frontal.** 0: bridged; 1: roofed.

The sensory canal on the frontal is roofed in most polynemids (Figs. 3–6) (character 8-1); however, a few complete and incomplete bridges are present on the dorsal surface of the frontal in *Polydactylus sextarius*, *Pentanemus quinquarius*, *Parapolynemus verekeri* and *Polynemus* (Fig. 7) (character 8-0). Such bridges are present in sciaenids (character 8-0) (e.g., Taniguchi, 1969; Sasaki, 1989; this study).

**TS 9. Basisphenoid.** 0: present; 1: absent.

The basisphenoid is present in polynemids (Figs. 3–7, 8A) (character 9-0), except for *Polydactylus macrochir* and *Polynemus*, in which it is absent (Fig. 8B, C) (character 9-1). The basisphenoid is present in most sciaenids (character 9-0), whereas it is absent in *Lonchurus*, *Ophioscion*, *Panna*, *Otolithoides* and *Stellifer* (character 9-1) (Sasaki, 1989).

**TS 10. Basisphenoid.** 0: Y-shaped; 1: stick-like.

When it is present, the basisphenoid is Y-shaped in polynemids (Figs. 3–7) (character 10-0), except for *Filimanus*, in which it is stick-like (Fig. 8A) (character 10-1). The basisphenoid is Y-shaped in sciaenids (character 10-0) (e.g., Taniguchi, 1969; Sasaki, 1989; this study). “?” is coded for species lacking the basisphenoid.

**TS 11. Basisphenoid and pterosphenoid.** 0: attached; 1: separated.

When the basisphenoid is present, it is attached with the pterosphenoid

dorslaterally in most polynemids (Figs. 3–5, 7) (character 11-0), whereas they are separated from each other in *Eleutheronema rhadinum* (Fig. 6) and *Filimanus* (Fig. 8A) (character 11-1). The basisphenoid is attached with the pterospheoid dorslaterally in sciaenids when it is present (character 11-0) (e.g., Green, 1941; Sasaki, 1989; this study). “?” is coded for species lacking the basisphenoid.

**TS 12. Basisphenoid and prootic.** 0: attached; 1: separated.

When the basisphenoid is present, it is attached with the prootic dorslaterally in most polynemids (Figs. 3, 4, 7) (character 12-0), whereas they are separated from each other in *Polydactylus nigripinnis*, *Polydactylus opercularis*, *Leptomelanosoma indicum* (Fig. 5), *Eleutheronema* (Fig. 6) and *Filimanus* (Fig. 8A) (character 12-1). The basisphenoid is present and attached with the prootic dorslaterally in sciaenids (character 12-0) (e.g., Green, 1941; Sasaki, 1989; this study). “?” is coded for species lacking the basisphenoid.

**TS 13. Dorsal margin of basisphenoid and parasphenoid.** 0: separated; 1: attached.

The dorsal margin of basisphenoid is separated from the parasphenoid in polynemids (Figs. 3–5, 7, 8A) (character 13-0), except for *Polydactylus nigripinnis*, *Polydactylus opercularis* and *Eleutheronema rhadinum*, in which the former is attached with the latter (Fig. 6) (character 13-1). The dorsal margin of basisphenoid is separated from the parasphenoid in sciaenids (character 13-0) (e.g., Green, 1941; Sasaki, 1989; this study). “?” is coded for species lacking the basisphenoid.

**TS 14. Pterosphenoid and parasphenoid.** 0: separated; 1: attached.

The pterosphenoid is attached to the parasphenoid in *Leptomelanosoma indicum*, *Eleutheronema*, *Polydactylus nigripinnis*, *Polydactylus opercularis*, *Parapolyneumus verekeri* and *Polynemus* (Figs. 5-7, 8C) (character 14-1), while they are separated from each other in other polynemids (Figs. 3, 4, 8A, B) (character 14-0). These two bones are separated by the prootic in sciaenids (character 14-0) (e.g., Taniguchi, 1969; Sasaki, 1989; this study).

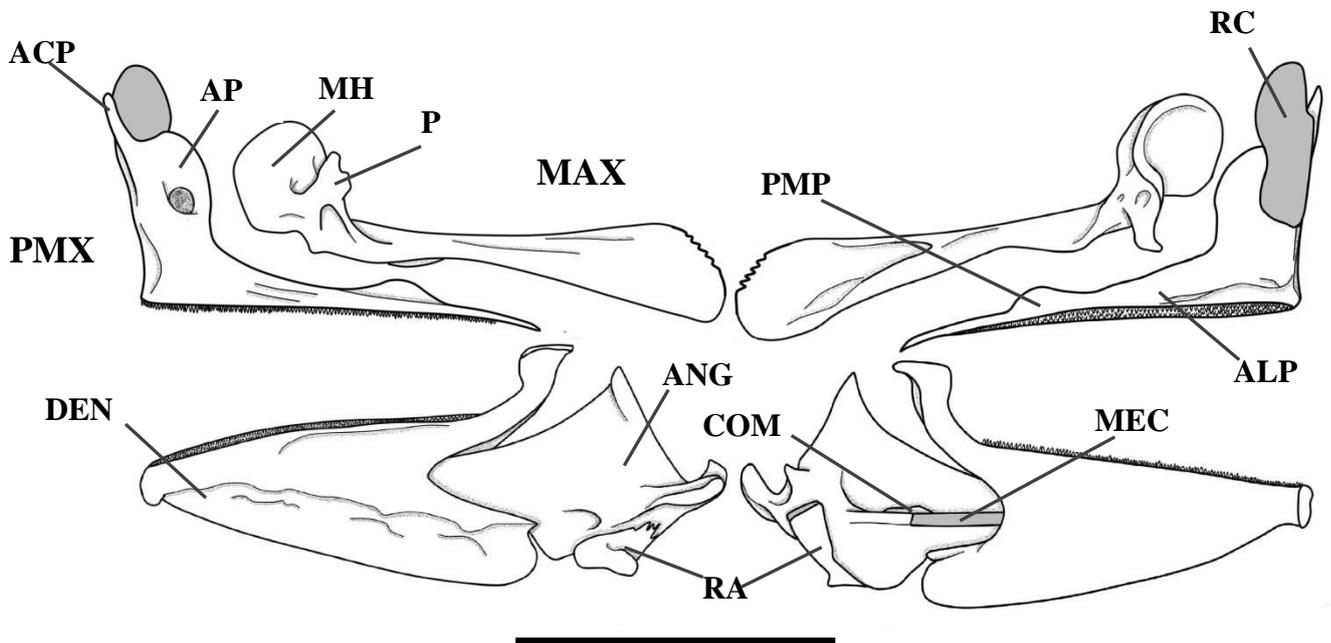
### **Other variations**

**Sphenotic on dorsal surface of neurocranium.** The sphenotic does not form on the dorsal surface of the neurocranium, whereas it is surrounded by the pterotic, parietal and frontal, and occupies its dorsal surface in *Leptomelanosoma indicum* (Fig. 5). The latter condition is unique among sciaenids (e.g., Sasaki, 1989; this study); therefore it is autapomorphic for this species.

**Foramen for nervus glossopharyngeus on intercalar.** A foramen for the nervus glossopharyngeus is present on the lateral surface of the exoccipital, whereas this foramen is present on the intercalar in *Parapolyneumus verekeri* (Fig. 7). Because the foramen is absent on the intercalar in sciaenids, it is considered as an autapomorphy of *P. verekeri*.

### 1-3 Jaws (Figs. 9–10)

**Description.** The jaws consist of the premaxilla and maxilla in the upper jaw, and the dentary, anguloarticular, retroarticular and coronomeckelian in the lower jaw. The supramaxillae are absent. The rostral cartilage in the upper jaw and Meckelian cartilage in the lower jaw are present.



**Fig. 9.** Lateral (upper left) and medial (upper right) views of upper jaw, and lateral (lower left) and medial (lower right) views of lower jaw in *Polydactylus sextarius*. ACP, ascending process; ALP, alveolar process; ANG, anguloarticular; AP, articular process; COM, coronomeckelian; DEN, dentary; MAX, maxilla; MEC, Meckelian cartilage; MH, maxillary head; P, process for insertion of primordial ligament; PMP, postmaxillary process; PMX, premaxilla; RA, retroarticular; RC, rostral cartilage. Bar indicates 10 mm.

The premaxilla is an L-shaped bone and includes four processes: the ascending, articular, alveolar and postmaxillary processes. The ascending process is rod-like and attached with the rostral cartilage posteromedially. The articular process is situated posterolateral to the ascending process and separated from the latter by a shallow and blunt notch (angle of notch between two

processes ca. 80–120 degree) in polynemids, except for *Parapolyneumus verekeri* and *Polyneumus*, in which a deep and sharp notch (ca. 30–40 degree) is present between the ascending and articular processes. A cavity is present on the center of the articular process laterally in most polynemids, whereas the cavity is absent in *Polydactylus nigripinnis* and *Polydactylus microstomus*. The alveolar process, having villiform teeth ventromedially, is 2 to 3 times longer than the ascending process in most polynemids, 0.5 to 1 time in *Galeoides decadactylus*, *Polydactylus microstomus* and *Polydactylus sextarius*, and about 5 times in *Polydactylus opercularis* and *Eleutheronema*. The postmaxillary process is situated on the middle portion of the alveolar process. The degree of development of the postmaxillary process are varied among polynemids (e.g., large in *Leptomelanosoma indicum* and *Polydactylus virginicus*; small in *Eleutheronema*; extremely small in *Filimanus*).

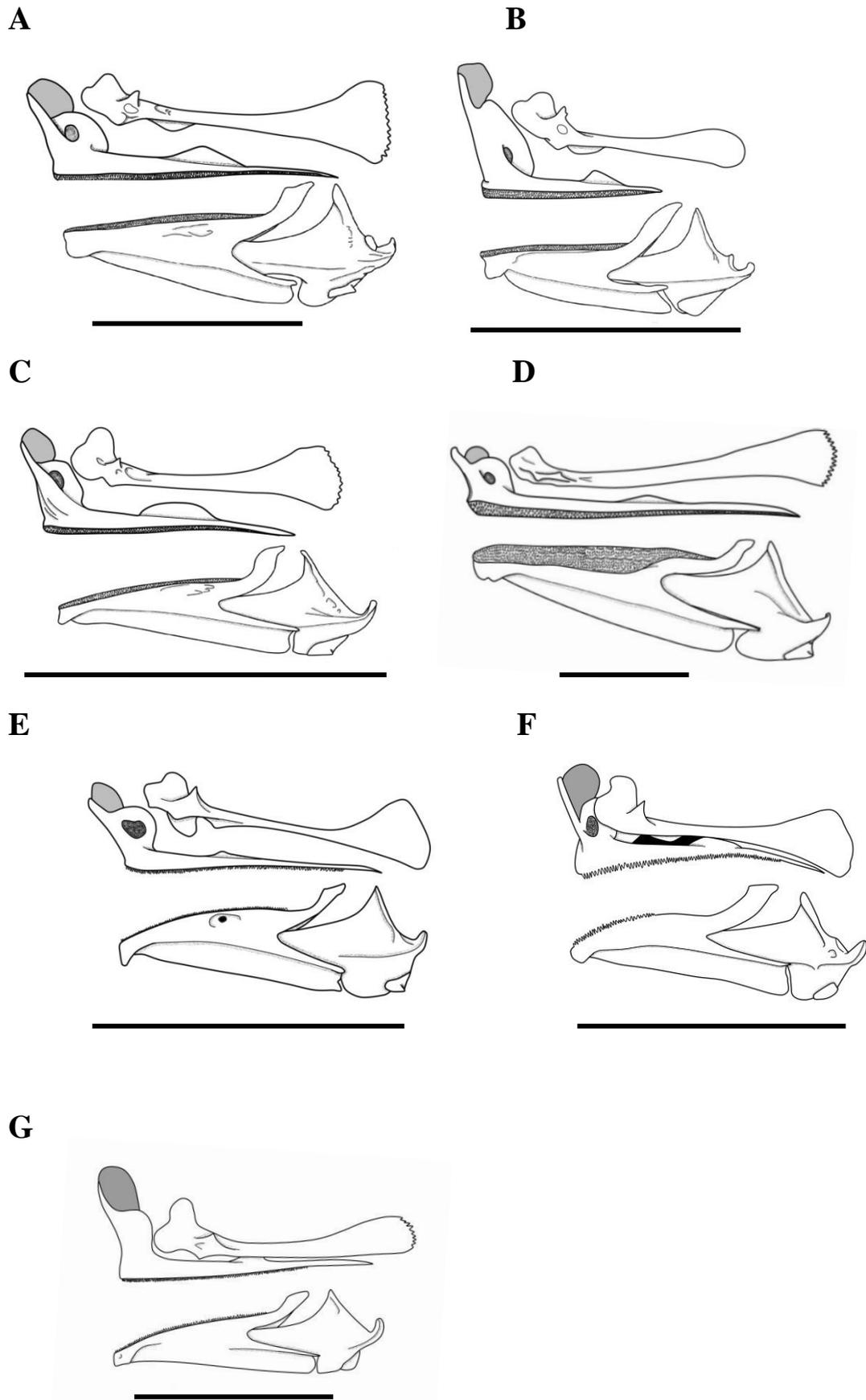
The maxilla is a rod-like bone and comprises a distinct maxillary head, bearing a process for the insertion of the primordial ligament posterolaterally, and a shaft. The maxillary head envelops the articular process of the premaxilla anteromedially. A ligament connects the ventrolateral part of the maxillary head and anterolateral surface of the ethmoid. The basal portion of the process for the insertion of the primordial ligament articulates with the anterior process of the palatine. The shaft is slender anteriorly and broad posteriorly. Its posterior margin is serrated in polynemids, except for *Galeoides decadactylus*, *Polyneumus multifilis*, *Polyneumus aquilonaris*, *Parapolyneumus verekeri*, *Pentanemus quinquarius* and *Filimanus*, in which it is smooth.

The dentary is a boomerang-shaped bone with a villiform tooth plate dorsally. The tooth plate is mainly situated on its dorsal surface in polynemids, except for *Polydactylus opercularis* and *Eleutheronema*, in which it well extends to the lateral surface. The dentary possesses a tubular structure forming the anterior portion of the preoperculo-mandibular sensory canal ventrally. The dentary is connected with the anguloarticular posteriorly and the Meckelian cartilage medially. A foramen is present on the upper center of the dentary in *Parapolyneumus verekeri* and *Filimanus*, while it is absent in the others.

The anguloarticular is a wedge-like bone and has an anterior projection inserted into a deep hollow of the dentary. It has a glenoid cavity posterodorsally for the articulation with the ventral portion of quadrate and is connected with the retroarticular posteroventrally. The anguloarticular bears the Meckelian cartilage and coronomeckelian medially. The sensory canal from the preopercle posteriorly runs through the tubular structure of this bone anteriorly to the dentary.

The retroarticular is a small bone, situated posteroventral to the anguloarticular. A strong ligament links the retroarticular with the interopercle.

The coronomeckelian is a tiny bone, connected with the medial surface of the anguloarticular and posterior end of the Meckelian cartilage. It is overlapped with the Meckelian cartilage medially.



**Fig. 10** Lateral views of upper (upper) and lower (lower) jaws. A, *Polydactylus virginicus*; B, *Galeoides decadactylus*; C, *Leptomelanosoma indicum*; D, *Eleutheronema rhadinum*; E, *Filimanus similis*; F, *Polynemus aquilonaris*; G, *Polydactylus nigripinnis*. Bars indicate 10 mm.

## Character recognition

**TS 15. Notch between ascending and articular processes.** 0: deep and sharp; 1: shallow and blunt.

The articular process is separated from the ascending process by a shallow and blunt notch (angle of notch between two processes ca. 80–120 degree) in polynemids (Figs. 9, 10A–E, G) (character 15-1), except for *Parapolyneumus verekeri* and *Polyneumus*, in which a deep notch (ca. 30–40 degree) is present between the ascending and articular processes (Fig. 10F) (character 15-0). The notch between the ascending and articular processes is deep in most sciaenids (character 15-0), whereas it is shallow in *Pachypops* and *Lonchurus lanceolatus* (character 15-1) (e.g., Green, 1941; Sasaki, 1989; this study).

**TS 16. Lateral cavity on center of articular process.** 0: present; 1: absent.

A cavity is present on the center of the articular process laterally in most polynemids (Figs. 9, 10A–F) (character 16-0), whereas the cavity is absent in *Polydactylus nigripinnis* (Fig. 10G) and *Polydactylus microstomus* (character 16-1). The presence of the cavity is a common character of Sciaenidae (character 16-0) (e.g., Sasaki, 1989; this study).

**TS 17. Lengths of alveolar and ascending processes.** 0: former 0.5 to 1 time longer than latter; 1: 2 to 3 times; 2: about 5 times. (ordered as 0-1-2)

The alveolar process is 2 to 3 times longer than the ascending process in most polynemids (Fig. 10A, C, E–G) (character 17-1), 0.5 to 1 time in *Galeoides decadactylus*, *Polydactylus microstomus* and *Polydactylus sextarius* (Figs. 9,

10B) (character 17-0), and about 5 times longer in *Polydactylus opercularis* and *Eleutheronema* (Fig. 10D) (character 17-2). In contrast, although Sasaki (1989) stated that “the ascending process usually longer than the alveolar process in the sciaenids with an inferior mouth” and “the length relationships of these two processes are varied in sciaenids”, he did not show concrete values of the relationships in sciaenids. Because the presence of character 17-2 in sciaenids is uncertain based on previous researches and limited materials examined in this study, the outgroup is coded as “?”.

**TS 18. Posterior margin of maxilla.** 0: smooth; 1: serrated.

The posterior margin of the maxilla is serrated in polynemids (Figs. 9, 10A, C–D, G) (character 18-1), except for *Galeoides decadactylus*, *Polynemus multifilis*, *Polynemus aquilonaris*, *Parapolynemus verekeri*, *Pentanemus quinquarius* and *Filimanus*, having a smooth posterior margin (Fig. 10B, E, F) (character 18-0). The posterior margin of the maxilla is smooth in sciaenids (character 18-0) (e.g., Green, 1941; Sasaki, 1989; this study).

**TS 19. Tooth plate on dentary.** 0: mainly situated on dorsal surface; 1: well extending to lateral surface.

The tooth plate is mainly situated on the dorsal surface of the dentary in most polynemids (Figs. 9, 10A–C, E–G) (character 19-0), while it well extends to the lateral surface in *Polydactylus opercularis* and *Eleutheronema* (Fig. 10D) (character 19-1). The dentary possesses the tooth band dorsally in sciaenids (character 19-0) (e.g., Topp and Cole, 1968; Sasaki, 1989; this study).

**TS 20. Dentary foramen.** 0: absent; 1: present.

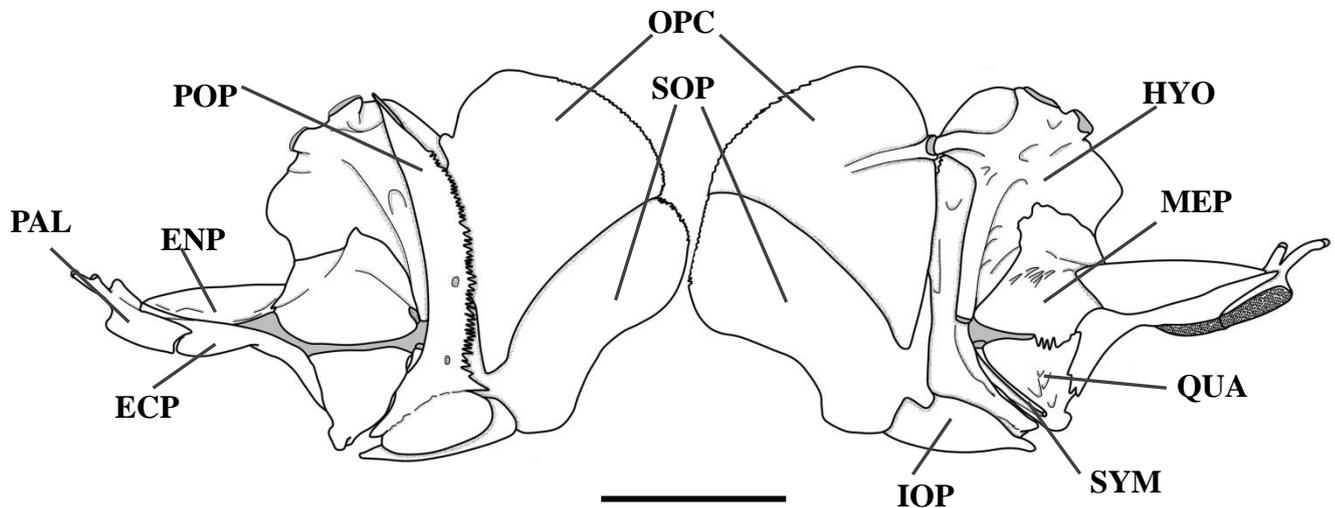
A foramen on the upper center of the dentary is absent in polynemids (Figs. 9 and 10A–D, F–G) (character 20-0), except for *Parapolynemus verekeri* and *Filimanus*, in which it is present (Fig. 10E) (character 20-1). In sciaenids, this foramen is usually absent (character 20-0), but it is present in *Larimus* and *Seriphus* (character 20-1) (Sasaki, 1989).

## **Other variations**

**Degree of development of postmaxillary process.** The degree of development of the postmaxillary process is varied among polynemids. For example, it is large in *Leptomelanosoma indicum* and *Polydactylus virginicus*, small in *Eleutheronema*, and extremely small in *Filimanus*. However, it is serially changed in polynemids and it is difficult to separate the variation into any distinct morphotypes. Subsequently, this variation is not used for the phylogenetic analysis.

#### 1-4 Suspensorium and opercular bones (Figs. 11–13)

**Description.** The suspensorium is situated on the lateral region of the head and is connected with the lower jaw, hyoid arch and cranium. It consists of seven elements: the palatine, ectopterygoid, endopterygoid, metapterygoid, hyomandibula, quadrate and symplectic. The opercular bones, situated posterior to the suspensorium, comprises four elements: the preopercle, opercle, subopercle and interopercle.



**Fig. 11.** Lateral (left) and medial (right) views of suspensorium and opercular bones in *Polydactylus approximans*. ECP, ectopterygoid; ENP, endopterygoid; HYO, hyomandibula; IOP, interopercle; MEP, metapterygoid; OPC, opercle; PAL, palatine; POP, preopercle; QUA, quadrate; SOP, subopercle; SYM, symplectic. Bar indicates 10 mm.

The palatine, a Z-shaped bone bearing a villiform tooth plate along its oral border, is connected with the endopterygoid posteromedially and the ectopterygoid posteroventrally. It possesses a cartilaginous cap anteriorly. The anterior process of the palatine articulates with the base of the process for the insertion of the primordial ligament on the maxilla anteroventrally, the first infraorbital anterodorsally and the prevomer anteriorly. The palatine has a socket

for the articulation with the lateral ethmoid dorsomedially in *Polydactylus opercularis*, *Leptomelanosoma indicum*, *Polynemus multifilis* and *Eleutheronema*, whereas an anteromedial process, instead of the socket, articulates with the ventrolateral condyle of the lateral ethmoid in other polynemids. The palatine greatly extends posteriorly and the length of its oral portion is longer than that of the ectopterygoid tooth plate in polynemids, except for *Polydactylus opercularis*, *Pentanemus quinquarius* and *Filimanus*, in which it slightly extends posteriorly and the length of its oral portion is shorter than that of the tooth plate of the ectopterygoid. The tooth plate on the palatine is separated from the ectopterygoid in most polynemids, whereas the tooth plate has a dorsomedial expansion that covering the anteroventral portion of the ectopterygoid dorsolaterally in *Eleutheronema*. The expansion and palatine medially and laterally sandwich the ectopterygoid.

The ectopterygoid with a villiform tooth plate on its ventromedial surface is connected with the palatine anterodorsally and the quadrate posteriorly. The ectopterygoid is also connected with the endopterygoid dorsomedially in most polynemids, while the former is fused with the latter in *Pentanemus quinquarius*, *Polydactylus nigripinnis*, *Polynemus paradiseus* and *Filimanus similis*. The ectopterygoid well elongates and its anterior margin attains to that of the endopterygoid. The ectopterygoid extends posterodorsally and is interdigitated (only in *Polydactylus opercularis*) or simply connected with the metapterygoid medially, whereas it is laterally separated from the latter by a long cartilaginous

band, which is present among the ectopterygoid, endopterygoid, metapterygoid and quadrate.

The endopterygoid is a thin, sheet-like bone, situated below the orbit, and is connected with the palatine anterolaterally, the ectopterygoid ventrolaterally and the metapterygoid posteriorly. The posterior portion of the endopterygoid covers the metapterygoid laterally. The endopterygoid is separated from the quadrate in polynemids, except for *Pentanemus quinquarius*, in which it is attached with the quadrate medially.

The metapterygoid is a rectangular or squared bone, sutured with the hyomandibula dorsoposteriorly and connected with the ectopterygoid anteroventrally. The metapterygoid is separated from the quadrate by a cartilaginous band laterally, while it is interdigitated with the latter medially. The anterior portion of the metapterygoid medially covers the posterior portion of the endopterygoid. The metapterygoid lamina supporting the levator arcus palatine is present.

The hyomandibula is a large fan-shaped bone, sutured with the metapterygoid ventroanteriorly and the preopercle posterolaterally. The hyomandibula is well developed and expands anteriorly, but separated from the endopterygoid by the metapterygoid in most polynemids. This bone has a much larger expansion and is connected with the endopterygoid in *Eleutheronema*. It has two dorsal and one posterodorsal condyles: the anterior dorsal one articulating with a socket formed by the prootic and sphenotic; the posterior dorsal one with a groove-like socket in the pterotic; and the posterodorsal one

with the anterior corner of the opercle. It is attached with the symplectic and interhyal through a cartilaginous interspace ventrally.

The quadrate is a triangular bone, having a condyle for the articulation with the anguloarticular anteriorly. It is interdigitated with the metapterygoid dorsomedially, connected with the ectopterygoid anteriorly and the preopercle posteroventrally, and medially possesses a long and narrow groove in which the symplectic is situated. A foramen is present on the ventral portion of the quadrate in *Polydactylus opercularis*.

The symplectic is a long rod-like bone, situated in the groove of the quadrate laterally. This bone has cartilaginous caps on its both tips and articulates with the interhyal at the dorsal tip.

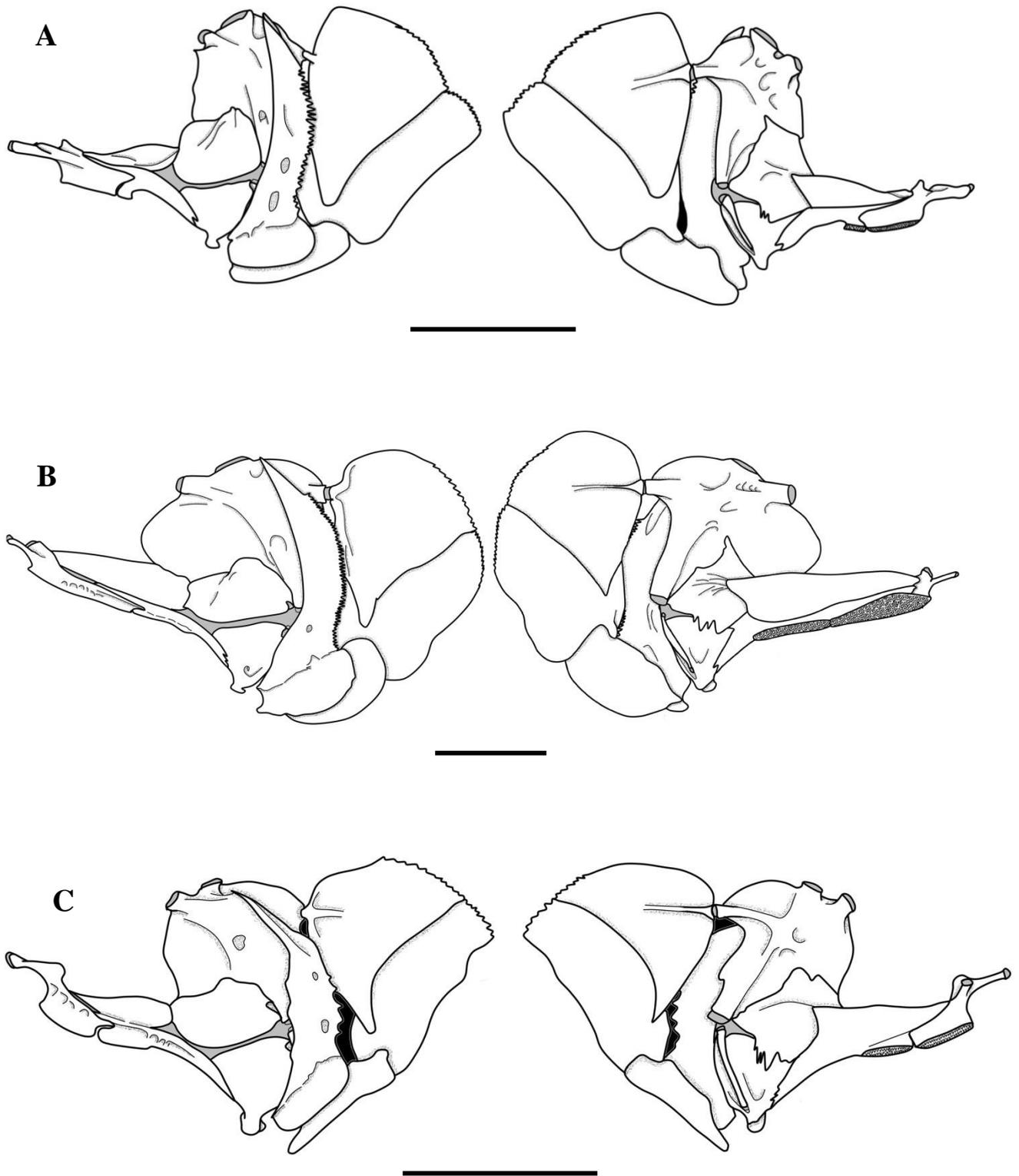
The preopercle is a large and crescentic bone supporting a tubular structure for the preoperculo-mandibular sensory canal. The lateral surface of the preopercle possesses two small pits on the middle portion and several bridges on the ventral portion in polynemids, except for *Parapolynemus verekeri* and *Pentanemus quinquarius*, in which several narrow bridges cover the lateral surface of this bone. The ventral part of the preopercle bears a well-developed thin semicircular sheet expansion covering the interopercle medially in polynemids, except for *Pentanemus quinquarius*, in which such an expansion is absent. The posterior margin of this bone is serrated in most polynemids, whereas it is smooth in *Parapolynemus verekeri* and *Pentanemus quinquarius*. The preopercle is sutured with the hyomandibula anterodorsally and the

quadrated anteroventrally, and medially covers the opercle, interopercle and subopercle partly.

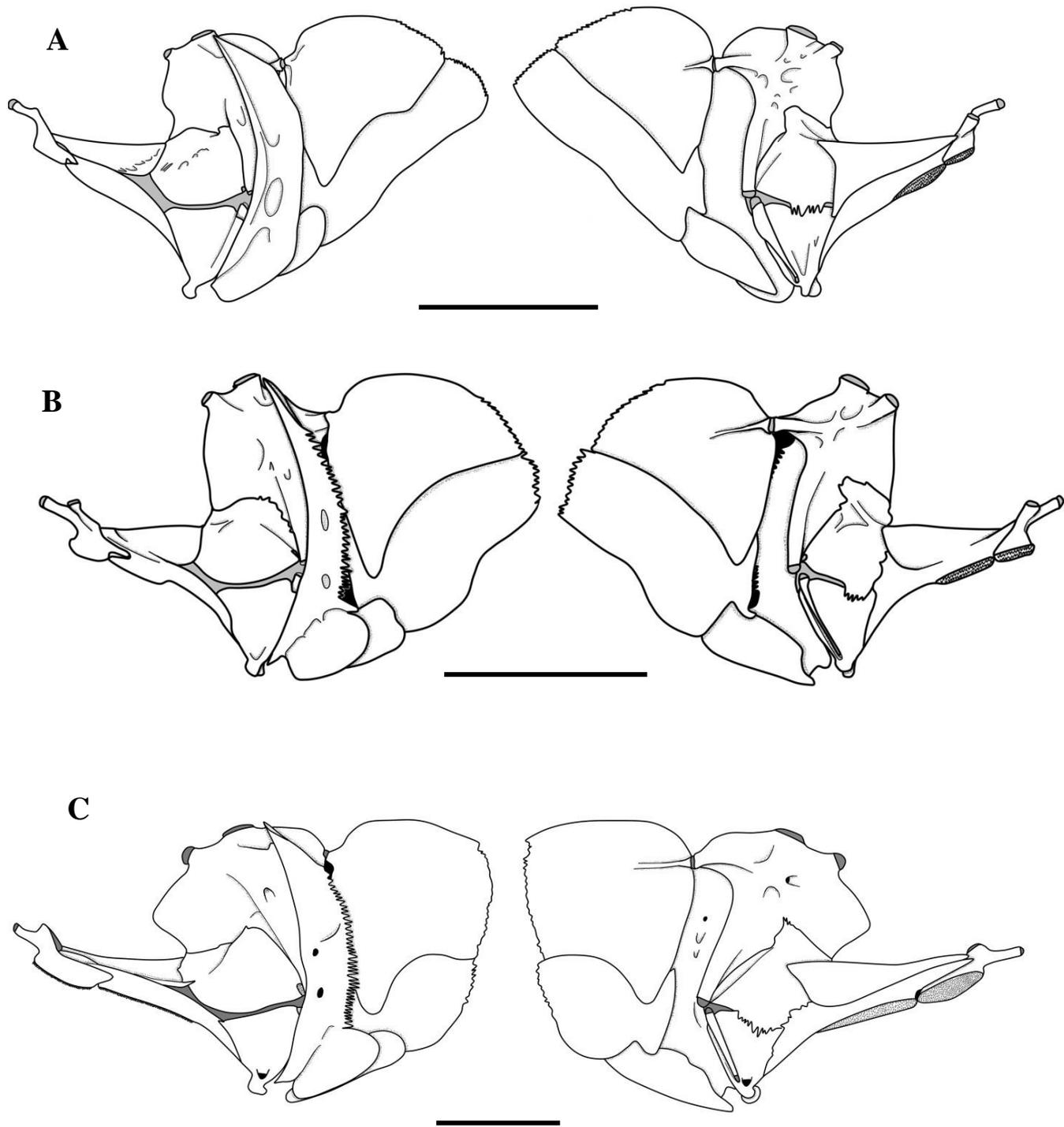
The opercle is a large thin fan-shaped bone, articulating with the hyomandibula anteriorly and slightly overlapping with the subopercle ventromedially. The opercle is covered by the preopercle anterolaterally and points posteriorly without spines. The dorsal margin of this bone is posteriorly serrated.

The subopercle is a sickle-shaped bone, partly overlapped with the ventral portion of the opercle and dorsal portion of the interopercle laterally. The subopercle is covered by the preopercle anterolaterally. The posterodorsal margin of this bone is serrated.

The interopercle is a thick bone, situated medial to the semicircular sheet-like process of the preopercle. This bone is overlapped with the ventral portion of the subopercle medially and is connected with the retroarticular anteriorly via a strong ligament.



**Fig. 12.** Lateral (left) and medial (right) views of suspensorium and opercular bones. A, *Galeoides decadactylus*; B, *Eleutheronema rhadinum*; C, *Polynemus paradiseus*. Bars indicate 10 mm.



**Fig. 13.** Lateral (left) and medial (right) views of suspensorium and opercular bones. A, *Pentanemus quinquarius*; B, *Filimanus similis*; C, *Polydactylus opercularis*. Bars indicate 10 mm.

## Character recognition

**TS 21. Anteromedial process of palatine.** 0: absent; 1: present.

The palatine has a socket for the articulation with the lateral ethmoid dorsomedially in *Polydactylus opercularis*, *Leptomelanosoma indicum*, *Polynemus multifilis* and *Eleutheronema* (character 21-0) (Figs. 12A, B, 13C), whereas an anteromedial process, instead of the socket, articulates with the ventrolateral condyle of the lateral ethmoid in other polynemids (character 21-1) (Figs. 11, 12C, 13A, B). Both conditions are present in Sciaenidae (characters 21-0 and 21-1) (e.g., Kim and Kim, 1965; Sasaki, 1989; this study).

**TS 22. Posterior portion of palatine.** 0: greatly extending; 1: slightly extending.

The palatine greatly extends posteriorly and the length of its oral portion is longer than that of ectopterygoid tooth plate in polynemids (character 22-0) (Figs. 11–12), except for *Polydactylus opercularis*, *Pentanemus quinquarius* and *Filimanus*, in which it slightly extends posteriorly and the length of its oral portion is shorter than that of the tooth plate of the ectopterygoid (character 22-1) (Fig. 13). This bone greatly extends posteriorly or posteroventrally in sciaenids (character 22-0) (e.g., Green, 1941; Kim and Kim, 1965; Sasaki, 1989; this study).

**TS 23. Tooth plate on palatine.** 0: separated from ectopterygoid; 1: covered by ectopterygoid dorsolaterally.

The tooth plate on the palatine is separated from the ectopterygoid in most polynemids (character 23-0) (Figs. 11, 12A, C, 13), while the tooth plate has a

dorsomedial expansion covered by the anteroventral portion of ectopterygoid dorsolaterally in *Eleutheronema* (character 23-1) (Fig. 12B). The tooth plate on palatine is absent in sciaenids (e.g., Sasaki, 1989; this study); thus the outgroup is coded as “?”.

**TS 24. Ectopterygoid and endopterygoid.** 0: autogenous; 1: fused.

The ectopterygoid is autogenous and connected with the endopterygoid in most polynemids (character 24-0) (Figs. 11, 12A, B, 13A, C), while the former is fused with the latter in *Pentanemus quinquarius*, *Polydactylus nigripinnis*, *Polynemus paradiseus* and *Filimanus similis* (character 24-1) (Figs. 12C, 13B). The endopterygoid and ectopterygoid are autogenous and connected in sciaenids (character 24-0) (e.g., Sasaki, 1989; this study).

**TS 25. Endopterygoid and quadrate.** 0: sutured medially; 1: separated medially.

The endopterygoid is sutured with the quadrate medially in *Pentanemus quinquarius* (character 25-0) (Fig. 13A), but two bones are separated from each other in other polynemids (character 25-1) (Figs. 11, 12, 13B, C). Only the former condition is found in sciaenids (character 25-0) (e.g., Green, 1941; Kim and Kim, 1965; Sasaki, 1989).

**TS 26. Hyomandibula and endopterygoid.** 0: separated; 1: connected.

The hyomandibula is separated with the endopterygoid by the metapterygoid in most polynemids (character 26-0) (Figs. 11, 12A, C, 13), whereas it has a much larger expansion and is connected with the endopterygoid

in *Eleutheronema* (character 26-1) (Fig. 12B). The two bones are separated in sciaenids (character 26-0) (e.g., Green, 1941; Sasaki, 1989; this study).

**TS 27. Well-developed thin semicircular sheet expansion of preopercle.**

0: absent; 1: present.

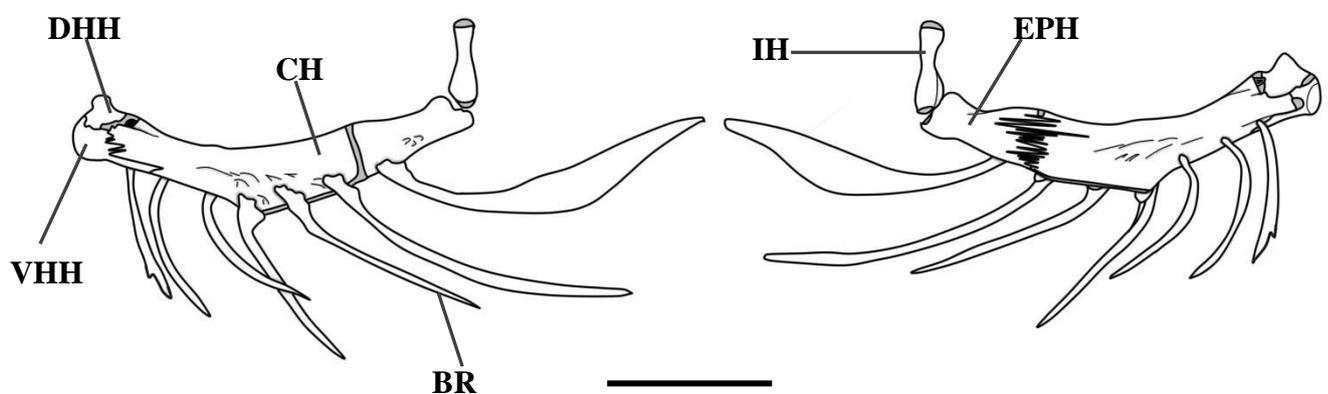
The ventral part of the preopercle bears a well-developed thin semicircular sheet expansion in most polynemids (character 27-1) (Figs. 11, 12, 13B, C), except for *Pentanemus quinquarius*, in which such a distinct semicircular expansion is absent (character 27-0) (Fig. 13A). The ventroposterior part of the preopercle in sciaenids is weakly developed and does not form the distinct semicircular expansion (character 27-0).

**TS 28. Posterior margin of preopercle.** 0: serrated; 1: smooth.

The posterior margin of the preopercle is serrated in polynemids (character 28-0) (Figs. 11–12, 13B, C), except for *Parapolynemus verekeri* and *Pentanemus quinquarius*, in which it is smooth (character 28-1) (Fig. 13A). The posterior margin of the preopercle is weakly serrated in sciaenids (character 28-0) (e.g., Sasaki, 1989; this study).

## 1-5 Hyoid arch (Figs. 14–17)

**Description.** The hyoid arch, situated on the lateral side of the head, connected with the branchial arch anteriorly and articulating with the suspensorium posteriorly, comprises the hypohyals, ceratohyal, epihyal, interhyal, branchiostegal rays, basihyal and urohyal.



**Fig. 14.** Lateral (left) and medial (right) views of hyoid arch in *Polydactylus approximans*. BR, branchiostegal ray; CH, ceratohyal; DHH, dorsal hypohyal; EPH, epihyal; IH, interhyal; VHH, ventral hypohyal. Bar indicates 10 mm.

The hypohyals, situated on the anteriormost part of the hyoid arch, consists of two elements, the dorsal and ventral hypohyals. The dorsal hypohyal is sutured with the ventral hypohyal ventrally, connected with the ceratohyal posteriorly via a cartilaginous insertion and posteriorly attached with the anterolateral surface of the first hypobranchial by a ligament. A foreman is present on the cartilaginous insertion. The ventral hypohyal is sutured with the dorsal hypohyal dorsally and the ceratohyal posteriorly. The posteroventral portion of the ventral hypohyal posteriorly extends beyond the first branchiostegal ray and partly suspends it in many polynemids, while the ventral

hypohyal does not extend beyond the first branchiostegal ray and is separated from it in *Leptomelanosoma indicum*, *Pentanemus quinquarius*, *Polydactylus microstomus*, *Polydactylus nigripinnis*, *Polydactylus multiradiatus*, *Polynemus aquilonaris*, *Polynemus melanochir melanochir*, *Parapolynemus verekeri* and *Polynemus paradiseus*.

The ceratohyal, a large flattened bone, is connected with the hypohyals anteriorly. The ceratohyal is connected with the epihyal via a narrow cartilaginous band on the lateral surface in polynemids, except for *Galeoides decadactylus*, *Parapolynemus verekeri*, *Polydactylus nigripinnis*, *Polydactylus opercularis*, *Pentanemus quinquarius*, *Polynemus* and *Filimanus*, in which the ceratohyal partly interdigitates with the epihyal laterally. This bone ventrally suspends the anterior six branchiostegal rays (anterior three medially and posterior three laterally) in polynemids, except for *Filimanus sealei*, in which it suspends the anterior seven branchiostegal rays (anterior four medially and posterior three laterally). A small concavity, suspending the third branchiostegal ray, is present on the ventral margin of the ceratohyal in *Leptomelanosoma indicum*, whereas it is absent in other polynemids.

The epihyal is a flattened, trapezoid bone, connected with the ceratohyal anteriorly. The epihyal articulates with the ventral end of the interhyal posterodorsally. The lateral surface of this bone anteroventrally suspends the posteriormost branchiostegal ray.

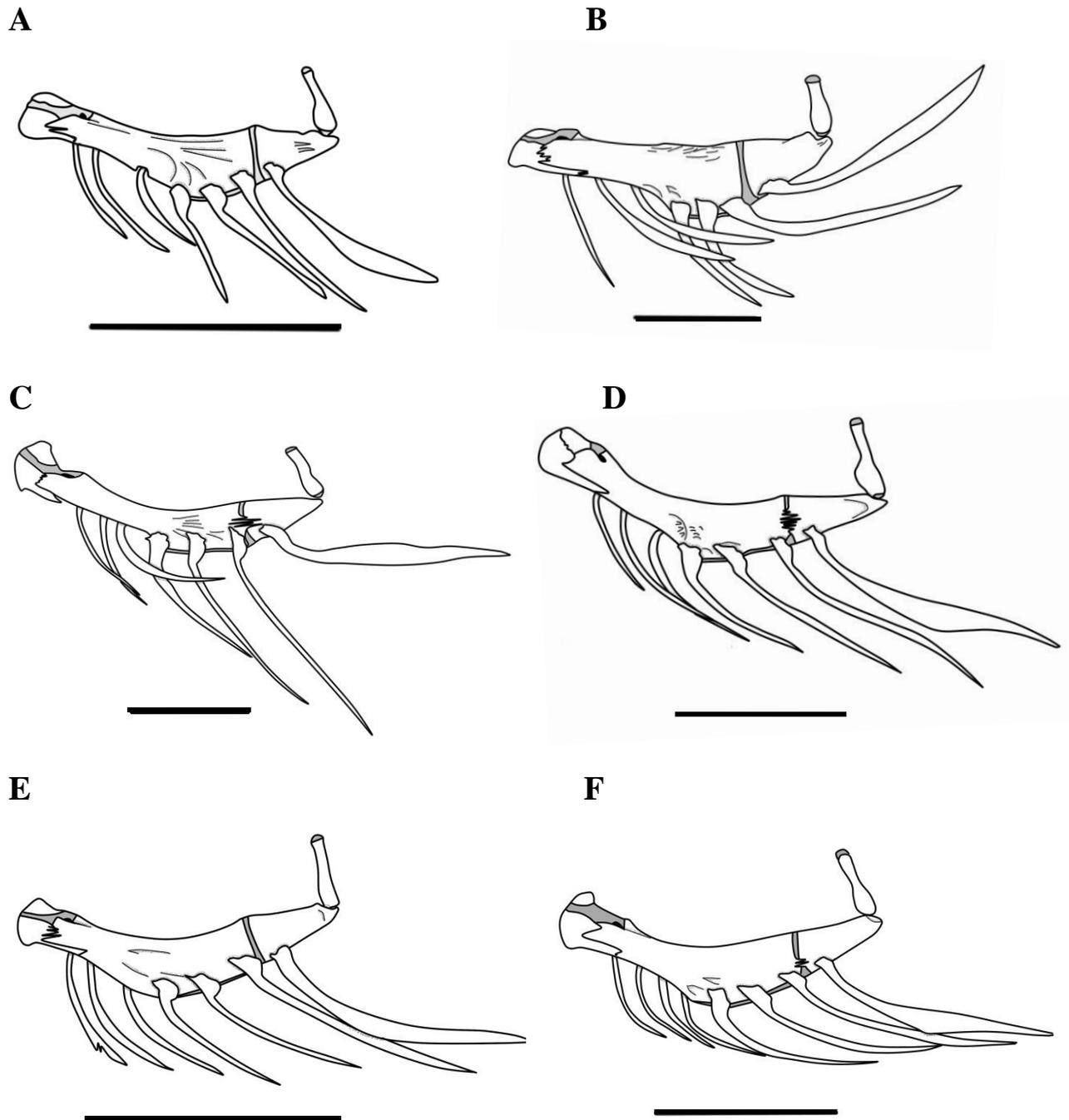
The interhyal is a short rod-like bone with cartilaginous caps on both ends. It articulates with the posterodorsal portion of the epihyal ventrally and the

cartilaginous glenoid cavity surrounded by the hyomandibula, preopercle and symplectic dorsally.

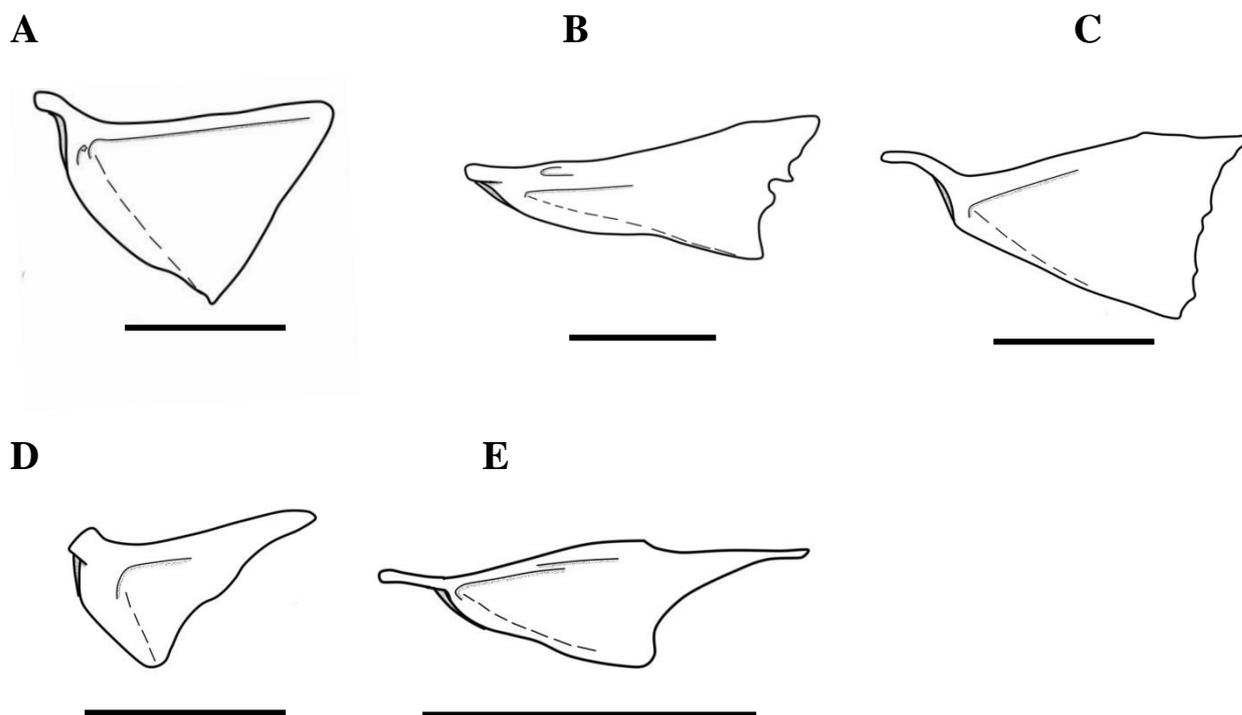
The branchiostegal rays are long and slender bones, suspended from the ceratohyal, epihyal or ventral hypohyal at their dorsal tips. The number of branchiostegal rays is seven in most polynemids, while it is eight in *Filimanus sealei*. The anterior three rays (or four rays in *Filimanus sealei*) are suspended by the ventral hypohyal or the anterior portion of the ceratohyal laterally, the middle three by the posterior portion of the ceratohyal medially, and the posterior one by the epihyal medially. The terminal tip of the first branchiostegal ray is pointed and smooth in polynemids, except for *Polydactylus plebeius*, *Polydactylus virginicus*, *Polydactylus approximans*, *Polydactylus multiradiatus*, *Polydactylus nigripinnis*, *Polydactylus opercularis*, *Polydactylus sexfilis*, *Polydactylus octonemus* and *Polydactylus oligodon*, in which it is broad and serrated.

The urohyal, an unpaired triangular bone, is connected to the ventral side of the first basibranchial dorsally. The anterior tip of the urohyal is connected with the medial portion of the ventral hypohyal via a ligament.

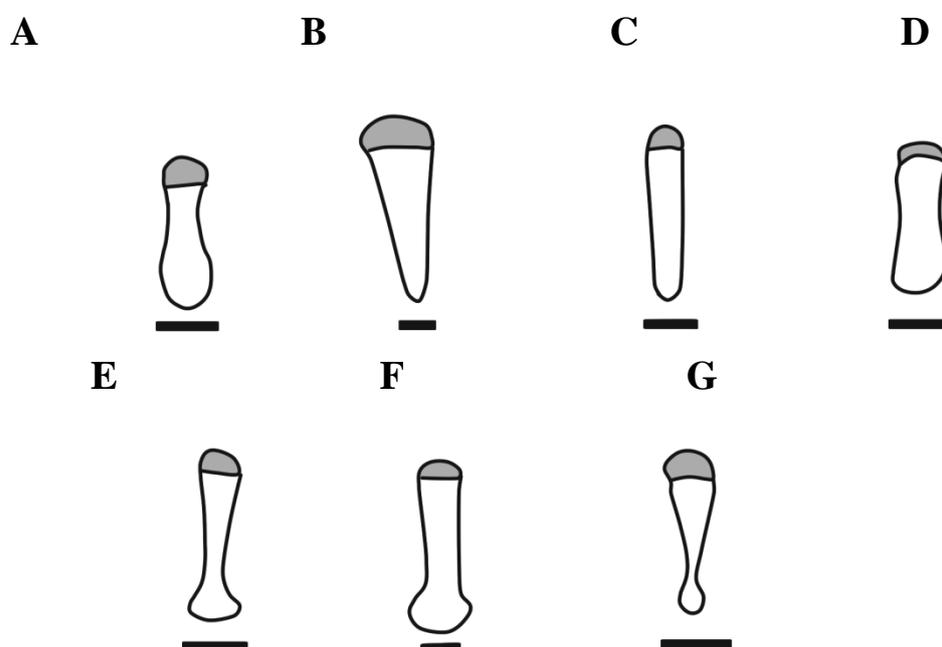
The basihyal is an unpaired rod-like bone with a cartilaginous cap anteriorly and attached with the first basibranchial posteroventrally.



**Fig. 15.** Lateral view of hyoid arch. A, *Leptomelanosoma indicum*; B, *Eleutheronema rhadinum*; C, *Pentanemus quinquarius*; D, *Filimanus similis*; E, *Polydactylus octonemus*; F, *Filimanus sealei*. Bars indicate 10 mm.



**Fig. 16.** Lateral view of urohyal. A, *Polydactylus virginicus*; B, *Eleutheronema rhadinum*; C, *Pentanemus quinquarius*; D, *Galeoides decadactylus*; E, *Parapolyneumus verekeri*. Bars indicate 5mm.



**Fig. 17.** Dorsal view of basihyal. A, *Polydactylus virginicus*; B, *Eleutheronema rhadinum*; C, *Pentanemus quinquarius*; D, *Galeoides decadactylus*; E, *Parapolyneumus verekeri*; F, *Leptomelanosoma indicum*; G, *Filimanus similis*. Bars indicate 1 mm.

## Character recognition

**TS 29. Posteroventral portion of ventral hypohyal.** 0: not extending beyond first branchiostegal ray; 1: beyond it.

The posteroventral portion of the ventral hypohyal posteriorly extends beyond the first branchiostegal ray and partly suspends it in many polynemids (character 29-1) (Fig. 15C), while the ventral hypohyal does not extend beyond the first branchiostegal ray and is separated from it in *Leptomelanosoma indicum*, *Pentanemus quinquarius*, *Polydactylus microstomus*, *Polydactylus nigripinnis*, *Polydactylus multiradiatus*, *Polynemus aquilonaris*, *Polynemus melanochir melanochir*, *Parapolynemus verekeri* and *Polynemus paradiseus* (character 29-0) (Figs. 14, 15A–B, D–F). The ventral hypohyal does not extend posteriorly and is separated from the first branchiostegal ray in Sciaenidae (character 29-0) (e.g., Kim and Kim, 1965; Sasaki, 1989; this study).

**TS 30. Connection of ceratohyal and epihyal on lateral surface.** 0: connected via cartilaginous band; 1: interdigitating.

The ceratohyal is connected with the epihyal via a narrow cartilage band on the lateral surface in polynemids (character 30-0) (Figs. 14, 15A–B, E), except for *Galeoides decadactylus*, *Parapolynemus verekeri*, *Polydactylus nigripinnis*, *Polydactylus opercularis*, *Pentanemus quinquarius*, *Polynemus* and *Filimanus*, in which the ceratohyal partly interdigitates with the epihyal laterally (character 30-1) (Fig. 14C, D, F). Both conditions are present in sciaenids (characters 30-0 and 30-1) (e.g., Green, 1941; Sasaki, 1989; this study).

**TS 31. Terminal tip of first branchiostegal ray.** 0: pointed and smooth;  
1: broad and serrated.

The terminal tip of the first branchiostegal ray is pointed and smooth in polynemids (character 31-0) (Fig. 15A–D, F), except for *Polydactylus plebeius*, *Polydactylus virginicus*, *Polydactylus approximans*, *Polydactylus multiradiatus*, *Polydactylus nigripinnis*, *Polydactylus opercularis*, *Polydactylus sexfilis*, *Polydactylus octonemus* and *Polydactylus oligodon*, in which it is broad and serrate (character 31-1) (Figs. 14, 15E). The terminal tip of the first branchiostegal ray is pointed in sciaenids (character 31-0) (e.g., Kim and Kim, 1965; Sasaki, 1989; this study).

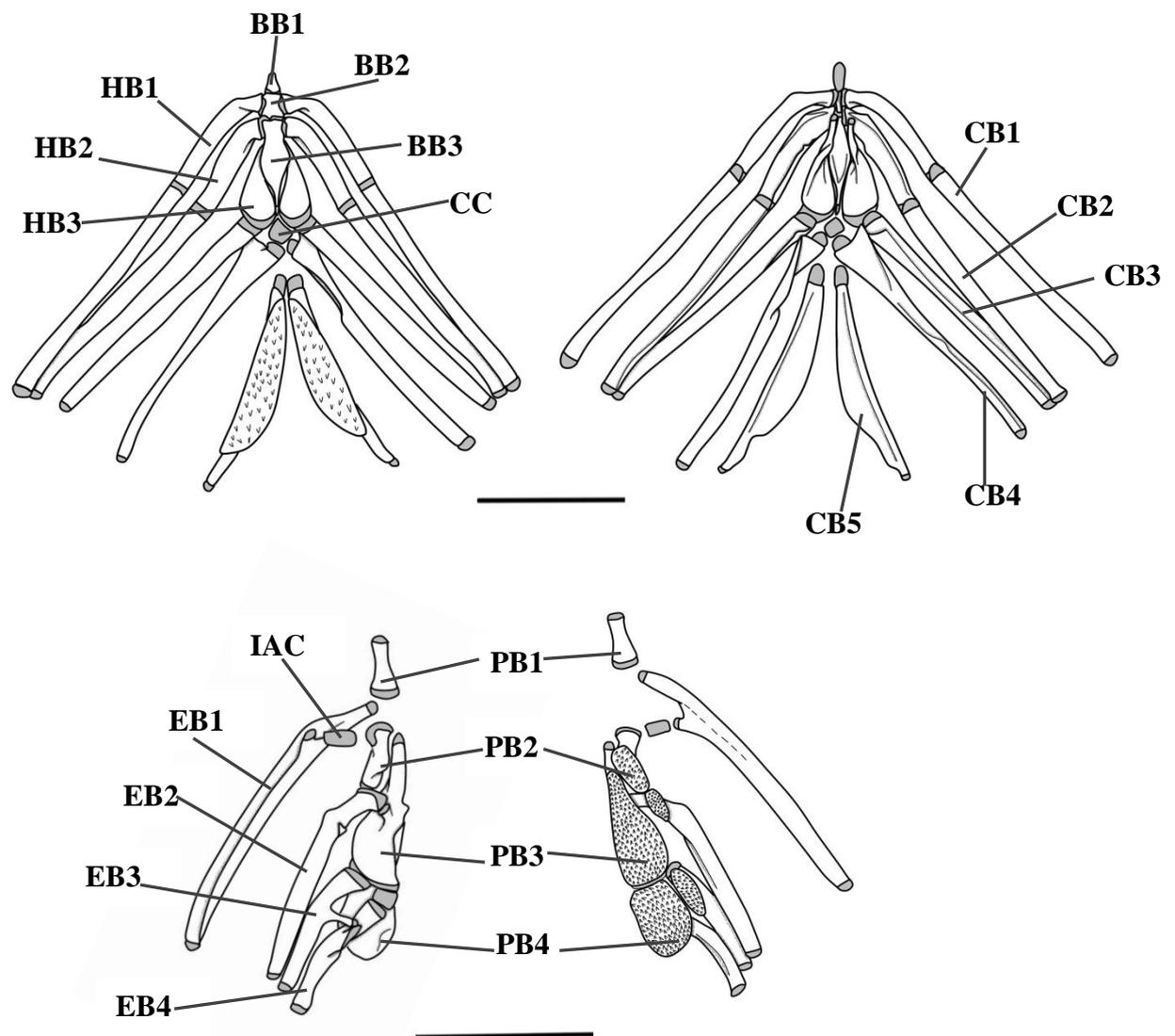
## **Other variations**

**Concavity on ventral margin of ceratohyal.** A small concavity, suspending the third branchiostegal ray, is present on the ventral margin of the ceratohyal in *Leptomelanosoma indicum* (Fig. 15A), whereas it is absent in other polynemids and sciaenids (e.g., Sasaki, 1989; this study). Therefore, the former character is an autapomorphy for the species.

**Eight branchiostegal rays.** The number of branchiostegal rays is seven in most polynemids, while it is eight in *Filimanus sealei* (Fig. 15F). Since sciaenids have seven branchiostegal rays (e.g., Topp and Cole, 1968; Sasaki, 1989; this study), the latter condition is considered to be an autapomorphy for *Filimanus sealei*.

## 1-6 Branchial arches (Figs. 18–23)

**Description.** The branchial arches supporting gill filaments and rakers comprise two parts, the lower and upper branchial arches. The lower branchial arch contains three unpaired basibranchials, one central cartilage, three pairs of the hypobranchials and five pairs of the ceratobranchials, and the upper branchial arch includes four pairs of the epibranchials and pharyngobranchials. A short rod-like interarcual cartilage is present between the first epibranchial and second pharyngobranchial.



**Fig. 18.** Dorsal (upper left) and ventral (upper right) views of lower branchial arches, and dorsal (lower left) and ventral (lower right) views of upper branchial arches in *Eleutheronema rhadinum*. BB1–3, first to third basibranchials; CB1–5, first to fifth ceratobranchials; CC, central cartilage; EB 1–4, first to fourth epibranchials; HB1–3, first to third hypobranchials; IAC, interarcual cartilage; PB 1–4, first to fourth pharyngobranchials. Bars indicate 10 mm.

The basibranchials are situated on the anterior midline of the lower branchial arches. The first basibranchial is a triangular bone, attached with the dorsal hypohyal laterally, and connected with the basihyal anterodorsally and with the second basibranchial posteriorly via a cartilaginous intervention. A cartilage is inserted into the interior of the first basibranchial ventrally. The second basibranchial is a cylindrical bone, sandwiched by the first hypobranchials anterolaterally and the second hypobranchials posterolaterally on both sides, respectively, and by the first basibranchial anteriorly and the third basibranchial posteriorly. The third basibranchial is upturned matress-like bone, situated between the third hypobranchials laterally and connected with the second basibranchial via a cartilaginous intervention anteriorly. This bone bears one and two tooth plates on its dorsal surface in *Polynemus aquilonaris*, and *Polynemus melanochir melanochir* and *Polynemus multifilis*, respectively, while it lacks tooth plates in other polynemids. The third basibranchial possesses a slender cartilaginous cap on the posterior tip, which points to the central cartilage. The central cartilage is rhombic and surrounded by cartilaginous parts on the third basibranchial, third hypobranchials, and third and fourth ceratobranchials.

The hypobranchials are three paired bones, situated between the basibranchials and ceratobranchials. The first hypobranchial, a hockey-stick-like bone, has an anteriorly-pointed projection laterally and cartilaginous caps on both ends, and is connected with the dorsal hypohyal anterolaterally by a ligament. The anteriorly-pointed projection is extremely small in polynemids,

except for *Filimanus* and *Pentanemus quinquarius*, in which it is large. The first hypobranchial articulates with the first and second basibranchials anteromedially, and the first ceratobranchial posterolaterally. The second hypobranchial is a rod-like bone with cartilaginous caps on both ends and articulates with the second and third basibranchials anteromedially, and the second ceratobranchial posterolaterally. The third hypobranchial is a teardrop-like bone; those on both sides sandwich the third basibranchial laterally. This bone has cartilaginous cap anteriorly and such margin posteriorly. Its anterior portion extends anteriorly beyond the second hypobranchial and its posterior margin articulates with the third ceratobranchial.

The ceratobranchials are consisted of five paired bones with cartilaginous caps on both ends. The first to third ceratobranchials are rod-like bones, articulating with the hypobranchials anteriorly and the epibranchials posterodorsally. The fourth ceratobranchial is a long, torch-like bone. It articulates with the central cartilage anteromedially and the fourth epibranchial posteriorly. The fifth ceratobranchial is a bow-like bone with a tooth plate on the dorsal surface. This bone is connected with the central cartilage by a strong ligament.

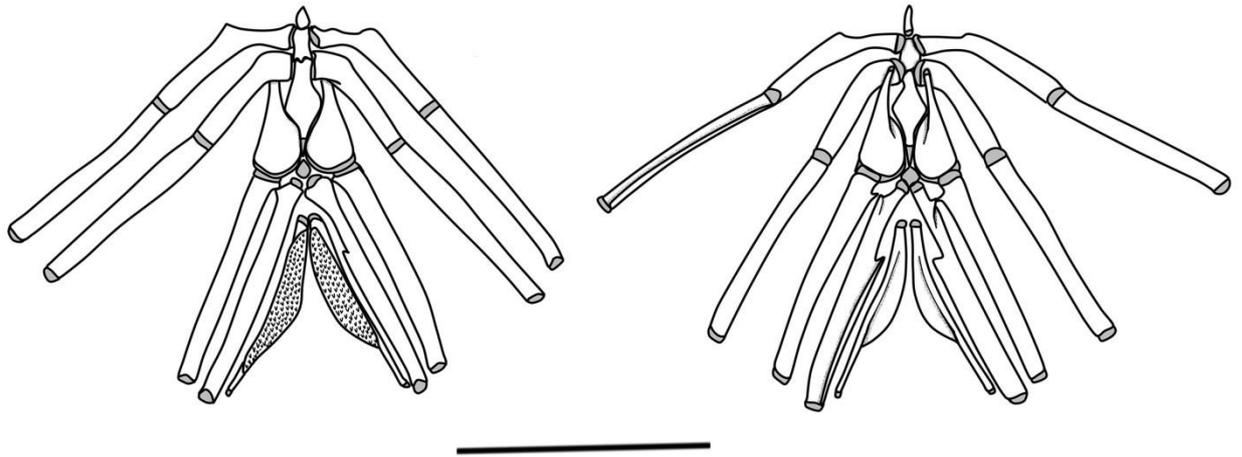
The epibranchials include four pairs of rod-like bones, situated between the pharyngobranchials and ceratobranchials, and have cartilaginous caps on both ends. The first epibranchial articulates with the first pharyngobranchial anterodorsally and the first ceratobranchial anteroventrally. This bone has an uncinat process, which articulates with the interarcual cartilage medially. The

second epibranchial articulates with the posterior region of the second pharyngobranchial and the anterolateral region of the third pharyngobranchial ventrally, and the second ceratobranchial anteroventrally. The second epibranchial is covered by an autogenous tooth plate anteroventrally. The third epibranchial articulates with the third pharyngobranchial anteromedially and the third ceratobranchial posteroventrally. A tooth plate is present on the anteroventral surface of the third epibranchial. This bone has a branched process, which articulates with the fourth epibranchial medially. The fourth epibranchial articulates with the cartilage of the fourth pharyngobranchial anteroventrally, the branch process of the third epibranchial laterally via its branched process, and the fourth ceratobranchial anteroventrally.

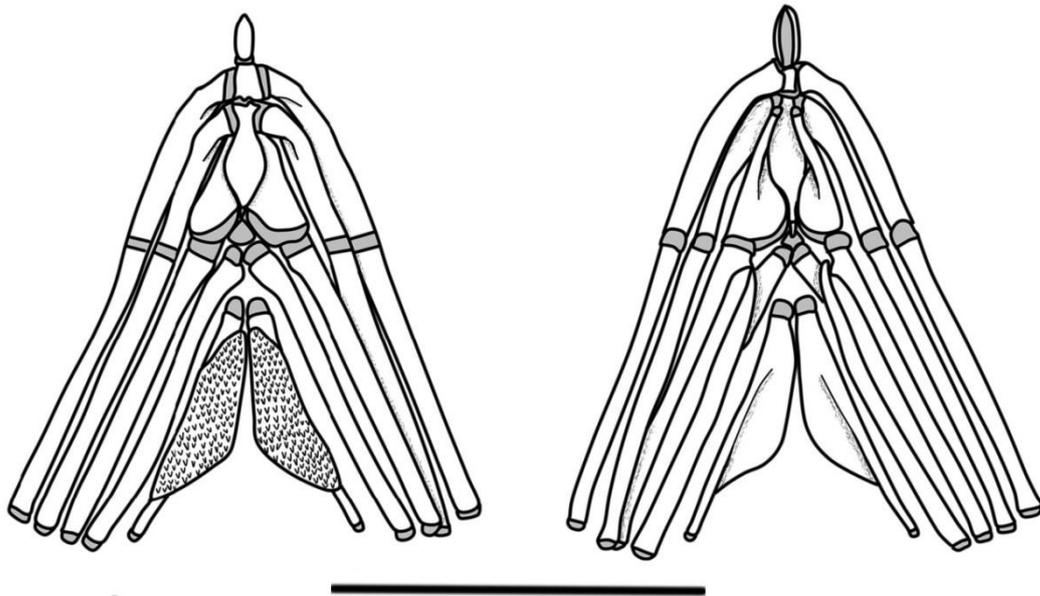
The pharyngobranchials are consisted of one pair of toothless bones (first), two pairs of toothed bones (second and third) and one pair of cartilaginous elements with circular pharyngeal tooth plates (fourth). The first pharyngobranchial is a tiny stick-like bone with two cartilaginous caps on its both tips, connected with the first epibranchial posteroventrally and suspended from the cranium anteromedially. The second pharyngobranchial, situated anterolateral to the third pharyngobranchial, is an L-shaped bone with a tooth plate ventrally. It has three cartilaginous caps on the anterior, dorsolateral and posterior tips, respectively, being autogenous from each other in polynemids, except for *Eleutheronema rhadinum* and *Polydactylus sexfilis*, in which the anterior and dorsolateral cartilaginous caps are fused with each other. The second pharyngobranchial articulates with the interarcual cartilage dorsolaterally

and the second epibranchial posterodorsally. The third pharyngobranchial is the largest toothed bone, articulating with the second epibranchial dorsolaterally, the third epibranchial posterolaterally, and the fourth pharyngobranchial posteriorly. The fourth pharyngobranchial is a rectangular cartilaginous bone with a tooth plate lacking the basal skeletal element. This bone articulates with the third pharyngobranchial anteriorly and the fourth epibranchial dorsoposteriorly.

A

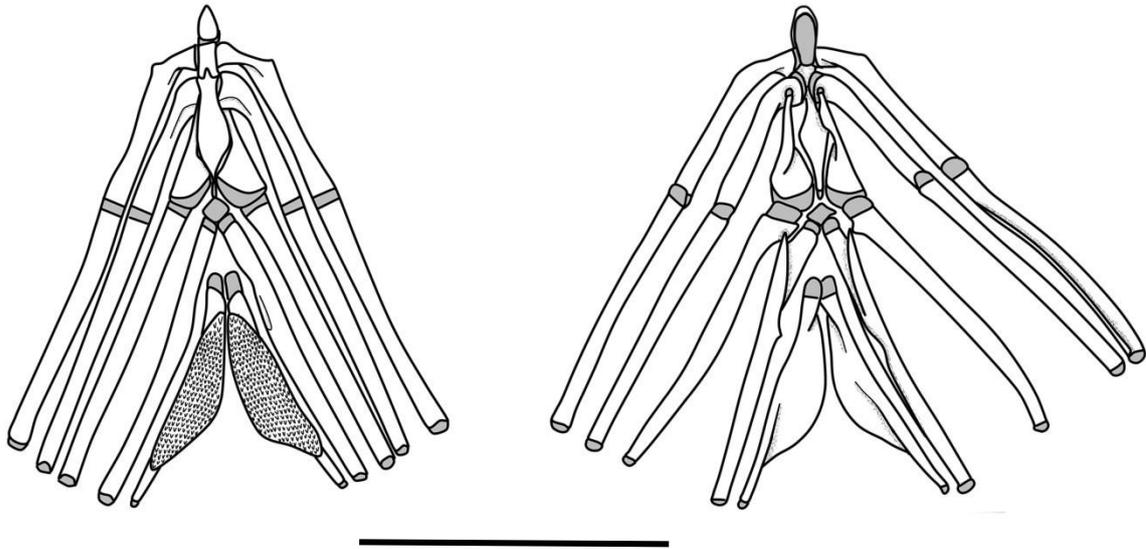


B

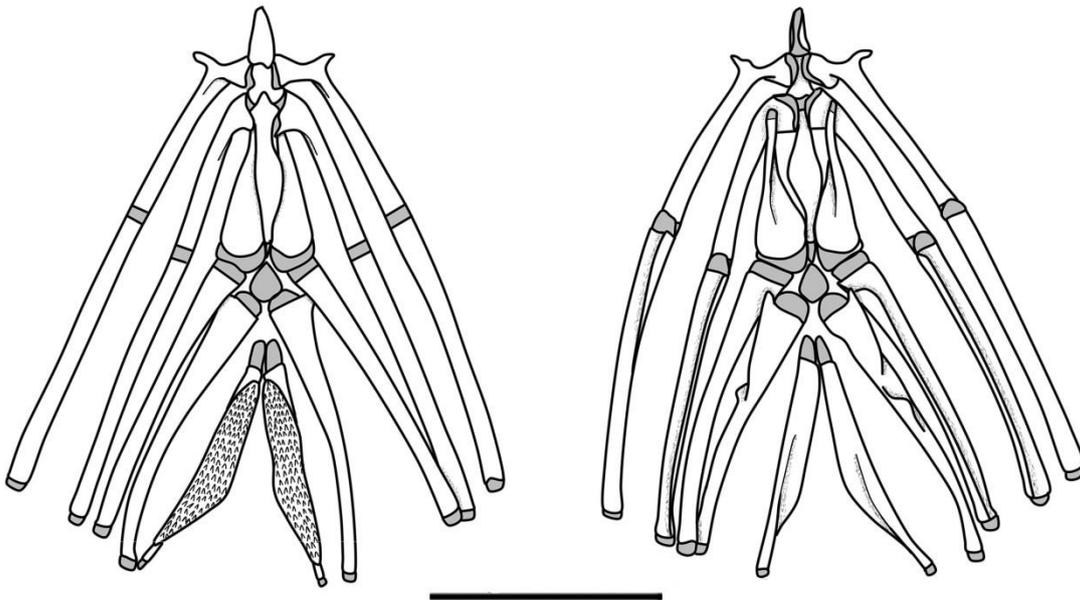


**Fig. 19.** Dorsal (left) and ventral (right) views of lower branchial arches. A, *Polydactylus sextarius*; B, *Leptomelanosoma indicum*. Bars indicate 10 mm.

**A**

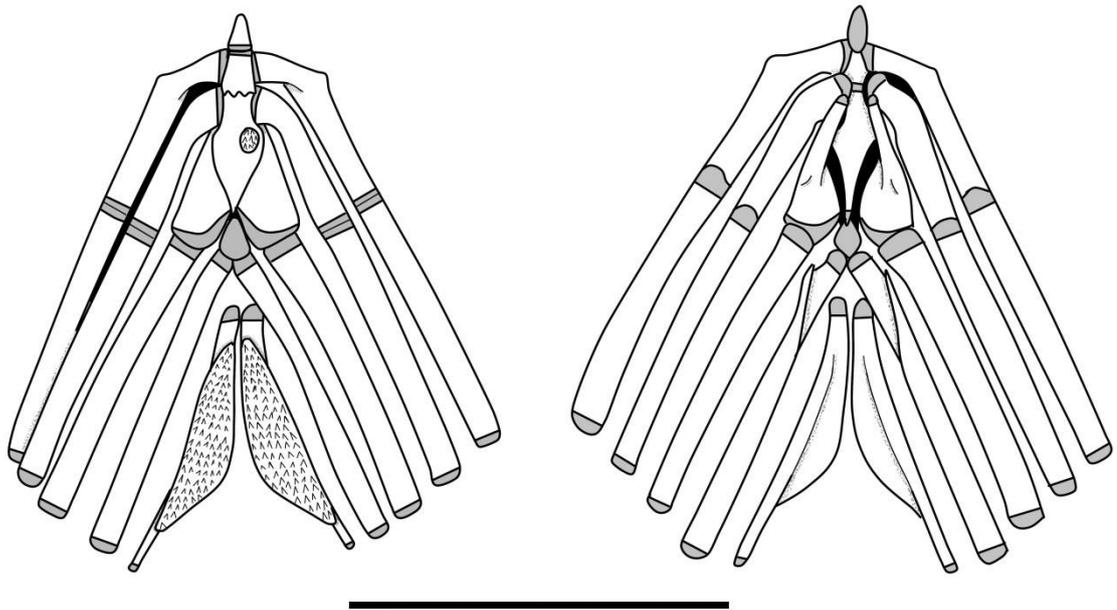


**B**

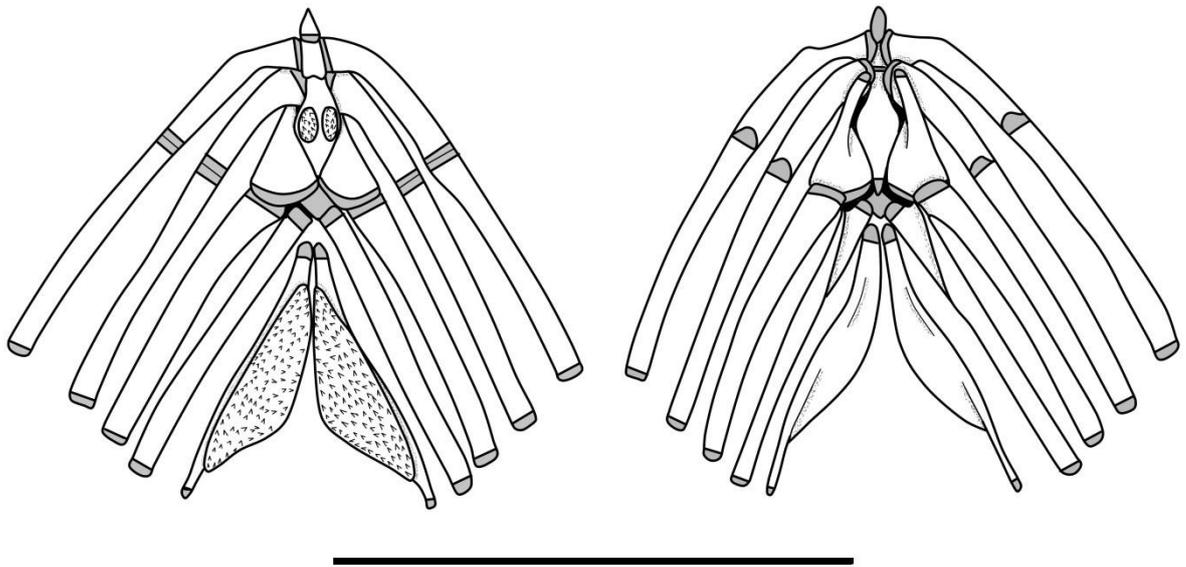


**Fig. 20.** Dorsal (left) and ventral (right) views of lower branchial arches. A, *Polynemus paradiseus*; B, *Pentanemus quinquarius*. Bars indicate 10 mm.

A

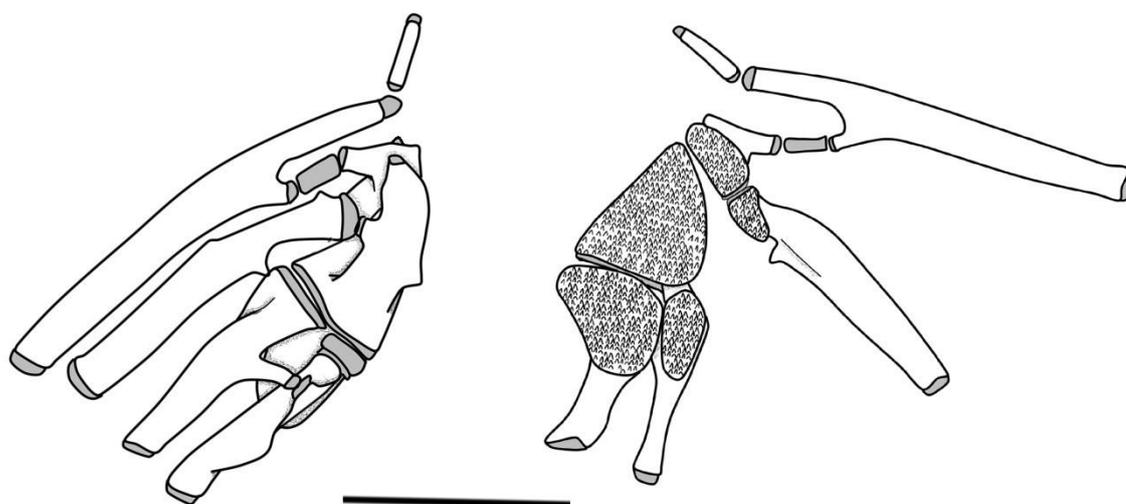


B

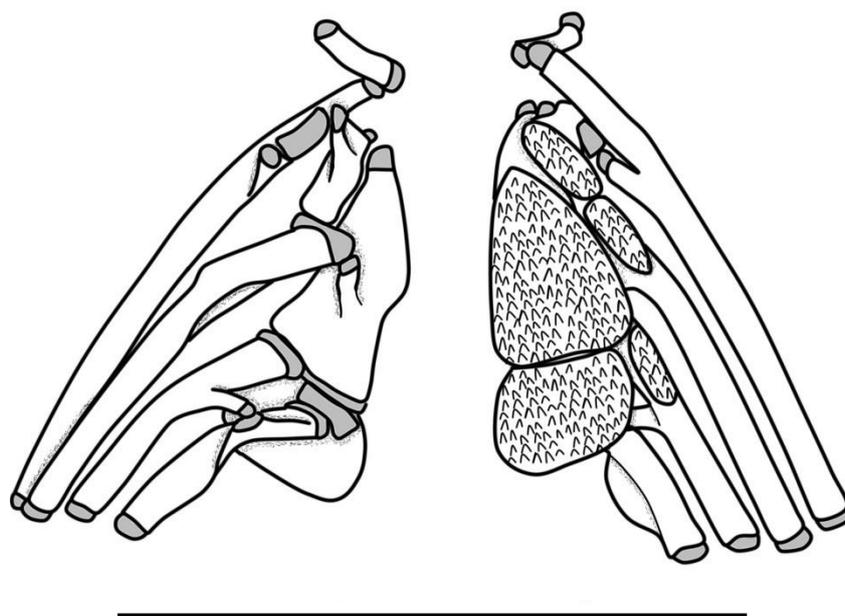


**Fig. 21.** Dorsal (left) and ventral (right) views of lower branchial arches. A, *Polynemus aquilonaris*; B, *Polynemus multifilis*. Bars indicate 10 mm.

**A**

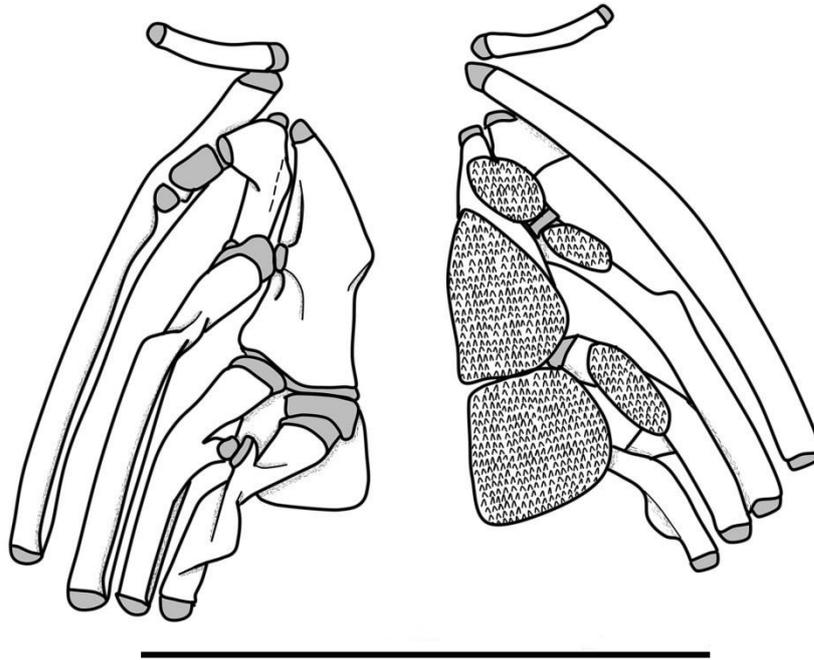


**B**

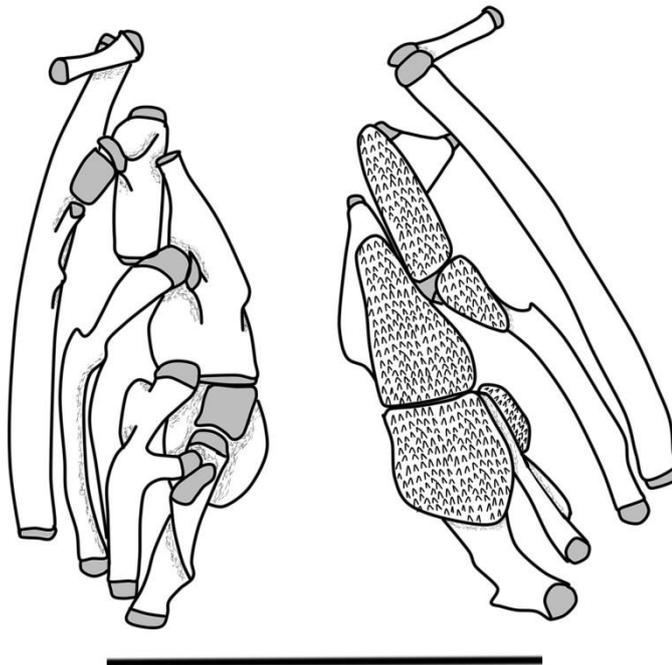


**Fig. 22.** Dorsal (left) and ventral (right) views of upper branchial arches. (A) *Polydactylus sextarius*; (B) *Leptomelanosoma indicum*. Bars indicate 10 mm.

A



B



**Fig. 23.** Dorsal (left) and ventral (right) views of upper branchial arches. A, *Polynemus paradiseus*; B, *Pentanemus quinquarius*. Bars indicate 10 mm.

## Character recognition

**TS 32. Tooth plates on dorsal surface of third basibranchial.** 0: absent; 1: one present; 2: two present (ordered as 0-1-2).

The third basibranchial bears one tooth plate on its dorsal surface in *Polynemus aquilonaris* (character 32-1) (Fig. 21A), and two in *Polynemus melanochir melanochir* and *Polynemus multifilis* (character 32-2) (Fig. 21B), while it lacks tooth plates in other polynemids (character 32-0) (Figs. 18–20). The tooth place on the dorsal surface of the third basibranchial is absent in Sciaenidae (character 32-0) (e.g., Kim and Kim, 1965; Sasaki, 1989; this study). Due to the lack of branchial arches of *Polydactylus opercularis*, the condition of it is coded as “?”.

**TS 33. Anteriorly-pointed projection on first hypobranchial.** 0: extremely small; 1: large.

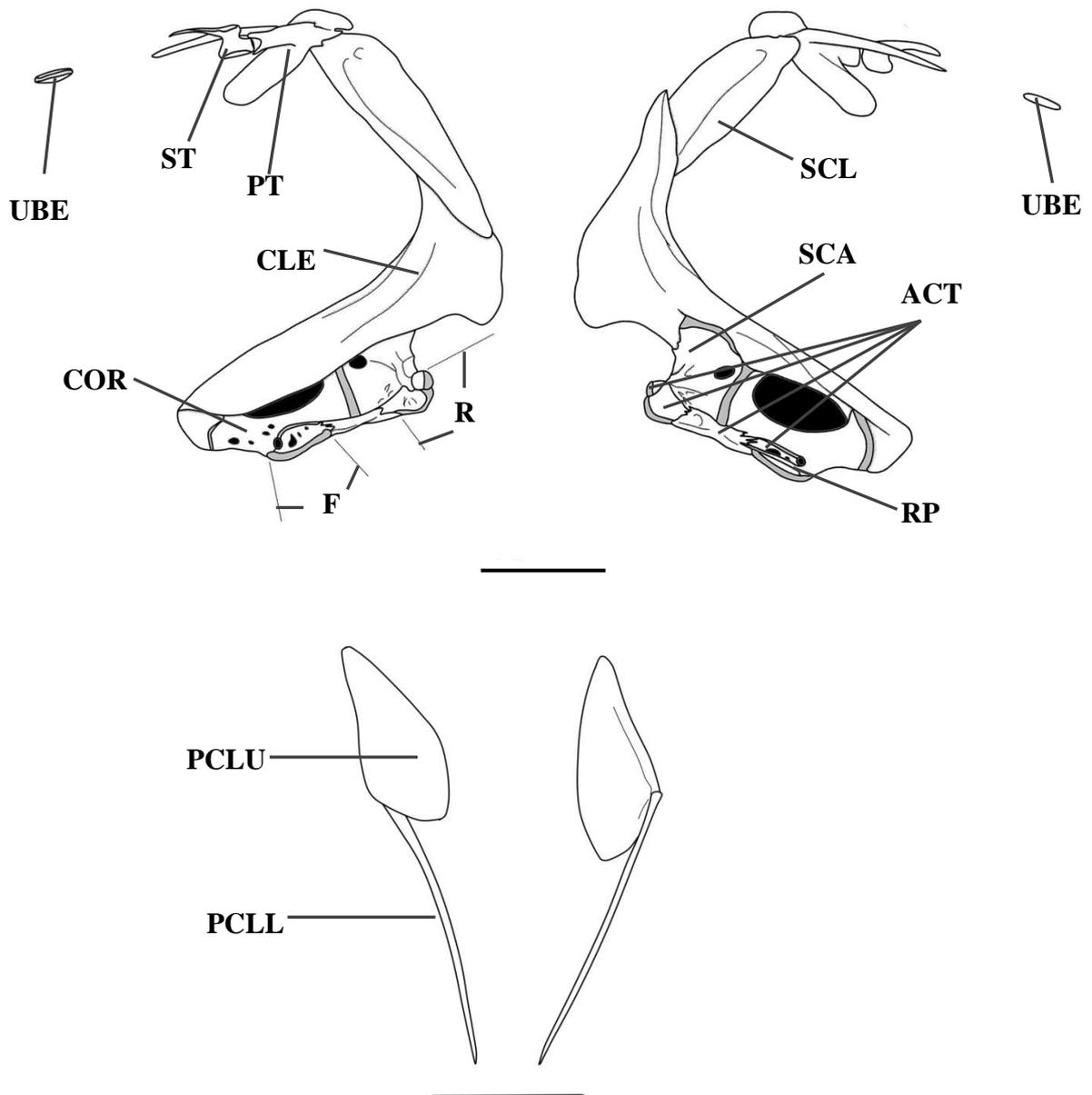
The first hypobranchial has an anteriorly-pointed projection laterally. This projection is extremely small in polynemids (character 33-0) (Figs. 18–19, 20A, 21), except for *Filimanus* and *Pentanemus quinquarius*, in which it is large (character 33-1) (Fig. 20B). Both conditions are present in sciaenids (e.g., extremely small in *Argyrosomus japonicas* and *Pennahia argentata*, and large in *Pentheroscion mbizi* and *Macrodon ancylodon*) (characters 33-0 and 33-1) (e.g., Green, 1941; Sasaki, 1989; this study). Due to the lack of branchial arches of *Polydactylus opercularis*, the condition of it is coded as “?”.

**TS 34. Anterior and dorsolateral cartilages on second pharyngobranchial.** 0: autogenous; 1: fused.

The second pharyngobranchial has three cartilaginous caps on anterior, dorsolateral and posterior tips, respectively, and the anterior cartilage is autogenous from the dorsolateral one in polynemids (character 34-0) (Figs. 19–21), except for *Eleutheronema rhadinum* and *Polydactylus sexfilis*, in which the anterior and dorsolateral cartilaginous caps are fused with each other (character 34-1) (Fig. 18). The anterior cartilage is present and autogenous from the dorsolateral one in sciaenids (character 34-0) (e.g., Sasaki, 1989; this study). Due to the lack of branchial arches of *Polydactylus opercularis*, the condition of it is coded as “?”.

## 1-7 Pectoral girdle (Figs. 24–28)

**Description.** The pectoral girdle is comprised of the supratemporal, posttemporal, supracleithrum, cleithrum, scapula, coracoid, actinosts and postcleithra. An unidentified bony element is also present in polynemids.



**Fig. 24.** Lateral (left, upper) and medial (right, upper) views of pectoral girdle, and lateral (left, lower) and medial (right, lower) views of postcleithra in *Eleutheronema rhadinum*. ACT, actinost; CLE, cleithrum; COR, coracoid; F, attachment site for lower filament-like rays; PCLU, upper postcleithrum; PCLL, lower postcleithrum; PT, posttemporal; R, attachment site for upper pectoral fin rays; RP, rod-like process; SCA, scapula; SCL, supracleithrum; ST, supratemporal; UBE, unidentified bony element. Bars indicate 10 mm.

The supratemporal (= extrascapulae, *sensu* Sasaki, 1989), situated on the posterodorsal region of the head, is a single forked tubular bone supporting the temporal sensory canal and loosely attached with the pterotic anteroventrally and the posttemporal posteriorly. The supratemporal is pipe-shaped and has one posterior, one lower and one upper pores for the sensory canal. This bone supports a sensory canal continuous with those of the posttemporal posteriorly and the pterotic anteriorly, and that of the dorsal surface of the head.

The posttemporal, situated between the supratemporal and supracleithrum, bears the dorsal and ventral limbs for the connection with the cranium. The anterior portion of the dorsal limb is firmly connected with the epiotic by a strong and thick ligament anteroventrally. The ventral limb is firmly attached with the intercalar by a short ligament ventrally. The posttemporal is connected with the supracleithrum posteromedially. The posterodorsal part of the posttemporal is a thin and semi-circular sheet. A tubular structure is present on the lateral surface of the posttemporal for the sensory canal continuous with those of the supracleithrum posteriorly and the supratemporal anteriorly.

The supracleithrum, a thick wedge-shaped bone, interconnects the posttemporal dorsolaterally and cleithrum ventromedially. The lateral line system runs through the dorsal portion of the supracleithrum. This bone is connected with the Baudelot's ligament medially.

The cleithrum is an L-shaped and the largest bone in the pectoral girdle, suspending the postcleithra posteromedially and bearing the dorsal and ventral limbs which form an obtuse angle. The dorsal limb is connected with the

supracleithrum dorsolaterally. It is weakly developed in *Parapolyneumus verekeri* and *Polyneumus*, while it is well developed in other polynemids. The ventral limb medially possesses a slender process which is connected with the scapula posterodorsally via a narrow cartilaginous band and the coracoid posteroventrally. A ventral process on the anteroventral tip of the ventral limb of the cleithrum extends posteroventrally and is attached with the ventral margin of the coracoid by a narrow cartilaginous band. A large space is present between the two connections of the cleithrum and coracoid. The ventral limb laterally bears a flange, forming a pocket receiving the lateral pectoral fin muscles. The flange extends posteriorly and is well developed in most polynemids, whereas it is weakly developed in *Parapolyneumus verekeri* and *Polyneumus*.

The scapula is a rectangular bone, containing the scapula foramen anteroventrally. It is connected with the cleithrum anteriorly and the coracoid ventrally via a narrow cartilaginous band. The scapula articulates with the first actinost, and is attached with the second and firmly connected with the dorsal half of the third actinost posteriorly.

The coracoid is a U-shaped bone situated on the ventroposterior region of the pectoral girdle. It has a dorsal process connected with the scapula dorsally and the cleithrum anteriorly, and a ventral process broadly attached with the cleithrum anteroventrally. The coracoid is sutured with the ventral half of the third actinost dorsoposteriorly and attached with the fourth actinost posteriorly via a narrow cartilaginous band. A rod-like process is present on the posterior margin of the coracoid, adjoining the ventral margin of the fourth actinost. The

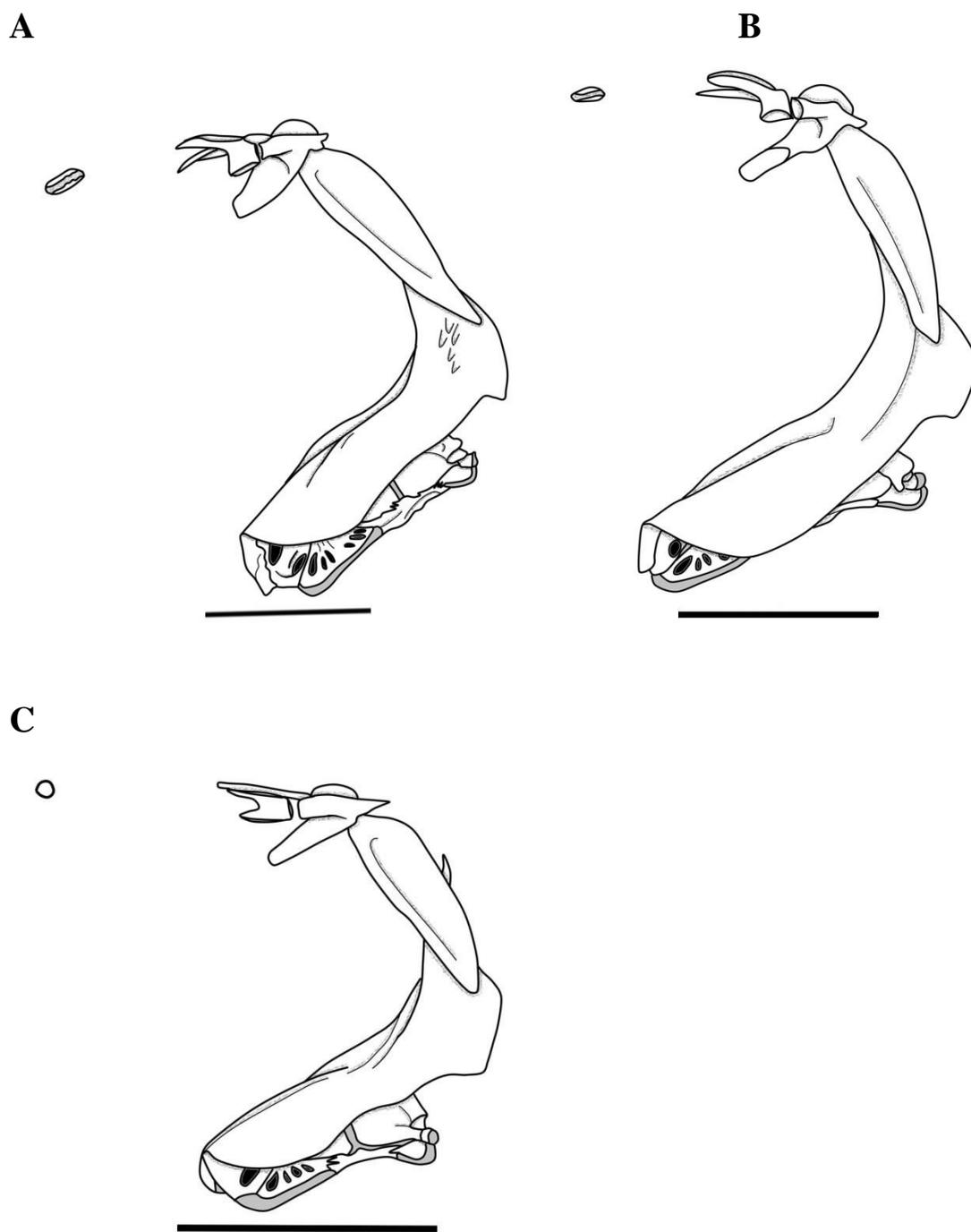
process is robust and long in *Parapolynemus verekeri*, *Pentanemus quinquarius* and *Polynemus*, whereas it is slender and short in other polynemids. The tip of this process is covered with a ligament.

The actinosts are comprised of four bones, serially arranged from small (upper) to large (lower), firmly attached with each other. The first actinost is the smallest one articulating with the scapula anteriorly. The second actinost is attached with the first actinost dorsally and the scapula anteriorly. These two actinosts supports the upper pectoral-fin rays posteriorly. The third actinost sutured with the second actinost dorsally, the fourth actinost ventrally, the scapula anterodorsally and the coracoid anteroventrally. It well extends ventrally and is equal to or longer than the fourth actinost in polynemids, except for *Polydactylus opercularis*, *Parapolynemus verekeri*, *Pentanemus quinquarius* and *Polynemus*, in which it weakly extends ventrally and is shorter than the fourth actinost. The third actinost does not support rays or filament-like rays. The fourth actinost is a fan-shaped bone supporting the lower filament-like rays posteriorly, sutured with the third actinost dorsally and attached with the coracoid anteriorly. This bone extends ventrally to the ventral margin of the coracoid in most polynemids, whereas it extends ventrally to the middle portion of the coracoid in *Parapolynemus verekeri*.

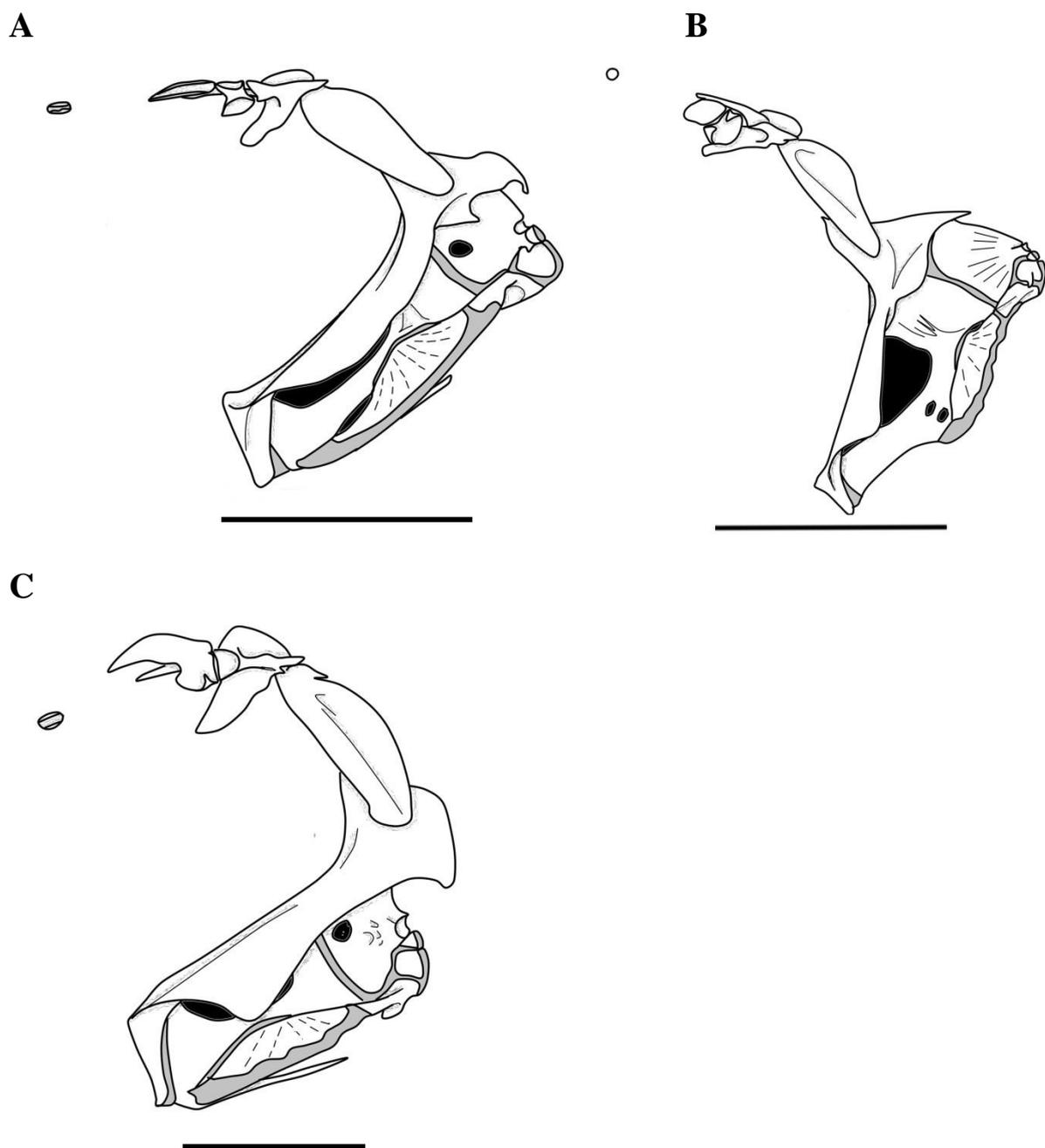
The postcleithra includes two bones: the leaf-like upper and rod-like lower elements in polynemids. These bones are situated on the posterior region of the pectoral girdle. The upper postcleithra is connected with the posterior process of the cleithrum dorsolaterally. It is attached with the lower postcleithrum medially

in polynemids, except for *Parapolynemus verekeri*, *Filimanus xanthonema*, *Pentanemus quinquarius*, *Polynemus multifilis*, *Polynemus aquilonaris* and *Polynemus paradiseus*, in which the fomer is attached with the latter posteriorly, and *Polynemus melanochir melanochir*, in which the former is fused with the latter. In *Polydactylus sextarius*, the lower postcleithra is divided into two parts in a specimen (HUMZ 33443), while such a division is absent in another specimen (USNM 278227).

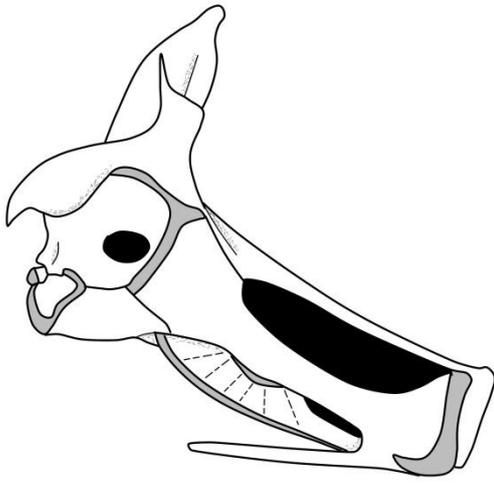
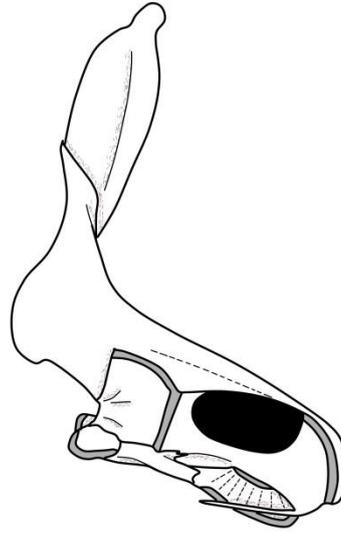
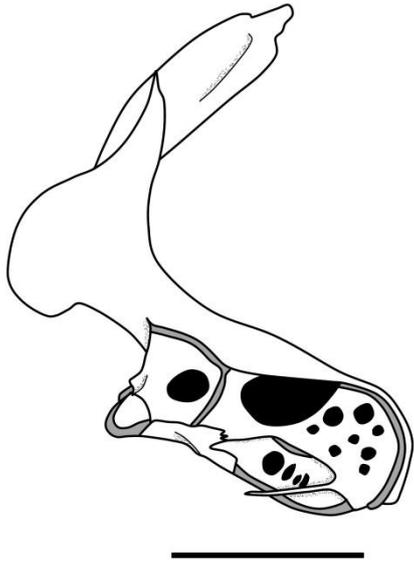
One unidentified bony element is present on the dorsal surface of the head. This bony element is a long elliptical bone with a tubular structure continuous with that of the supratemploral via a long skinny sensory canal from the supratemploral in polynemids, except for *Parapolynemus verekeri* and *Leptomelanosoma indicum*, in which it is a round bone, and *Polydactylus nigripinnis*, in which it is a cartilaginous element, also having the long skinny sensory canal. The skinny sensory canal extends anteriorly from the unidentified bony element, and those on both sides meet medially and run anteriorly in parallel.



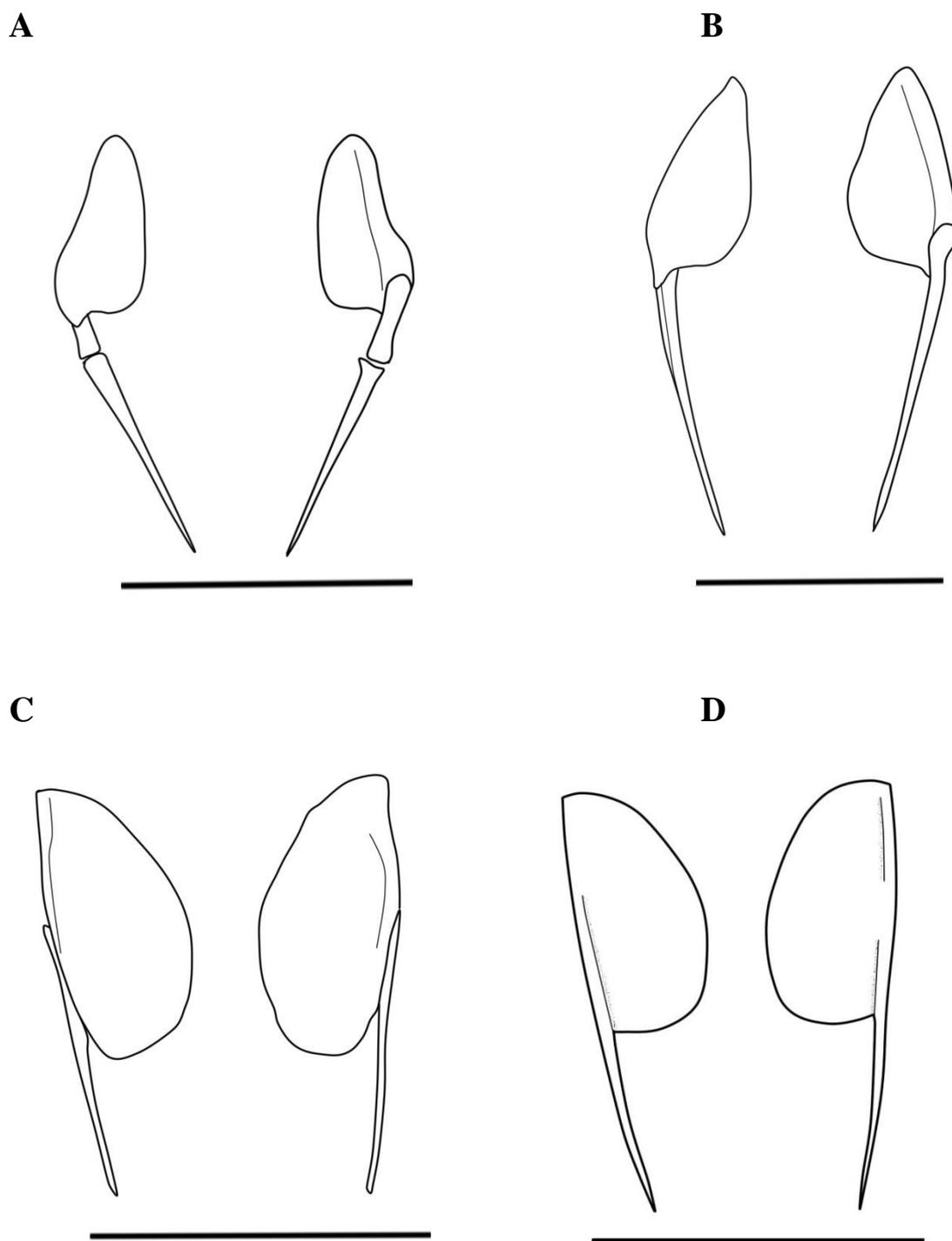
**Fig. 25.** Lateral view of pectoral girdle. A, *Polydactylus virginicus*; B, *Galeoides decadactylus*; C, *Leptomelanosoma indicum*. Bars indicate 10 mm.



**Fig. 26.** Lateral view of pectoral girdle. A, *Polynemus paradiseus*; B, *Parapolyneumus verekeri*; C, *Pentanemus quinquarius*. Bars indicate 10 mm.

**A****B****C**

**Fig. 27.** Medial view of pectoral girdle after remove posttemporal and supratemporal. A, *Polynemus multifilis*; B, *Filimanus sealei*; C, *Polydactylus nigripinnis*. Bars indicate 10 mm.



**Fig. 28.** Lateral (left, lower) and medial (right, lower) views of postcleithra. A, *Polydactylus sextarius*; B, *Galeoides decadactylus*; C, *Polynemus paradiseus*; D, *Polynemus melanochir melanochir*. Bars indicate 10 mm.

## Character recognition

**TS 35. Dorsal limb of cleithrum.** 0: well developed; 1: weakly developed.

The dorsal limb of the cleithrum is weakly developed in *Parapolynemus verekeri* and *Polynemus* (character 35-1) (Fig. 27A), while it is well developed in other polynemids (character 35-0) (Fig. 27B–C). The dorsal limb of the cleithrum is well developed in sciaenids (character 35-0) (e.g., Green, 1941; Sasaki, 1989; this study).

**TS 36. Flange on cleithrum.** 0: weakly developed; 1: well developed.

The flange on the ventral limb of cleithrum extends posteriorly and is well developed in most polynemids (character 36-1) (Figs. 24–25, 26C), whereas it is weakly developed in *Parapolynemus verekeri* and *Polynemus* (character 36-0) (Fig. 26A–B). In sciaenids, this structure is absent or weakly developed (character 36-0) (e.g., Kim and Kim, 1965; Sasaki, 1989; this study).

**TS 37. Rod-like process.** 0: slender and short; 1: robust and long.

A rod-like process is present on the posterior margin of the coracoid. It is robust and long in *Parapolynemus verekeri*, *Pentanemus quinquarius* and *Polynemus* (character 37-1) (Figs. 27A), whereas it is slender and short in other polynemids (character 37-0) (Figs. 24, 27B–C). Because sciaenids lack this rod-like process on the coracoid, the outgroup is coded as “?”.

**TS 38. Third actinost.** 0: shorter than fourth actinost; 1: equal to or longer than fourth actinost.

The third actinost well extends ventrally and is equal to or longer than the fourth actinost in polynemids (character 38-1) (Figs. 24–25, 27B–C), except for *Polydactylus opercularis*, *Parapolynemus verekeri*, *Pentanemus quinquarius* and *Polynemus*, in which it weakly extends ventrally and is shorter than the fourth actinost (character 38-0) (Fig. 26, 27A). The third actinost is shorter than the fourth actinost in sciaenids (character 38-0) (e.g., Sasaki, 1989; this study).

**TS 39. Relation of upper and lower postcleithra.** 0: former attached with latter medially; 1: former attached with latter posteriorly; 2: fused.  
(unordered)

The upper postcleithra is attached with the lower postcleithra medially in polynemids (character 39-0) (Figs. 24, 28A–B), except for *Parapolynemus verekeri*, *Filimanus xanthonema*, *Pentanemus quinquarius*, *Polynemus multifilis*, *Polynemus aquilonaris* and *Polynemus paradiseus*, in which the former is attached with the latter posteriorly (character 39-1) (Fig. 28C), and *Polynemus melanochir melanochir*, in which the former is fused with the latter (character 39-2) (Fig. 28D). In sciaenids, the former is attached with the latter medially (character 39-0) (e.g., Kim and Kim, 1965; Sasaki, 1989; this study).

**TS 40. Structure of unidentified bony element.** 0: long elliptical bone with tubular structure; 1: round bone with tubular structure; 2: cartilaginous.  
(unordered)

This bony element is a long elliptical bone with a tubular structure continuous with that of the supratemploral via a long skinny sensory canal in polynemids (character 40-0) (Figs. 24, 25A–B, 26A, C), except for

*Parapolyneumus verekeri* and *Leptomelanosoma indicum*, in which it is a round bone with a tubular structure (character 40-1) (Figs. 25C, 26B), and *Polydactylus nigripinnis*, in which it is a cartilaginous element, also having the long skinny sensory canal (character 40-2). This bony element is absent in sciaenids (e.g., Sasaki, 1989; this study), therefore the outgroup is coded as “?”.

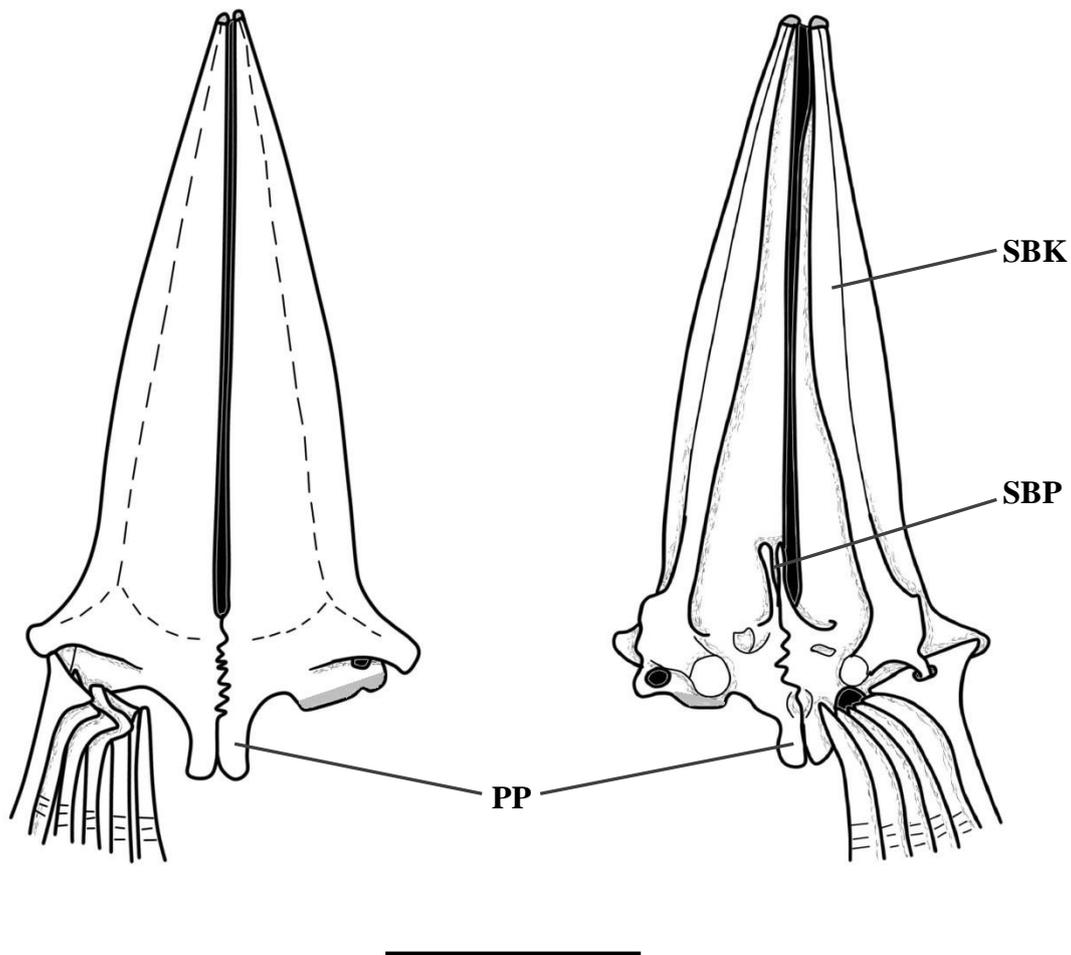
### **Other variations**

**Fourth actinost extending ventrally to middle of coracoid.** The fourth actinost extends ventrally to the ventral margin of the coracoid in most polynemids, whereas it extends ventrally to the middle portion of the coracoid only in *Parapolyneumus verekeri*. The fourth actinost does not extend or weakly extends ventrally to the dorsal margin of the coracoid in sciaenids (e.g., Sasaki, 1989; this study). Therefore the latter character is an autapomorphy for the species.

**Division of lower postcleithra.** In *Polydactylus sextarius*, the lower postcleithra is divided into two parts in a specimen (HUMZ 33443) (Fig. 28A), while such a division is absent in another specimen (USNM 278227). In other polynemids and sciaenids, the element is not divided into any parts, as well as typical percoids (e.g., Tominaga, 1968; Fraser, 1972; Sasaki, 1989; this study). This study regards that the division is an abnormal condition of the specimen.

## 1-8 Pelvic girdle (Figs. 29–30)

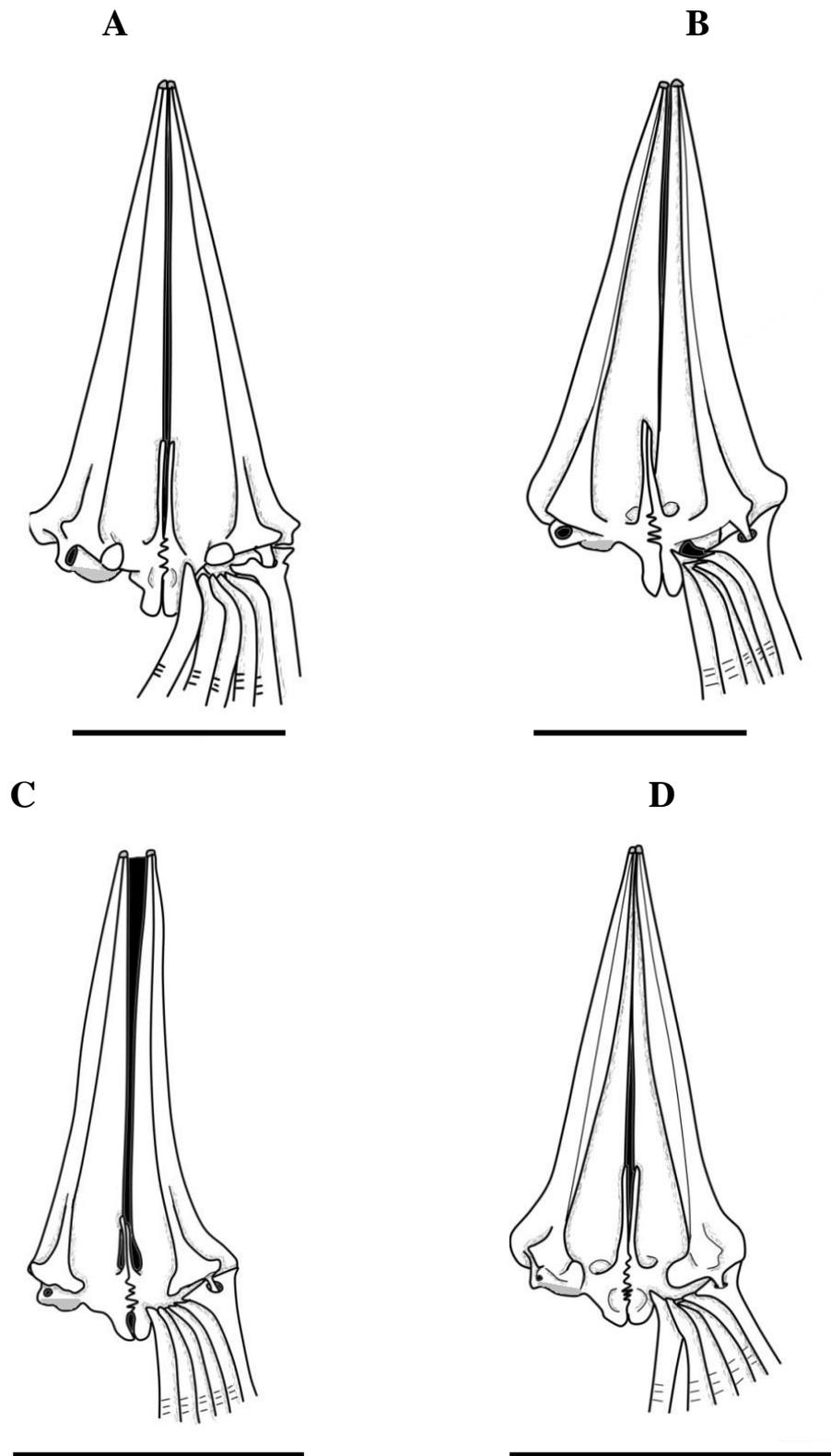
**Description.** The pelvic girdle consists of a pair of elongated triangular pelvic bones, situated posteroventral to the pectoral girdle. It bears a pair of pelvic fins posteriorly.



**Fig. 29.** Dorsal (left) and ventral (right) views of pelvic fin in *Polynemus paradiseus*. PP, postpelvic process; SBK, subpelvic keel; SBP, subpelvic process. Bar indicates 5 mm.

The pelvic bone has a small cartilaginous cap anteriorly and possesses a very thin cartilaginous pad, supporting the pelvic fin rays posteriorly. A small penetrated pore, interlocked with the ring-like structure of the pelvic spine, is present on the posterolateral corner of the pelvic bone. The pelvic bone forms

the subpelvic keel, and subpelvic and postpelvic processes. An accessory subpelvic keel is absent. The subpelvic keel is situated on the ventral margin of the pelvic bone and extends medially. This process is well developed in *Polydactylus opercularis*, *Galeoides decadactylus*, *Leptomelanosoma indicum*, *Filimanus*, *Polynemus* and *Parapolynemus verekeri*, whereas it is weakly developed or absent in other polynemids. The subpelvic process is well developed and slender, and situated on the posteromedial portion of the pelvic bone. The postpelvic process is situated on the posterior end of this bone.



**Fig. 30.** Ventral view of pelvic fin. A, *Polydactylus approximans*; B, *Eleutheronema rhadinum*; C, *Pentanemus quinquarius*; D, *Filimanus similis*. Bars indicate 10 mm.

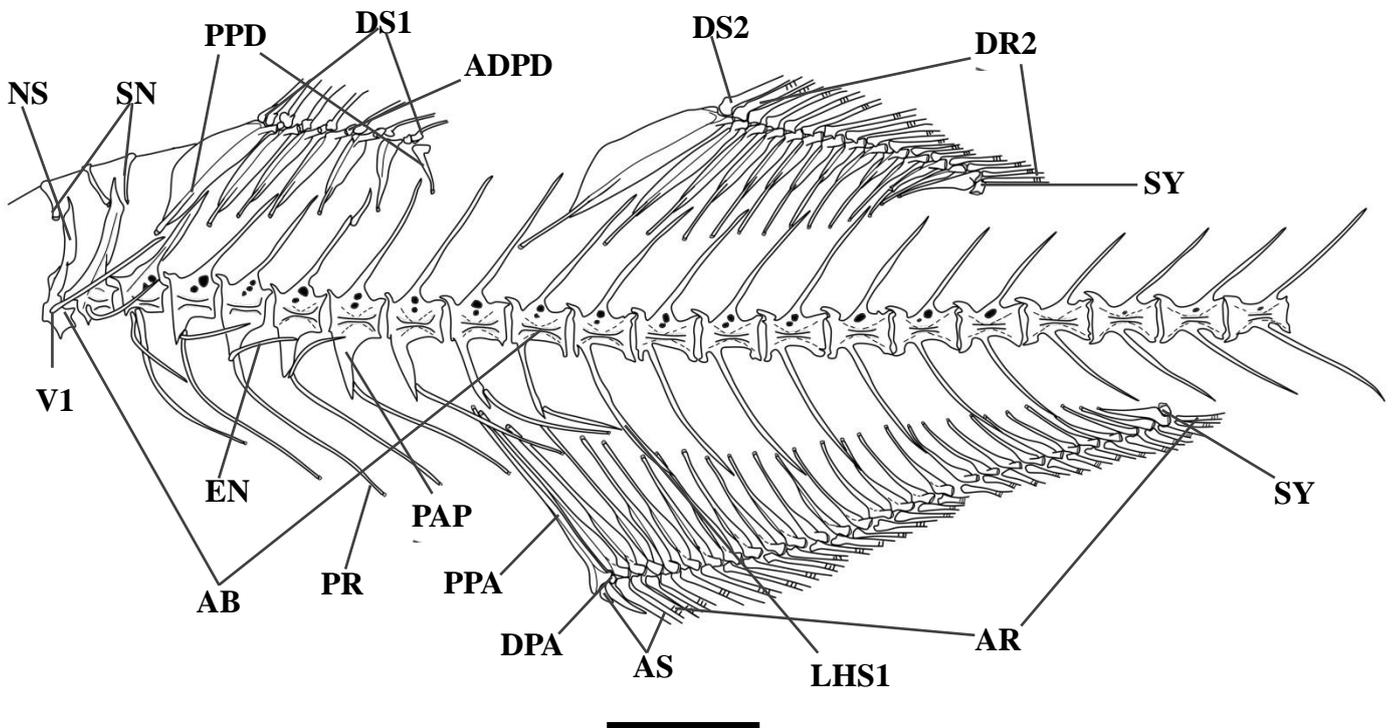
## Character recognition

**TS 41. Subpelvic keel.** 0: well developed; 1: weakly developed or absent.

The subpelvic process is well developed in *Polydactylus opercularis*, *Galeoides decadactylus*, *Leptomelanosoma indicum*, *Filimanus*, *Polynemus* and *Parapolynemus verekeri* (character 41-0) (Figs. 29, 30D), whereas it is weakly developed or absent in other polynemids (character 41-1) (Fig. 30A–C). The subpelvic process is well developed in sciaenids (character 41-0) (e.g., Sasaki, 1989; this study).

## 1-9 Axial skeleton and median fin supports (Figs. 31–35)

**Description.** The axial skeleton is consisted of the vertebrae, epineurals and pleural ribs. The median fins include the first and second dorsal, and anal fins having spines and soft rays, and supported by proximal and distal pterygiophores, and stay. The supraneurals are present, while the medial pterygiophores are absent.



**Fig. 31.** Abdominal and caudal vertebrae and associated bones in *Pentanemus quinquarius*. AB, abdominal vertebrae; ADPD, anterior distal pterygiophore of dorsal fin; AS, anal spine of anal fin; AR, anal soft rays of anal fin; DPA, distal pterygiophore of anal fin; DS1, dorsal spine of first dorsal fin; DS2, dorsal spine of second dorsal fin; DR2, dorsal soft rays of second dorsal fin; EN, epineural; LHS1, first long hemal spine; NS, neural spine; PAP, parapophysis; PPA, proximal pterygiophore of anal fin; PPD, proximal pterygiophore of dorsal fin; PR, pleural rib; SN, supraneural; SY, stay; V1, first vertebra. Bar indicates 10 mm.

Axial skeleton.—The vertebrae are situated on the midline of the body, comprised of two (abdominal and caudal) elements. The number of the abdominal vertebrae is ten. They possess the neural arches and neural spines

dorsally. The abdominal vertebrae, except for anterior two elements, possess a pair of parapophyses ventrolaterally supporting pleural ribs posteriorly. The parapophysis progressively becomes longer posteriorly. The first abdominal vertebra articulates with the exoccipitals on both sides anterodorsally and the basioccipital anteroventrally. A ligament bonds the prezygapophysis of the second vertebra with the posterior portion of the first vertebra. The caudal vertebrae are situated posterior to the abdominal vertebrae, possessing neural spines and neural arches dorsally, and hemal spines and hemal arches ventrally. The number of the caudal vertebrae is fourteen in polynemids, except for *Polynemus* and *Eleutheronema*, in which it is fifteen.

The epineurals, paired slender rod-like bones, are 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 number of the epineurals is various in polynemids (for example, six in *Galeoides decadactylus*, *Polydactylus sextarius*, *Pentanemus quinquarius* and *Filimanus*, seven in *Polydactylus approximans*, *Polydactylus virginicus*, *Polydactylus plebeius*, *Polydactylus sexfilis*, *Polydactylus macrochir*, *Parapolynemus verekeri* and *Eleutheronema*, eight in *Leptomelanosoma indicum* and *Polydactylus opercularis*).

The pleural ribs are paired slender rod-like bones, attached with the dorsolateral portions of the parapophyses of the third to tenth abdominal vertebrae and situated under the epineurals when the epineurals are present. The number of pleural ribs is eight.

Median fin support.—The proximal pterygiophores of the dorsal and anal fins are leaf-like bones supporting the dorsal and anal fin rays, respectively. The proximal pterygiophores are inserted into the intersapce between neural and hemal spines. The first proximal pterygiophores of the first dorsal and anal fins bear two spines (one very short and one long), respectively, in most polynemids, whereas they bear a single long spine on each one and the first spines are absent in *Polynemus paradiseus*. Therefore the proximal pterygiophores of the first dorsal fin support eight spines, and the proximal pterygiophores of the anal fin support three spines in most polynemids, whereas they support seven and two, respectively, in *Polynemus paradiseus*.

The number of the proximal pterygiophores of the first dorsal fin is seven. The first proximal pterygiophore of the first dorsal fin is inserted between the second and third neural spines in polynemids, except for *Parapolynemus verekeri*, in which it is inserted between the third and fourth neural spines. The second proximal pterygiophore of the first dorsal fin is inserted between the third and fourth neural spines. The third proximal pterygiophore of the first dorsal fin is inserted between the third and fourth neural spines in polynemids, except for *Polydactylus nigripinnis*, *Polynemus melanochir melanochir*, *Polynemus aquilonaris*, *Polynemus paradiseus* and *Parapolynemus verekeri*, in which it is inserted between the fourth and fifth neural spines. The fourth proximal pterygiophore of the first dorsal fin is inserted between the fourth and fifth neural spines in polynemids, except for *Parapolynemus verekeri*, in which it is inserted between the fifth and sixth neural spines. The fifth proximal

pterygiophore of the first dorsal fin is inserted between the fifth and sixth neural spines. The sixth proximal pterygiophore of the first dorsal fin is inserted between the sixth and seventh neural spines in polynemids, except for *Eleutheronema*, in which it is inserted between the fifth and sixth neural spines. The seventh proximal pterygiophore of the first dorsal fin is inserted between the seventh and eighth neural spines in polynemids, except for *Leptomelanosoma indicum*, *Polydactylus sexfilis* and *Eleutheronema*, in which it is inserted between the fifth and sixth neural spines.

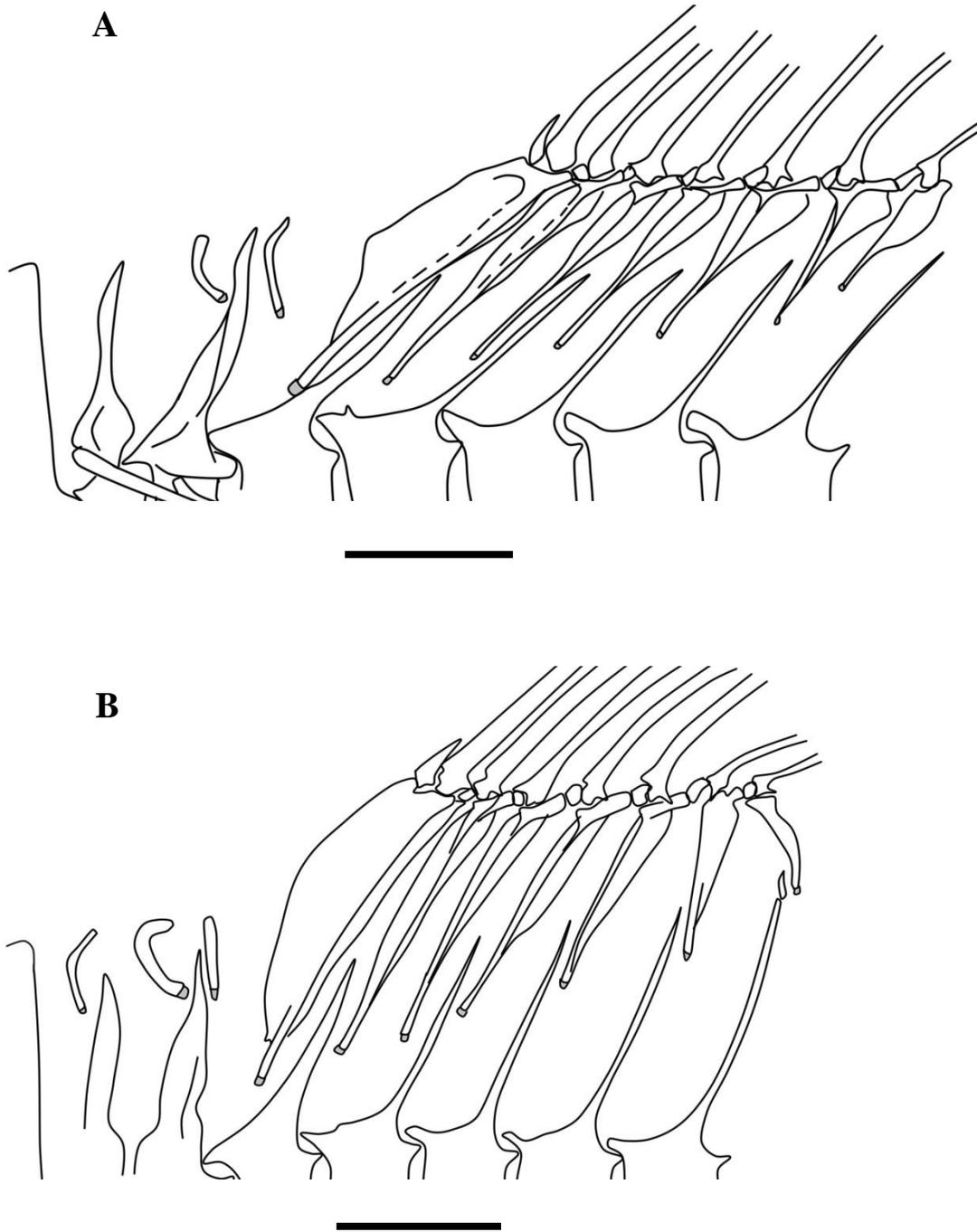
The number of the proximal pterygiophores of the second dorsal fin is 11 to 14. They are widely separated from the proximal pterygiophores of the first dorsal fin anteriorly and support one spine and 12 to 15 soft rays.

One anteriormost proximal pterygiophore of the anal fin is situated anterior to the first long hemal spine in most polynemids, two in *Parapolynemus verekeri* and seven in *Pentanemus quinquarius*. The number of the anal proximal pterygiophores is 10 to 15 in polynemids, except for *Pentanemus quinquarius*, in which it is 27.

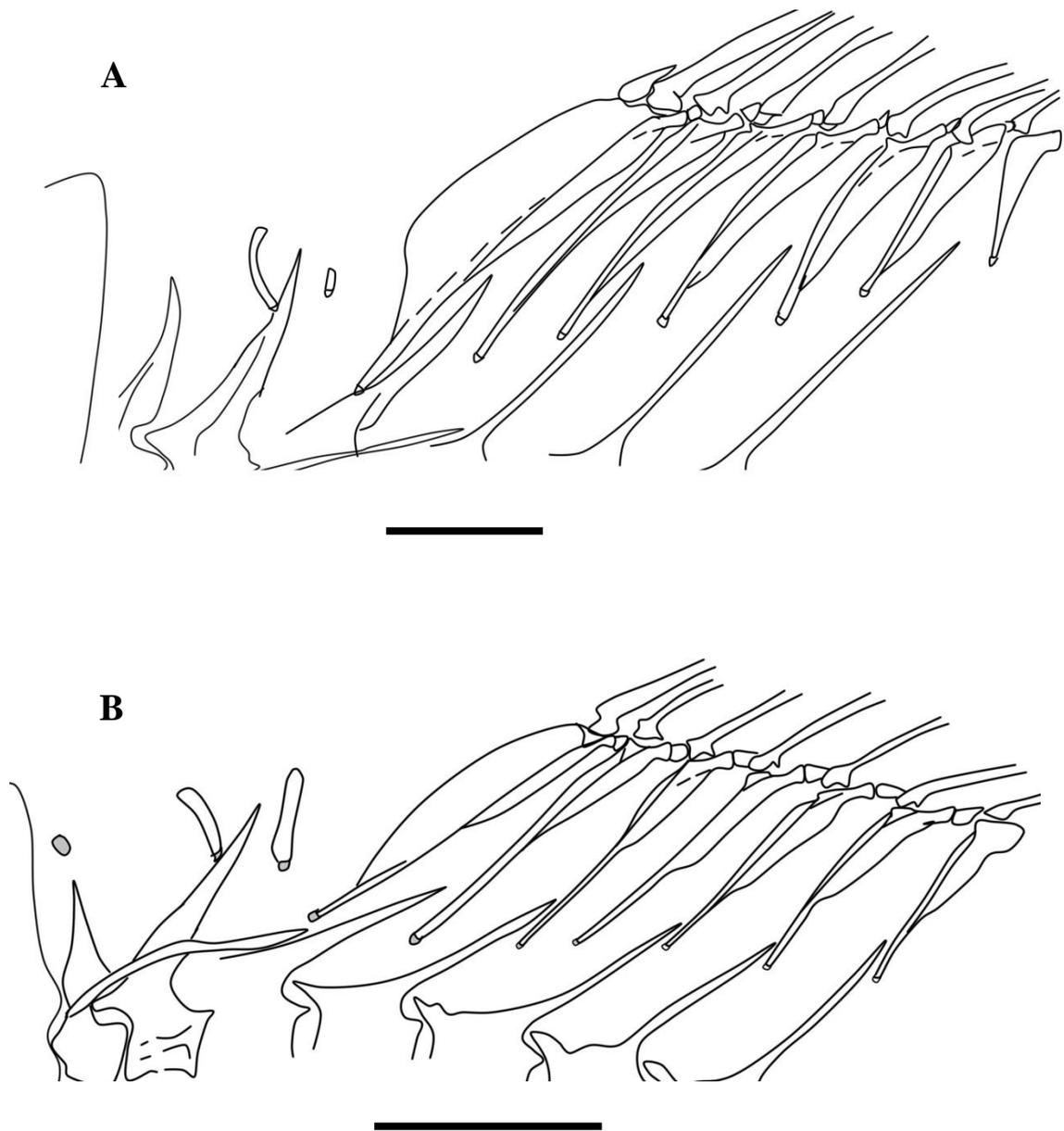
The distal pterygiophores are small bony elements, located on the posterior tips of the proximal pterygiophores, except for the last second dorsal and anal proximal pterygiophores lacking them. These bones supporting the spines are unpaired, while those supporting soft rays are paired.

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

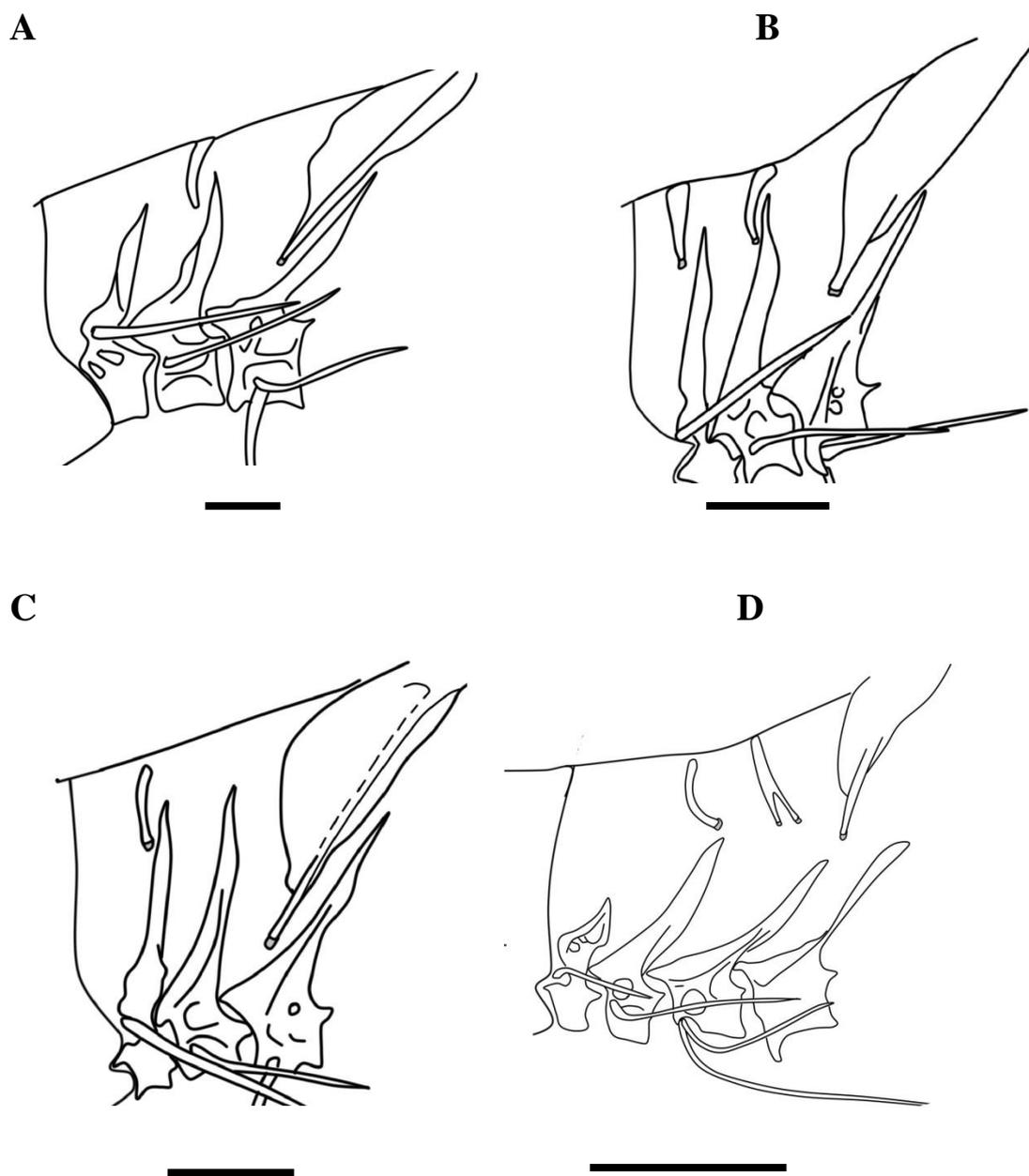
The supraneurals are rod-like bones, situated anterior to the first proximal pterygiophore of the first dorsal fin. The number of the bone is three in most polynemids. The first supraneural is inserted between the neurocranium and the first neural spine. The first supraneural is ossified in polynemids, except for *Polynemus paradiseus*, in which it is cartilaginous, and *Eleutheronema*, *Leptomelanosoma indicum*, *Polydactylus opercularis*, *Polydactylus octonemus*, *Polydactylus oligodon*, *Polynemus melanochir melanochir*, *Polynemus multifilis*, *Polynemus aquilonaris* and *Parapolynemus verekeri* lacking it. The second supraneural is inserted between the first and second neural spines in polynemids, except for *Galeoides decadactylus*, in which it is absent. The third supraneural is inserted between the second neural spine and the first proximal pterygiophore of the first dorsal fin in polynemids, except for *Eleutheronema tetradactylum*, *Polydactylus oligodon*, *Polydactylus sextarius* and *Galeoides decadactylus* lacking it.



**Fig. 32.** Elements of first dorsal fin, associated vertebrae and supraneurals. A, *Leptomelanosoma indicum*; B, *Polydactylus approximans*. Bar indicates 5 mm.

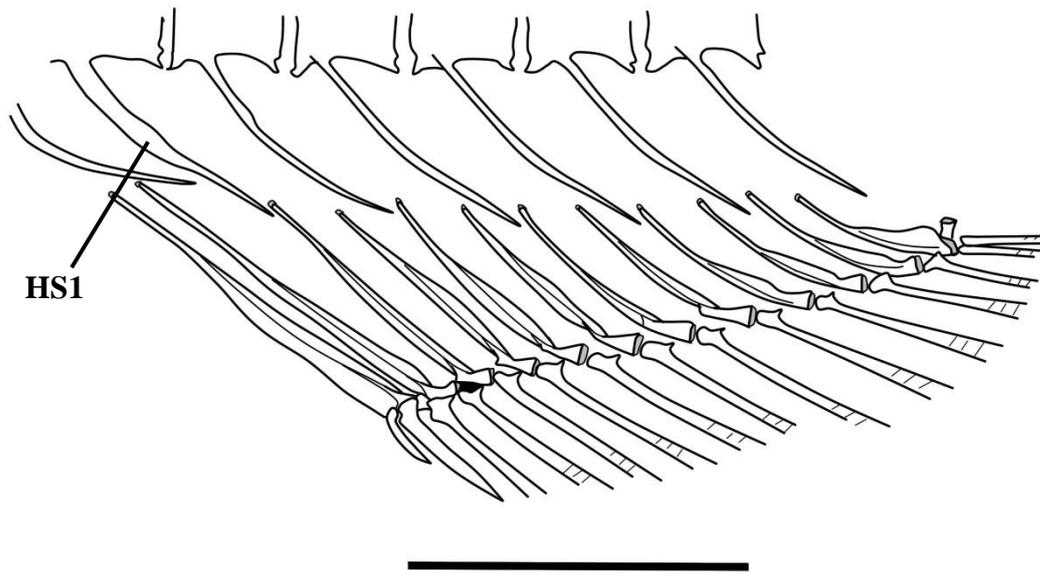


**Fig. 33.** Elements of first dorsal fin, associated vertebrae and supraneurals. A, *Eleutheronema rhadinum*; B, *Polynemus paradiseus*. Bars indicate 10 mm.

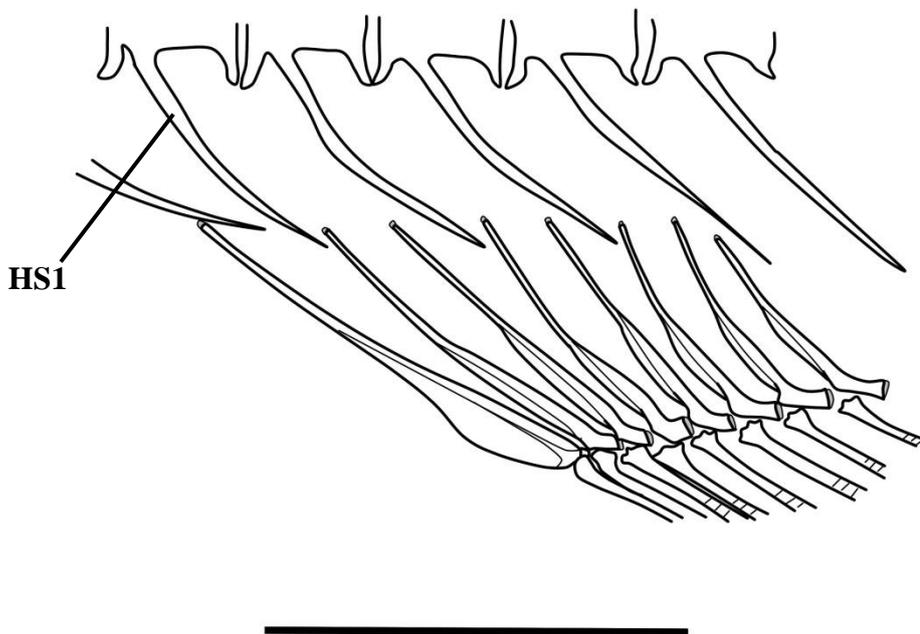


**Fig. 34.** Supraneurals and associated bones. A, *Eleutheronema tetradactylum*; B, *Polydactylus sextarius*; C, *Galeoides decadactylus*; D, *Parapolyneemus verekeri*. Bars indicate 5 mm.

A



B



**Fig. 35.** Anal fin proximal pterygiophores and associated vertebrae. A, *Parapolyneumus verekeri*; B, *Polynemus paradiseus*. HS1, hemal spine on first caudal vertebra. Bars indicate 10 mm.

## Character recognition

**TS 42. Number of caudal vertebrae.** 0: 14; 1: 15.

The number of the caudal vertebrae is 14 in polynemids (character 42-0), except for *Polynemus* and *Eleutheronema*, in which it is 15 (character 42-1). The number of the caudal vertebrae is varied from 14 to 20 in sciaenids (e.g., Sasaki, 1989; this study); therefore the outgroup is coded as “?”.

**TS 43. Insertion of third proximal pterygiophore of first dorsal fin.** 0: between third and fourth neural spines; 1: between fourth and fifth neural spines.

The third proximal pterygiophore of the first dorsal fin is inserted between the third and fourth neural spines in polynemids (character 43-0) (Figs. 31, 32, 33A), except for *Polydactylus nigripinnis*, *Parapolynemus verekeri*, *Polynemus aquilonaris*, *Polynemus melanochir melanochir* and *Polynemus paradiseus*, in which it is inserted between the fourth and fifth neural spines (character 43-1) (Fig. 33B). The third proximal pterygiophore of the first dorsal fin is indefinite in sciaenids (e.g., Sasaki, 1989: fig. 51; this study); therefore the outgroup is coded as “?”.

**TS 44. Insertion of sixth proximal pterygiophore of first dorsal fin.** 0: between sixth and seventh neural spines; 1: between fifth and sixth neural spines.

The sixth proximal pterygiophore of the first dorsal fin is inserted between the sixth and seventh neural spines in polynemids (character 44-0) (Figs. 31, 32, 33B), except for *Eleutheronema*, in which it is inserted between the fifth and sixth neural spines (character 44-1) (Fig. 33A). The insertion of the sixth

proximal pterygiophore of the first dorsal fin is variable in sciaenids (e.g., Sasaki, 1989; this study); therefore the outgroup is coded as “?”.

**TS 45. Insertion of seventh proximal pterygiophore of first dorsal fin.**

0: between seventh and eighth neural spines; 1: between sixth and seventh neural spines.

The seventh proximal pterygiophore of the first dorsal fin is inserted between the seventh and eighth neural spines in polynemids (character 45-0) (Figs. 31, 32B, 33B), except for *Leptomelanosoma indicum*, *Polydactylus sexfilis* and *Eleutheronema*, in which it is inserted between the fifth and sixth neural spines (character 45-1) (Figs. 32A, 33A). Because the insertion of the sixth proximal pterygiophore of the first dorsal fin is variable in sciaenids (e.g., Sasaki, 1989; this study), the outgroup is coded as “?”.

**TS 46. First supraneural.** 0: ossified; 1: cartilaginous; 2: absent.

(unordered)

The first supraneural is ossified in polynemids (character 46-0) (Figs. 31, 30A, 31B, C), except for *Polynemus paradiseus*, in which it is cartilaginous (character 46-1) (Fig. 33B), and *Eleutheronema*, *Polydactylus opercularis*, *Polynemus melanochir melanochir*, *Polynemus aquilonaris*, *Polynemus multifilis*, *Polydactylus octonemus*, *Polydactylus oligodon*, *Leptomelanosoma indicum* and *Parapolynemus verekeri* lacking it (character 46-2) (Figs. 32A, 33A, 34A, D). The first supraneural is ossified (e.g., *Pennahia argentata*, *Argyrosomus japonicas* and *Pentheroscion mbizi*) and absent (e.g., *Macrodon ancylodon* and

*Cynoscion squamipinnis*) in sciaenids (characters 46-0 and 46-2) (e.g., Sasaki, 1989; this study).

**TS 47. Third supraneural.** 0: present; 1: absent.

The third supraneural is present in polynemids (Figs. 31–33, 34D) (character 47-0), except for *Polydactylus sextarius*, *Polydactylus oligodon*, *Eleutheronema tetradactylum* and *Galeoides decadactylus* lacking it (Fig. 34A–C) (character 47-1). Both conditions are present in sciaenids (characters 47-0 and 47-1; for example, it is present in *Larimichthys polyactis*, *Pennahia argentata* and *Pareques iwamotoi*, and absent in *Equetus lanceolatus*) (e.g., Sasaki, 1989, this study).

## Other variations

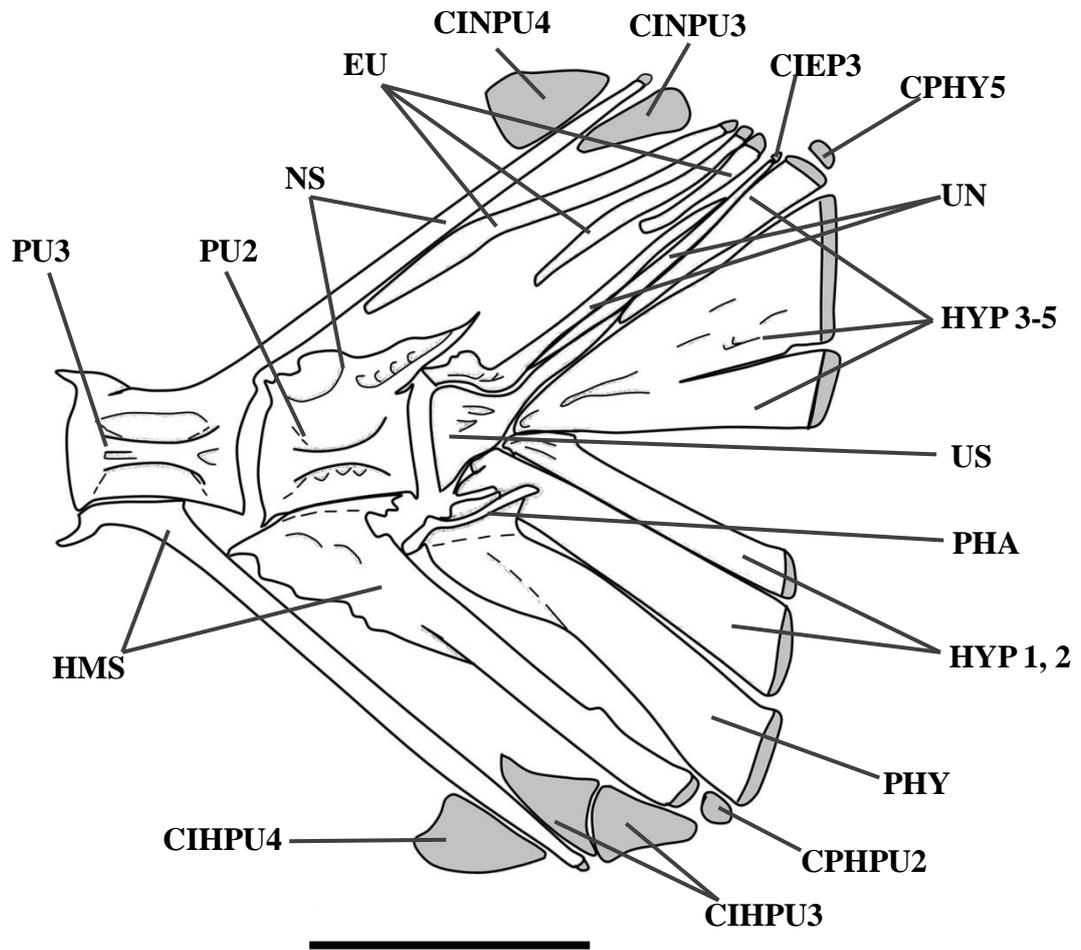
**First spines on first proximal pterygiophores of first dorsal and anal fins.** The first proximal pterygiophores of the first dorsal and anal fins bear two spines, respectively, in most polynemids, whereas they bear a single spine on each one and the first spines are absent in *Polynemus paradiseus*. The latter condition is considered as an autapomorphy for *Polynemus paradiseus*, because the first proximal pterygiophores of the first dorsal and anal fins bear two spines, respectively, in sciaenids (e.g., Sasaki, 1989; this study).

**Second supraneural.** The second supraneural is present and inserted between the first and second neural spines in polynemids, except for *Galeoides decadactylus* lacking it. This bone is present in sciaenids (e.g., Sasaki, 1989; this

study). Therefore, the absence of this bone is considered to be an autapomorphy for the species.

## 1-10 Caudal skeleton (Figs. 36–37)

**Description.** The caudal skeleton is a fan-like part and spreads out from the posteriormost centrum, consisting of the hypurals, parhypural, uroneurals, epurals and urostyle, plus the second and third preural centra with the neural and hemal spines on them. The posterior margin of the caudal skeleton bears the caudal rays and radial cartilages.



**Fig. 36.** Lateral view of caudal skeleton in *Polydactylus approximans*. CIEP, inter-epural cartilage; CIHPU, inter-hemal spine cartilage of preural; CINPU, inter-neural spine cartilage of preural; CPHY, post-hypural cartilage; CPHPU, post-hemal spine cartilage; EU, epural; NS, neural spine; HMS, hemal spine; HYP, hypural; PHA, parhypurapophysis; PHY, parhypural; PU, preural centra; UN, uroneural; US, urostyle. Bar indicates 10 mm.

The hypurals, situated on the posterior portion of the urostyle, consist of five plate-like bones and support the caudal fin rays posteriorly. The first and second hypurals are contained in the lower caudal lobe. They are attached with each other in polynemids, except for *Polynemus paradiseus*, in which their posterior portions are fused with each other. The first hypural is connected with the parhypural ventrally. The third to fifth hypurals are contained in the upper caudal lobe. The anterior portions of the third and fourth hypurals are fused with each other in most polynemids, whereas they are completely fused in *Polynemus paradiseus*. The fifth hypural is a slender element, attached with the urostyle anteriorly, the uroneural anterodorsally and the fourth hypural ventrally.

The parhypural is a plate-like bone with a distinct parhypurapophysis on its lateral surface. The parhypural is attached with the first hypural dorsally and situated posterior to the posteriormost hemal spine.

The uroneurals are consisted of two slender rod-like bones, situated above the urostyle and fifth hypural. The first uroneural is attached with the urostyle ventrally and well extends posteriorly to the interspace below the posterior epural in most polynemids, while it is fused with the urostyle on the middle portion in *Pentanemus quinquarius*. The second uroneural is inserted into the interspace between the fifth hypural and first uroneural.

The epurals, situated above the uroneurals, are three rod-like bones. The anterior epural is the longest one among them, attached with the posteriormost neural spine anteriorly and a large radial cartilage dorsoposteriorly. The epurals become progressively shorter posteriorly.

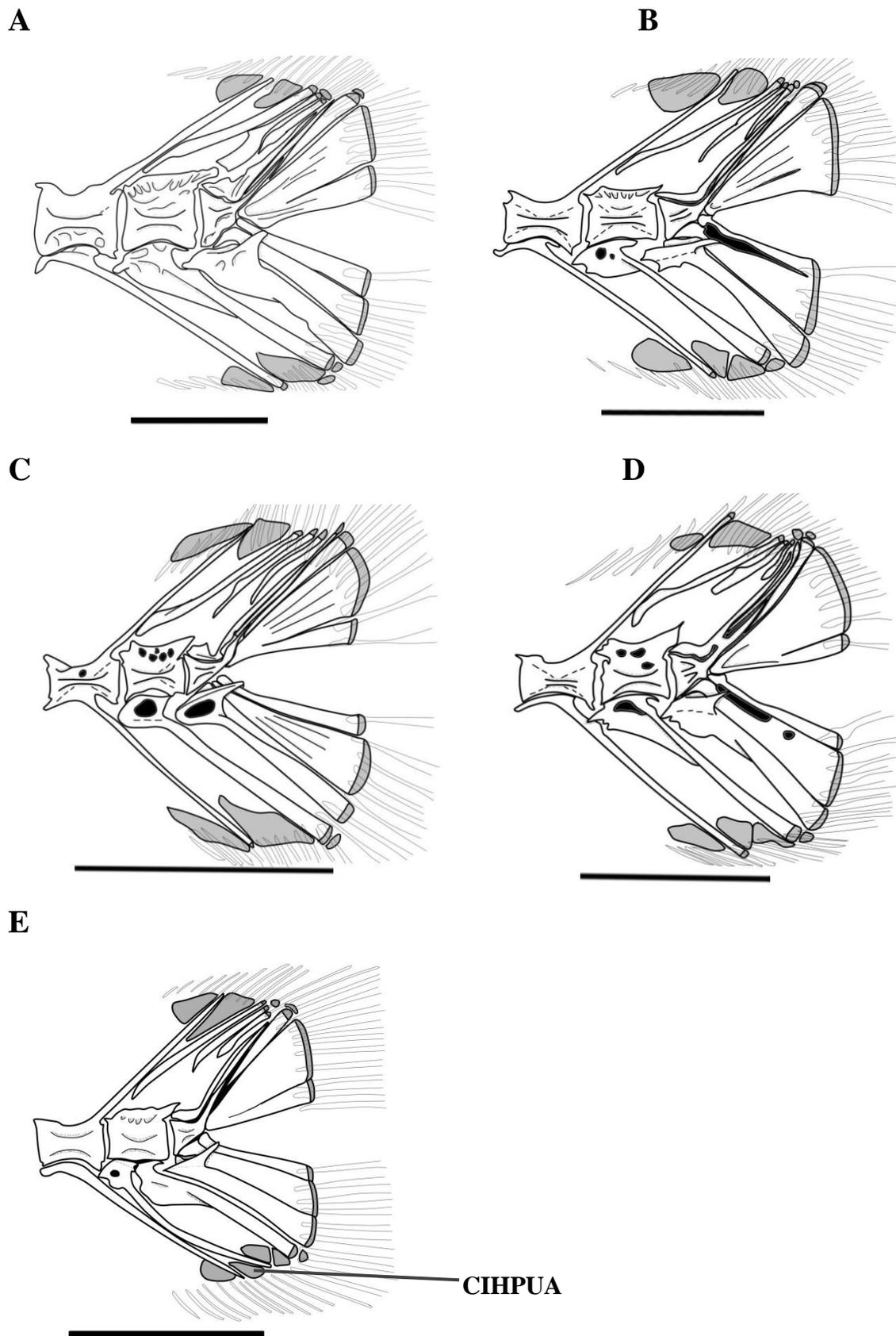
The urostyle is a tadpole-like bone, articulating with the second preural centrum anteriorly, and attached with the hypurals posteriorly, the uroneurals dorsally and the parhypural ventrally. It posteriorly possesses a long spine inserted into the interspace between the uroneurals and third to fifth hypurals.

The second preural centrum is situated anterior to the urostyle, bearing a short wedge-like neural spine dorsally. The third preural centrum is situated anterior to the second one and bears a long rod-like spine dorsally. These two bones are ventrally connected with an autogenous hemal spine, respectively, in most polynemids, whereas the third preural centrum is fused with the third hemal spine in *Parapolyneumus verekeri*, and the second preural centrum is connected with two autogenous hemal spines in *Polydactylus microstomus*.

The caudal fin rays consist of 16–18 principal rays and 22–27 procurrent rays (11–15 in upper lobe, 11–12 in lower lobe). The procurrent rays of the caudal fin are situated on the upper and lower margins of the fin. Both upper and lower lobes support one unbranched ray on the outer corner. The upper caudal lobe supports eight branched rays, and the lower caudal lobe seven.

The radial cartilages are present around the distal tips of the third preural centra, epurals, fifth hypural, and hemal spines of the second and third preural centra. The third and fourth inter-neural spine cartilages of the preural are large cartilages, situated between the distal tips of the neural spine of the third preural centra and the anterior epural, and anterior to the distal tips of the neural spine of the third preural centra, respectively. The third inter-epural cartilage is a tiny cartilage, posterodorsal to the epurals and uroneurals. The fifth post-hypural

cartilage is tiny and attached with the fifth hypural anteroventrally in polynemids, except for *Parapolyneumus verekeri*, in which it is absent. The second post-hemal spine cartilage is small and posteroventral to the parhypural. The third inter-hemal spine cartilage of the preural, situated between the distal tips of the second and third hemal spines, is separated into two parts in most polynemids, while it is a single one in *Parapolyneumus verekeri*. The fourth inter-hemal spine cartilage of the preural is a large cartilage, anteroventral to the distal tip of the third hemal spine. An additional inter-hemal spine cartilage of the preural is present in *Polydactylus microstomus*, whereas it is absent in other polynemids.



**Fig. 37.** Lateral view of caudal skeleton. A, *Eleutheronema rhadinum*; B, *Polynemus paradiseus*; C, *Parapolynemus verekeri*; D *Pentanemus quinquarius*; E, *Polydactylus microstomus*. CIHPUA, additional inter-hemal spine cartilage of preural. Bars indicate 10 mm.

## Character recognition

**TS 48. Fifth post-hypural cartilage.** 0: present; 1: absent.

The fifth post-hypural cartilage is tiny and attached with the fifth hypural anteroventrally in polynemids (character 48–0), except for *Parapolynemus verekeri*, in which it is absent (character 48–1) (Fig. 37C). Both presence (e.g., *Nebris microps*) and absence (e.g., *Pennahia argentata* and *Johnius*) of this cartilage are found in sciaenids (characters 48–0 and 48–1) (e.g., Sasaki, 1989; Fujita, 1990; this study).

## Other variations

**Fusion of posterior portions of hypurals.** The anterior portions of the third and fourth hypurals are fused with each other in most polynemids, whereas the third and fourth hypurals are completely fused in *Polynemus paradiseus*. In addition, the first and second hypurals are attached with each other in polynemids, except for *Polynemus paradiseus*, in which the posterior portions of them are fused (Fig. 37B). The five hypurals are autogenous in sciaenids (e.g., Fujita, 1990); therefore the fusion of the posterior portions of the third and fourth hypurals, and the first and second hypurals in *Polynemus paradiseus* are treated as autapomorphies of this species.

**Fusion of first uroneural and urostyle.** The first uroneural is attached with the urostyle ventrally in most polynemids, while it is fused with the urostyle on the middle portion in *Pentanemus quinquarius* (Fig. 37D). The first uroneural is attached with the urostyle in Sciaenidae (e.g., Sasaki, 1989; Fujita, 1990; this

study). Therefore the latter character is considered as an autapomorphy of *Pentanemus quinquarius*.

**Fusion of third preural centrum and third hemal spine.** The third preural centrum is ventrally connected with an autogenous plate-like third hemal spine. In contrast, the third preural centrum is fused with the third hemal spine in *Parapolyneumus verekeri* (Fig. 37C). The third preural centrum is autogenous from the third hemal spine in sciaenids (e.g., Sasaki, 1989; Fujita, 1990); therefore the fusion of the third preural centrum and third hemal spine is an autapomorphy of *Parapolyneumus verekeri*.

**Single third inter-hemal spine cartilage of preural.** The third inter-hemal spine cartilage of the preural, situated between the distal tips of the second and third hemal spines, is separated into two parts in most polynemids, while it is a single one in *Parapolyneumus verekeri*. The number of this cartilage is two in sciaenids (e.g., Fujita, 1990); thus a single third inter-hemal spine cartilage of the preural is an autapomorphy of *Parapolyneumus verekeri*.

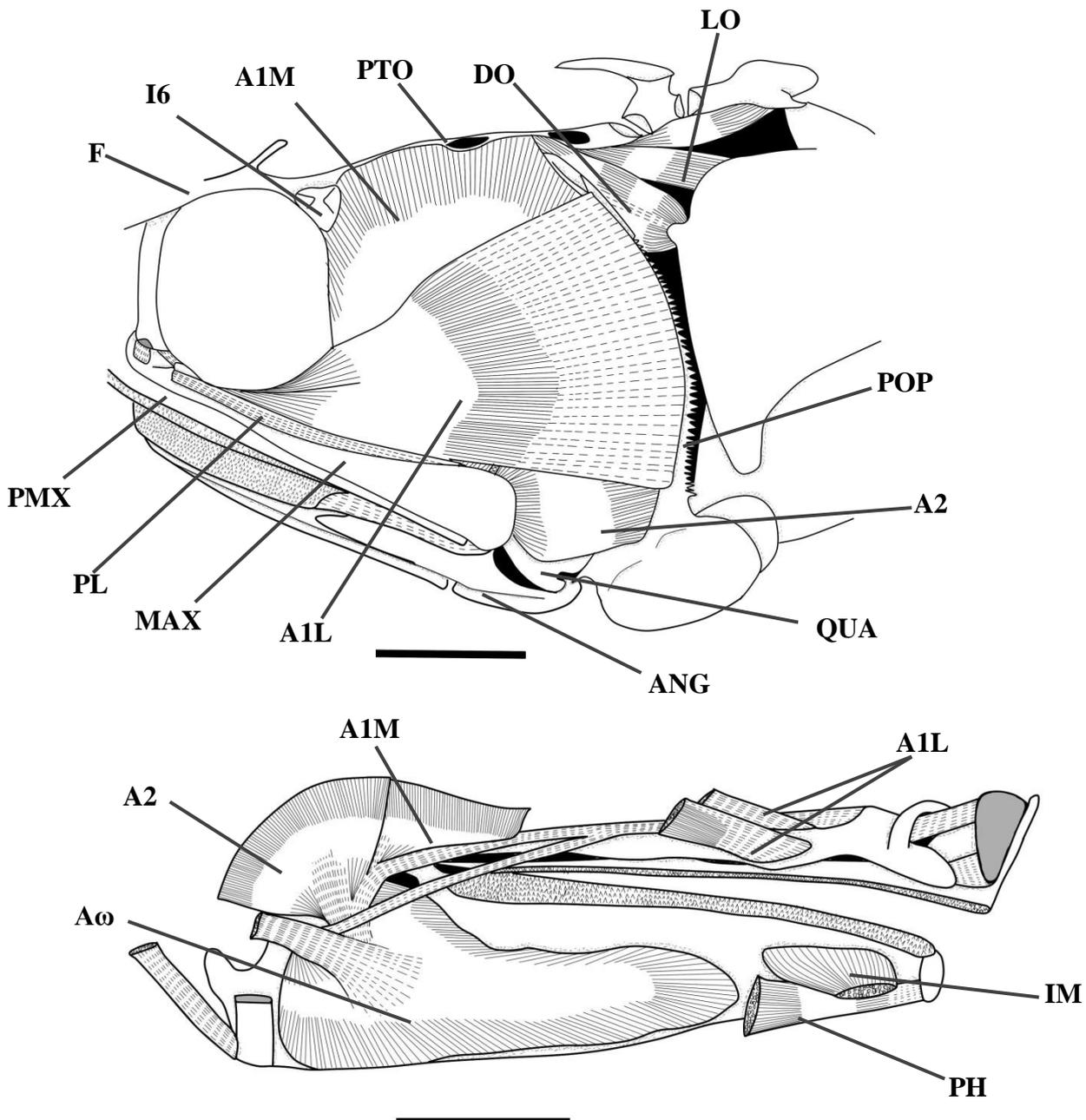
**Presence of additional hemal spine and inter-hemal spine cartilage of preural** (Fig. 37E). One autogenous hemal spine is connected with the second preural centrum in polynemids, except for *Polydactylus microstomus*, in which one more autogenous hemal spine is connected with the second preural centrum. In addition, one more inter-hemal spine cartilage of preural, associated with the additional hemal spine, is also present only in *Polydactylus microstomus*. The additional hemal spine and inter-hemal spine cartilage of preural are absent in

sciaenids (e.g., Sasaki, 1989; Fujita, 1990); thus their presence is an autapomorphy of *Polydactylus microstomus*.

## 2. Myology

### 2-1 Cheek muscle (Figs. 38–41)

**Description.** The cheek muscle consists of the adductor mandibulae (A), which is divided into three sections, A1, A2 and A $\omega$ . A distinct section A3 is absent.



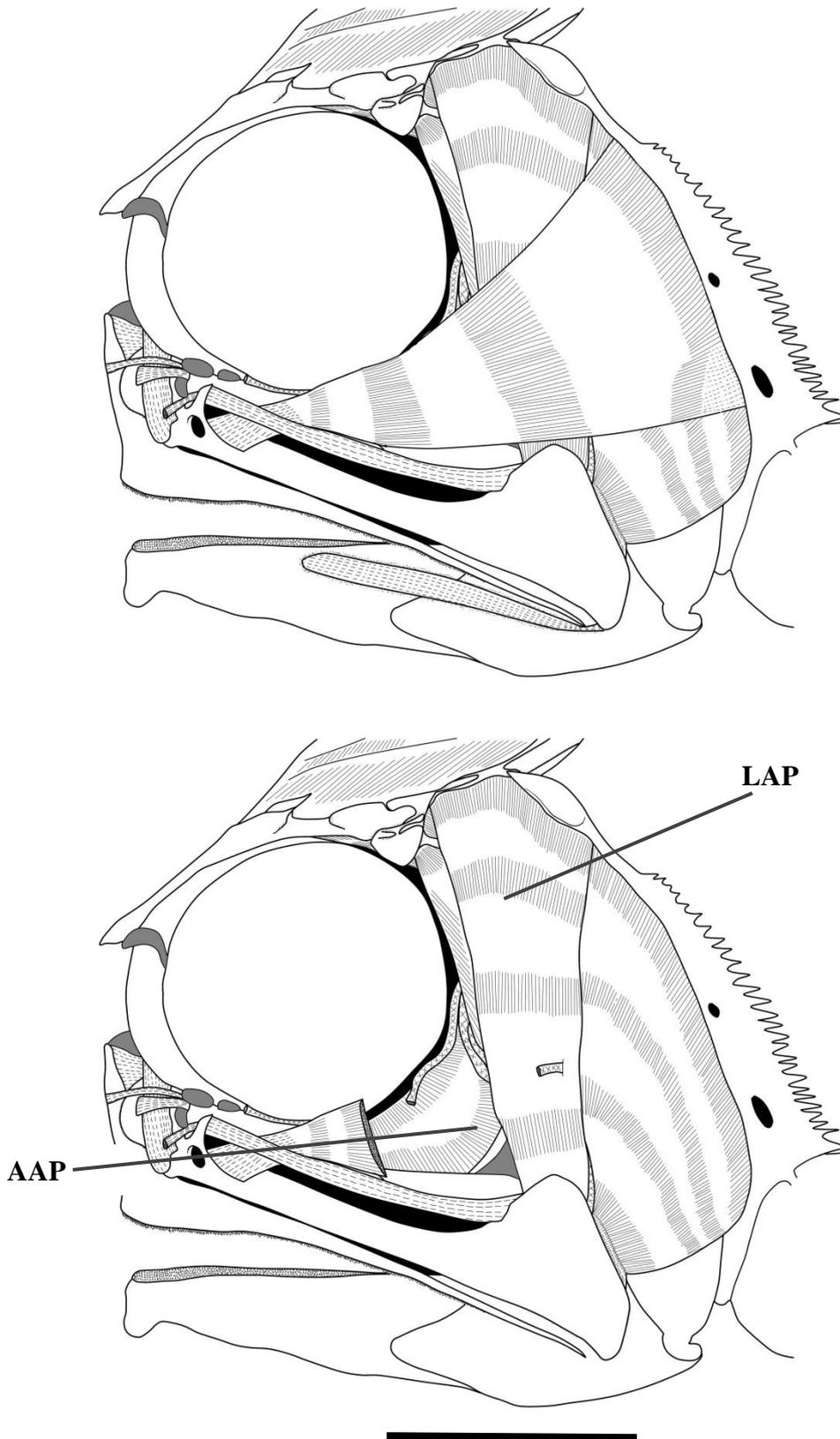
**Fig. 38** Lateral (upper) and medial (lower) views of cheek muscles in *Eleutheronema rhadinum*. A1L and A1M, lateral and medial elements of adductor mandibulae section 1, respectively; A2 and A $\omega$ , adductor mandibulae section 2 and  $\omega$ , respectively; ANG, anguloarticular; DO, dilatator operculi; F, frontal; IM, intermandibularis; LO, levator operculi; MAX, maxilla; PH, protractor hyohyoidei; PL, primordial ligament; PMX, premaxilla; POP, preopercle; PTO, pterotic; QUA, quadrate. Bars indicate 10 mm.

The section A1 is clearly divided into two subsections, the lateral and medial elements (A1L and A1M, respectively). The A1L, the outermost cheek muscle, originates from the preopercle in polynemids, except for *Polynemus melanochir melanochir* and *Polynemus paradiseus*, in which it originates from the preopercle and pterotic. This muscle is attached to the preopercle via a broad and thin tendon in many polynemids, whereas its muscular fibres are also partly attached to the preopercle in *Polydactylus plebeius*, *Polydactylus nigripinnis*, *Polydactylus octonemus*, *Polydactylus macrochir*, *Parapolynemus verekeri*, *Pentanemus quinquarius*, *Leptomelanosoma indicum* and *Filimanus*. The A1L is inserted onto the anterior portion of the maxilla via short lateral and medial tendons. The A1M, located medial to A1L and anterolateral to the section A2, originates from the preotic, hyomandibula and preopercle, and is inserted onto the posterior portion of the primodial ligament, which connects an extended process on the anterior portion of the maxilla and posterolateral surface of the angular (posteriorly, a thin division of the primodial ligament is attached to the posteromedial portion of the maxilla). A branch of the primodial ligament, divided from its middle portion, is fused with the strong tendon of the section A $\omega$  posteriorly.

The section A2, situated posteromedial to the A1M element, originates from the preopercle, hyomandibula, metapterygoid and quadrate, and is inserted onto the medial surface of the anguloarticular and continued with the section A $\omega$ .

The section A $\omega$ , lying on the medial surface of the anguloarticular and dentary, is connected with the primodial ligament and the tendon of the section

A2 dorsally, and preopercle and quadrate posteriorly by a strong tendon. It is weakly developed and restricted to the posterior region of the dentary in polynemids, except for *Polydactylus opercularis* and *Eleutheronema*, in which it is well developed and extends to the anterior portion of the dentary.

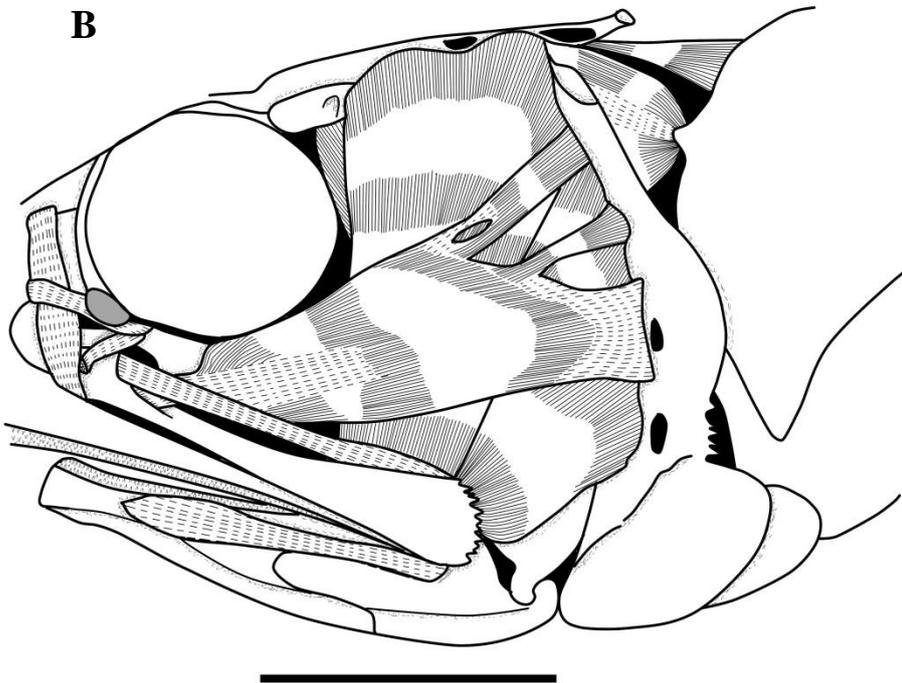


**Fig. 39** Lateral views of cheek muscles in *Filimanus similis*. AAP, adductor arcus palatini; LAP, levator arcus palatini. Bar indicates 10 mm.

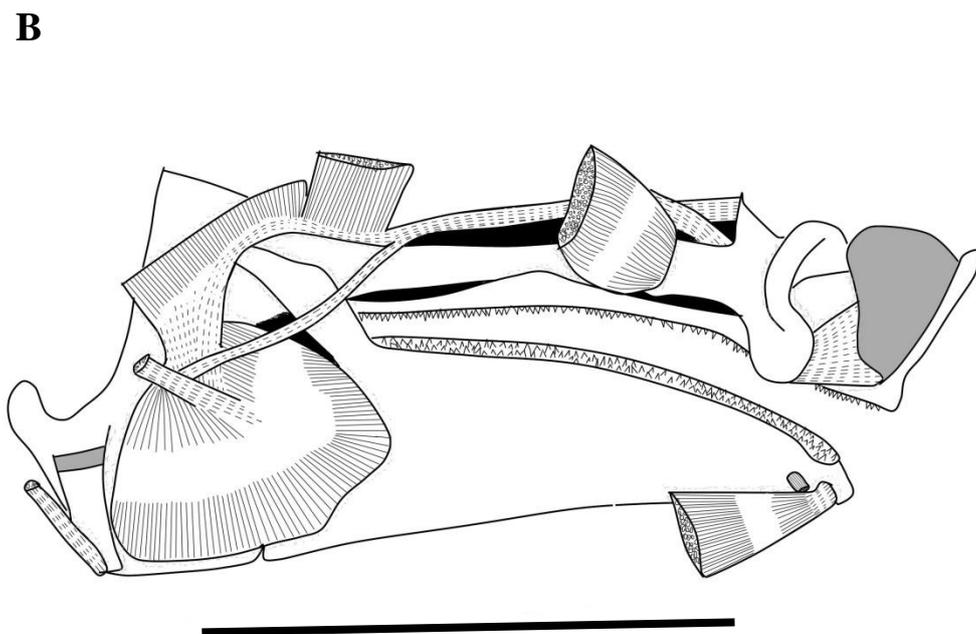
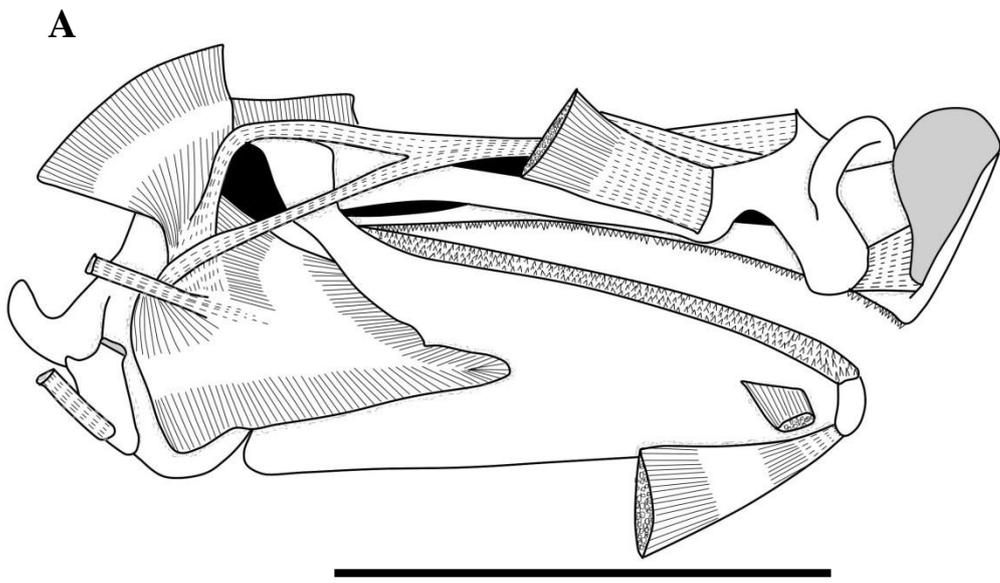
A



B



**Fig. 40** Lateral views of cheek muscles. A, *Polynemus melanochir melanochir*; B, *Polydactylus nigripinnis*. Bars indicate 10 mm.



**Fig. 41** Medial views of cheek muscles and jaws. A, *Polydactylus virginicus*; B, *Polynemus melanochir melanochir*. Bars indicate 10 mm.

## Character recognition

**TS 49. Origin of A1L.** 0: preopercle; 1: preopercle and pterotic.

The A1L, the outermost cheek muscle, originates from the preopercle in polynemids (character 49–0) (Figs. 38–29, 40B), except for *Polynemus melanochir melanochir* and *Polynemus paradiseus*, in which it originates from the preopercle and pterotic (character 49–1) (Fig. 40A). Sasaki (1989) recognized two A1 subsections in sciaenids: the subsection A1 $\alpha$ , situated dorsolateral to A2 and originated from the preopercle and hyomandibula, and subsection A1 $\beta$ , situated medial to A1 $\alpha$  and originated from the palatine and metapterygoid. Kang et al. (2017) considered that “it is possible to assume that section A1 was independently divided into two elements in the two families, resulting different position and origin of the lateral element of A1 in Polynemidae and section A1 $\beta$  in Sciaenidae”. Accordingly, because it can be inferred that the homologous muscular element with A1L is absent in sciaenids, the outgroup is coded as “?”.

**TS 50. Attachment of A1L to preopercle.** 0: via tendon; 1: via tendon and muscle.

The A1L element is attached to the preopercle via a broad and thin tendon in many polynemids (character 50–0) (Figs. 38, 40A), whereas its muscular fibres are also partly attached to the preopercle in *Polydactylus plebeius*, *Polydactylus nigripinnis*, *Polydactylus octonemus*, *Polydactylus macrochir*, *Parapolynemus verekeri*, *Pentanemus quinquarius*, *Leptomelanosoma indicum*

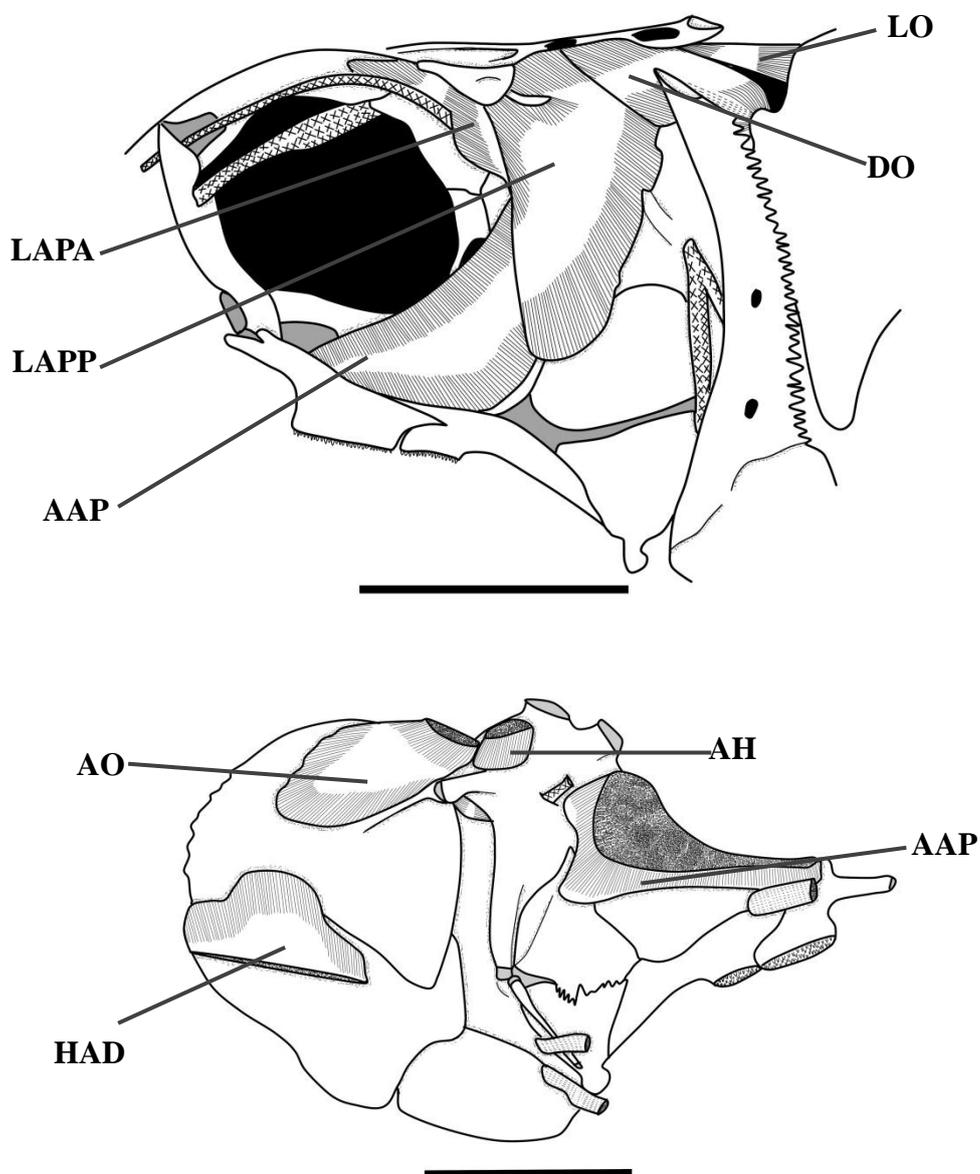
and *Filimanus* (character 50–1) (Figs. 39, 40B). As mentioned in the discussion on TS49 above, the outgroup is coded as “?”.

**TS 51. Section A $\omega$ .** 0: weakly developed and not extending anteriorly; 1: well developed and extending anteriorly.

The section A $\omega$  is weakly developed and restricted to the posterior region of the dentary in polynemids (character 51–0) (Fig. 38), except for *Polydactylus opercularis* and *Eleutheronema*, in which it is well developed and extends to the anterior portion of the dentary (character 51–1) (Fig. 41). Both conditions are present in sciaenids (characters 51-0 and 51-1; for example, it is weakly developed in *Larimichthys polyactis*, *Pennahia argentata* and *Pareques iwamotoi*, and well developed in *Argyrosomus japonicas* and *Sciaenops ocellata*) (e.g., Sasaki, 1989, this study).

## 2-2 Cephalic muscles between cranium and suspensorium-opercular bones (Figs. 38-43)

**Description.** The cephalic muscles between the cranium and suspensorium-operculum are consisted of the adductor arcus palatini, levator arcus palatini, dilatator operculi, adductor operculi, adductor hyomandibulae and levator operculi.



**Fig. 42** Lateral view of cephalic muscles after removal of jaws and cheek muscles (upper), and medial view of cephalic muscles and ventral muscles of head (lower) in *Polydactylus microstomus*. AAP, adductor arcus palatini; AH, adductor hyomandibulae; AO, adductor opercula; DO, dilatator operculi; HAD, hyohyoideus adductores; LAPA and LAPP, anterior and posterior subsections of levator arcus palatini, respectively; LO, levator operculi. Bars indicate 10 mm.

The adductor arcus palatini, a meniscus-shaped thick muscle, is situated on the floor of the orbit and the anterodorsal margin of the suspensorium. It originates from the prevomer, parasphenoid and prootic, and is inserted onto the lateral surface of the endopterygoid and the medial surfaces of the hyomandibula and metapterygoid.

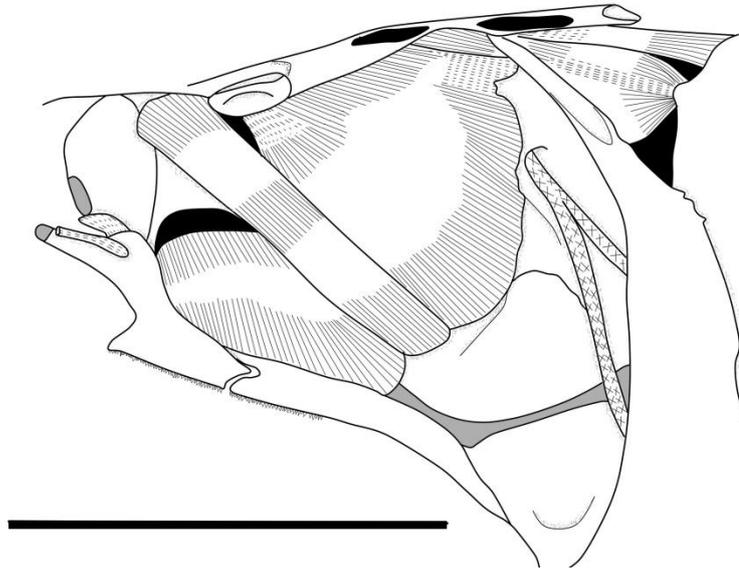
The levator arcus palatini is divided into the anterior and posterior subsections. The anterior subsection originates from the ventral surfaces of the frontal and sphenotic. It is inserted onto the anterior edge of the hyomandibula in most polynemids, while it is inserted onto the lateral surfaces of the endopterygoid and metapterygoid in *Polynemus*. The posterior subsection, covering the adductor arcus palatini medially, is located on the posterodorsal region of the suspensorium. It originates from the sphenotic and pterotic, and is inserted onto the hyomandibula and metapterygoid.

The dilatator operculi originates from the sphenotic, pterotic and hyomandibula, and is inserted onto the anterodorsal corner of the opercle.

The levator operculi, a thin and small muscle, originates from the pterotic and is inserted onto the dorsal margin of the opercle.

The adductor hyomandibulae originates from the pterotic and intercalar, and is inserted onto the posteromedial portion of the hyomandibula.

The adductor operculi, tightly adjoining to the adductor hyomandibulae anteriorly, originates from the pterotic and intercalar, and is inserted onto the anteromedial portion of the opercle.



**Fig. 43** Lateral view of cephalic muscles after removal of jaws and cheek muscles in *Polynemus melanochir melanochir*. Bar indicates 10 mm.

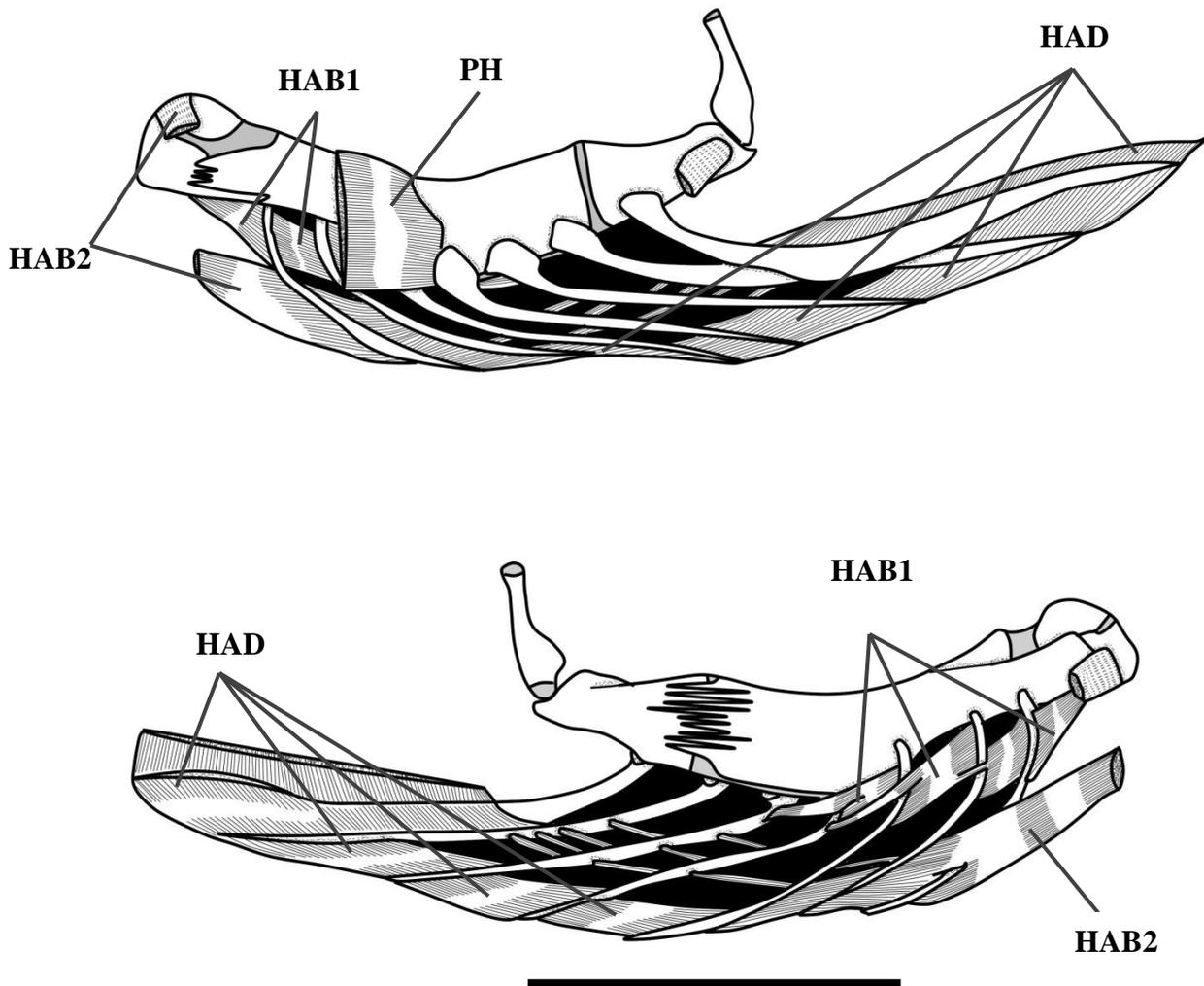
## Character recognition

**TS 52. Insertion of anterior subsection of levator arcus palatini.** 0: hyomandibula; 1: endopterygoid and metapterygoid.

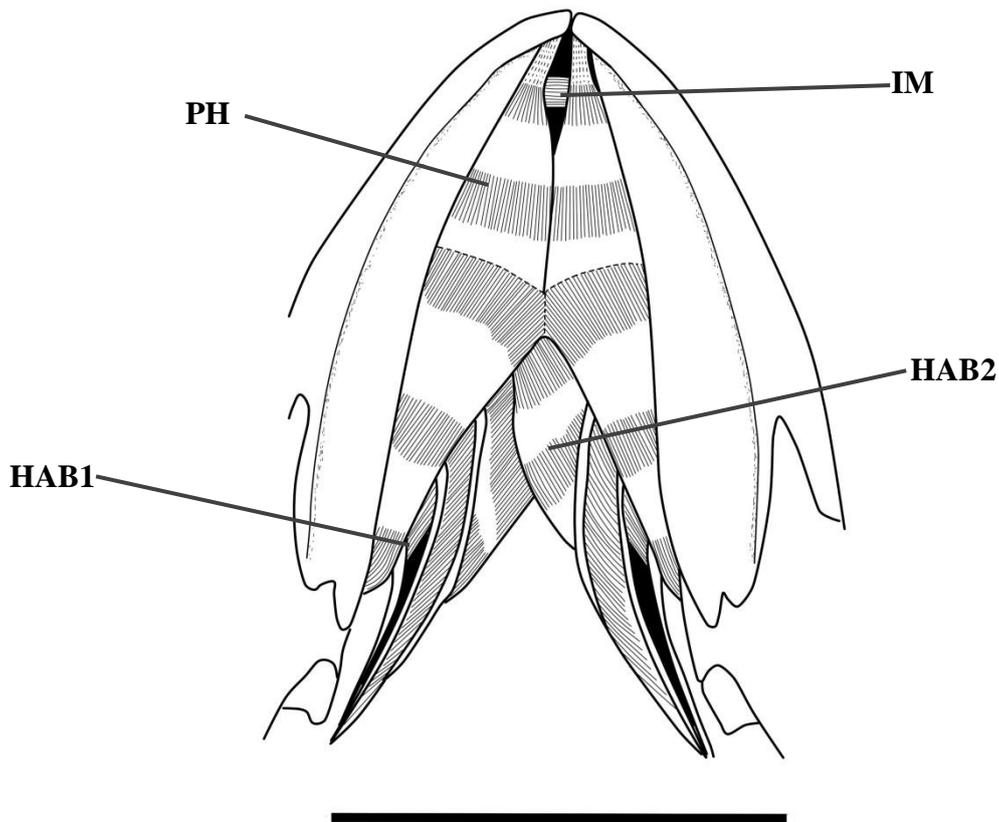
The anterior subsection of the levator arcus palatini is inserted onto the anterior edge of the hyomandibula in most polynemids (character 52–0) (Fig. 42), while it is inserted onto the lateral surface of the endopterygoid and metapterygoid in *Polynemus* (character 52–1) (Fig. 43). The levator arcus palatini is not divided into two subsections in Sciaenidae (e.g., Sasaki, 1989, this study); thus the outgroup is coded as “?”.

### 2-3 Ventral muscles of head (Figs. 38, 41, 44–45)

**Description.** The ventral muscles of the head are composed of the intermandibularis, protractor hyoidei, hyohyoidei abductores and hyohyoidei adductores.



**Fig. 44.** Lateral (upper) and medial (lower) views of ventral muscles of head in *Polydactylus sextarius*. HAB1 and 2, first and second hyohyoidei abductors, respectively; HAD, hyohyoidei adductor; PH, protractor hyoidei. Bar indicates 10 mm.



**Fig. 45.** Ventral view of ventral muscles of head in *Polydactylus sextarius*. HAB1 and 2, first and second hyoidei abductores, respectively; IM, intermandibularis; PH, protractor hyoidei. Bar indicates 10 mm.

The intermandibularis, lying on the anterior portion of dentary and connecting the dentaries on both sides, is a small and weakly-developed muscle in most polynemids, whereas it is large and well developed in *Polydactylus opercularis* and *Eleutheronema*.

The protractor hyoidei is a robust muscle, situated medial to the lower jaw and lateral to the hyoid arch. It originates from the anteromedial region of the dentary via a short tendon and is inserted onto the lateral surface of the ceratohyal. The protractor hyoidei on both sides are fused with each other on the midline.

The hyohyoidei abductores comprises two sections, the sections 1 and 2. The section 1 originates from the anteroventral region of the ceratohyal and is inserted onto the proximal portion of the anterior five branchiostegal rays. The section 2 originates from the dorsal hypohyal via a tendon, and is inserted onto the first and second branchiostegal rays on the other side. These muscles on both sides cross each other, and the left element is ventral to the right element.

The hyohyoidei adductor, a sheet-like muscle, connects all the branchiostegal rays and opercle. It is fused with the hyohyoidei abductor section 2 anteriorly.

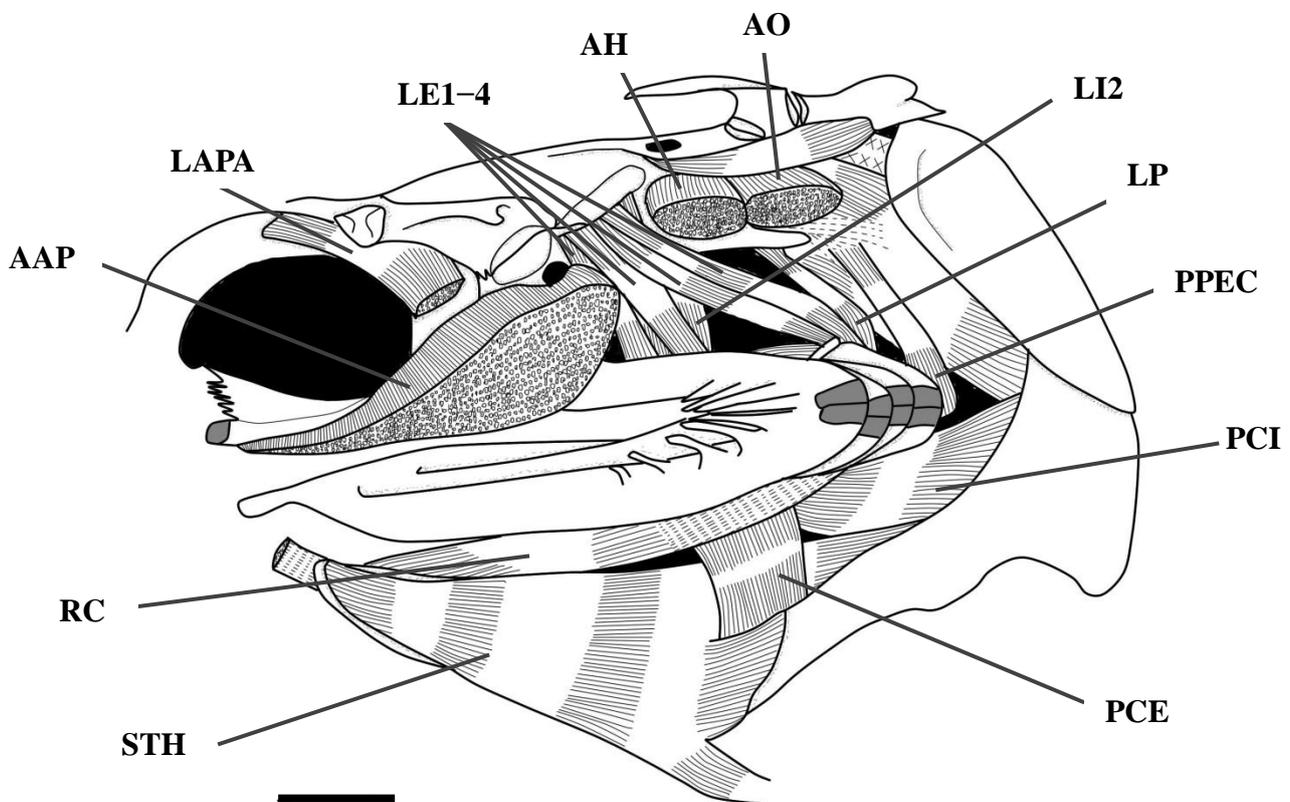
### **Character recognition**

**TS 53. Intermandibularis.** 0: weakly developed; 1: well developed.

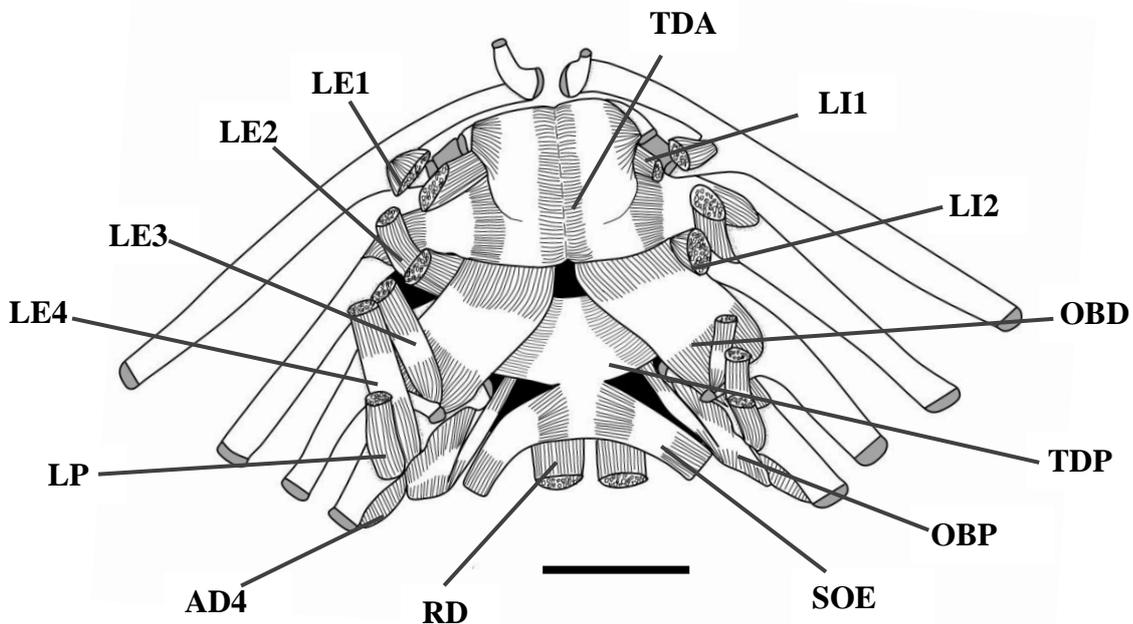
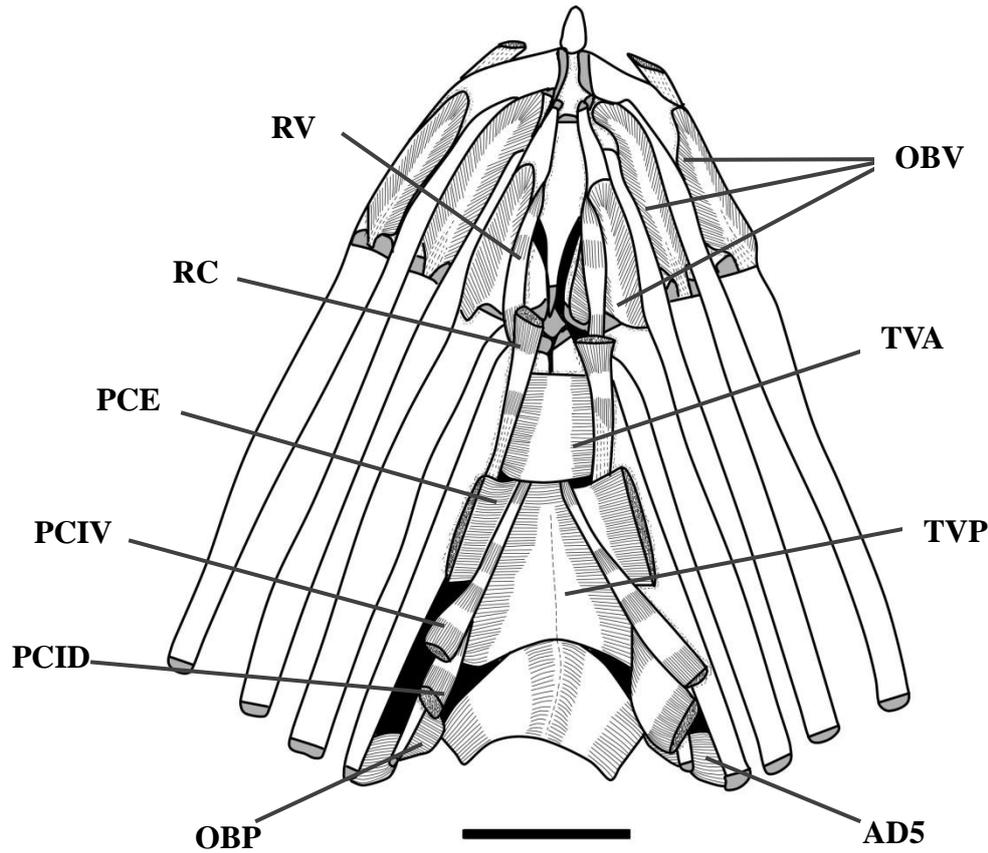
The intermandibularis is a small and weakly-developed muscle in most polynemids (character 53–0) (Fig. 41), whereas it is large and well developed in *Polydactylus opercularis* and *Eleutheronema* (character 53–1) (Fig. 38). Both conditions are present in sciaenids (characters 53-0 and 53-1; for example, it is weakly developed in *Larimichthys polyactis* and *Pareques iwamotoi*, and well developed in *Pennahia argentata* and *Sciaenops ocellata*) (this study).

## 2-4 Branchial muscles (Figs. 46-49)

**Description.** The branchial muscles include the levator externus, levator internus, levator posterior, transversus dorsalis, obliquus dorsalis, retractor dorsalis, rectus communis, pharyngoclavicularis, rectus ventralis, obliquus ventralis, transversus ventralis, sphincter oesophagi, adductores and obliquus posterior.



**Fig. 46.** Lateral view of head in *Eleutheronema rhadinum* after removal of infraorbitals, jaws, suspensorium, hyoid arch and their associated muscles. AAP, adductor arcus palatini; AH, adductor hyomandibulae; AO, adductor operculi; LAPA, anterior subsection of levator arcus palatini; LE1-4, first to fourth levator externus; LI2, second levator internus; LP, levator posterior; PCE, pharyngoclavicularis externus; PCI, pharyngoclavicularis internus; PPEC, protractor pectoralis; RC, rectus communis; STH, sternohyoideus. Bar indicates 10 mm.



**Fig. 47.** Ventral (upper) and dorsal (lower) views of muscles serving lower and upper branchial arches, respectively, in *Polydactylus virginicus*. AD 4 and 5, fourth and fifth adductores; LE1–4, first to fourth levator externus; LI–2, first and second levator internus; LP, levator posterior; OBD, obliquus dorsalis; OBP, obliquus posterior; OBV, obliquus ventralis; PCE, pharyngoclavicularis externus; PCID and PCIV, dorsal and ventral subsections of pharyngoclavicularis internus, respectively; RC, rectus communis; RD, retractor dorsalis; RV, rectus ventralis; SOE, sphincter oesophagi; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior; TVA, transversus ventralis anterior, TVP, transversus ventralis posterior. Bars indicate 10 mm.

The levator externi consist of four elements, the first to fourth levator externi. These muscles originate from the dorsolateral region of the prootic and pterotic in polynemids, except for *Pentanemus quinquarius* and *Parapolynemus verekeri*, in which they originate only from the pterotic. The levator externi are inserted onto the dorsal surface of the first to fourth epibranchials, respectively.

The levator interni, situated medial to the levator externi, include two elements, the first and second levator interni. They originate from the pterotic and prootic. The first levator internus is inserted onto the dorsal surface of the second pharyngobranchial and the second levator internus onto the dorsolateral region of the third pharyngobranchial.

The levator posterior originates from the posterior edge of the intercalar and is inserted onto the posterodorsal portion of the fourth epibranchial.

The transversus dorsalis, located on the dorsal portion of the upper gill arch, is comprised with two elements, the transversus dorsalis anterior and posterior. The transversus dorsalis anterior is branched into two bundles. The anterior and posterior bundles connect the dorsal portions of the second pharyngobranchials on both sides, and the medial portions of the second epibranchials on both sides, respectively. The anterior bundle is robust in most polynemids, whereas it is slender in *Parapolynemus verekeri*. The posterior bundle is commonly robust in polynemids. The transversus dorsalis posterior bonds the third and fourth pharyngobranchials on both sides.

The obliquus dorsalis originates from the third pharyngobranchial and is inserted onto the third and fourth epibranchials.

The retractor dorsalis originates from the medial margin of the third and fourth pharyngobranchials and is inserted onto the ventrolateral face of the second abdominal vertebra.

The rectus communis originates from the dorsal surface of the urohyal and is inserted onto the ventrolateral face of the fifth ceratobranchial.

The pharyngoclavicularis, including two elements (the externus and internus), connects gill arches with the cleithrum. The pharyngoclavicularis externus originates from the anteroventral portion of the cleithrum and is inserted onto the ventral surface of the fifth ceratobranchial. The origin of the pharyngoclavicularis externus on the cleithrum is sandwiched by the posterior portion of the sternohyoideus. The pharyngoclavicularis internus originates from the dorsoanterior margin of the cleithrum. The anterior part of it is divided into two subsections. The ventral subsection is inserted onto the tip of the fourth ceratobranchial via a tendon, and the dorsal subsection onto the posterior portion of the fifth ceratobranchial.

The rectus ventralis connects the third hypobranchial with the fourth ceratobranchial.

The obliquus ventralis, composed with three elements, interconnects the first to third hypobranchials with the first to third ceratobranchials, respectively.

The transversus ventralis consists of two muscles (the transversus ventralis anterior and posterior), connecting the fourth and fifth ceratobranchials on both sides with each other, respectively. The posterior margin of the transversus ventralis anterior covers the anterior portion of the transversus ventralis posterior

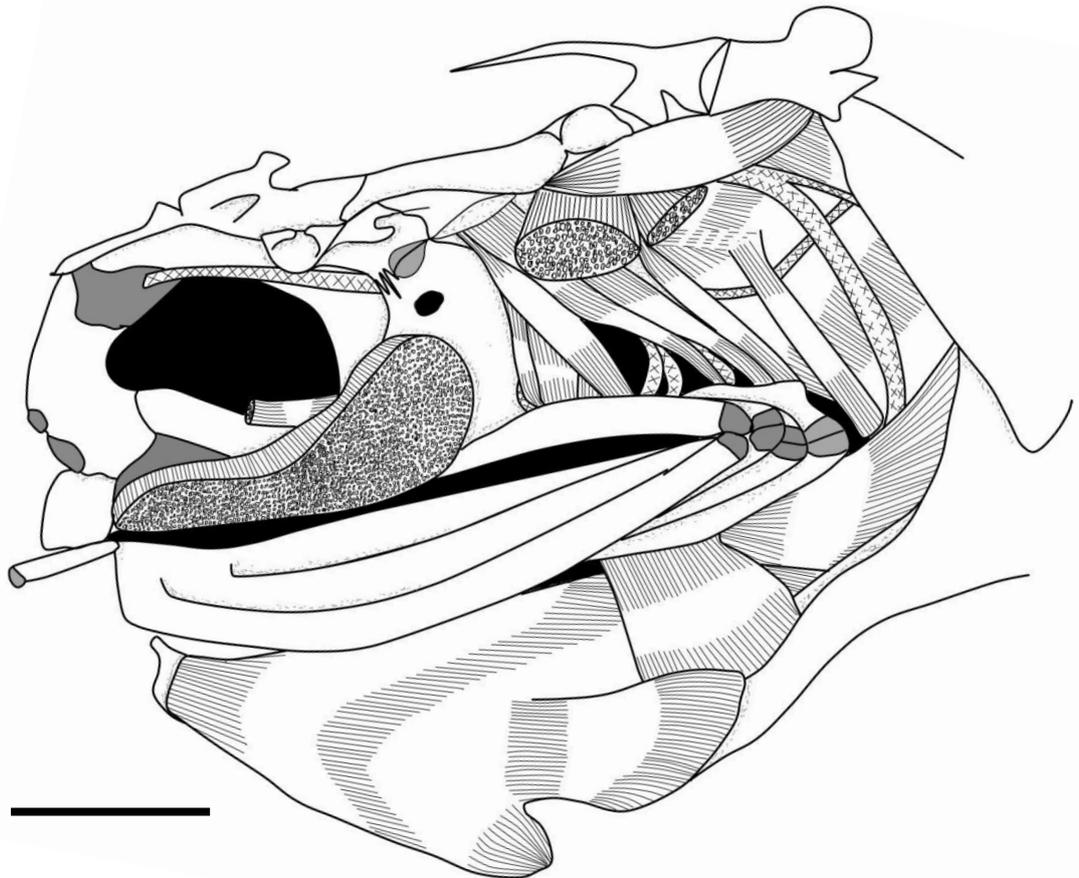
dorsally.

The sphincter oesophagi wrap up the esophagus in the posterior portion of the branchial arch.

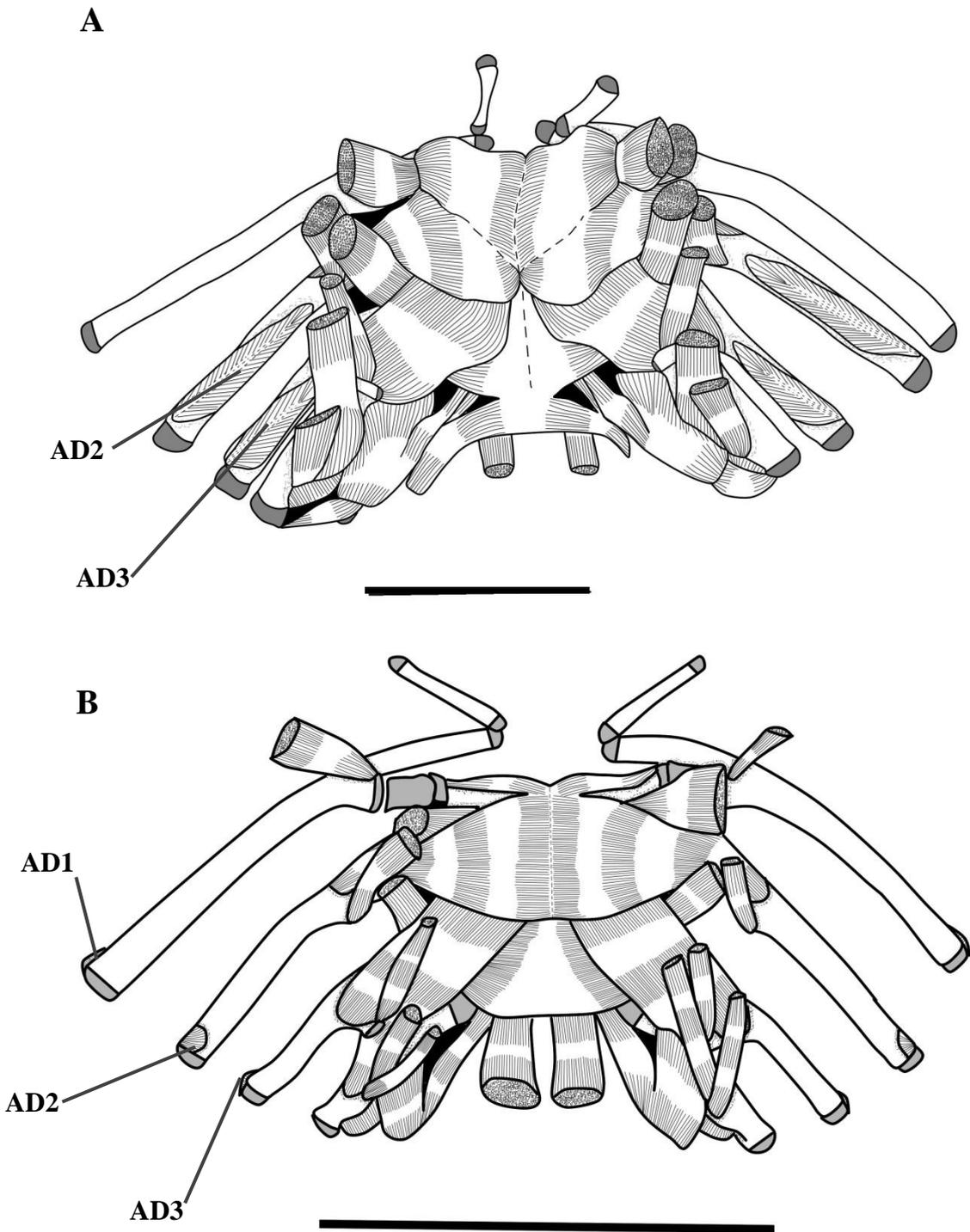
The obliquus posterior connects the fourth epibranchial with the fifth ceratobranchial.

The adductores include five small sections. The first to third sections interconnect the posterolateral surfaces of the first to third epibranchials with ceratobranchials, respectively. The first section is restricted to the posterolateral surface of the first epibranchial and ceratobranchial. The second section is restricted to the posterolateral surface of the second epibranchial and ceratobranchial in polynemids, except for *Galeoides decadactylus*, *Polydactylus sextarius*, *Polydactylus multiradiatus*, *Polydactylus nigripinnis* and *Polydactylus microstomus*, in which they extend onto the posterodorsal surfaces of the second epibranchial. The third section is restricted to the posterolateral surface of the third epibranchial and ceratobranchial in polynemids, except for *Pentanemus quinquarius*, *Galeoides decadactylus*, *Filimanus sealei*, *Polydactylus sextarius*, *Polydactylus multiradiatus*, *Polydactylus nigripinnis*, *Polydactylus microstomus*, *Polydactylus macrochir*, *Parapolynemus verekeri*, *Polynemus multifilis* and *Polynemus aquilonari*, in which they extend onto the posterodorsal surfaces of the third epibranchial. The fourth and fifth sections are robust muscles, interconnecting the posteromedial portions of the fourth epibranchial with the fourth ceratobranchial, and the posteromedial portion of the fourth ceratobranchial with the posterodorsal portion of the fifth ceratobranchial,

respectively.



**Fig. 48** Lateral view of head in *Pentanemus quinquarius* after removal of infraorbitals, jaws, suspensorium, hyoid arch and their associated muscles. Bar indicates 10 mm.



**Fig. 49** Dorsal views of muscles serving upper branchial arches. A, *Galeoides decadactylus*; B, *Parapolyneumus verekeri*. AD 1, 2 and 3, first, second and third adductor. (a small first adductor is present and hidden in A) Bars indicate 10 mm.

## Character recognition

**TS 54. Origin of levator externi.** 0: prootic and pterotic; 1: pterotic.

The levator externi originate from the dorsolateral region of the prootic and pterotic in polynemids (character 54-0) (Fig. 46), except for *Pentanemus quinquarius* and *Parapolynemus verekeri*, in which they originate only from the pterotic (character 54-1) (Fig. 48). The levator externi originate from the dorsolateral region of the prootic and pterotic in sciaenids (character 54-0) (e.g., Sasaki, 1989; this study).

**TS 55. Adductor section 2.** 0: extending onto the posterodorsal surface; 1: restricted to the posterolateral surface.

The adductor section 2 is restricted to the posterolateral surface of the second epibranchial in polynemids (character 55-1) (Fig. 47), except for *Galeoides decadactylus*, *Polydactylus sextarius*, *Polydactylus multiradiatus*, *Polydactylus nigripinnis* and *Polydactylus microstomus*, in which it extends onto the posterodorsal surface of the second epibranchial (character 55-0) (Fig. 49). Due to the lack of the gill arch of the specimen *Polydactylus opercularis*, the condition of this species is unknown; thus its value is coded as “?”. The adductor section 2 extends onto the posterodorsal surface of the second epibranchial in sciaenids (character 55-0) (this study).

**TS 56. Adductor section 3.** 0: extending onto the posterodorsal surface; 1: restricted to the posterolateral surface.

The adductor section 3 is restricted to the posterolateral surface of the third epibranchial in polynemids (character 56-1) (Fig. 47, 49B), except for

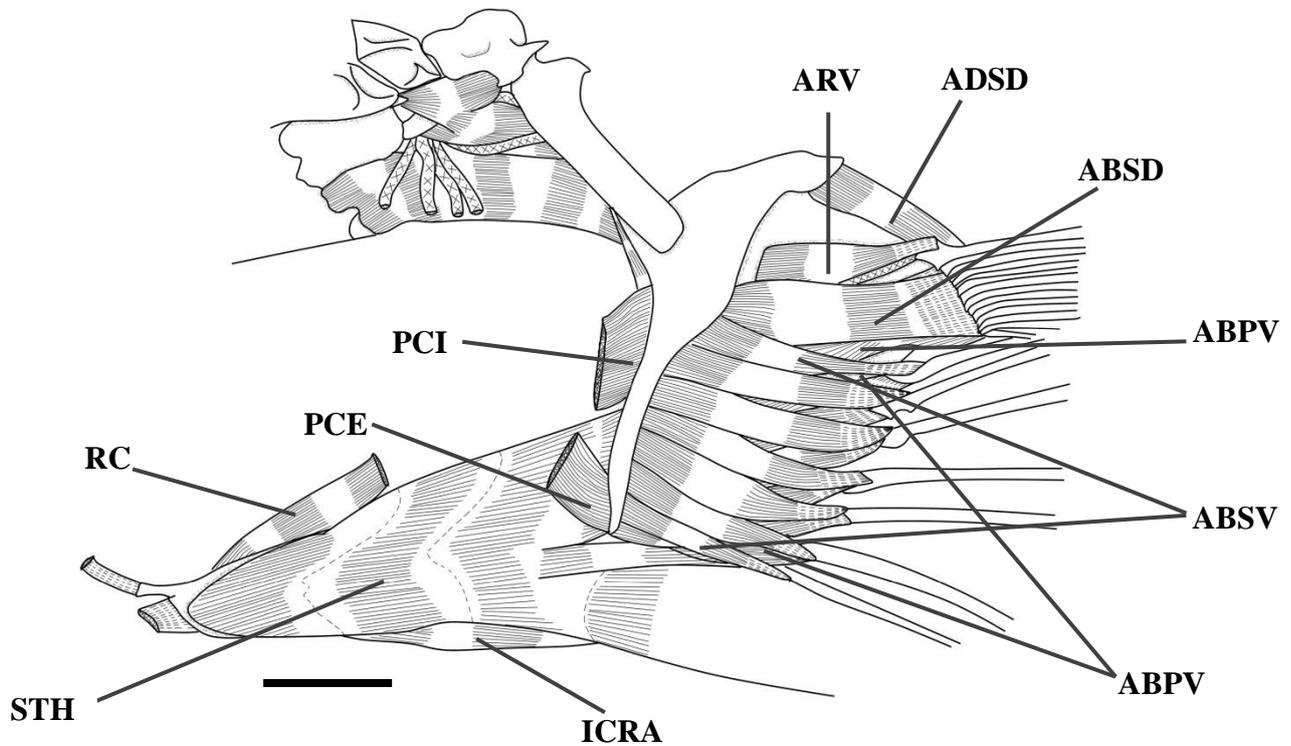
*Pentanemus quinquarius*, *Galeoides decadactylus*, *Filimanus sealei*,  
*Polydactylus sextarius*, *Polydactylus multiradiatus*, *Polydactylus nigripinnis*,  
*Polydactylus microstomus*, *Polydactylus macrochir*, *Parapolynemus verekeri*,  
*Polynemus multifilis* and *Polynemus aquilonaris*, in which they extend onto the  
posterodorsal surface of the third epibranchial (character 56-0) (Fig. 49A). Due  
to the lack of the gill arch of the specimen *Polydactylus opercularis*, the  
condition of this species is unknown; thus its value is coded as “?”. The adductor  
section 3 extends onto the posterodorsal surface of the third epibranchial in  
sciaenids (character 56-0) (this study).

**TS 57. Anterior bundle of transversus dorsalis anterior.** 0: robust; 1:  
slim.

The anterior bundle of the transversus dorsalis anterior is robust in most  
polynemids (character 57-0) (Fig. 47, 49A), whereas it is slender in  
*Parapolynemus verekeri* (character 57-1) (Fig. 49B). Due to the lack of the gill  
arch of the specimen *Polydactylus opercularis*, the condition of this species is  
unknown; thus it is coded as “?”. Because the transversus dorsalis anterior in  
sciaenids is not branched into two bundles (e.g., Sasaki, 1989; this study), the  
outgroup is coded as “?”.

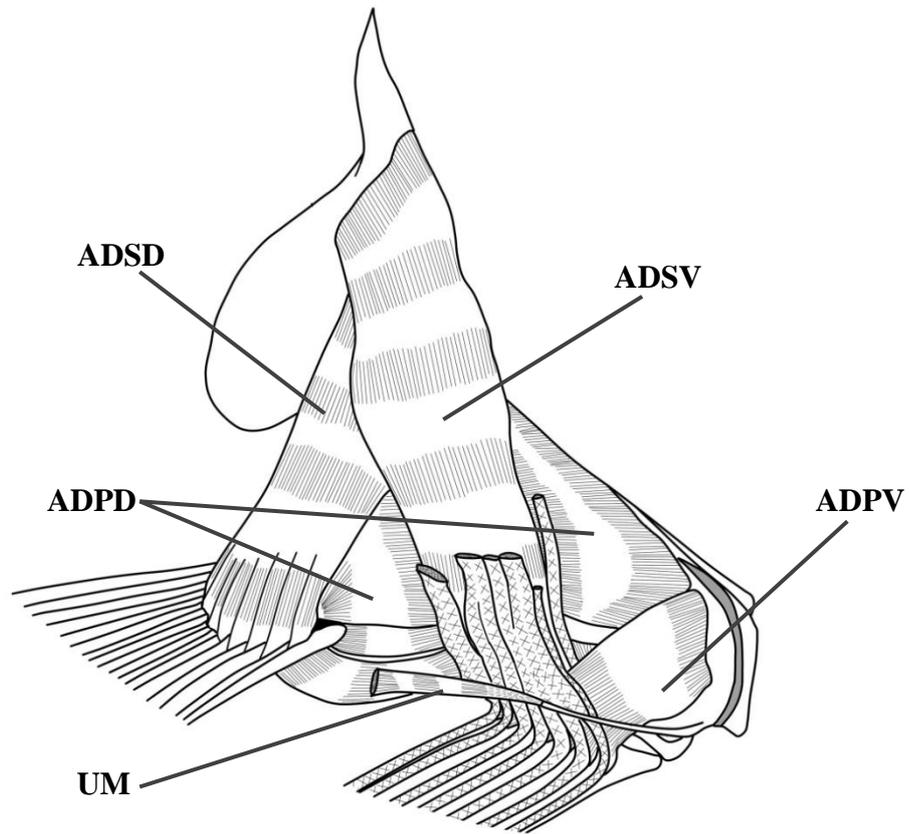
## 2-5 Pectoral fin muscles (Figs. 46, 48, 50–52)

**Description.** The pectoral muscles comprise the abductor superficialis, abductor profundus, arrector ventralis, adductor superficialis, adductor profundus, adductor radialis and arrector dorsalis. The coracoradialis is absent. The levator pectoralis, protractor pectoralis, and an unidentified muscle, situated between the rod-like process of the coracoid and postcleithrum, are also described here.

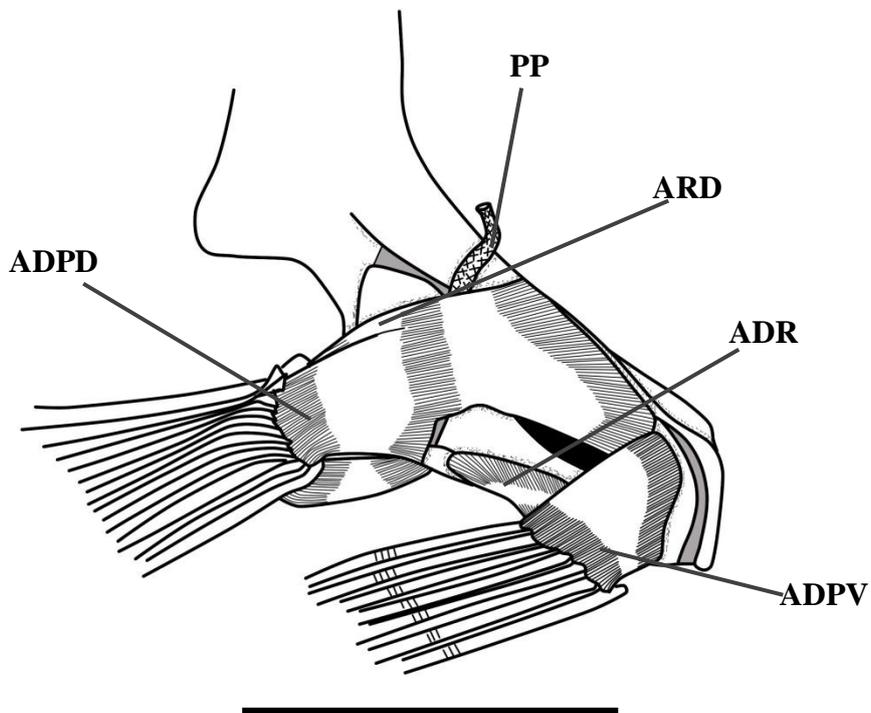


**Fig. 50.** Lateral view of pectoral girdle of *Parapolyneumus verekeri*. ABPD and ABPV, dorsal and ventral elements of abductor profundus, respectively; ABSD and ABSV, dorsal and ventral elements of abductor superficialis, respectively; ARV, arrector ventralis; ICRA, infracarinalis anterior; PCE, pharyngoclavicularis externus; PCI, pharyngoclavicularis internus; RC, rectus communis; STH, sternohyoideus. Bar indicates 10 mm.

A



B



**Fig. 51.** Medial view of pectoral girdle of *Filimanus similis*. A, superficial view; B, medial view after removal of the adductor superficialis. ADPD and ADPV, dorsal and ventral elements of adductor profundus, respectively; ADR, adductor radialis; ADSD and ADSV, dorsal and ventral elements of adductor superficialis, respectively; ARD, arrector dorsalis; PP, pectoral plexus nerve; UM, unidentified muscle. Bar indicates 10 mm.

The abductor superficialis, the outer muscle on the lateral surface of the pectoral girdle, is divided into two subsections, the dorsal and ventral subsections. The dorsal subsection originates from the medial side of the cleithrum flange and is inserted onto the bases of all upper pectoral fin rays except for the uppermost one. The ventral subsection originates from the medial side of the ventral portion of the cleithrum flange and the lateral surface of the coracoid, and is inserted onto the bases of all lower filament like rays. It is continuous to form a single mass in most polynemids, while it is split into several bundles connecting the respective filaments in *Pentanemus quinquarius*, *Leptomelanosoma indicum*, *Parapolynemus verekeri* and *Polynemus*.

The abductor profundus, situated medial to the abductor superficialis on the lateral surface of the pectoral girdle, is also divided into two subsections, the dorsal and ventral subsections. The dorsal subsection originates from the medial side of the cleithrum flange and the lateral surfaces of the coracoid, scapula and the second and third actinosts, and is inserted onto the bases of all upper pectoral fin rays. The ventral subsection originates from the lateral surfaces of the ventral portion of the cleithrum, the coracoid and the fourth actinost, and is inserted onto the bases of all lower filament like rays.

The arrector ventralis lies medial to the abductor superficialis and dorsal to the abductor profundus. This muscle originates from the medial surface of the cleithrum flange and the lateral surface of the scapula, and is inserted onto the base of the anteromedial portion of the uppermost ray via a tendon.

The adductor superficialis, situated on the medial surface of the pectoral

girdle, is the innermost muscle divided into two subsections, the dorsal and ventral subsections. The dorsal subsection originates from the medial surface of the cleithrum, and is inserted onto the bases of all upper pectoral fin rays except for the uppermost one. The ventral subsection, covering the dorsal subsection laterally, originates from the medial surface of the dorsal portion of the cleithrum, and is inserted onto the bases of all lower filament like rays.

The adductor profundus, situated lateral to the adductor superficialis, is divided into two subsections, the dorsal and ventral subsections. The dorsal subsection originates from the medial surface of the cleithrum, scapula, coracoid, the second and third actinosts, and is inserted onto the bases of all upper pectoral rays, except for the uppermost one. It is fused with the arrector dorsalis dorsally. The ventral subsection originates from the medial surface of the ventral portion of the cleithrum, the coracoid and the fourth actinost, and is inserted onto the bases of all lower filament like rays.

The arrector dorsalis lies lateral to the adductor superficialis and dorsal to the adductor profundus. It originates from the medial surface of the cleithrum, coracoid and scapula, and is inserted onto the base of the uppermost ray. It is fused with the dorsal subsection of the adductor profundus ventrally. This muscle is separated from the dorsal subsection of the adductor superficialis by a branch of the pectoral plexus nerve.

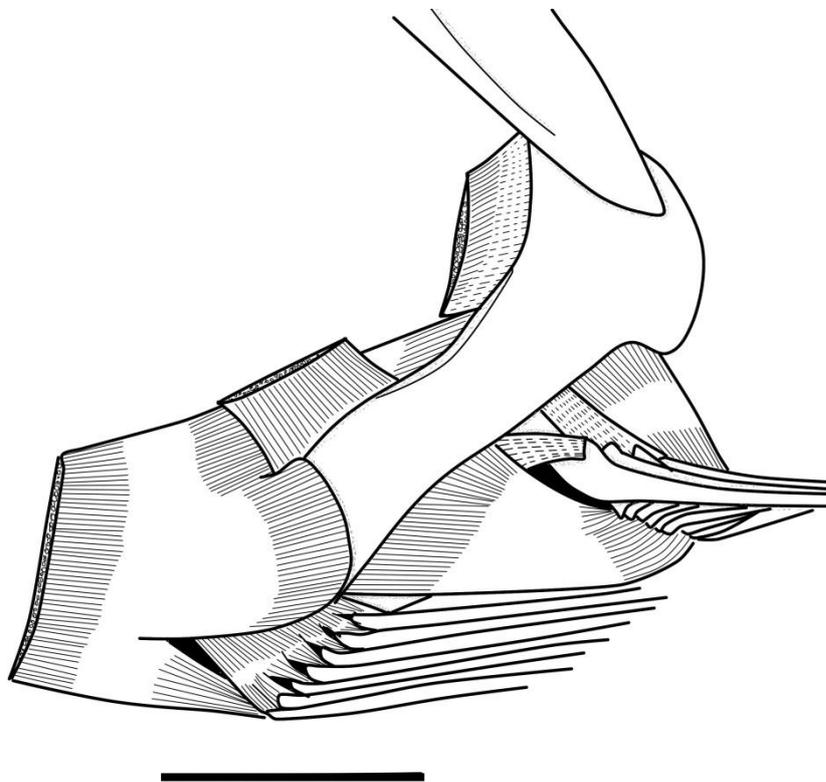
The adductor radialis is a small sheet-like muscle, located lateral to the ventral subsection of the adductor profundus. It originates from the coracoid, and third and fourth actinosts, and is inserted onto the bases of all lower filament like

rays.

The levator pectoralis originates from the posterior region of the cranium, and is inserted onto the supracleithrum and the dorsal tip of the cleithrum.

The protractor pectoralis is a slender muscle. It originates from the pterotic and is inserted onto the cleithrum via a membranaceous tendon.

The unidentified muscle, partly fused with the body muscle, connects the rod-like process of the coracoid and lower postcleithrum.



**Fig. 52.** Lateral view of pectoral girdle of *Polydactylus virginicus*. Bar indicates 10 mm.

**Remarks.** Identification of arrector dorsalis. The arrector dorsalis is a muscle situated lateral to the adductor superficialis and dorsal to the adductor profundus, also being lateral to the adductor superficialis. Winterbottom (1974) described

that the arrector dorsalis was usually inserted onto the uppermost pectoral fin ray. In contrast, Winterbottom (1974) also noticed that the insertion of the adductor profundus were all the pectoral fin rays except for the uppermost one. Furthermore, the arrector dorsalis is usually separated from the adductor superficialis by a branch of the pectoral plexus nerve (this study). In polynemids, an independent arrector dorsalis is absent. In contrast, a muscular mass situated lateral to the dorsal subsection of the adductor superficialis is inserted onto the bases of all upper pectoral rays. In addition, this muscular mass is separated from the dorsal subsection of the adductor superficialis by the branch of the pectoral plexus nerve. Thus this study assumed that the arrector dorsalis is present and fused with the dorsal subsection of the adductor profundus to form the muscular mass.

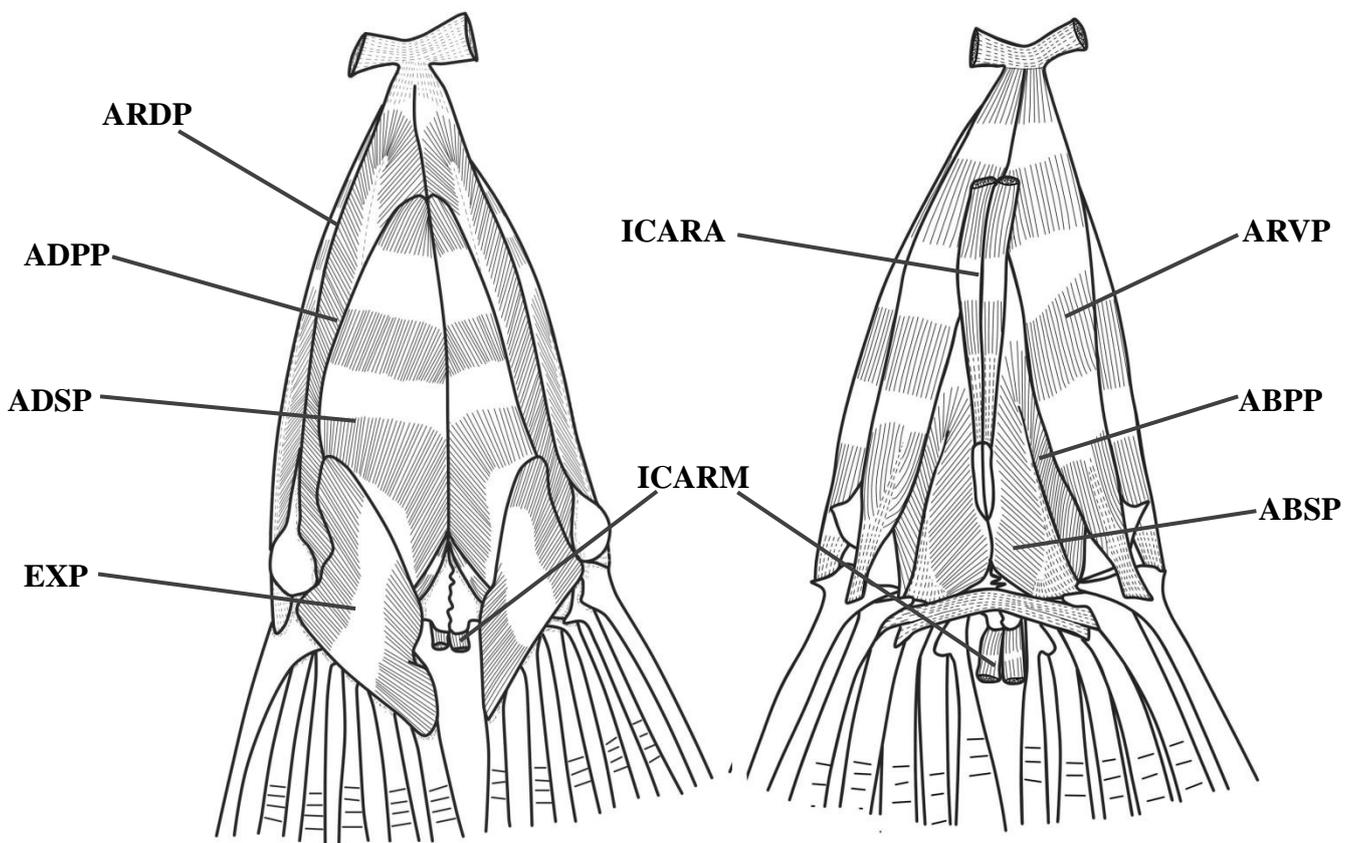
### **Character recognition**

**TS 58. Ventral subsection of abductor superficialis.** 0: continuous to form a single mass; 1: split into several bundles.

The ventral subsection of the abductor superficialis is continuous to form a single mass in most polynemids (character 58-0) (Fig. 52), while it is split into several bundles connecting the respective lower filament like rays in *Pentanemus quinquarius*, *Leptomelanosoma indicum*, *Parapolynemus verekeri* and *Polynemus* (character 58-1) (Fig. 50). The abductor superficialis is not divided into two subsections in sciaenids, but the lower portion is not split into any bundles (character 58-0) (e.g., Sasaki, 1989; this study).

## 2-6 Pelvic fin muscles (Figs. 53)

**Description.** The pelvic muscles comprise the adductor superficialis pelvici, adductor profundus pelvici, arrector dorsalis pelvici, extensor proprius, abductor superficialis pelvici, abductor profundus pelvici and arrector ventralis pelvici.



**Fig. 53.** Dorsal (left) and ventral (right) views of pelvic fin muscles of *Parapolyneemus verekeri*. ABPP, abductor profundus pelvici; ABSP, abductor superficialis pelvici; ADPP, adductor profundus pelvici; ADSP, adductor superficialis pelvici; ARDP, arrector dorsalis pelvici; ARVP, arrector ventralis pelvici; EXP, extensor proprius; ICARA, infracarinalis anterior; ICARM, infracarinalis medius. Bar indicates 10 mm.

The adductor superficialis pelvici covers the adductor profundus pelvici ventrally and is attached by the extensor proprius dorsolaterally. This muscle is inserted onto the bases of the soft rays and spine.

The adductor profundus pelvici originates from the dorsal surface of the pelvis and is inserted onto the bases of the soft rays and spine.

The arrector dorsalis pelvici originates from the lateral surface of the pelvis and is inserted onto the base of the pelvic spine.

The extensor proprius, situated dorsal to the adductor superficialis pelvici and adductor profundus pelvici, is inserted onto the innermost ray.

The abductor superficialis pelvici lies ventral to the abductor profundus, and is inserted onto the bases of the soft rays and spine via a tendon. It is attached with the subpelvic process.

The abductor profundus pelvici, situated dorsal to the abductor superficialis pelvici and arrector ventralis pelvici, originates from the ventral surface of the pelvis, and is inserted onto the bases of the soft rays.

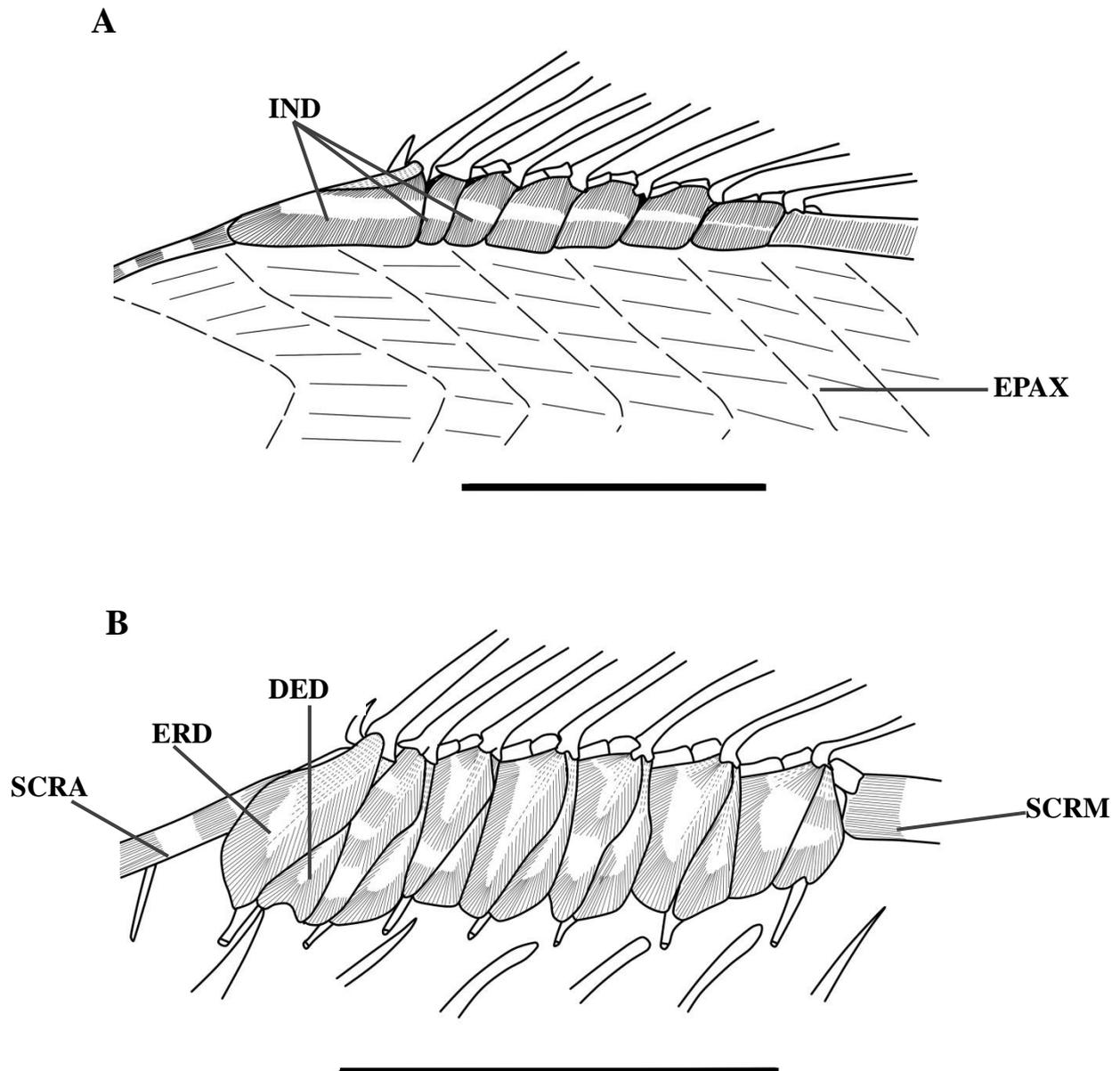
The arrector ventralis pelvici, situated ventrolateral to the abductor superficialis pelvici and abductor profundus pelvici, originates from the ventrolateral aspect of the pelvis and is inserted onto the base of the pelvic spine.

### **Character recognition**

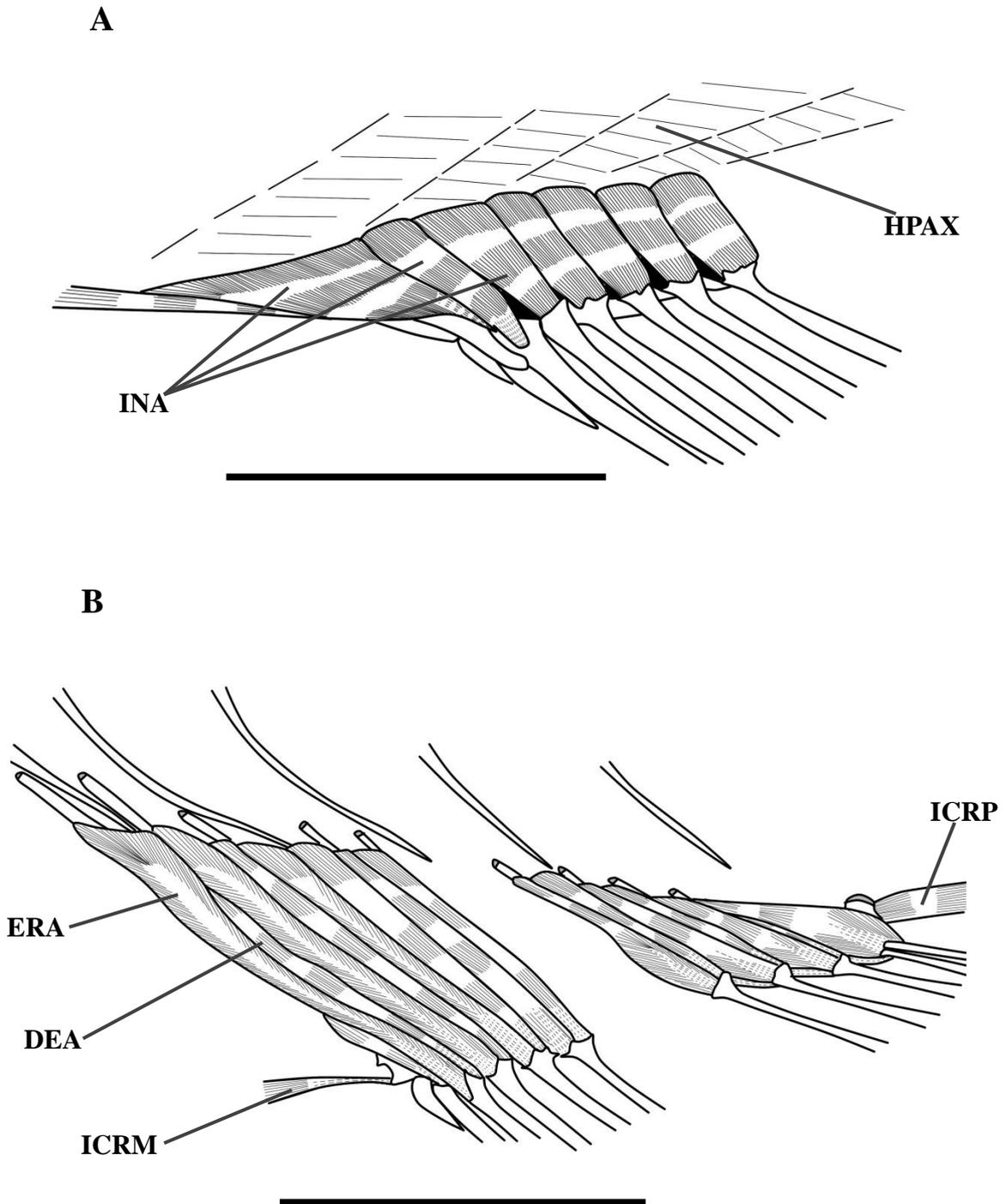
No characters available for phylogenetic analysis were recognized.

## 2-7. Muscles associated with median fins (Figs. 54–56)

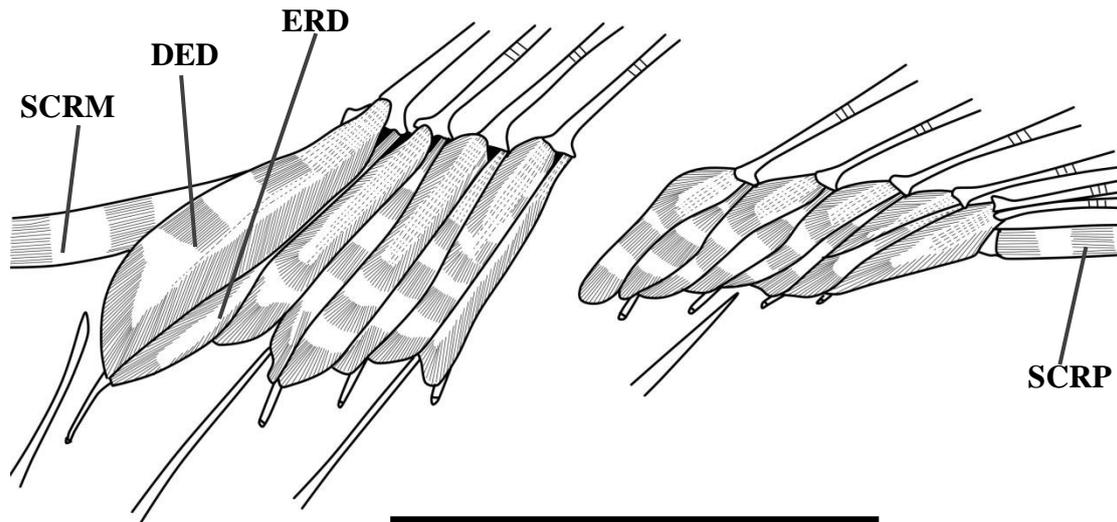
**Description.** Median fin muscles include three muscular categories, the erector, depressor and inclinator. The carinal muscles are also described here.



**Fig. 54.** Lateral aspect of muscles associated with first dorsal fin in *Parapolyneumus verekeri*. A, first dorsal fin after removal of skin; B, first dorsal fin after removal of inclinatores dorsales and epaxialis. DED, depressores dorsales; ERD, erectores dorsales; EPAX, epaxialis; IND, inclinatores dorsales; SCRA, supracarinalis anterior; SCRUM, supracarinalis medius. Bars indicate 10 mm.



**Fig. 55.** Lateral aspect of muscles associated with anal fin in *Leptomelanosoma indicum*. A, anal fin after removal of skin; B, anal fin after removal of inclinatores anales and hypaxialis. DEA, depressores anales; ERA, erectores anales; HPAX, hypaxialis; ICRM, infracarinalis medius; ICRM, infracarinalis posterior; INA, inclinatores anales. Bars indicate 10 mm.



**Fig. 56.** Lateral aspect of muscles associated with second dorsal fin after removal of inclinatore dorsalis and epaxialis in *Parapolyneemus verekeri*. DED, depressores dorsales; ERD, erectores dorsales; SCRMP, supracarinalis posterior; SCRMP, supracarinalis medius. Bar indicates 10 mm.

The dorsal fin muscles are composed with the inclinatore dorsales, erectores dorsales and depressores dorsales.

The inclinatore dorsales are superficial sheet-like muscles, lying on the epaxialis. These muscles originate from the fascia between the skin and epaxialis and are inserted onto the lateral bases of the spines and soft rays of dorsal fin. The inclinatore dorsalis inserted onto the last spine of the first dorsal fin is continuous with that of the anteriormost spine of the second dorsal fin.

The erectores dorsales originate from the anterolateral surfaces of the dorsal fin proximal pterygiophores, with which the spines or the soft rays articulate, and the posterolateral surfaces of the preceding dorsal fin proximal pterygiophores, except for the anteriormost ones of the first and second dorsal fins, which only originate from the lateral surfaces of the anteriormost dorsal fin proximal pterygiophores in both the first and second dorsal fins, respectively.

The *erectores dorsales* are inserted onto the bases of the dorsal fin spines and soft rays anteromedially.

The *depressores dorsales* originate from the lateral surfaces of the dorsal fin proximal pterygiophores, with which the spines or the rays articulate, and are inserted onto the posterolateral bases of the dorsal fin spines and soft rays.

The anal fin muscles consist of the *inclinatores anales*, *erectores anales* and *depressores anales*.

The *inclinatores anales* are superficial sheet-like muscles, lying on the hypaxialis. These muscles originate from the fascia between the skin and hypaxialis and are inserted onto the lateral bases of spines and soft rays of the anal fin.

The *erectores anales* originate from the anterolateral surfaces of the anal fin proximal pterygiophores, with which the spines or the rays articulate, and the posterolateral surfaces of the preceding anal fin proximal pterygiophores, except for the anteriormost one, which only originates from the lateral surface of the anteriormost anal fin proximal pterygiophore. These muscles are inserted onto the bases of the anal fin spines and soft rays anteromedially.

The *depressores anales* originate from the lateral surfaces of the anal fin proximal pterygiophores, with which the spines or soft rays articulate, and are inserted onto the posterolateral bases of the anal fin spines and soft rays.

The carinal muscles include the *supracarinalis anterior*, *supracarinalis medius*, *supracarinalis posterior*, *infracarinalis anterior*, *infracarinalis medius* and *infracarinalis posterior*.

The supracarinalis anterior connects the posterodorsal portion of the supraoccipital and the anterior portion of the first proximal pterygiophore of the first dorsal fin.

The supracarinalis medius is a slender muscle, connecting the last proximal pterygiophore of the first dorsal fin and the anteriormost proximal pterygiophore of the second dorsal fin.

The supracarinalis posterior is a rod-like muscle, situated between the last proximal pterygiophore of the second dorsal fin and the neural spine on the third preural centrum.

The infracarinalis anterior connects the anteroventral portion of the cleithrum and the anterior tip of the subpelvic process.

The infracarinalis medius is a paired muscle, connecting the postpelvic process and the anteroventral portion of the first proximal pterygiophore of anal fin.

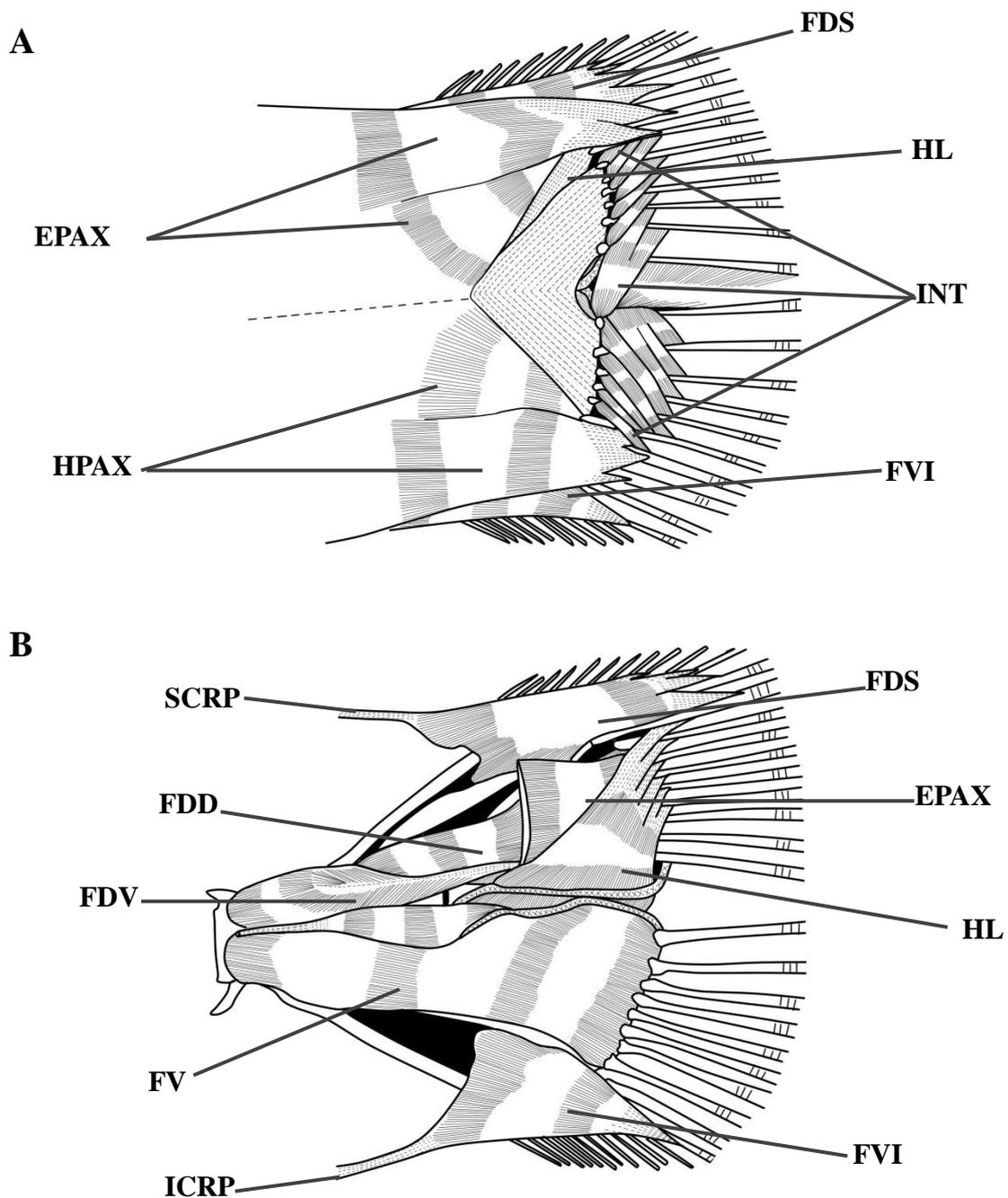
The infracarinalis posterior is a rod-like muscle, situated between the last proximal pterygiophore of the anal fin and the hemal spine on the third preural centrum.

### **Character recognition**

No characters available for phylogenetic analysis were recognized.

## 2-8 Caudal fin muscles (Fig. 57)

**Description.** The caudal fin muscles consist of the interradialis, hypochordal longitudinalis, flexor dorsalis superior, flexor dorsalis, flexor ventralis and flexor ventralis inferior. The adductor dorsalis is absent. An independent flexor ventralis externus is also absent.



**Fig. 57.** Lateral aspect of muscles associated with caudal fin in *Polydactylus opercularis*. A, caudal fin after removal of skin; B, caudal fin after removal of interradialis, hypaxialis and epaxialis. EPAX, epaxialis; FDD and FDV, dorsal and ventral subsections of flexor dorsalis, respectively; FDS, flexor dorsalis superior; FV, flexor ventralis; FVI, flexor ventralis inferior; HL, hypochochordal longitudinalis; HPAX, hypaxialis; ICRP, infracarinalis posterior; INT, interradialis; SCRCP, supracarinalis posterior. Bar indicates 10 mm.

The interradiialis is located between the caudal fin rays and split into the dorsal and ventral elements, associated with the dorsal and ventral lobes of the caudal fin, respectively.

The hypochordal longitudinalis, a triangular muscle, originates from the urostyle, parhypurapophysis, and the first and second hypurals, and is inserted onto the upper six principle caudal fin rays on the upper dorsal lobe via tendons.

The flexor dorsalis superior originates from the neural spines of the second and third preural centra, and epurals, and is inserted onto several caudal fin rays including procurrent and principle rays on the posterodorsal corner of upper caudal skeletons.

The flexor dorsalis is divided into two subsections, the dorsal and ventral subsections. The dorsal subsection originates from the second preural centra, uroneural, urostyle, and third to fifth hypurals, and is inserted onto the bases of the branched caudal fin rays of the upper lobe. The ventral subsection originates from the second and third preural centra, and is inserted onto the bases of the lowermost two branched caudal fin rays of the upper lobe via a tendon. The anterior portion of the ventral subsection is slightly partly fused with the dorsal subsection in a few polynemids.

The flexor ventralis, a thick muscular mass located ventral to the hypochordal longitudinalis and flexor dorsalis, originates from the hemal spine and centra of the second to third preural centra, urostyle, first and second hypurals and parhypural, and is inserted onto the bases of all eight principle caudal fin rays of the lower lobe.

The flexor ventralis inferior originates from the parhypural and hemal spines of the second to third preural centra, and is inserted onto bases of several procurrent caudal fin rays on the posteroventral corner of the lower caudal skeletons of the lower lobe.

**Remarks.** Absence of independent flexor ventralis externus. The flexor ventralis externus is a muscle lying lateral to the flexor ventralis. Winterbottom (1974) described that it arose from the hemal spines and passed posteriorly (or posterodorsally) to insert on the two or three uppermost rays of the ventral half of the caudal fin in many perciforms, while it was absent in some taxa. In polynemids, an independent flexor ventralis externus is absent, showing two possibilities; 1) this element was lost, and 2) it was fused with the flexor ventralis. However, because it cannot be determined which one was occurred, further study, including ontogenetic examination, is needed.

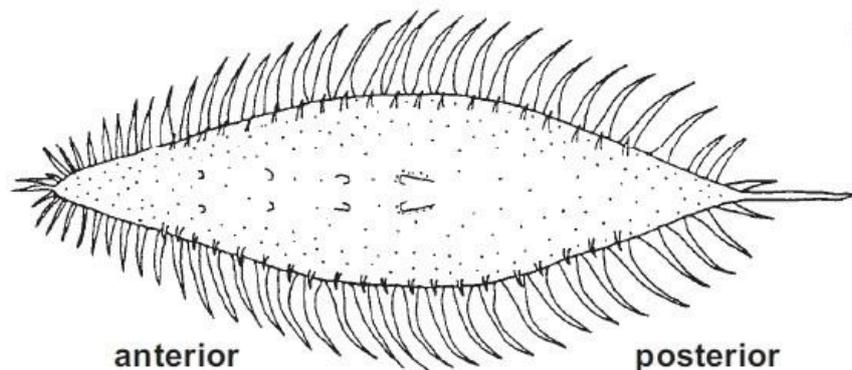
### **Character recognition**

No characters available for phylogenetic analysis were recognized.

### 3. Others

#### 3-1 Swimbladder (Fig. 58)

**Description.** The swimbladder is present in polynemids, except for *Eleutheronema*, *Polydactylus multiradiatus*, *Polydactylus nigripinnis*, *Polydactylus opercularis*, *Polynemus melanochir melanochir* and *Polynemus paradiseus*, in which it is absent. The swimbladder is simple and lacks specialized structures in polynemids when it is present, except for *Leptomelanosoma indicum*, in which it possesses many appendages inserted onto lateral walls of the abdominal cavity. The muscles associated with the swimbladder are absent.



**Fig. 58.** Dorsal view of swimbladder in *Leptomelanosoma indicum* (from Motomura, 2004).

#### Character recognition

**TS 59. Swimbladder.** 0: present; 1: absent.

The swimbladder is present in polynemids (character 59-0), except for *Eleutheronema*, *Polydactylus multiradiatus*, *Polydactylus nigripinnis*, *Polydactylus opercularis*, *Polynemus melanochir melanochir* and *Polynemus*

*paradiseus*, in which it is absent (character 59-1). The swimbladder is present in Sciaenidae (character 59-0) (e.g., Sasaki, 1989; this study).

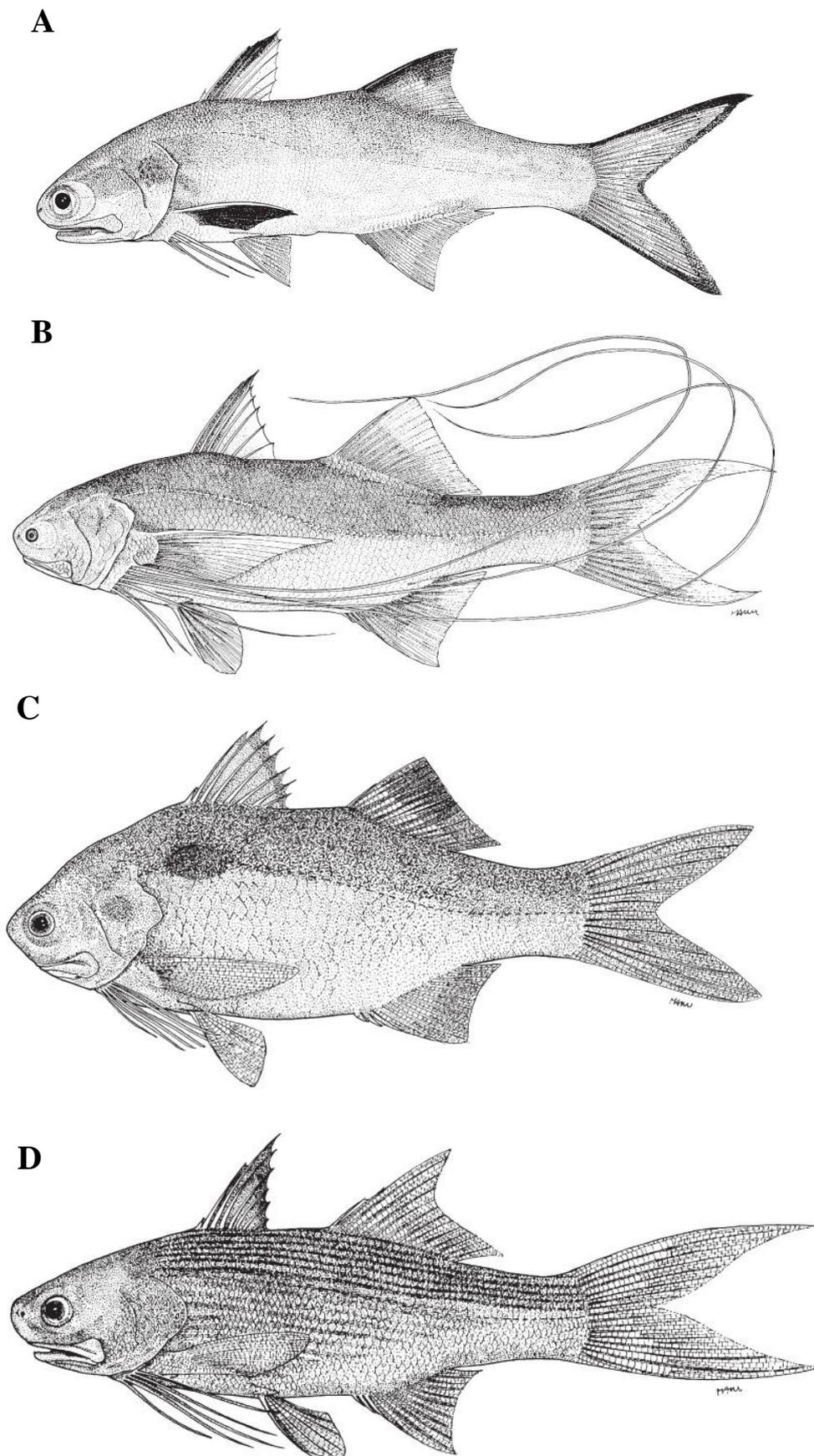
**TS 60. Appendages of swimbladder.** 0: absent; 1: present.

The swimbladder is simple and lacks specialized structures in polynemids when it is present (character 60-0), except for *Leptomelanosoma indicum*, in which it possesses many appendages inserted onto lateral walls of the abdominal cavity (character 60-1) (Fig. 58). Polynemid species lacking the swimbladder is coded as “?”. Both conditions are present in sciaenids; for example, the swimbladder is simple in *Equetus*, *Pareques*, *Leiostomus*, *Ctenosciaena*, *Umbrina*, *Menticirrhus* and *Cheilotrema*, while it has some appendages in *Protonibea*, *Megalonibea*, *Roncador*, *Genyonemus*, *Pogonias* and *Larimichthys* (characters 60-0 and 60-1) (e.g., Sasaki, 1989; this study).

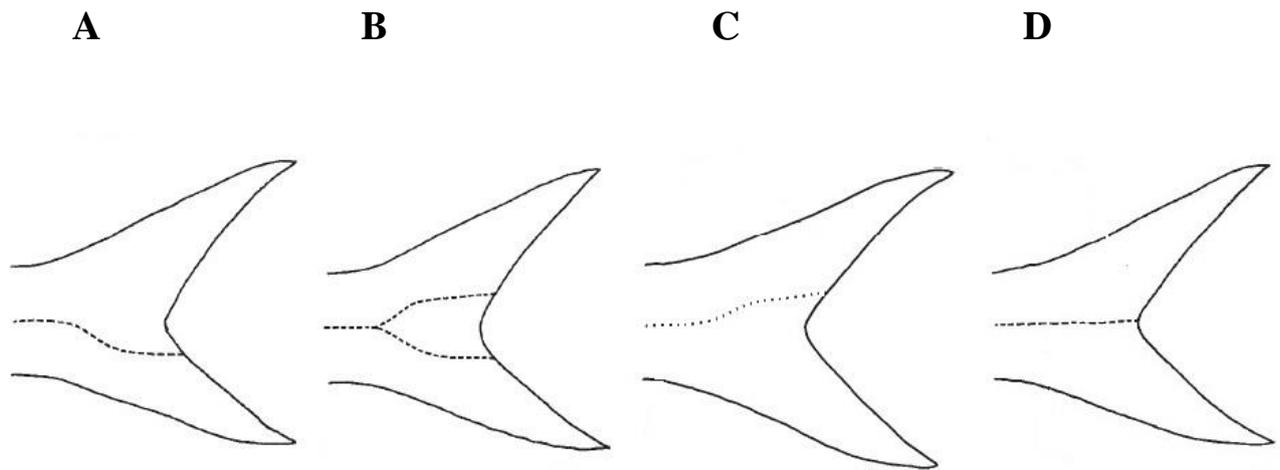
### 3-2 External morphology (Figs. 59–61)

**Description.** The polynemids have an obtusely conical, overhanging snout and an inferior mouth which is near-horizontal and large. The maxilla extends beyond the level of the posterior margin of the eye. Teeth are villiform on the broad bands on the jaws, vomer, palatines and ectopterygoids (vomerine teeth is absent in some species). The adipose eyelid (firm transparent gelatinous tissue) covers the eye and extends dorsally to the surface of the neurocranium under the skin. The body is elongated to deep and compressed. The polynemids have two well-separated dorsal fins. The first dorsal fin contains eight spines (seven spines in two species of *Polynemus*), and the second dorsal fin a single spine and 11 to 18 soft rays. The anal fin contains three spines and 10 to 18 soft rays (two spines in two species of *Polynemus* and 24 to 30 soft rays in *Pentanemus quinquarius*). The pectoral fin is divided into two sections: the upper part with 12 to 19 rays joined by the membrane and the lower part with 3 to 16 individually-separated filament-like rays. The filament-like rays are slightly elongate but and the longest one does not reach to the caudal fin in polynemids, except for *Pentanemus quinquarius*. *Parapolynemus verekeri* and *Polynemus*, in which the filament-like rays are well elongate and the longest one extends to the causal fin. The pectoral-fin insertion is well below the midline of the body in polynemids, except for *Parapolynemus verekeri* and *Polynemus*, in which the pectoral-fin insertion is near the midline of the body. The pelvic fin contains a single spine and five soft rays. The caudal fin is deeply forked to lunate. Body scales are weakly ctenoid and some small scales cover most of the dorsal, pectoral, anal

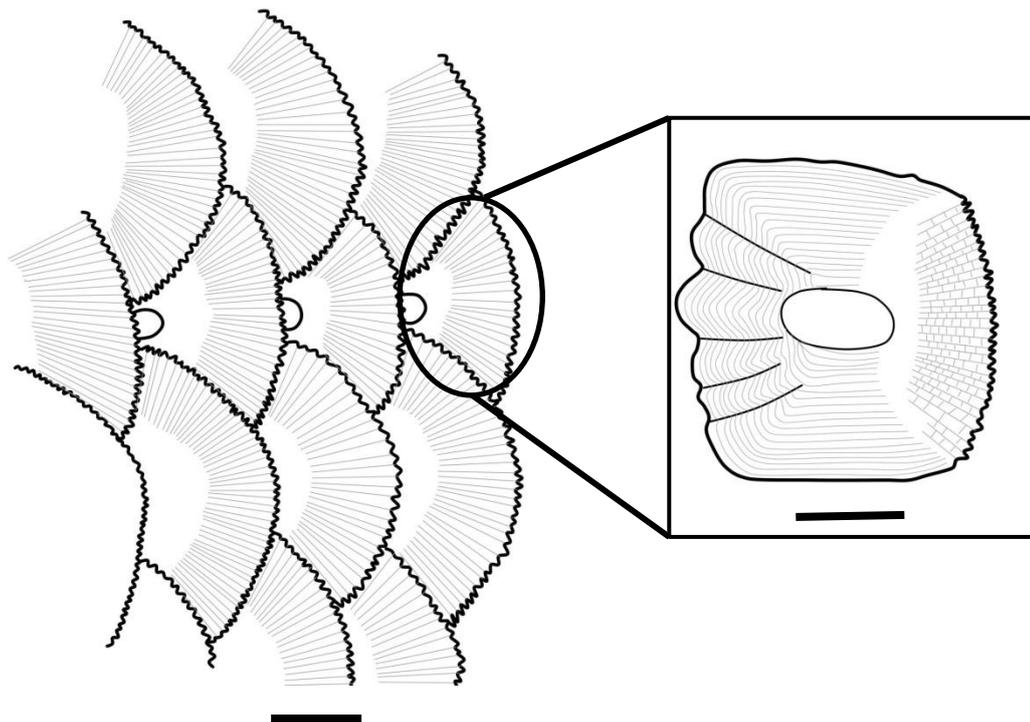
and caudal fins. The lateral line is simple and extends from the upper end of the gill opening to the posterior margin of the caudal-fin membrane. The posterior portion of the lateral line on the caudal-fin membrane extends along the midline of the caudal fin in *Filimanus*, *Pentanemus quinquarius* and *Polynemus*. It bifurcates on the caudal-fin base, and the upper branch extending to the lower end of the upper caudal-fin lobe and the lower branch extending to the middle of the lower caudal-fin lobe in *Polydactylus approximans*, *Polydactylus octonemus*, *Polydactylus oligodon* and *Polydactylus virginicus*. It extends to the lower end of the upper caudal-fin lobe in *Galeoides decadactylus*, and to the upper end of the lower caudal-fin lobe in other polynemids. A black spot is present above the anterior portion of the lateral line in *Polydactylus sextarius* and *Polydactylus microstomus*, and it is present below the latter in *Galeoides decadactylus*, while it is absent in other polynemids. Several longitudinal stripes are present along the body axis in *Polydactylus plebeius*, *Polydactylus sexfilis* and *Galeoides decadactylus*, whereas they are absent in other polynemids.



**Fig. 59.** Lateral sketches of four polynemids (from Motomura, 2004). A, *Eleutheronema rhadinum*; B, *Polynemus paradiseus*; C, *Polydactylus sextarius*; D, *Polydactylus plebeius*.



**Fig. 60.** Diagrammatic illustrations of lateral-line patterns on caudal fin. A, *Polydactylus plebeius*; B, *Polydactylus virginicus*; C, *Galeoides decadactylus*; D, *Filimanus similis*.



**Fig. 61.** Lateral view of lateral line and scales in *Polydactylus oligodon*. Bars = 1 mm.

## Character recognition

**TS 61. Length of filament-like rays.** 0: not elongate; 1: slightly elongate; 2: well elongate. (ordered)

The filament-like rays are slightly elongate but the longest one does not reach to the caudal fin in polynemids (character 61-1) (Fig. 59A, C, D), except for *Pentanemus quinquarius*, *Parapolynemus verekeri* and *Polynemus*, in which the filament-like rays are well elongate and the longest one extends to the caudal fin (character 61-2) (Fig. 59B). Sciaenids lack the filament-like rays, but no pectoral fin rays are elongate (character 61-0).

**TS 62. Posterior portion of lateral line.** 0: extending along midline of caudal fin; 1: bifurcating, upper branch extending to lower end of upper caudal-fin lobe and lower branch secondarily extending to middle of lower caudal-fin lobe; 2: extending to upper end of lower caudal-fin lobe; 3: extending to lower end of upper caudal-fin lobe. (unordered)

The posterior portion of the lateral line on the caudal-fin membrane extends along the midline of the caudal fin in *Filimanus*, *Pentanemus quinquarius* and *Polynemus* (character 62-0) (Fig. 60D). It bifurcates on the caudal-fin base, and the upper branch extending to the lower end of the upper caudal-fin lobe and the lower branch extending to the middle of the lower caudal-fin lobe in *Polydactylus approximans*, *Polydactylus octonemus*, *Polydactylus oligodon* and *Polydactylus virginicus* (character 62-1) (Fig. 60B). It extends to the lower end of the upper caudal-fin lobe in *Galeoides decadactylus* (character 62-3) (Fig.

60C), and to the upper end of the lower caudal-fin lobe in other polynemids (character 62-2) (Fig. 60A). The posterior portion of the lateral line on the caudal-fin membrane extends along the midline of the caudal fin in sciaenids (character 62-0) (e.g., Sasaki, 1989; this study).

**TS 63. Black spot.** 0: absent; 1: present above anterior portion of lateral line; 2: below anterior portion of lateral line. (unordered)

A black spot is present on the anterior portion of the lateral line in *Polydactylus sextarius* and *Polydactylus microstomus* (character 63-1) (Fig. 59C), and it is present below the latter in *Galeoides decadactylus* (character 63-2), while it is absent in other polynemids (character 63-0) (Fig. 59A, B, D). Sciaenids lack this black spot on the area (character 63-0) (e.g., Sasaki, 1989; this study).

**Remarks.** The position of the black spot in *Polydactylus sextarius* and *Polydactylus microstomus* is different from but near to that in *Galeoides decadactylus* as mentioned above and in Description. Both conditions are derived, whereas their homology is unclear; thus they were coded as different characters and unordered to retain two possibilities, (1) they were independently derived from the primitive character 63-0 and (2) one of them was derived from another derived character.

**TS 64. Longitudinal stripes along body axis.** 0: absent; 1: present.

Several longitudinal stripes are present along the body axis in *Polydactylus plebeius*, *Polydactylus sexfilis* and *Galeoides decadactylus* (character 64-1) (Fig. 59D), whereas they are absent in other polynemids (character 64-0) (Fig.

59A–C). Such stripes are absent in sciaenids (character 64-0), although the juveniles of *Umbrina ronchus* have oblique stripes on the body (the stripes are absent in its adults) (e.g., Sainsbury *et al*, 1984; Smith and Heemstra, 1986; Randall, 1995; this study). However, these stripes in polynemids and sciaenids are considered to be non-homologous, because their directions are different.

## **Other variation**

**Insertion of pectoral fin base well below midline of body.** The pectoral-fin insertion is well below the midline of the body in polynemids (Fig. 59A, C, D), except for *Parapolynemus verekeri* and *Polynemus*, in which the pectoral-fin insertion is near the midline of the body. The pectoral-fin insertion is near the midline of the body in sciaenids (this study). The former condition is possessed by the species having the well-developed dorsal limb of the cleithrum (character 35-0), while the latter condition is possessed by the species having the weakly-developed dorsal limb of the cleithrum (character 35-1) (see TS 35). It can be assumed that the position of the pectoral-fin insertion is well associated with the development degree of the dorsal limb of the cleithrum. Therefore, the character on the pectoral-fin insertion is not separately used for the phylogenetic analysis in this study.

## VII. Phylogenetic relationships of Polynemidae

Phylogenetic relationships of Polynemidae are reconstructed by characters in 64 transformation series (Table 2). The characters matrix is showed in Table 3. Four most parsimonious trees of Polynemidae were obtained as the result of the phylogenetic analysis. The consistency index was 0.49, rescaled consistency index 0.35 and tree length 153. A strict consensus tree of four most parsimonious trees is shown in Figure 61. The characters commonly supporting each clade in all four most parsimonious trees are described below and in Figure 62. Reversal characters are labeled by “r”. Asterisk represents an autapomorphic character. “A” and “D” are characters according to ACCTRAN and DELTRAN.

Clade A includes all examined polynemids. After the phylogenetic analysis, the monophyly of the family Polynemidae is also unambiguously supported by the following three synapomorphies: fourth infraorbital covering fifth laterally (character 4-1), adductor section 2 restricted to posterolateral surface of second epibranchial (character 55-1), filament-like rays slightly elongate (character 61-1). This clade is also supported by three synapomorphies according to ACCTRAN: endopterygoid and quadrate separated medially (character 25-1), well-developed thin semicircular sheet expansion of preopercle present (character 27-1) and flange on cleithrum well developed (character 36-1). All of them have the reversal or change to further derived characters. Thus, the monophyly of the family Polynemidae is strongly supported by 20 unambiguous synapomorphies and three (plus three according to ACCTRAN) potential synapomorphies. Clade A is divided into clades B1 and B2.

## **Description of relationships and characters supporting clades**

**Clade B1.** Includes all examined polynemids, except for *Pentanemus quinquarius*, *Parapolynemus verekeri* and *Polynemus*, and is unambiguously supported by four synapomorphies: 5-1, 8-1\*, 29-1 and 38-1\*. Clade B1 is divided into clades C1 and C2.

**Clade B2.** Includes *Pentanemus quinquarius*, *Parapolynemus verekeri* and *Polynemus*, and is unambiguously supported by four synapomorphies: 37-1\*, 39-1, 58-1 and 61-2\*. This clade is also supported by two synapomorphies (28-1 and 54-1) according to ACCTTRAN. Clade B2 is divided into clades E1 and E2.

**Clade C1.** Includes *Polydactylus*, *Galeoides decadactylus*, *Leptomelanosoma indicum* and *Eleutheronema*, and is unambiguously supported by three synapomorphies: 18-1, 30-0r and 62-2. Clade C1 is divided into clades D1, D2, D3, D4, D5 and D6.

**Clade C2.** Includes the genus *Filimanus*, and is unambiguously supported by four synapomorphies: 4-2, 10-1\*, 20-1 and 22-1. This clade is also supported by one synapomorphy (12-1) according to DELTRAN. Clade C2 is divided into clades L1 and L2.

**Clade D1.** Includes *Polydactylus plebeius*, *Polydactylus sexfilis*, *Polydactylus virginicus*, *Polydactylus approximans*, *Polydactylus octonemus* and *Polydactylus oligodon*. No common synapomorphies support this clade in four most parsimonious trees (31-1 in one tree and 56-1 in three). Clade D1 is divided into clades F1 and F2.

**Clade D2.** Includes *Polydactylus opercularis*, *Leptomelanosoma indicum* and *Eleutheronema*, and is unambiguously supported by three synapomorphies: 14-1, 21-0r and 46-2. This clade is also supported by two synapomorphies (45-1 and 60-1\*) according to ACCTRAN, and by one synapomorphy (12-1) according to DELTRAN. Clade D2 is divided into clades G1 and G2.

**Clade D3.** Includes *Galeoides decadactylus*, *Polydactylus sextarius* and *Polydactylus microstomus*, and is unambiguously supported by two synapomorphies, 17-0\* and 63-1. This clade is also supported by one synapomorphy (4-2) according to ACCTRAN. Clade D3 is divided into clades K1 and K2.

**Clade D4.** Includes *Polydactylus multiradiatus*, and has one derived character, 6-1.

**Clade D5.** Includes *Polydactylus nigripinnis*, and possesses eight derived characters: 3-1, 13-1, 14-1, 24-1, 30-1r, 40-2\*, 43-1 and 50-1r. This clade also has two derived characters (12-1 and 16-1) according to DELTRAN.

**Clade D6.** Includes *Polydactylus macrochir*, and has one derived character, 9-1.

**Clade E1.** Includes *Pentanemus quinquarius*, and has four derived characters: 3-1, 22-1, 24-1 and 41-1. This clade also possesses two derived characters (25-0r\* and 27-0r\*) according to ACCTRAN, and two derived characters (28-1 and 54-1) according to DELTRAN.

**Clade E2.** Includes *Parapolynemus verekeri* and *Polynemus*, and is unambiguously supported by six synapomorphies: 2-1\*, 7-1\*, 15-0\*, 35-1\*, 43-1

and 46-2. This clade is also supported by two synapomorphies (1-1 and 36-0r) according to ACCTRAN. Clade E2 is divided into clades H1 and H2.

**Clade F1.** Includes *Polydactylus plebeius* and *Polydactylus sexfilis*, and is unambiguously supported by one synapomorphy, 64-1. Clade F1 is divided into clades N1 and N2.

**Clade F2.** Includes *Polydactylus virginicus*, *Polydactylus approximans*, *Polydactylus octonemus* and *Polydactylus oligodon*, and is unambiguously supported by one synapomorphy, 62-1\*. Clade F2 is divided into clades I1, I2 and I3.

**Clade G1.** Includes *Polydactylus opercularis* and *Eleutheronema*, and is unambiguously supported by five synapomorphies: 17-2\*, 19-1\*, 51-1\*, 53-1\* and 59-1. This clade is also supported by one synapomorphy (13-1) according to ACCTRAN. Clade G1 is divided into clades J1 and J2.

**Clade G2.** Includes *Leptomelanosoma indicum*, and unambiguously has three derived characters: 29-0r, 40-1 and 58-1. This clade also has two derived characters (45-1 and 60-1\*) according to DELTRAN.

**Clade H1.** Includes *Parapolyneumus verekeri*, and unambiguously possesses six derived characters: 4-0r\*, 20-1, 40-1, 48-1\*, 57-1\* and 62-2. This clade also has three derived characters (1-1, 28-1 and 54-1) according to DELTRAN.

**Clade H2.** Includes the genus *Polynemus*, and is unambiguously supported by four synapomorphies: 9-1, 42-1, 50-0r and 52-1\*. This clade is also supported by three synapomorphies (28-0r, 32-1 and 54-0r) according to ACCTRAN. Clade H2 is divided into clades M1 and M2.

**Clade I1.** Includes *Polydactylus virginicus*. This clade has no derived characters.

**Clade I2.** Includes *Polydactylus approximans*, having no derived characters.

**Clade I3.** Includes *Polydactylus octonemus* and *Polydactylus oligodon*, and is unambiguously supported by one synapomorphy, 46-2. Clade I3 is divided into clades O1 and O2.

**Clade J1.** Includes the genus *Eleutheronema*, and is unambiguously supported by four synapomorphies: 23-1\*, 26-1\*, 42-1 and 44-1\*. This clade is also supported by one synapomorphy (45-1) according to DELTRAN. Clade J1 is divided into clades P1 and P2.

**Clade J2.** Includes *Polydactylus opercularis*, and has four derived characters: 22-1, 30-1r, 31-1 and 38-0r. This clade also has one derived character (45-0r) according to ACCTTRAN, and one derived character (13-1) according to DELTRAN.

**Clade K1.** Includes *Galeoides decadactylus* and *Polydactylus sextarius*, and is unambiguously supported by two synapomorphies, 6-1 and 47-1. Clade K1 is divided into clades Q1 and Q2.

**Clade K2.** Includes *Polydactylus microstomus*, and has two derived characters (4-2 and 16-1) according to DELTRAN.

**Clade L1.** Includes *Filimanus similis* and *Filimanus xanthonema*, and is unambiguously supported by one synapomorphy, 56-1. Clade L1 is divided into clades R1 and R2.

**Clade L2.** Includes *Filimanus sealei*, having no derived characters.

**Clade M1.** Includes *Polynemus multifilis* and *Polynemus aquilonaris*, and is unambiguously supported by one synapomorphy, 5-1. This clade is also supported by one synapomorphy (1-0r) according to ACCTTRAN, and by one synapomorphy (32-1) according to DELTRAN. Clade M1 is divided into clades S1 and S2.

**Clade M2.** Includes *Polynemus melanochir melanochir* and *Polynemus paradiseus*, and is unambiguously supported by four synapomorphies: 18-1, 49-1\*, 56-1 and 59-1. This clade is also supported by one synapomorphy (1-1) according to DELTRAN. Clade M2 is divided into clades T1 and T2.

**Clade N1.** Includes *Polydactylus plebeius*, and unambiguously has one derived character, 50-1r.

**Clade N2.** Includes *Polydactylus sexfilis*, and unambiguously possesses three derived characters: 6-1, 34-1 and 45-1.

**Clade O1.** Includes *Polydactylus octonemus*, and unambiguously has one derived character, 50-1r.

**Clade O2.** Includes *Polydactylus oligodon*, and unambiguously has two derived characters, 4-3\* and 47-1.

**Clade P1.** Includes *Eleutheronema tetradactylum*, unambiguously having one derived character, 47-1. This clade also has one derived character (13-0r) according to ACCTTRAN.

**Clade P2.** Includes *Eleutheronema rhadinum*, and unambiguously has two derived characters: 11-1 and 34-1. This clade also has one derived character (13-1) according to DELTRAN.

**Clade Q1.** Includes *Galeoides decadactylus*, unambiguously having six derived characters: 18-0r, 30-1r, 41-0r, 62-3\*, 63-2\* and 64-1. This clade also has one derived character (4-1r) according to ACCTTRAN.

**Clade Q2.** Includes *Polydactylus sextarius*, and unambiguously possesses one derived character, 8-0r. This clade also possesses one derived character (4-2) according to DELTRAN.

**Clade R1.** Includes *Filimanus similis*, and unambiguously has one derived character, 24-1.

**Clade R2.** Includes *Filimanus xanthonema*, and unambiguously has two derived characters: 5-0r and 39-1.

**Clade S1.** Includes *Polynemus multifilis*, unambiguously having four derived characters: 21-0r, 29-1, 32-2 and 43-0r.

**Clade S2.** Includes *Polynemus aquilonaris*. This clade has no derived characters.

**Clade T1.** Includes *Polynemus melanochir melanochir*, and unambiguously has two derived characters: 32-2 and 39-2\*. This clade also possesses one derived character (28-1r) according to ACCTTRAN, and one derived character (28-1) according to DELTRAN.

**Clade T2.** Includes *Polynemus paradiseus*, and unambiguously has two derived characters: 24-1 and 46-1\*. This clade also has one derived character (32-0r) according to ACCTTRAN.

**Table 2. List of the transformation series (TS) and characters used in the analysis**

---

---

TS 1. Arrangement of infraorbitals. 0: semi-circular; 1: deeply V-shape.
TS 2. Subocular shelf on third infraorbital. 0: present; 1: absent.
TS 3. First and second infraorbitals. 0: first covering second medially; 1: posterodorsal part of first lateral to second and posteroventral part of first medial to second.
TS 4. Fourth and fifth infraorbitals. 0: not overlapped; 1: fourth covering fifth laterally; 2: fourth covering fifth medially; 3: anterodorsal portion of fourth lateral to anteroventral portion of fifth and posterodorsal portion of former medial to posteroventral portion of latter. (unordered)
TS 5. Tooth plate on prevomer. 0: absent; 1: present.
TS 6. Lateral portion of ethmoid. 0: broad; 1: narrow.
TS 7. Lateral ethmoid and pterosphenoid. 0: separated; 1: connected.
TS 8. Sensory canal on frontal. 0: bridged; 1: roofed.
TS 9. Basisphenoid. 0: present; 1: absent.
TS 10. Basisphenoid. 0: Y-shaped; 1: stick-like.
TS 11. Basisphenoid and pterosphenoid. 0: attached; 1: separated.
TS 12. Basisphenoid and prootic. 0: attached; 1: separated.
TS 13. Dorsal margin of basisphenoid and parasphenoid. 0: separated; 1: attached.
TS 14. Pterosphenoid and parasphenoid. 0: separated; 1: attached.
TS 15. Notch between ascending and articular processes. 0: deep and sharp; 1: shallow and blunt.
TS 16. Lateral cavity on center of articular process. 0: present; 1: absent.
TS 17. Lengths of alveolar and ascending processes. 0: former 0.5 to 1 time longer than latter; 1: 2 to 3 times; 2: about 5 times. (ordered as 0-1-2)
TS 18. Posterior margin of maxilla. 0: smooth; 1: serrated.
TS 19. Tooth plate on dentary. 0: mainly situated on dorsal surface; 1: well extending to lateral surface.
TS 20. Dentary foramen. 0: absent; 1: present.
TS 21. Anteromedial process of palatine. 0: absent; 1: present.
TS 22. Posterior portion of palatine. 0: greatly extending; 1: slightly extending.
TS 23. Tooth plate on palatine. 0: separated from ectopterygoid; 1: covered by ectopterygoid dorsolaterally.
TS 24. Ectopterygoid and endopterygoid. 0: autogenous; 1: fused.
TS 25. Endopterygoid and quadrate. 0: sutured medially; 1: separated medially.
TS 26. Hyomandibula and endopterygoid. 0: separated; 1: connected.
TS 27. Well-developed thin semicircular sheet expansion of preopercle. 0: absent; 1: present.
TS 28. Posterior margin of preopercle. 0: serrated; 1: smooth.
TS 29. Posteroventral portion of ventral hypohyal. 0: not extending beyond first branchiostegal ray; 1: beyond it.
TS 30. Connection of ceratohyal and epihyal on lateral surface. 0: connected via cartilaginous band; 1: interdigitating.
TS 31. Terminal tip of first branchiostegal ray. 0: pointed and smooth; 1: broad and serrated.

---

**Table 2. Continued**

---

TS 32. Tooth plates on dorsal surface of third basibranchial.	0: absent; 1: one present; 2: two present. (ordered as 0-1-2)
TS 33. Anteriorly-pointed projection on first hypobranchial.	0: extremely small; 1: large.
TS 34. Anterior and dorsolateral cartilages on second pharyngobranchial.	0: autogenous; 1: fused.
TS 35. Dorsal limb of cleithrum.	0: well developed; 1: weakly developed.
TS 36. Flange on cleithrum.	0: weakly developed; 1: well developed.
TS 37. Rod-like process.	0: slender and short; 1: robust and long.
TS 38. Third actinost.	0: shorter than fourth actinost; 1: equal to or longer than fourth actinost.
TS 39. Relation of upper and lower postcleithra.	0: former attached with latter medially; 1: former attached with latter posteriorly; 2: fused. (unordered)
TS 40. Structure of unidentified bony element.	0: long elliptical bone with tubular structure; 1: round bone with tubular structure; 2: cartilaginous. (unordered)
TS 41. Subpelvic keel.	0: well developed; 1: weakly developed or absent.
TS 42. Number of caudal vertebrae.	0: 14; 1: 15.
TS 43. Insertion of third proximal pterygiophore of first dorsal fin.	0: between third and fourth neural spines; 1: between fourth and fifth neural spines.
TS 44. Insertion of sixth proximal pterygiophore of first dorsal fin.	0: between sixth and seventh neural spines; 1: between fifth and sixth neural spines.
TS 45. Insertion of seventh proximal pterygiophore of first dorsal fin.	0: between seventh and eighth neural spines; 1: between sixth and seventh neural spines.
TS 46. First supraneural.	0: ossified; 1: cartilaginous; 2: absent. (unordered)
TS 47. Third supraneural.	0: present; 1: absent.
TS 48. Fifth post-hypural cartilage.	0: present; 1: absent.
TS 49. Origin of A1L.	0: preopercle; 1: preopercle and pterotic.
TS 50. Attachment of A1L to preopercle.	0: via tendon; 1: via tendon and muscle.
TS 51. Section A $\omega$ .	0: weakly developed and not extending anteriorly; 1: well developed and extending anteriorly.
TS 52. Insertion of anterior subsection of levator arcus palatini.	0: hyomandibula; 1: endopterygoid and metapterygoid.
TS 53. Intermandibularis.	0: weakly developed; 1: well developed.
TS 54. Origin of levator externus.	0: prootic and pterotic; 1: pterotic.
TS 55. Adductor section 2.	0: extending onto posterodorsal surface; 1: restricted to posterolateral surface.
TS 56. Adductor section 3.	0: extending onto posterodorsal surface; 1: restricted to posterolateral surface.
TS 57. Anterior bundle of transversus dorsalis anterior.	0: robust; 1: slim.
TS 58. Ventral subsection of abductor superficialis.	0: continuous to form a single mass; 1: split into several bundles.
TS 59. Swimbladder.	0: present; 1: absent.
TS 60. Appendages of swimbladder.	0: absent; 1: present.

---

**Table 2. Continued**

---

---

TS 61. Length of filament-like rays. 0: not elongate; 1: slightly elongate; 2: well elongate. (ordered)

TS 62. Posterior portion of lateral line. 0: extending along midline of caudal fin; 1: bifurcating, upper branch extending to lower end of upper caudal-fin lobe and lower branch secondarily extending to middle of lower caudal-fin lobe; 2: extending to upper end of lower caudal-fin lobe; 3: extending to lower end of upper caudal-fin lobe. (unordered)

TS 63. Black spot. 0: absent; 1: present above anterior portion of lateral line; 2: below anterior portion of lateral line. (unordered)

TS 64. Longitudinal stripes along body axis. 0: absent; 1: present.

---

---

**Table 3.** Matrix of characters in transformation series used in phylogenetic analysis (Polymorphism is shown in parenthesis)

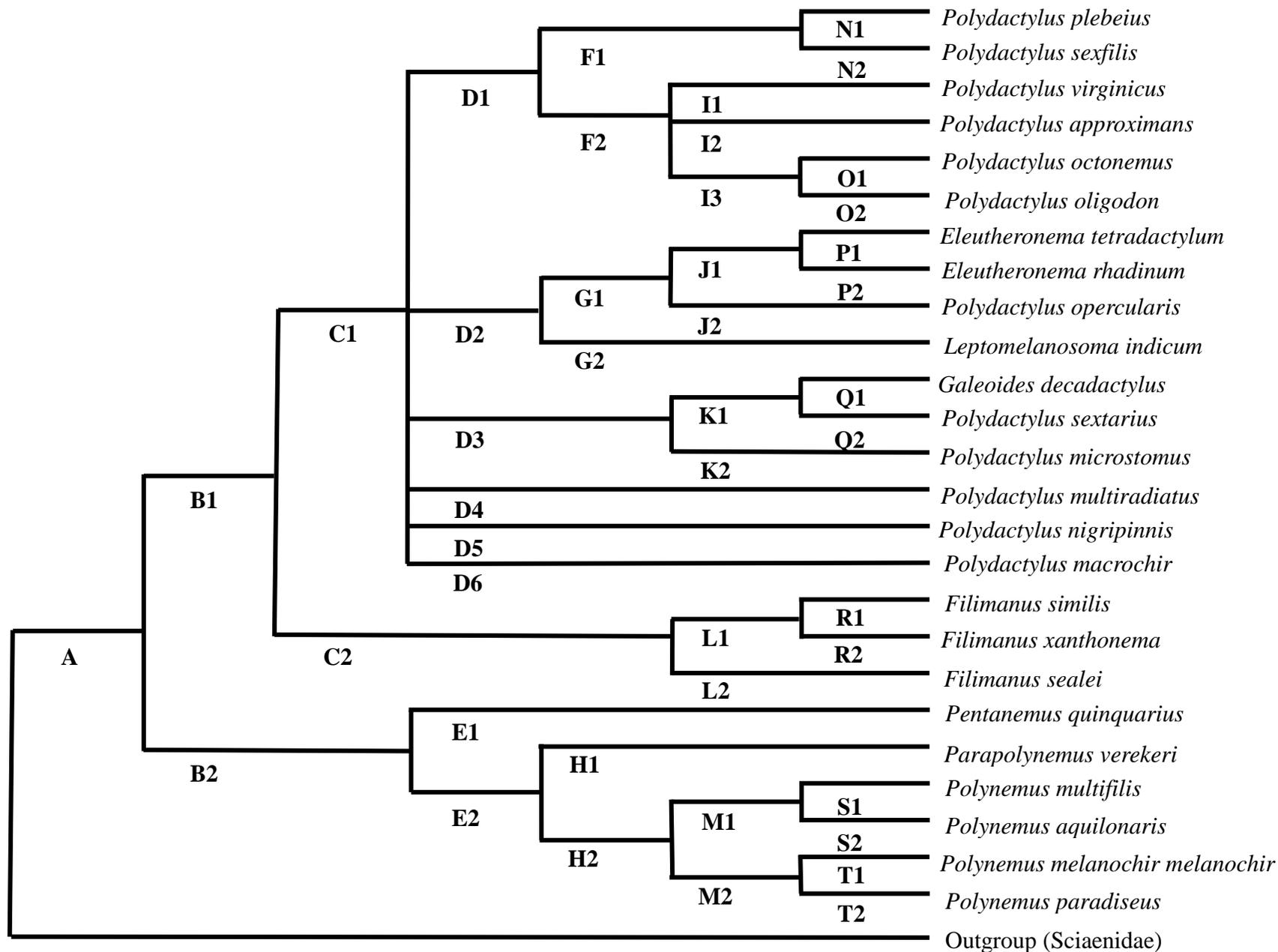
Taxon	Transformation series and characters				
	1-5	6-10	11-15	16-20	21-25
Outgroup (Sciaenidae)	0(01)(01)00	(01)(01)0(01)0	0000(01)	0?00(01)	(01)0?00
<i>Polydactylus plebeius</i>	00011	00100	00001	01100	10001
<i>Polydactylus sexfilis</i>	00011	10100	00001	01100	10001
<i>Polydactylus virginicus</i>	00011	00100	00001	01100	10001
<i>Polydactylus approximans</i>	00011	00100	00001	01100	10001
<i>Polydactylus octonemus</i>	00011	00100	00001	01100	10001
<i>Polydactylus oligodon</i>	00031	00100	00001	01100	10001
<i>Galeoides decadactylus</i>	00010	10100	00001	00000	10001
<i>Polydactylus sextarius</i>	00020	10000	00001	00100	10001
<i>Polydactylus microstomus</i>	00020	00100	00001	10100	10001
<i>Polydactylus nigripinnis</i>	00110	00100	01111	11100	10011
<i>Polydactylus multiradiatus</i>	00011	10100	00001	01100	10001
<i>Eleutheronema tetradactylum</i>	00011	00100	01011	02110	00101
<i>Eleutheronema rhadinum</i>	00011	00100	11111	02110	00101
<i>Polydactylus opercularis</i>	00011	00100	01111	02110	01001
<i>Leptomelanosoma indicum</i>	00011	00100	01011	01100	00001
<i>Polydactylus macrochir</i>	00011	0011?	???01	01100	10001
<i>Filimanus similis</i>	00021	00101	11001	01001	11011
<i>Filimanus sealei</i>	00021	00101	11001	01001	11001
<i>Filimanus xanthonema</i>	00020	00101	11001	01001	11001
<i>Pentanemus quinquarius</i>	00110	00000	00001	01000	11010
<i>Parapolyneumus verekeri</i>	11000	01000	00010	01001	10001
<i>Polynemus multifilis</i>	01011	0101?	???10	01000	00001
<i>Polynemus aquilonaris</i>	01011	0101?	???10	01000	10001
<i>Polynemus melanochir melanochir</i>	11010	0101?	???10	01100	10001
<i>Polynemus paradiseus</i>	11010	0101?	???10	01100	10011

**Table 3. Continued.**

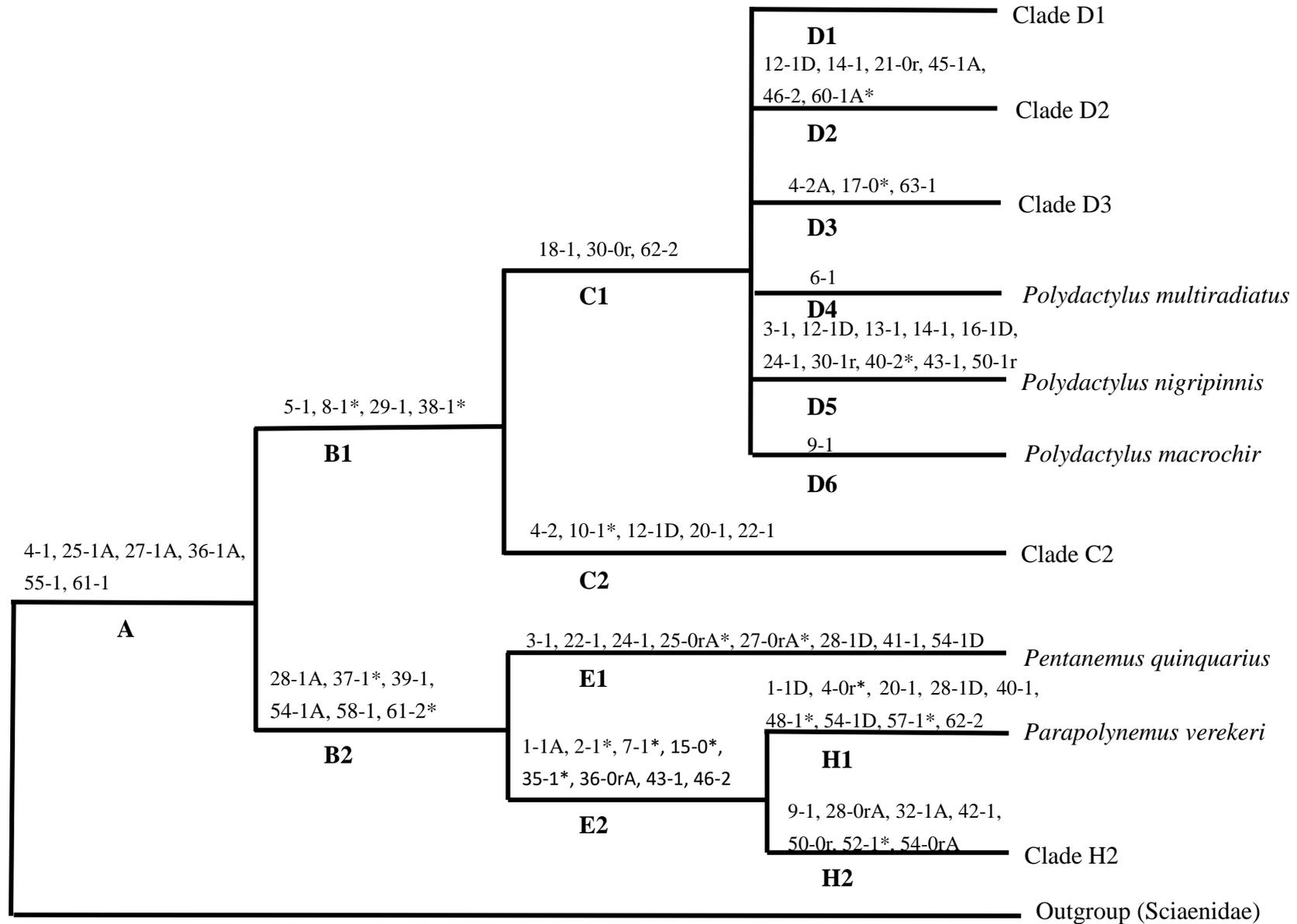
Taxon	Transformation series and characters				
	26-30	31-35	36-40	41-45	46-50
Outgroup (Sciaenidae)	0000(01)	00(01)00	0?00?	0????	(02)(01)(01)??
<i>Polydactylus plebeius</i>	01010	10000	10100	10000	00001
<i>Polydactylus sexfilis</i>	01010	10010	10100	10001	00000
<i>Polydactylus virginicus</i>	01010	10000	10100	10000	00000
<i>Polydactylus approximans</i>	01010	10000	10100	10000	00000
<i>Polydactylus octonemus</i>	01010	10000	10100	10000	20001
<i>Polydactylus oligodon</i>	01010	10000	10100	10000	21000
<i>Galeoides decadactylus</i>	01011	00000	10100	00000	01000
<i>Polydactylus sextarius</i>	01010	00000	10100	10000	01000
<i>Polydactylus microstomus</i>	01000	00000	10100	10000	00000
<i>Polydactylus nigripinnis</i>	01001	10000	10102	10100	00001
<i>Polydactylus multiradiatus</i>	01000	10000	10100	10000	00000
<i>Eleutheronema tetradactylum</i>	11010	00000	10100	11011	21000
<i>Eleutheronema rhadinum</i>	11010	00010	10100	11011	20000
<i>Polydactylus opercularis</i>	01011	1???0	10000	00000	20000
<i>Leptomelanosoma indicum</i>	01000	00000	10101	00001	20001
<i>Polydactylus macrochir</i>	01010	00000	10100	10000	00001
<i>Filimanus similis</i>	01011	00100	10100	00000	00001
<i>Filimanus sealei</i>	01011	00100	10100	00000	00001
<i>Filimanus xanthonema</i>	01011	00100	10110	00000	00001
<i>Pentanemus quinquarius</i>	00101	00100	11010	10000	00001
<i>Parapolyneumus verekeri</i>	01101	00001	01011	00100	20101
<i>Polynemus multifilis</i>	01011	02001	01010	01000	20000
<i>Polynemus aquilonaris</i>	01001	01001	01010	01100	20000
<i>Polynemus melanochir melanochir</i>	01101	02001	01020	01100	20010
<i>Polynemus paradiseus</i>	01001	00001	01010	01100	10010

**Table 3. Continued.**

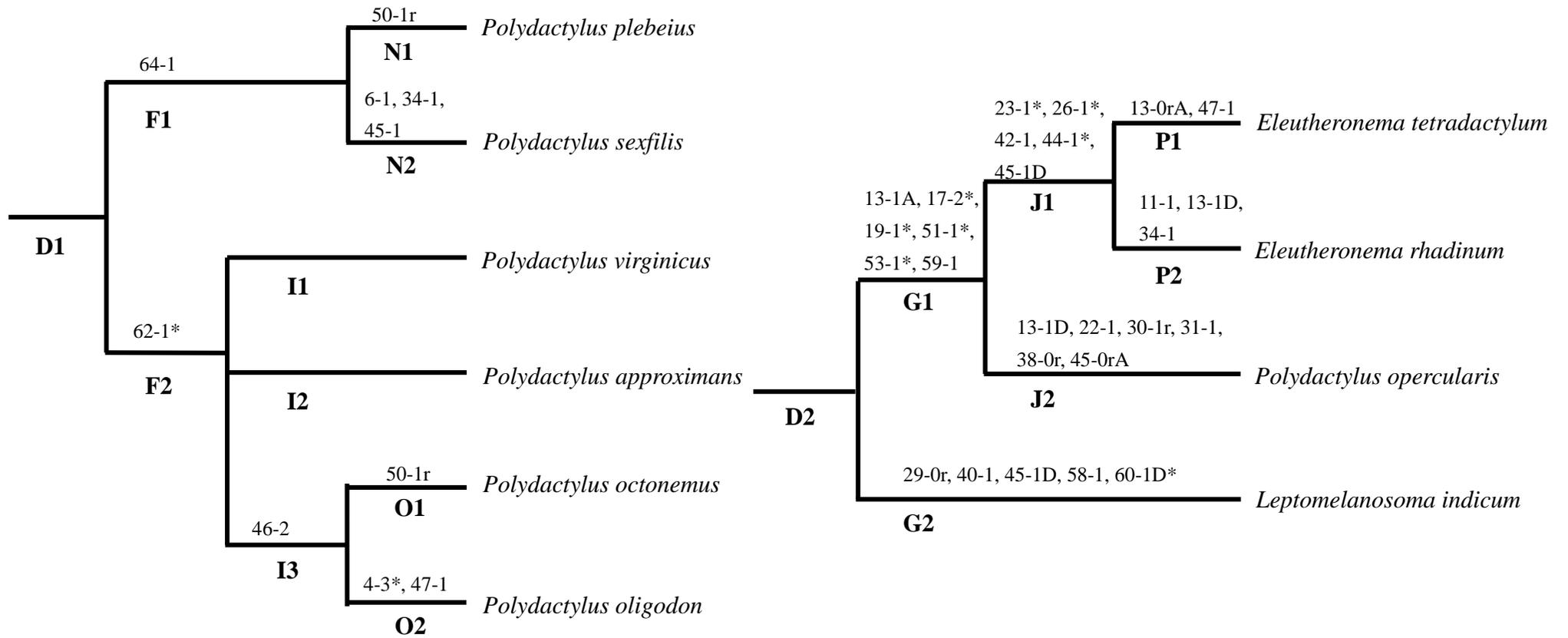
Taxon	Transformation series and characters		
	51-55	56-60	61-64
Outgroup (Sciaenidae)	(01)?(01)00	0?00(01)	0000
<i>Polydactylus plebeius</i>	00001	10000	1201
<i>Polydactylus sexfilis</i>	00001	10000	1201
<i>Polydactylus virginicus</i>	00001	10000	1100
<i>Polydactylus approximans</i>	00001	10000	1100
<i>Polydactylus octonemus</i>	00001	10000	1100
<i>Polydactylus oligodon</i>	00001	10000	1100
<i>Galeoides decadactylus</i>	00000	00000	1321
<i>Polydactylus sextarius</i>	00000	00000	1210
<i>Polydactylus microstomus</i>	00000	00000	1210
<i>Polydactylus nigripinnis</i>	00000	0001?	1200
<i>Polydactylus multiradiatus</i>	00000	0001?	1200
<i>Eleutheronema tetradactylum</i>	10101	1001?	1200
<i>Eleutheronema rhadinum</i>	10101	1001?	1200
<i>Polydactylus opercularis</i>	1010?	??01?	1200
<i>Leptomelanosoma indicum</i>	00001	10101	1200
<i>Polydactylus macrochir</i>	00001	00000	1200
<i>Filimanus similis</i>	00001	10000	1000
<i>Filimanus sealei</i>	00001	00000	1000
<i>Filimanus xanthonema</i>	00001	10000	1000
<i>Pentanemus quinquarius</i>	00011	00100	2000
<i>Parapolynemus verekeri</i>	00011	01100	2200
<i>Polynemus multifilis</i>	01001	00100	2000
<i>Polynemus aquilonaris</i>	01001	00100	2000
<i>Polynemus melanochir melanochir</i>	01001	1011?	2000
<i>Polynemus paradiseus</i>	01001	1011?	2000



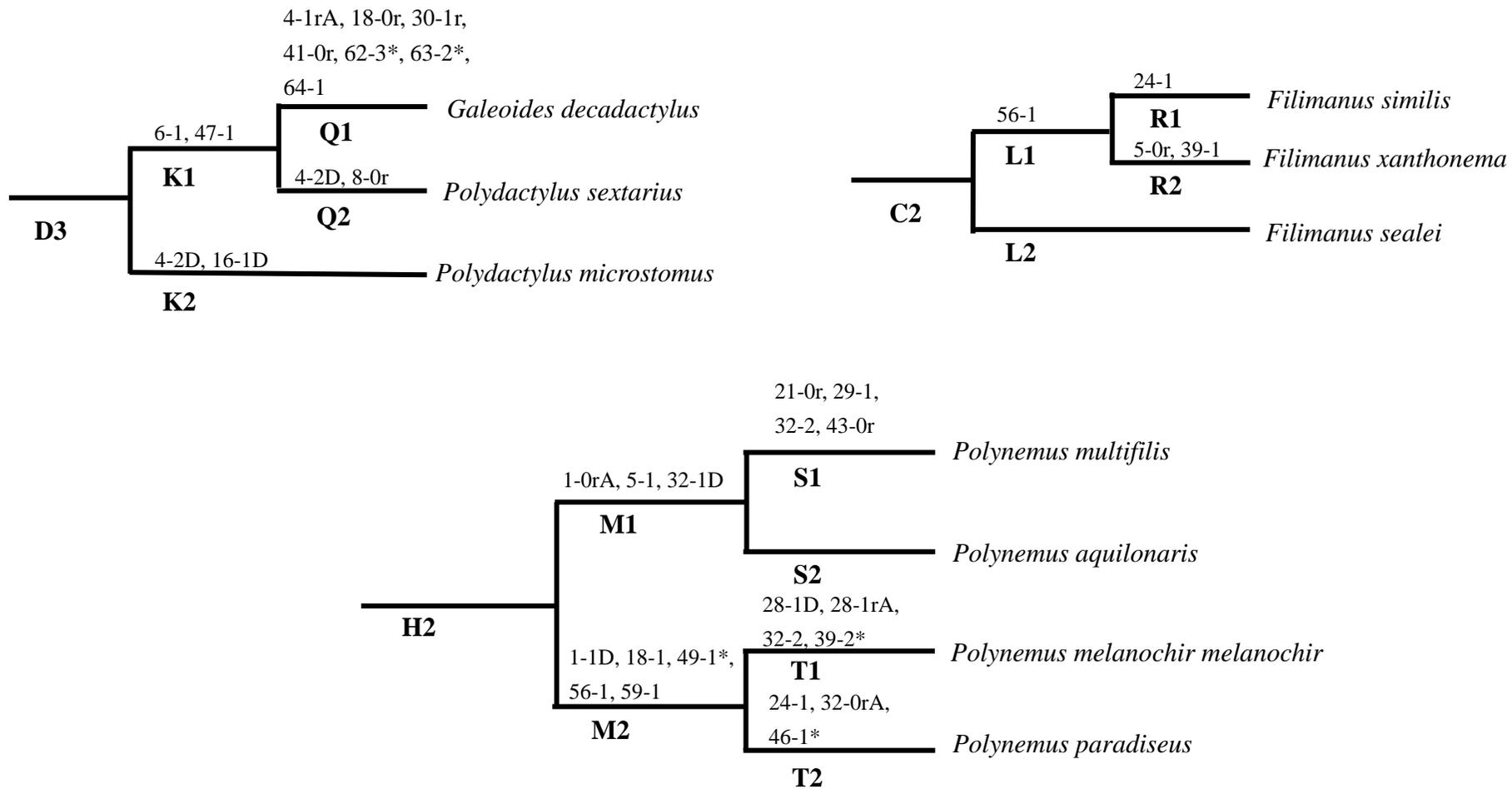
**Fig. 62.** Strict consensus tree of four most parsimonious phylogenetic relationships of Polynemidae.



**Fig. 63.** Clades A to E and H in phylogenetic relationships of Polynemidae.



**Fig. 64.** Interrelationships of D1 (left) and D2 (right) in phylogenetic relationships of Polynemidae.



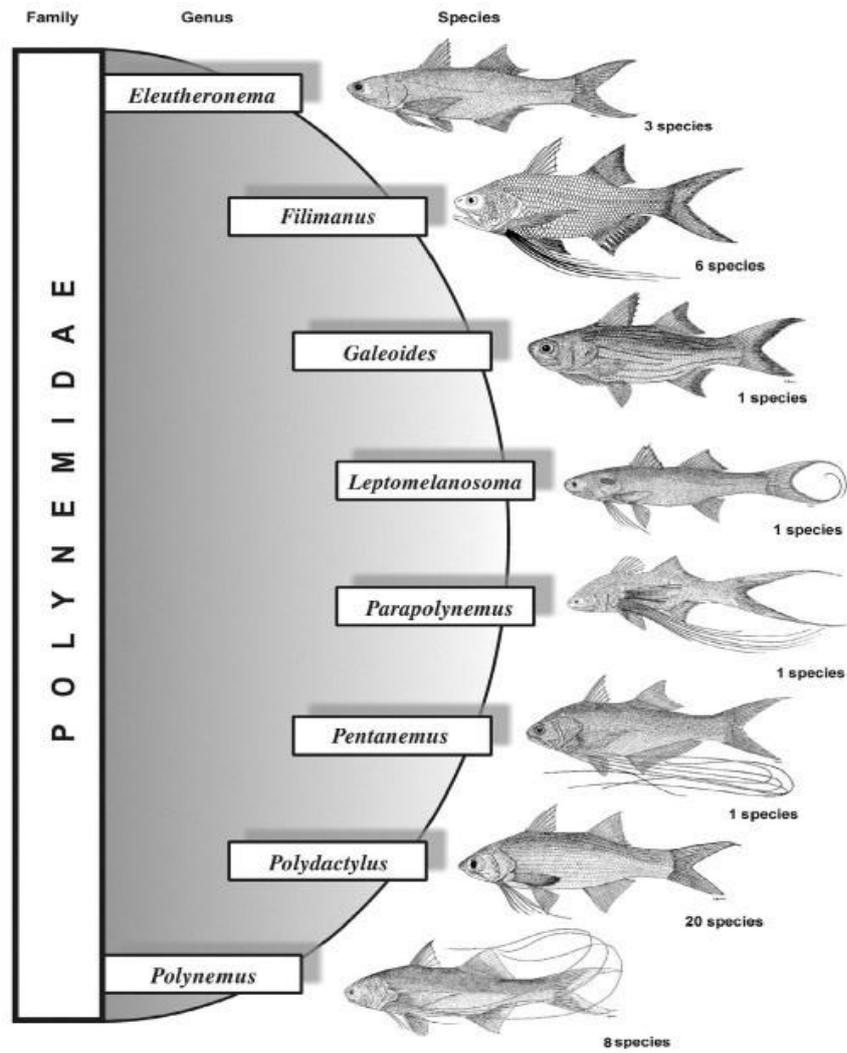
**Fig. 65.** Interrelationships of D3 (upper, left), C2 (upper, right) and H2 (lower) in phylogenetic relationships of Polynemidae.

## VIII. Classification

The family Polynemidae has been variously classified by many ichthyologists previously (see chapter Introduction). Recently, Polynemidae was classified by Motomura (2004) into eight genera, *Eleutheronema* Bleeker, 1862, *Filimanus* Myers, 1936, *Galeoides* Günther, 1860, *Leptomelanosoma* Motomura and Iwatsuki, 2001, *Parapolynemus* Feltes, 1993, *Pentanemus* Günther, 1860, *Polydactylus* Lacepède, 1803 and *Polynemus* Linnaeus, 1758 (Fig. 66). After Motomura (2004), this classification has been adopted by several ichthyologists, such as Nelson (2006), Nakabo (2013) and Nelson et al. (2016). However, it is not based on the cladistic methodology, and the phylogenetic relationships providing the basis of the classification have not been reconstructed in Polynemidae. Accordingly, this study proposes a new classification of Polynemidae based on the reconstructed phylogenetic relationships (Fig. 62).

In the inferred relationships in this study, clades C2, E1, H1 and H2 include species of the genera *Filimanus*, *Pentanemus*, *Parapolynemus* and *Polynemus*, respectively (Fig. 69). Especially the monophyly of each of *Filimanus* and *Polynemus* is retained. Therefore, the validity of each of these genera is supported in this study. However, the genus *Polydactylus* was assumed to be a non-monophyletic group in the four most parsimonious trees (Figs. 67, 68). All examined species of *Polydactylus* are included in clade C1 with *Eleutheronema*, *Leptomelanosoma* and *Galeoides*. Accordingly, if these three genera are retained, previous *Polydactylus* (see Motomura2004) becomes invalid cladistically. To

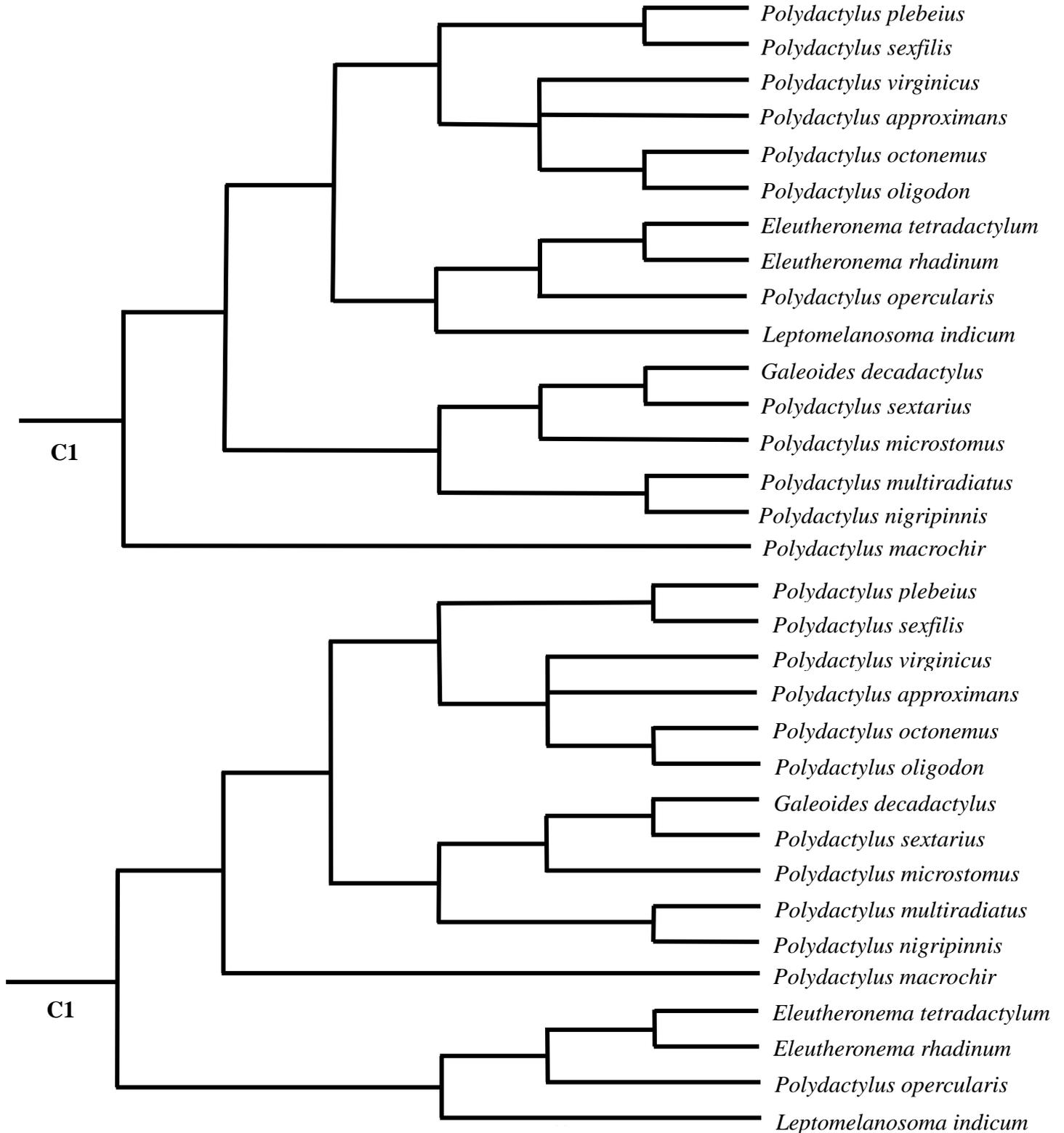
avoid to recognize the cladistically invalid genus, this study propose a newly-defined genus including species of *Polydactylus*, *Eleutheronema*, *Leptomelanosoma* and *Galeoides* to clade C1.



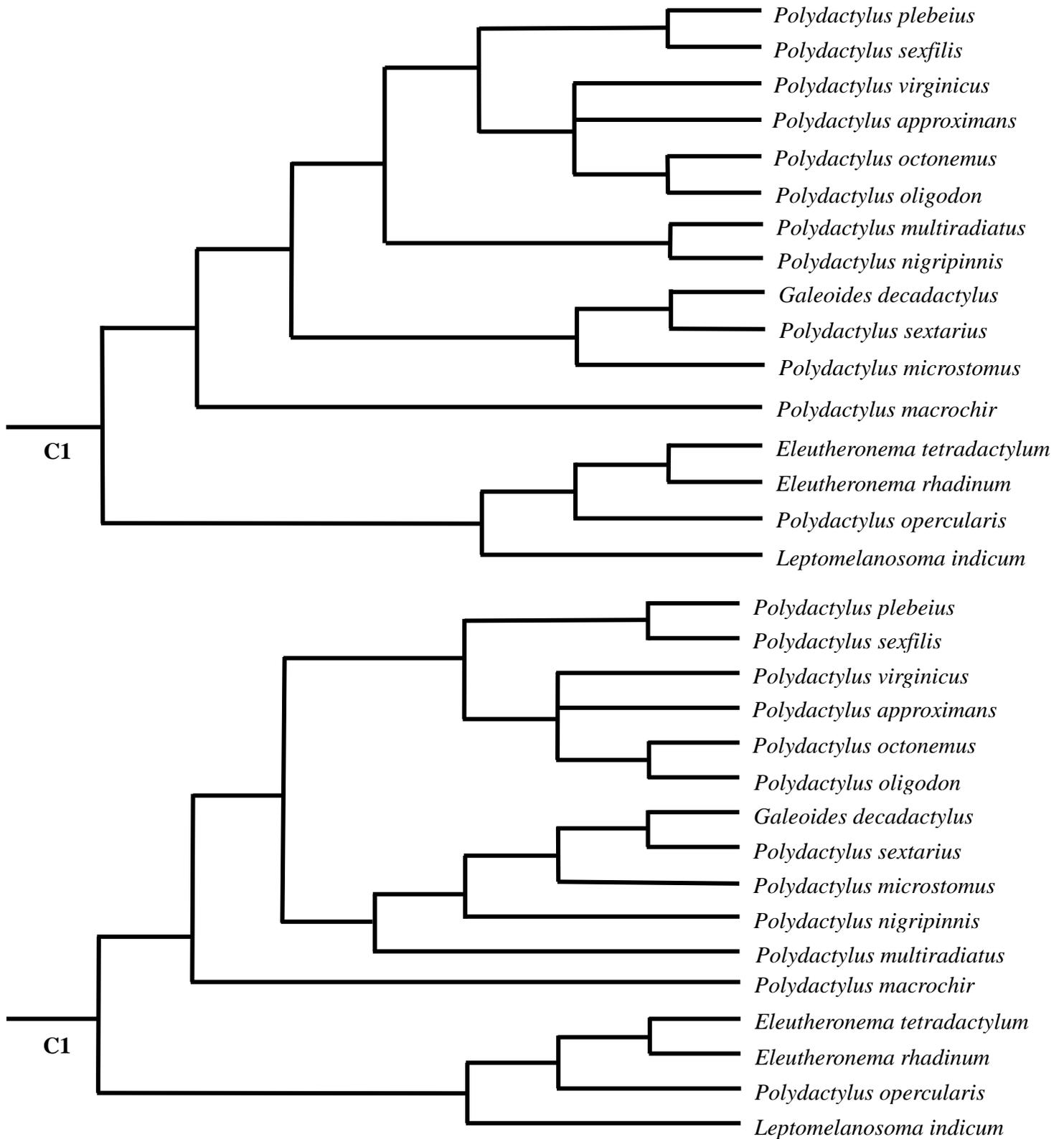
**Fig. 66.** Classification of the family Polynemidae described by Motomura (2004).

Of the four genera, *Polydactylus* is the oldest name having the priority over three other genera; thus *Polydactylus* is adapted to clade C1. This clade is well

supported by three unambiguous synapomorphies, 18-1 (posterior margin of maxilla serrated), 30-0r (lateral surface of ceratohyal connected epihial via cartilaginous band), 62-2 (posterior portion of lateral line extending to upper end of lower caudal-fin lobe).

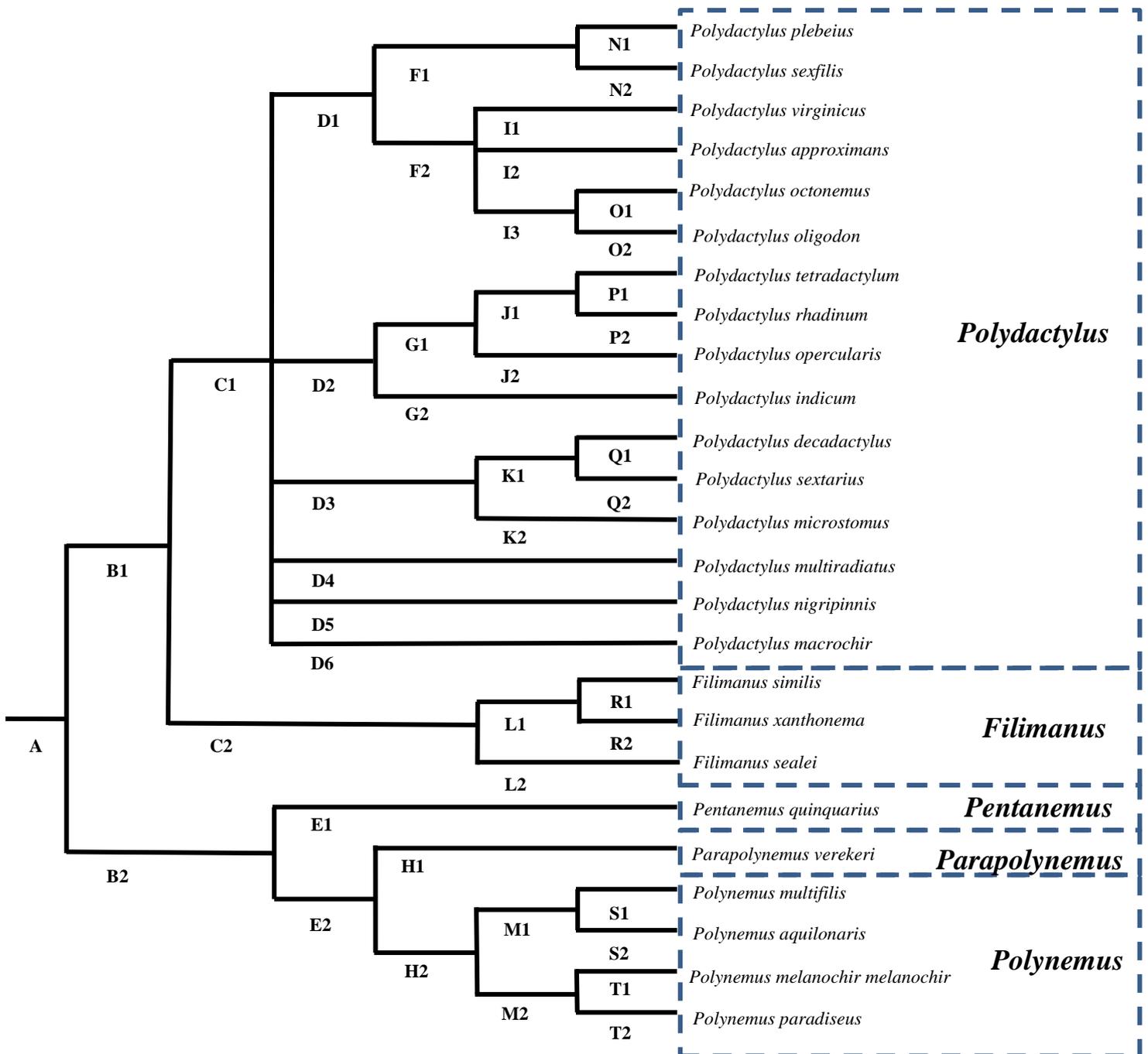


**Fig. 67.** Two interrelationships of clade C1 among four most parsimonious trees.



**Fig. 68.** Two interrelationships of clade C1 among four most parsimonious trees.

In conclusion, after phylogenetic analysis, this study redefined Polynemidae as a family including five genera, *Filimanus* Myers, 1936, *Parapolynemus* Feltes, 1993, *Pentanemus* Günther, 1860, *Polydactylus* Lacepede, 1803 and *Polynemus* Linnaeus, 1758 (Fig. 69). This study represents the first one showing such a classification.



**Fig. 69.** Strict consensus tree obtained in this study showing new classification of Polynemidae.

## Family Polynemidae

**Diagnosis.** Adipose eyelid (firm transparent gelatinous tissue) covering eye; fourth infraorbital covering fifth laterally (except for *Parapolynemus verekeri*, *Polydactylus oligodon*, *Polydactylus sextarius*, *Polydactylus microstomus* and *Filimanus*); intercalar and epiotic connected; supramaxilla absent; tooth plate present on ectopterygoid; ectopterygoid strongly elongated; metapterygoid and quadrate interdigitated medially; a single branchiostegal ray suspended by epihyal; pectoral fins divided into an upper part with 12 to 19 rays joined by membrane and a lower part with 3 to 11 separate rays (= pectoral filaments sensu Motomura, 2004); filament-like rays slightly elongate (except for *Pentanemus quinquarius*, *Parapolynemus verekeri* and *Polynemus*); an unnamed bone present on cephalic sensory canal extending from supratemporal; ventral process of cleithrum present; third actinost not supporting pectoral-fin rays; rod-like process extending from the ventral margin of the coracoid; pelvis and pelvic spine interlocked; posterior portions of pelvic bones on both sides interdigitated; median pterygiophores absent in dorsal and anal fins; third and fourth hypurals fused anteriorly; lateral line simple, posteriorly extending to posterior margin of caudal-fin membrane; adductor mandibulae section 1 comprised the lateral and medial elements; levator arcus palatini divided into anterior and posterior subsections; adductor section 2 restricted to posterolateral surface of second epibranchial (except for *Polydactylus decadactylus*, *Polydactylus sextarius*, *Polydactylus multiradiatus*, *Polydactylus nigripinnis* and *Polydactylus microstomus*); abductor superficialis, abductor

profundus, adductor superficialis and adductor profundus all separated into dorsal and ventral subdivisions; coracoradialis absent; division of obliquus inferioris present between lower postcleithrum and rod-like process on coracoid; anterior extension of nasal canal present.

**Remark.** The following five genera are recognized in Polynemidae in this study based on the reconstructed relationships (Fig. 69): *Polydactylus* Lacepède, 1803, *Filimanus* Myers, 1936, *Pentanemus* Günther, 1860, *Parapolynemus* Feltes, 1993, and *Polynemus* Linnaeus, 1758.

## Key to the genera of Polynemidae

- 1a. Pectoral filament-like rays well elongate and longest one extending to caudal fin.....2
- 1b. Pectoral filament-like rays slightly elongate and longest one not extending to caudal fin.....4
- 2a. Eye large and eye diameter 7% or more of SL.....*Pentanemus*
- 2b. Eye small and eye diameter 4% or less of SL.....3
- 3a. Posterior portion of lateral line extending along the midline of caudal fin.....*Polynemus*
- 3b. Posterior portion of lateral line extending to upper end of lower caudal-fin lobe.....*Parapolynemus*
- 4a. Palatine tooth plate equal to or longer than that of ectopterygoid.....*Polydactylus*
- 4b. Palatine tooth plate shorter than that of ectopterygoid.....*Filimanus*

## Genus *Polydactylus* Lacepède, 1803

*Polydactylus* Lacepède, 1803: 419 [type species: *Polydactylus plumierii* Lacepède, 1803, presently regarded as a junior synonym of *Polydactylus virginicus* (Linnaeus, 1758)].

*Galeoides* Günther, 1860: 319, 332 [type species: *Polynemus polydactylus* Vahl, 1798, presently regarded as a junior synonym of *Galeoides decadactylus* (Bloch, 1795)].

*Eleutheronema* Bleeker, 1862a: 110 (type species: *Polynemus tetradactylus* Shaw, 1804).

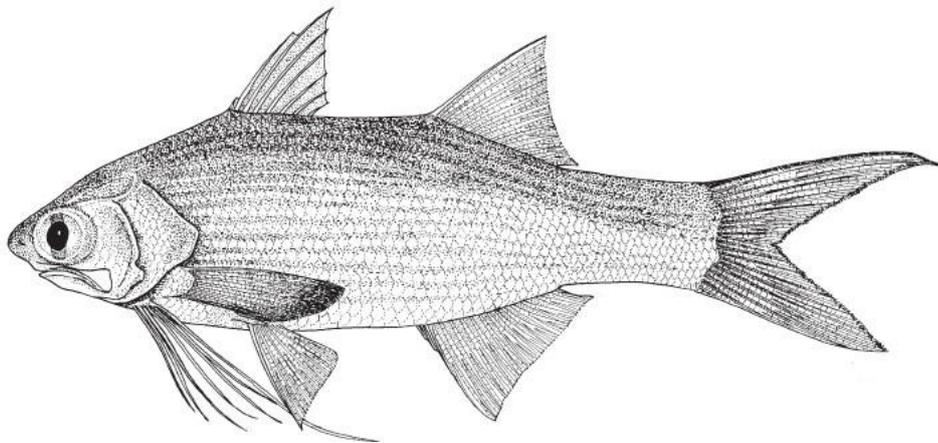
*Leptomelanosoma* Motomura and Iwatsuki, 2001a: 13 (type species: *Polynemus indicus* Shaw, 1804).

**Diagnosis.** Eye large or small, and eye diameter 3-9% SL; infraorbitals arranged in semicircular; subocular shelf on third infraorbital present; tooth plate on prevomer present or absent; sensory canal on frontal roofed (except for *Polydactylus sextarius*); shallow and blunt notch present between ascending and articular processes; posterior margin of maxilla serrated (except for *Polydactylus decadactylus*); posterior portion of palatine well extending and its tooth plate equal to or longer than that of ectopterygoid; endopterygoid separated from quadrate medially; well-developed thin semicircular sheet expansion of preopercle present; posterior margin of preopercle serrated; lateral surface of ceratohyal connected epihyal via cartilaginous band (except for *Polydactylus decadactylus*, *Polydactylus*

*nigripinnis* and *Polydactylus opercularis*); anteriorly-pointed projection on first hypobranchial extremely small; dorsal limb of cleithrum well developed; flange on cleithrum well developed; rod-like process slender and short; third actinost equal to or longer than fourth actinost; fourth actinost extending ventrally to ventral margin of coracoid; subpelvic keel weakly developed or absent (except for *Polydactylus decadactylus*, *Polydactylus indicum* and *Polydactylus opercularis*); 14 or 15 caudal vertebrae; first supraneural present or absent; levator externi originating from prootic and pterotic; ventral subsection of abductor superficialis continuous to form a single mass (except for *Polydactylus indicum*); swimbladder present or absent; filament-like rays slightly elongate and longest one not extending to caudal fin; posterior portion of lateral line extending to upper end of lower caudal-fin lobe or lower end of upper caudal-fin lobe or bifurcating.

**Remark.** As mentioned above, the genera *Eleutheronema*, *Leptomelanosoma* and *Galeoides* are synonymized under *Polydactylus*, based on the inferred phylogenetic relationships in this study. At present, this genus comprises at least the following 25 species: *Polydactylus approximans* Lay and Bennett, 1839, *Polydactylus bifurcus* Motomura, Kimura and Iwatsuki, 2001, *Polydactylus longipes* Motomura, Okamoto and Iwatsuki, 2001, *Polydactylus macrochir* Günther, 1867, *Polydactylus macrophthalmus* Bleeker, 1858, *Polydactylus malagasyensis* Motomura and Iwatsuki, 2001, *Polydactylus microstomus* Bleeker, 1851, *Polydactylus mullani* Hora, 1926, *Polydactylus multiradiatus* Günther, 1860, *Polydactylus nigripinnis* Munro, 1964, *Polydactylus octonemus* Girard, 1858,

*Polydactylus oligodon* Günther, 1860, *Polydactylus opercularis* Gill, 1863, *Polydactylus persicus* Motomura and Iwatsuki, 2001, *Polydactylus plebeius* Broussonet, 1782, *Polydactylus quadrifilis* Cuvier, 1829, *Polydactylus sexfilis* Valenciennes, 1831, *Polydactylus sextarius* Bloch and Schneider, 1801, *Polydactylus siamensis* Motomura, Iwatsuki and Yoshino, 2001, *Polydactylus virginicus* Linnaeus, 1758, *Polydactylus decadactylus* Bloch, 1795, *Polydactylus indicum* Shaw, 1804, *Polydactylus rhadinum* Jordan and Evermann, 1902, *Polydactylus tetradactylum* Shaw, 1804 and *Polydactylus tridactylum* Bleeker, 1849. Of them, *P. decadactylus*, *P. indicum*, and *P. rhadinum*, *P. tetradactylum* and *P. tridactylum* have been classified in *Galeoide*, *Leptomelanosoma* and *Eleutheronema*, respectively.



**Fig. 70.** Lateral view of *Polydactylus virginicus*, type species of the genus *Polydactylus* (from Motomura, 2004).

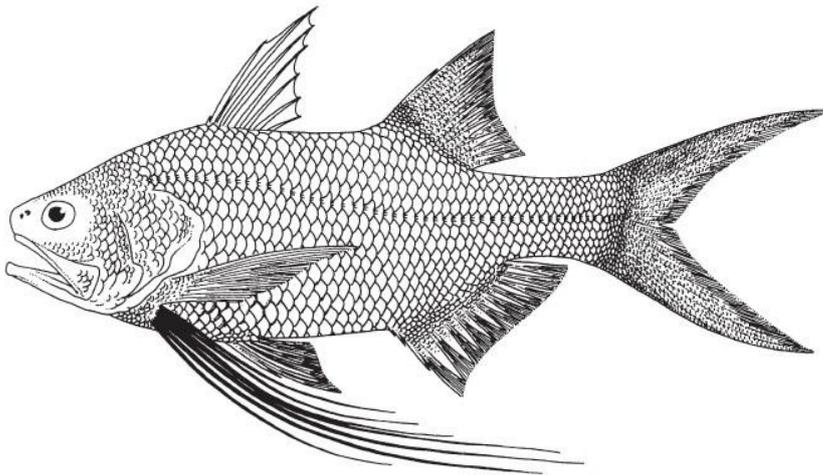
## Genus *Filimanus* Myers, 1936

*Filimanus* Myers, 1936: 379 [type species: *Polynemus melanochir* (misidentified, not of Valenciennes in Cuvier and Valenciennes, 1831); later identified as *Filimanus perplexa* Feltes, 1991 by Feltes (1991)].

**Diagnosis.** Eye large and eye diameter 6% or more of SL; infraorbitals arranged in semicircular; subocular shelf on third infraorbital present; fourth infraorbital covering fifth medially; tooth plate on prevomer present or absent; sensory canal on frontal roofed; basisphenoid stick-like; shallow and blunt notch present between ascending and articular processes; a foramen present on the upper center of the dentary; posterior portion of palatine slightly extending and its tooth plate shorter than that of ectopterygoid; endopterygoid separated from quadrate medially; well-developed thin semicircular sheet expansion of preopercle present; posterior margin of preopercle serrated; ceratohyal interdigitating with epihyal on lateral surface; anteriorly-pointed projection on first hypobranchial large; dorsal limb of cleithrum well developed; flange on cleithrum well developed; rod-like process slender and short; third actinost equal to or longer than fourth actinost; fourth actinost extending ventrally to ventral margin of coracoid; subpelvic keel well developed; 14 caudal vertebrae; first supraneural present; levator externi originating from prootic and pterotic; ventral subsection of abductor superficialis continuous to form a single mass; swimbladder present; filament-like rays slightly elongate and longest one not extending to caudal fin; posterior portion of lateral line extending along the midline of caudal fin.

**Remark.** Myers (1936) described *Filimanus* as a new genus on the basis of a single specimen (USNM 72742, 114 mm SL), but had misidentified the latter as *Polynemus melanochir* (see Feltes, 1991). The specimen used by Myers (1936) in his description of *Filimanus* was identified by Feltes (1991) as *F. perplexa*, which was recognized as the type species of *Filimanus* later.

Six valid species, *Filimanus heptadactyla* Cuvier, 1829, *Filimanus hexanema* Cuvier, 1829, *Filimanus perplexa* Feltes, 1991, *Filimanus sealei* Jordan and Richardson, 1910, *Filimanus similis* Feltes, 1991 and *Filimanus xanthonema* Valenciennes, 1831, are included in the genus *Filimanus* at present.



**Fig. 71.** Lateral view of *Filimanus perplexa*, type species of the genus *Filimanus* (from Motomura, 2004).

### **Genus *Pentanemus* Günther, 1860**

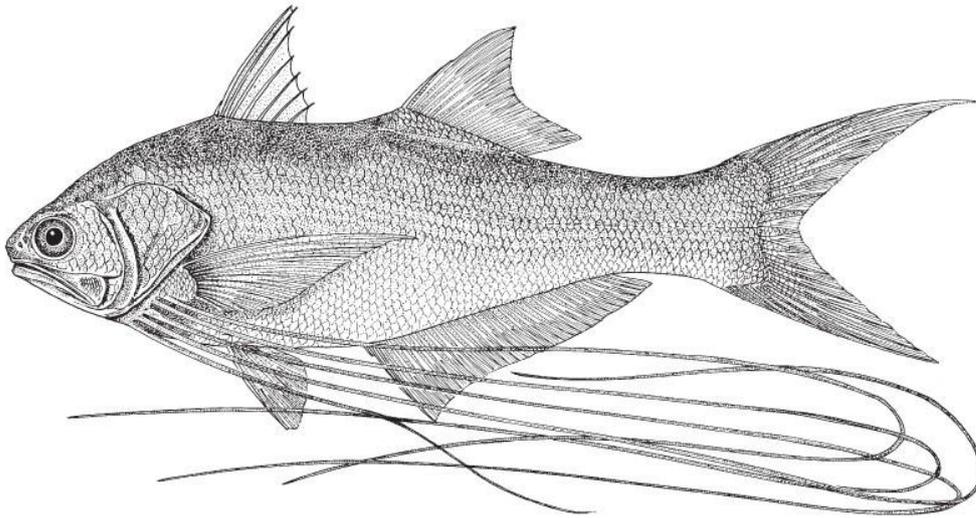
*Pentanemus* Günther, 1860: 330 (type species: *Polynemus quinquarius* Linnaeus, 1758).

**Diagnosis.** Eye large and eye diameter 7% or more of SL; infraorbitals

arranged in semicircular; subocular shelf on third infraorbital present; posterodorsal and posteroventral parts of first infraorbital situated lateral and medial to second infraorbital, respectively; tooth plate on prevomer absent; sensory canal on frontal bridged; shallow and blunt notch present between ascending and articular processes; posterior portion of palatine slightly extending and its tooth plate shorter than that of ectopterygoid; ectopterygoid fused with endopterygoid; endopterygoid sutured with quadrate medially; well-developed thin semicircular sheet expansion of preopercle absent; posterior margin of preopercle smooth; ceratohyal interdigitating with epihyal on lateral surface; anteriorly-pointed projection on first hypobranchial large; dorsal limb of cleithrum well developed; flange on cleithrum well developed; rod-like process robust and long; third actinost equal to or longer than fourth actinost; fourth actinost extending ventrally to ventral margin of coracoid; subpelvic keel weakly developed or absent; 14 caudal vertebrae; first supraneural present; first uroneural fused with urostyle; levator externi originating from pterotic; ventral subsection of abductor superficialis split into several bundles; swimbladder present; filament-like rays well elongate and longest one extending to caudal fin; anal-fin rays 24 to 30; posterior portion of lateral line extending along the midline of caudal fin.

**Remark.** Günther (1860) described *Pentanemus* with diagnosis such as anal-fin rays 24 to 30 (less than 18 in all other genera); anal-fin base greater than head length; and width of tooth band on upper and lower jaws less than space (on

symphysis) separating tooth bands on opposing premaxillae. The validity of this genus is also supported in this study. The genus is monotypic, including only *Pentanemus quinquarius* Linnaeus, 1758.



**Fig. 72.** Lateral view of *Pentanemus quinquarius*, type species of the genus *Pentanemus* (from Motomura, 2004).

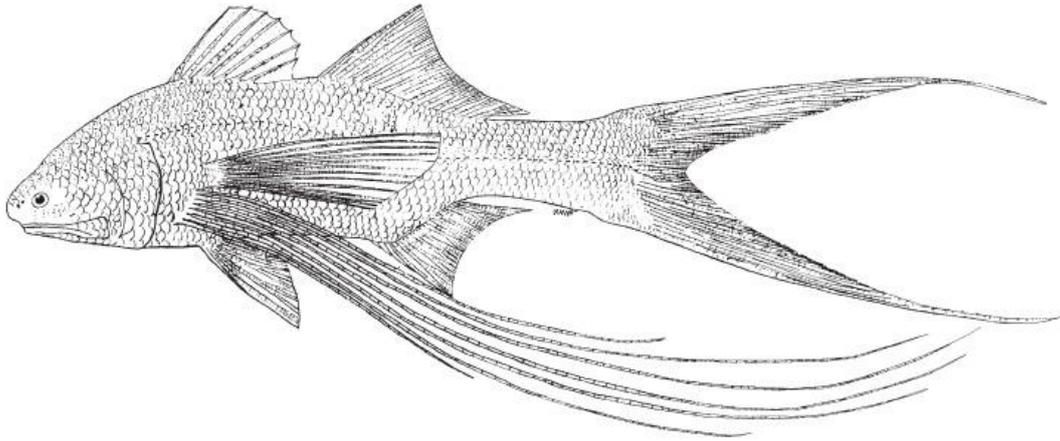
### **Genus *Parapolynemus* Feltes, 1993**

*Parapolynemus* Feltes, 1993: 207 (type species: *Polynemus verekeri* Saville-Kent, 1889).

**Diagnosis.** Eye small and eye diameter 3% or less of SL; infraorbitals arranged in deeply V-shape; subocular shelf on third infraorbital absent; third and fourth infraorbitals fused; tooth plate on prevomer absent; lateral ethmoid connected with pterosphenoid; sensory canal on frontal bridged; pterosphenoid attached to parasphenoid; foramen for nervus glossopharyngeus present on intercalar; deep and sharp notch present between ascending and articular processes; a foramen present on the upper center of the dentary; posterior portion of palatine

well extending and its tooth plate equal to or longer than that of ectopterygoid; endopterygoid separated from quadrate medially; well-developed thin semicircular sheet expansion of preopercle present; posterior margin of preopercle smooth; ceratohyal interdigitating with epihyal on lateral surface; anteriorly-pointed projection on first hypobranchial extremely small; dorsal limb of cleithrum weakly developed; flange on cleithrum weakly developed; rod-like process robust and long; third actinost shorter than fourth actinost; fourth actinost extending ventrally to middle of coracoid; subpelvic keel well developed; 14 caudal vertebrae; first supraneural absent; fifth post-hypural cartilage absent; third preural centrum fused with third hemal spine; single third inter-hemal spine cartilage of preural; levator externi originating from pterotic; anterior bundle of transversus dorsalis anterior slim; ventral subsection of abductor superficialis split into several bundles; swimbladder present; filament-like rays well elongate and longest one extending to caudal fin; posterior portion of lateral line extending to upper end of lower caudal-fin lobe.

**Remark.** The genus is monotypic, including only *Parapolyneumus verekeri* Saville-Kent, 1889, and established by Feltes (1993). After the phylogenetic analysis, this study agrees with the validity of the genus.



**Fig. 73.** Lateral view of *Parapolyneumus verekeri*, type species of the genus *Parapolyneumus* (from Motomura, 2004).

### **Genus *Polynemus* Linnaeus, 1758**

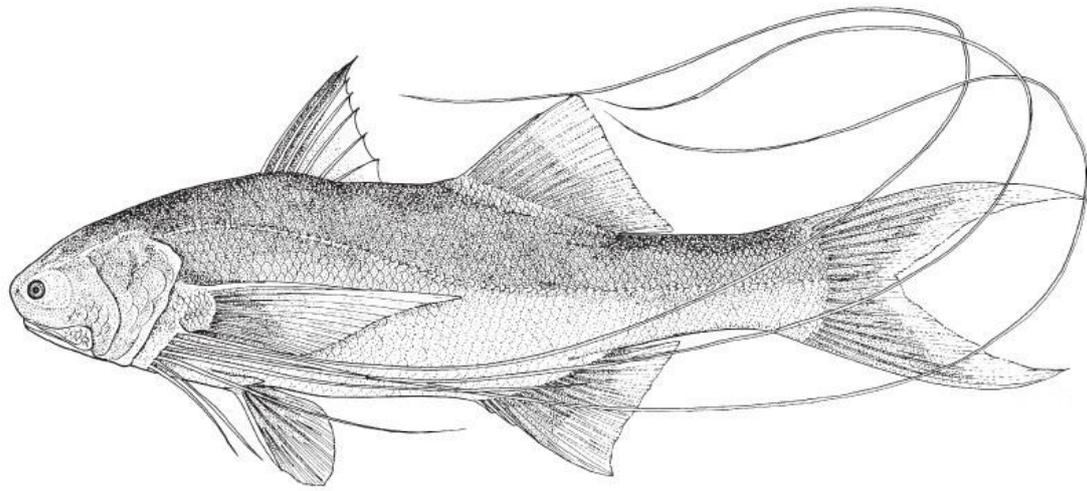
*Polynemus* Linnaeus, 1758: 317 (type species: *Polynemus paradiseus* Linnaeus, 1758).

*Polistonemus* Gill, 1861: 277 (type species: *Polynemus multifilis* Temminck and Schlegel, 1843; recognized as junior synonym of *Polynemus* Linnaeus, 1758).

**Diagnosis.** Eye small and eye diameter 4% or less of SL; subocular shelf on third infraorbital absent; lateral ethmoid connected with pterosphenoid; sensory canal on frontal bridged; basisphenoid absent; pterosphenoid attached to parasphenoid; deep and sharp notch present between ascending and articular processes; posterior portion of palatine well extending and its tooth plate equal to or longer than that of ectopterygoid; endopterygoid separated from quadrate medially; well-developed thin semicircular sheet expansion of preopercle present; posterior margin of preopercle serrated; ceratohyal interdigitating with epihyal on

lateral surface; anteriorly-pointed projection on first hypobranchial extremely small; dorsal limb of cleithrum weakly developed; flange on cleithrum weakly developed; rod-like process robust and long; third actinost shorter than fourth actinost; fourth actinost extending ventrally to ventral margin of coracoid; subpelvic keel well developed; 15 caudal vertebrae; first supraneural absent or cartilaginous; anterior subsection of levator arcus palatine inserted onto endopterygoid and metapterygoid; levator externi originating from prootic and pterotic; ventral subsection of abductor superficialis split into several bundles; swimbladder present or absent; filament-like rays well elongate and longest one extending to caudal fin; posterior portion of lateral line extending along the midline of caudal fin.

**Remark.** *Polynemus*, the oldest genus of Polynemidae, was originally described by Linnaeus (1758). At present, it includes the following eight species at least: *Polynemus aquilonaris* Motomura, 2003, *Polynemus dubius* Bleeker, 1854, *Polynemus hornadayi* Myers, 1936, *Polynemus kapuasensis* Motomura and van Oijen, 2003, *Polynemus melanochir dulcis* Motomura and Sabaj, 2002, *Polynemus melanochir melanochir* Valenciennes, 1831, *Polynemus multifilis* Temminck and Schlegel, 1843 and *Polynemus paradiseus* Linnaeus, 1758.



**Fig. 74.** Lateral view of *Polynemus paradiseus*, type species of the genus *Polynemus* (from Motomura, 2004).

## IX. Summary

The present study was made to describe the osteological, myological and other morphological characters of the family Polynemidae (sensu Motomura, 2004), to evaluate the monophyly of this family and the sister relationship of Polynemidae and Sciaenidae, to reconstruct its phylogenetic relationships based on morphological characters, and to propose a new classification of Polynemidae.

The conclusions of this study are summarized below:

1. The monophyly of Polynemidae was strongly supported by 20 synapomorphies. In addition, after the phylogenetic analysis, it is also supported by three unambiguous synapomorphies (plus three synapomorphies according to ACCTTRAN).
2. The sister relationship of Polynemidae and Sciaenidae was supported by six synapomorphies (Kang et al., 2017). This study sustains this conclusion, and use the sister group, Sciaenidae, as the outgroup for the phylogenetic analysis of Polynemidae.
3. Four most parsimonious trees of Polynemidae were obtained as the result of the phylogenetic analysis based on the morphological characters in 64 transformation series of 8 genera and 25 species of Polynemidae. It was assumed that *Eleutheronema*, *Leptomelanosoma* and *Galeoides* were inferred to be nested within *Polydactylus*.
4. This study redefined Polynemidae as a family including five genera, *Filimanus* Myers, 1936, *Parapolynemus* Feltes, 1993, *Pentanemus*

Günther, 1860, *Polydactylus* Lacepède, 1803 and *Polynemus* Linnaeus, 1758. The genera *Eleutheronema*, *Leptomelanosoma* and *Galeoides* were synonymized under *Polydactylus*, based on the inferred phylogenetic relationships in this study.

## **X. Acknowledgments**

I sincerely wish to thank Prof. Mamoru Yabe, Prof. Yutaka Watanuki, Prof. Hisashi Imamura and Dr. Toshio Kawai, for their guidance during this study and critical reading of the draft manuscript. I am most grateful to the following persons for giving us permission to examine specimens of their institutions: Jeffrey T. Williams (USNM), David Catania (CAS), Michael Hammer and Gavin Daly (NTM), Hiroyuki Motomura (KAUM), Yukio Iwatsuki (MUFS), Seishi Kimura (FRLM) and Hsuan-Ching Ho (NMMB). I especially thank to Dr. Hiroyuki Motomura, who gave much valuable advice on fish specimen collections and polynemid taxonomy. I am greatly indebted to the China Scholarship Council and Office of Hakodate City, which supported her scholarship and funding throughout this study.

## XI. Literature Cited

- Betancur-R, R., Broughton, R.E., Wiley, E.O., Carpenter, K., Lopez, J.A., Li, C., Holcroft, N.I., Arcila, D., Sanciangco, M., Cureton, J., Zhang, F., Buser, T., Campbell, M.A., Ballesteros, J.A., Roa-Varon, A., Willis, S., Borden, W.C., Rowley, T., Reneau, P.C., Hough, D.J., Lu, G., Grande, T., Arratia, G. & Orti, G. (2013) The tree of life and a new classification of bony fishes. *PLoS Currents Tree of Life*, <http://dx.doi.org/10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288>
- Betancur-R, R., Wiley, E., Bailly, N., Miya, M., Lecointre, G. & Orti, G. (2014) Phylogenetic classification of bony fishes—Version 3. [http://dx.doi.org/www.deepfin.org/Classification\\_v3.htm](http://dx.doi.org/www.deepfin.org/Classification_v3.htm).
- Bleeker, P. (1862) Sixième mémoire sur la faune ichthyologique de l'île de Batjan. *Versl. Akad. Amsterdam*, 14, 99–112.
- Eschmeyer, W.N. (1998) Collection abbreviations. *In*: Eschmeyer, W.N. (ed), *Catalog of Fishes, Vol 1*. California Academy of Sciences, San Francisco, pp. 16–22.
- Farris, J.A. (1970) Method for computing Wagner tree. *Syst. Zool.*, 19, 83–92.
- Feltes, R.M. (1991) Revision of the polynemid fish genus *Filimanus*, with the description of 2 new species. *Copeia*, 1991, 302–322.
- Feltes, R.M. (1993) *Parapolynemus*, a new genus for the polynemid fish previously known as *Polynemus verekeri*. *Copeia*, 1993, 207–215.
- Feltes, R.M. (2003) Polynemidae. *In*: K.E. Carpenter (ed.), *The living marine*

*resources of the Western Central Atlantic. Vol. 3: Bony fishes part 2 (Opistognathidae to Molidae), sea turtles and marine mammals. FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication. No 5. FAO, Rome, pp. 1578–1582.*

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

Fraser, T.H. (1972) Comparative osteology of the shallow water cardinal fishes (Perciformes: Apogonidae) with reference to the systematics and evolution of the family. *Ichthyol. Bull.*, 34, 1–105.

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

Gill, T.N. (1861) Synopsis of the polynematoids. *Proc. Acad. Nat. Sci. Phila.*, 13, 271–282.

Gosline, W.A. (1968) The suborders of perciform fishes. *Proc. US. Natl. Mus.*, 124, 1–78.

Gosline, W.A. (1971) *Functional morphology and classification of teleostean fishes*. University Press of Hawaii, Honolulu.

Green, M. (1941) The cranial and appendicular osteology of *Aplodinotus grunniens* Rafinesque. *Trans. Kansas Acad. Sci.*, 44, 400–413.

Grove, J.S. & Lavenberg, R.J. (1997) *The fishes of the Galápagos Islands*. Stanford University Press, Stanford, 863 pp.

- Günther, A. (1860) *Catalogue of the acanthopterygian fishes in the collection of the British Museum (Natural History). Vol. 2, Squamipinnes, Cirrhitidae, Triglidae, Trachinidae, Sciaenidae, Polynemidae, Sphyraenidae, Trichiuridae, Scombridae, Carangidae, Xiphiidae*. British Museum, London, xxi + 548 pp.
- Hennig, W. (1966) *Phylogenetic systematics*. University of Illinois Press, Urbana, 263 pp.
- Imamura, H. (1996) Phylogeny of the family Platycephalidae and related taxa (Pisces: Scorpaeniformes). *Spec. Divers.*, 1, 123–233.
- Johnson, G.D. (1993) Percomorph phylogeny: progress and problem. *Bull. Mar. Sci.*, 52, 3–28.
- Kang, S.H., Imamura, H. & Kawai, T. (2017) Morphological evidence supporting the monophyly of the family Polynemidae (Teleostei: Perciformes) and its sister relationship with Sciaenidae. *Ichthyol. Res.*, <https://dx.doi.org/10.1007/s10228-017-0591-6>.
- Kim, S.Y. (2012) Phylogenetic systematics of the family Pentacerotidae (Actinopterygii: order Perciformes). *Zootaxa*, 3366, 1–111.
- Kim, Y.U. & Kim, I.B. (1965) Osteological study of fishes from Korea (1). Comparative osteology of the family Sciaenidae. *Bull. Pusan Fish. Coll.*, 6, 61–76.
- Lacepède, B.G.E. (1803) *Histoire naturelle des poissons*. Plassan, Paris, lxviii+803 pp.
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes*,

*ordines, genera, species, cum characteribus, differentiis, synonymis, locis.*

Tomus I. Editio decima, reformata. Holmiae. Systema Naturae, Ed. X.V. 1,  
ii+824 pp.

Longhurst, A.R. (1965) The biology of west African polynemid fishes. *ICES Journal of Marine Science*, 30(1), 58–74.

<https://dx.doi.org/10.1093/icesjms/30.1.58>

Maddison, W. P. & Maddison, D. R. (2000) *MacClade, version. 4*. Sinaur Associates, Sunderland, Massachusetts.

Motomura, H. (2004) *Threadfin of the world. FAO species catalogue for fishery purposes*. No. 3. FAO, Rome, 117 pp.

Motomura, H. & Iwatsuki Y. (2001b) Review of *Polydactylus* species (Perciformes: Polynemidae) characterized by a large black anterior lateral line spot, with descriptions of two new species. *Ichthyol. Res.*, 48, 337–354.

Motomura, H. & Iwatsuki, Y. (2001f) A new genus, *Leptomelanosoma*, for the polynemid fish previously known as *Polydactylus indicus* (Shaw, 1804) and a redescription of the species. *Ichthyol. Res.*, 48, 13–21.

Motomura, H. & Iwatsuki, Y. (2003) A new species of freshwater threadfin, *Polynemus aquilonaris*, from Indochina, and redescription of *P. dubius* Bleeker, 1853, (Perciformes: Polynemidae). *Ichthyol. Res.*, 50(2), 154–163.

Motomura, H., Iwatsuki, Y. & Kimura, S. (2001c) Redescription of *Polydactylus sexfilis* (Valenciennes in Cuvier and Valenciennes, 1831), a senior synonym of *P. kuru* (Bleeker, 1853) with designation of a lectotype (Perciformes:

Polynemidae). *Ichthyol. Res.*, 48(1), 83–89.

Motomura, H., Iwatsuki, Y. & Kimura, S. (2001d) A poorly known polynemid fish,

*Polynemus astrolabi* Sauvage, 1881, a junior synonym of *Galeoides*

*decadactylus* (Bloch, 1795). *Ichthyol. Res.*, 48(2), 197–202.

Motomura, H., Iwatsuki, Y., Kimura, S. & Yoshino, T. (2000) Redescription of

*Polydactylus macrochir* (Günther, 1867), a senior synonym of *P. sheridani*

(Macleay, 1884) (Perciformes: Polynemidae). *Ichthyol. Res.*, 47(4), 327–333.

Motomura, H., Iwatsuki, Y., Kimura, S. & Yoshino, T. (2002d) Revision of the

Indo-West Pacific polynemid fish genus *Eleutheronema* (Teleostei:

Perciformes). *Ichthyol. Res.*, 49, 47–61.

Motomura, H., Iwatsuki, Y. & Yoshino, T. (2001a) A new species, *Polydactylus*

*siamensis*, from Thailand and redescription of *P. plebeius* (Broussonet, 1782)

with designation of a neotype (Perciformes: Polynemidae). *Ichthyol. Res.*,

48(2), 117–126.

Motomura, H., Johnson, J.W. & Iwatsuki, Y. (2002c) A taxonomic assessment and

redescription of *Polydactylus multiradiatus* (Günther, 1860), with a synopsis

of other Australian species in the genus (Perciformes: Polynemidae). *Austral.*

*J. Zool.*, 50(3), 267–279.

Motomura, H., Kimura, S. & Iwatsuki, Y. (2002b) Revision of the threadfin genus

*Polydactylus* (Perciformes: Polynemidae) from the eastern Pacific Ocean.

*Ichthyol. Res.*, 49, 358–366.

Motomura, H. & Sabaj, M.H. (2002e) A new subspecies, *Polynemus melanochir*

- dulcis*, from Tonle Sap Lake, Cambodia, and redescription of *P. m. melanochir* Valenciennes in Cuvier and Valenciennes, 1831 with designation of a neotype. *Ichthyol. Res.*, 49(2), 181–190.
- Motomura, H., Sado T. & Kimura, S. (2002a) Feeding behavior of *Polydactylus plebeius* (Perciformes: Polynemidae) in an aquarium. *Jpn. J. Ichthyol.*, 49, 156–157.
- Motomura, H., Seshagiri Rao, B.V., Ratnamala, B. & Iwatsuki, Y. (2001e) *Polydactylus konadaensis* Mishra and Krishnan, 1993, a junior synonym of *Filimanus xanthonema* (Valenciennes in Cuvier and Valenciennes, 1831) (Perciformes: Polynemidae). *Ichthyol. Res.*, 48(2), 203–206.
- Myers, G.S. (1936) A new polynemid fish collected in the Sadong River, Sarawak by Dr William T. Hornaday. *J. Wash. Acad. Sci.*, 26(9), 376–382.
- Nakabo, T. (ed.) (2013) *Fishes of Japan with pictorial keys to the species, 3rd edition*. Tokai University Press, Tokyo, 2428 pp.
- Near, T.J., Dornburg, A., Eytan, R.I., Keck, B.P., Smith, W.L., Kuhn, K.L., Moore, J.A., Price, S.A., Burbrink, F.T., Friedman, M. & Wainwright, P.C. (2013) Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *Proc. Nat. Acad. Sci.*, 110:12738–12743.
- Nelson, J.S. (1984) *Fishes of the world. 2nd edition*. John Wiley & Sons, New York, xv+475 pp.
- Nelson, J.S. (2006) *Fishes of the world. 4th edition*. John Wiley & Sons, New York, xix+601 pp.

- Nelson, J.S., Grande T.C. & Wilson M.V.H. (2016) *Fishes of the world, 5th edition*.  
John Wiley & Sons, Hoboken, xvi+707 pp.
- Randall, J.E. (1995) *Coastal fishes of Oman*. Crawford House Publ. Pty Ltd,  
Bathurst, 439 pp.
- Rosen, D.E. (1964) The relationships and taxonomic position of the halfbeaks,  
killifishes, silversides, and their relatives. *Bull. Mus. Nat. Hist.*, 27, 219–267.
- Sainsbury, K.J., Kailila, P.J. & Leyland, G.G. (1984) *Fishes of northern and  
north-western Australia*. Canberra Times, Canberra, 375 pp.
- Sanciango, M.D., Carpenter, K. & Betancur-R, R. (2015) Phylogenetic placement  
of enigmatic percomorph families (Teleostei: Percomorphaceae). *Mol.  
Phylogenet. Evol.*, 94 (Part B), 565–576.
- Sasaki, K. (1989) Phylogeny of the family Sciaenidae, with notes on its  
zoogeography (Teleostei, Perciformes). *Mem. Fac. Fish. Hokkaido Univ.*, 36,  
1–137.
- Smith, C.L. & Bailey, R.M. (1962) The subocular shelf of fishes. *J. Morphol.*, 110,  
1–17.
- Smith, M.M. & Heemstra, P.C. (1986) *Smiths' sea fishes*. Berlin: Springer-Verlag,  
1047 pp.
- Swofford, D.L. (2002) PAUP\*. *Phylogenetic analysis using parsimony (\*and  
other methods)*, version 4.0b10. Sinaur Associated, Sunderland,  
Massachusetts.
- Taniguchi, N. (1969) Comparative osteology of the sciaenid fishes from Japan and

- its adjacent waters-I. Neurocranium. *Jpn. J. Ichthyol.*, 16, 55–67.
- Topp, R.W. & Cole, C.F. (1968) An osteological study of the sciaenid genus, *Sciaenops* Gill (Teleostei, Sciaenidae). *Bull. Mar. Sci.*, 18, 902–945.
- Watrous, L.E. & Wheeler, Q.D. (1981) The out-group comparison method of character analysis. *Syst. Zool.*, 30, 1–11.
- Winterbottom, R. (1974) A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. Philadelphia*, 125, 235–317.
- Wiley, E.O. (1981) *Phylogenetic: the theory and practice of phylogenetic systematic*. John Wiley and Sons, New York, xv+439 pp.
- Yabe, M. (1985) Comparative osteology and myology of the superfamily Cottoidea (Pisces: Scorpaeniformes), its phylogenetic classification. *Mem. Fac. Fish. Hokkaido Univ.*, 32, 1–130.