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ORIGINAL PAPER

Comparative osteology of the superfamily Congiopodoidea (Pisces: Scorpaenoidei)

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Abstract

A detailed study of the structure of bone elements of the neurocranium and pectoral girdle and of the structure of pelvis of all three genera of the family Congiopodidae: *Congiopodus*, *Alertichthys*, and *Zanclorhynchus,* was carried out in the present paper. It resulted in the discovery of new complex apomorphies of Congiopodidae s.l., which are an additional and very convincing confirmation of the separate position of this family in the suborder Scorpaenoidei. These include the features of the posterior neurocranium structure: location, shape, and size of the parietal and supraoccipital, location of these bones in relation to the anterior pterygiophores D1, position of the first vertebrae in relation to the neurocranium and the highly complex structure of the cleithrum. Based on the osteological data, it was concluded that the taxonomic status of the family could be increased to superfamily Congiopodoidea, and its subfamilies, respectively, to the rank of the families Congiopodidae and Zanclorhynchidae.

Keywords Comparative osteology · Taxonomy · Phylogeny · Congiopodoidea · *Zanclorhynchus* · *Alertichthys* · *Congiopodus*

Introduction

The fishes of the three genera, *Congiopodus* Perry 1811, *Alertichthys* Moreland 1960, and *Zanclorhynchus* Günther 1880 inhabit the shelves and tops of seamounts in the subtropical, temperate, and subantarctic waters of the Southern Hemisphere at depths of up to 800 m. The monotypic genus *Alertichthys* is endemic to New Zealand (Stewart and Struders 2015). Fishes of the genus *Zanclorhynchus* inhabit the waters of the Southern Ocean. The genus encompasses two species: *Z. chereshnevi* Balushkin et Zhukov 2016, found off the Crozet Islands and the Prince Edward Islands (Balushkin and Zhukov 2016; Zhukov 2020a), and polytypic species *Z. spinifer* Günther 1880 with four subspecies. *Z. spinifer spinifer* Günther 1880 inhabits shelves and seamounts on Kerguelen Plateau (Meyer et al. 2000; Zhukov 2019), *Z. spinifer armatus* Zhukov 2019—waters off the Crozet Islands and the Prince Edward Islands (Zhukov 2019), *Z. spinifer macquariensis* Zhukov 2019—the Macquarie Island Shelf (Zhukov 2019), *Z. spinifer heracleus* Zhukov et Balushkin 2018 inhabits the tops of seamounts of the Ridge of Hercules (Pacific-Antarctic Ridge) (Zhukov and Balushkin 2018). Genus *Congiopodus* includes a total of six valid species, which inhabit the following locations pairwise: *C. kieneri* (Sauvage 1878) and *C. peruvianus* (Cuvier 1829)—shelf of the southern South America (Hureau 1971; Pequeño 1989), *C. spinifer* (Smith 1839) and *C. torvus* (Gronow 1772)—southern Africa (Day et al. 1970; Poss 1986), *C. leucopaecilus* (Richardson 1846) and *C. coriaceus* Paulin et Moreland 1979—waters off southern Australia and New Zealand (Stewart and Struders 2015; Zhukov 2020b).

The taxonomic rank of all three genera of the family has been revised by different authors. Regan discovered differences in the structure of the skeleton of Congiopodidae (Regan 1913), which are quite noticeable between the genera *Congiopodus* and *Zanclorhynchus*, including the differences in location of the anterior rays of D1 either on the head or the occiput, in the origin of posttemporal attachment to the skull bones, and in the length ratio of the pelvis. Regan (1913) indicated the significant importance for the taxonomic position of the Congiopodidae of the close location of the medial margins of the epioccipital behind the supraoccipital, which he considered an apomorphy of the

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Congiopodidae, similar to the connection of these bones in Pataecidae. Regan placed the Congiopodidae in its own order Congiopodiformes, based on examination of osteology and external morphology. Next, a number of authors classified Congipodoidei as an independent suborder of Scorpaniformes according to the listed characters (Greenwood et al. 1966; Lindberg 1971; Nelson 1976; Lauder and Liem 1983).

Mandrytsa (2001) noted that Scorpaenoidei and Congipodoidei differ in the position of the two anterior pterygiophores of the first dorsal fin in relation to the neural processes of the first vertebra, as well as in a number of the structural features of the bony elements of the splanchnocranium and seismosensory system. This was also the view of Smith and others (2018) in their work on the molecular biology and phylogeny of Scorpaeniformes. These apomorphies gave the authors the opportunity to revise the taxonomic rank of the Congiopodoidei suborder. The taxonomic rank of the suborder Congipodoidei was lowered to the family level in the work of Andriashev (1993) based on the functional morphology of the pectoral and pelvic fins, and later by Ishida (1994) and Eschmeyer (1998) based on osteological and myological study of Scorpaenoidei, and, respectively, the rank of the families Congiopodidae and Zanclorinchidae was lowered to the level of subfamilies (Imamura 2004; Ishii and Imamura 2008). Ishida (1994) identified eight characters in the structure of the neurocranium and the pectoral girdle, which are autapomorphies or synapomorphies of all three genera in Congiopodidae, and also partially unite them with other Scorpaenoidei: the lateral ethmoid and vomer are separated by the articulation of the mesethmoid and parasphenoid or a large mass of cartilage; vomer without teeth; basisphenoid is absent in *Alertichthys* and *Zanclorhynchus*. In Congiopodidae (group 53–1 of Ishida 1994), the epioccipitals meet in the midline, thus separating the supraoccipital and exoccipital (this character is not shown in Ishida’s Fig. 26, which he cites); in Congiopodidae and Aploactinidae (group 54–1 of Ishida 1994), the intercalar is small, occupying a more posterior position, where it meets anteriorly with the posterior margin of the pterotic, and is separated from the prootic by the connection of the pterotic and exoccipital and the dermosphenotic is absent. In *Alertichthys* and *Zanclorhynchus*, the scapula is fused with the uppermost radial. Imamura (2004) recognized ten apomorphies in the structure of the neurocranium and pectoral girdle of Congiopodidae: tubercles on neurocranium present; nasal firmly attached to cranium; vomerine teeth absent; pterosphenoid and parasphenoid connected in *Alertichthys*; prootic and intercalary separated; intercalar and posttemporal sutured; spines associated with the seismosensory canal on the parietal present in *Zanclorhynchus* and *Alertichthys*; Baudelot's ligament absent; medial extrascapular absent; lateral extrascapular is a single element (longitudinal tube) with two sensory openings; uppermost radial and scapula fused in *Alertichthys*. Ishii and Imamura (2008) supported the monophyly of the Congiopodidae by these apomorphies, and also recognized the taxonomic rank of subfamilies of the families Congiopodidae and Zanclorhynchidae previously claimed by Mandritsa (2001). At the same time, the authors recognized enough high specialization in Congiopodidae s.l. to separate it from other Scorpaenoidei.

Recently, studying radiographs and tomograms of *Congiopodus*, we found in this genus a very unusual, previously undescribed structure of the neurocranium, further separating it from *Alertichthys* and *Zanclorhynchus*. Among that, the study of the neurocranium and the skeleton of the pectoral girdle of all three genera revealed the characters of the occipital region of neurocranium, the first vertebra, and the bones of the pectoral girdle and pelvis, which are unique in Scorpaenoidei. In our opinion, these features support recognition of the family rank of the subfamilies Congiopodinae Gill 1889 and Zanclorhynchinae Andriashev 1993 (Andriashev 1993; Balushkin and Zhukov 2016) and to place then in a separate superfamily Congioipodoidea of the suborder Scorpaenoidei. Since we did not find a description of the structure of the neurocranium of congiopodids in any previous studies works, we provide a detailed description and complete drawings of the neurocranium and the skeleton of the pectoral girdles of all three genera of Congiopodidae, a cladistic analysis that includes osteological characters and features of the seismosensory system, as well as rationale of our taxonomic conclusions.

Materials and methods

Studied specimens are deposited at the Zoological Institute of the Russian Academy of Sciences.

Alertichthys blacki ZIN 45669–31 TL 241 mm, SL 203 mm, southern Campbell Plateau, depth 200 m, LFT «Ekvator», Dec. 1971, collector Svirskij VG; *Congiopodus coriaceus* ZIN 50281–24 TL 137.3 mm, SL 116.3 mm, SRV «Dmitriy Mendeleev», Cruise 16, St. 1278, Southern Ocean, north off Campbell Island, 51°46’ S, 169°35’ E, depth 286–230 m, 15 Jan.1976, collectors Andriashev AP, Pirodina VP; *Zanclorhynchus spinifer spinifer* ZIN 45691–26 TL 139 mm, SL 107 mm, Kerguelen Island, 47°25’ S, 68°36’ E, SSS «Skif», Cruise 3, St. 1072/161, Trawl 113, depth 189 m, 02 January 1971 г., collector Pushkin AF.

Comparative material: *Pataecus fronto* ZIN 39183 TL 179 mm, SL 155 mm, Great Australian Bight, 33°10’ S, 126°23’ E, FT «Seskar», depth 104–99 m, 17 February 1966, collector Tsarev VI; *Gnathanacanthus goetzeei* ZIN 49794 TL 234 mm, SL 178 mm, Victoria (Australia), Horns point at Wilsons Promontory, 39°10’ S, 146°28’ E, depth 10 m, 08 February 1982, collectors Kuiter RH, McDonald M.

Computed tomography was performed on Toshiba Aqulion Prime 64 equipment. X-ray images was obtained on a PRDU-02 X-ray diffractometer. Osteological examinations were made on specimens stained with Alizarin Red-S and Alcian Blue followed with clearing in KOH:glycerin solutions (Potthoff 1984). Abbreviations used: D—dorsal fin, FT—fish trawler, LFT—large fish trawler, SL—standard length, SRV—scientific-research vessel, SSS—scientific-search ship, TL—total length, V—ventral fin, ZIN—Zoological Institute of the Russian Academy of Sciences. We have adopted the following order of presentation of the results. First, a description of the structure of the skeleton or its details at *Congiopodus* is given. After that, the structural features of Zanclorhynchynae as a whole are given, and then separately in *Zanclorhynchys* and *Alerthichtys*.

Results

Neurocranium

The neurocranium of *Congiopodus, Zanclorhynchus* and *Alertichthys* in dorsal and ventral views have the shape of an elongated triangle, (Figs. 1A–C, 2A–C). The height of the upper profile of the cranium in *Congiopodus* increases significantly at the level of the vertical plate of the lateral ethmoid and further increases above the eye, remaining unchanged posteriorly. In *Zanclorhynchus*, the upper cranium profile rises less significantly and steadier, and above the eye is also quite high due to the formation of large, upwardly directed lateral frontal ridges, between which a groove is formed medially in the interorbital space. Posterior to the eye, the upper profile decreases slightly, forming a small notch of the upper profile of the cranium, and then its height increases slightly again. In *Alertichthys*, the lateral ridges of the frontals are less developed. The ethmoid region of the lower profile of the neurocranium at the level of the vertical plate of the lateral ethmoid in *Congiopodus* is noticeably inclined downward anteriorly, in *Zanclorhynchus* and *Alertichthys* the lower profile of the neurocranium is straight along its entire length (Fig. 3A–C).

Roof

The nasal of *Congiopodus* is firmly attached to the frontal posteriorly, to the mesethmoid medially and laterally to the vertical plate of the lateral ethmoid. The nasal contains the first segment of the supraorbital canal of the seismosensory system. In *Congiopodus*, the bone is straight, elongated, sharpened at the anterior end, dorsally covering almost ¾ of the ethmoid region and medially bears a small spine on posteromedially. In *Zanclorhynchus*, the nasal is short, covering no more than half of the ethmoid region. In contrast to *Congiopodus*, the anterior half of the nasal bends laterally,

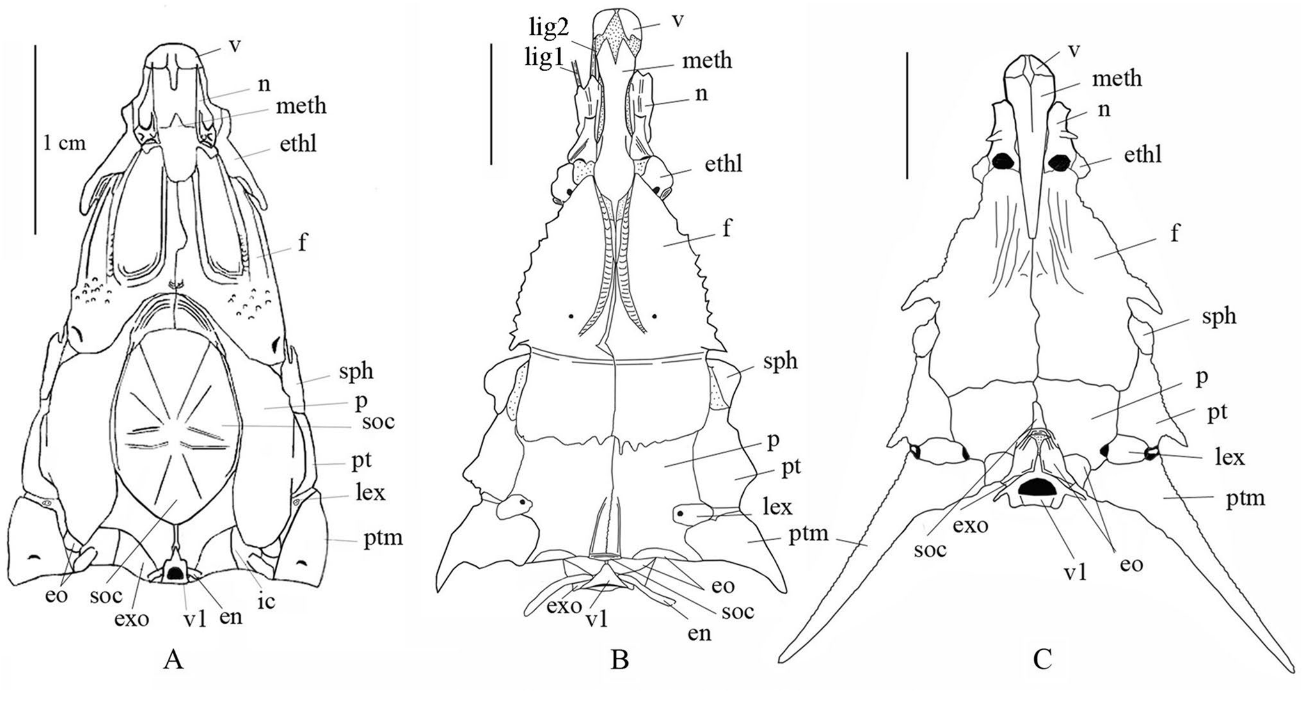

Fig. 1 Neurocranium (dorsal view). *Congiopodus coriaceus* ZIN 50281-24 (**A**), *Alertichthys blacki* ЗИН 45669-31 (**B**), *Zanclorhynchus spinifer spinifer* ZIN 45691-26 (**C**); *eo* epioccipital, *ethl* lateral ethmoid, *exo* exoccipital, *f* frontal, *lex* lateral extrascapular, *meth* mesethmoid, *n* nasal, *p* parietal, *pt* pterotic, *ptm* posttemporal, *soc* supraoccipital, *sph* sphenotic, *v* vomer, *v1* first vertebra

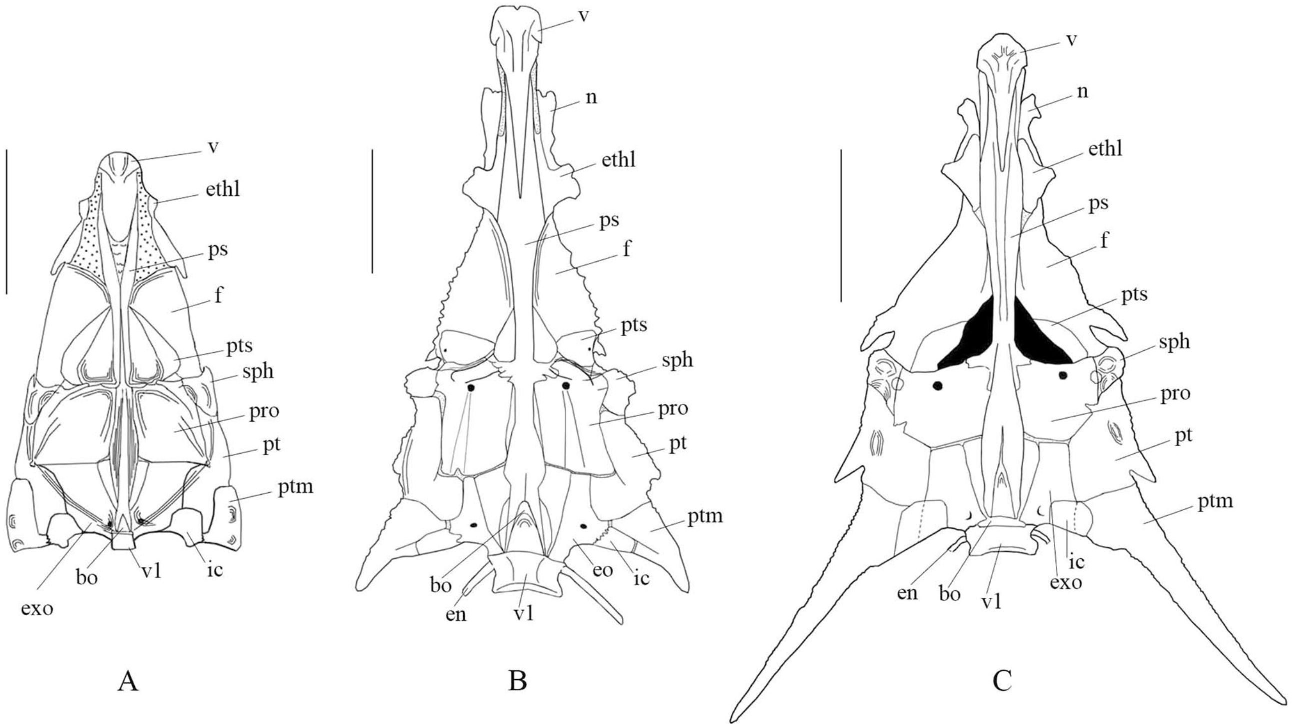

Fig. 2 Neurocranium (ventral view). *Congiopodus coriaceus* ZIN 50281-24 (**A**), *Alertichthys blacki* ZIN 45669-31 (**B**), *Zanclorhynchus spinifer spinifer* ZIN 45691-26 (**C**); *bo* basioccipital, *en* epineural, *ethl* lateral ethmoid, *exo* exoccipital, *f* frontal, *ic* intercalar, *pro* prootic, *ps* parasphenoid, *pt* pterotic, *ptm* posttemporal, *pts* pterosphenoid, *sph* sphenotic, *v* vomer, *v1* first vertebrae

remaining wide anteriorly. And the posteromedial spine is larger than that of *Congiopodus*. *Alertichthys* has the longest nasal. It almost completely covers the ethmoid region, and it expands and slightly forks anteriorly. A short ligament attaches its lateral part to the head of the palatine laterally. The inner surface of the anterior expansion of the nasal provides an attachment site for another ligament that extends to the vomer and attaches to the posterior edge of this bone.

In *Congiopodus*, the frontal forms an elongated anterior tip, then expands laterally and ends with an expanded and almost straight margin located at the level of the sphenotic; it does not contact the pterotic, unlike in other genera. Medially, the posteriormost tips of the frontals form the anterior portion of the ridge, bordering anteriorly and laterally a very deep supraoccipital fossa and providing an attachment site for the anteriormost of the m. rectus dorsalis, which on both sides passes into the supraoccipital fossa. Between them are five anterior proximal pterygiophores so that only the dorsal fin spines attached to them rise above the upper profile of the cranium. The posterior, longest and highest portion of the ridge of the supraoccipital fossa is formed by the medial margins of the parietals. The dorsolateral surface of this bone does not bear the spine of the supratemporal commissure, which in *Congiopodus* is interrupted and has only a lateral segment located on the lateral extrascapular. The parietals are separated from each other throughout, being widely divided by the very large supraoccipital. In *Zanclorhynchus* and *Alertichthys*, the frontal is also narrowed anteriorly, but is longer than in *Congiopodus*. Its straight posterior margin situated at the level of the anteriormost extent of the pterotic. The bone does not form the ridge of the supraoccipital fossa and does not participate in its formation, far from reaching it anterior margin. Dorsal to the eye, the lateral edge of the frontal forms a high ridge, strongest in *Zanclorhynchus*. A longitudinal medial notch is formed between the right and left ridges on the dorsal surface of the neurocranium. Posterodorsal to the eye, the lateral ridge of the frontal bears a long sharp spine, which is absent in *Congiopodus*. This spine is most strongly developed in *Zanclorhynchus*, wherein, the anterior halves of the right and left parietals are connected anteriorly along the midline of the cranium. The posterior halves of these bones medially enclose a small triangular supraoccipital, which bears a large number of minute spines on its dorsal surface. Posteriorly the parietals slightly expand, lose their external sculpture and become smooth. The medial margins of the parietals and supraoccipital form a shallow supraoccipital pit located medially at the posteriormost portion of the cranium. The right parietal bears posteriorly a small, backward-curved

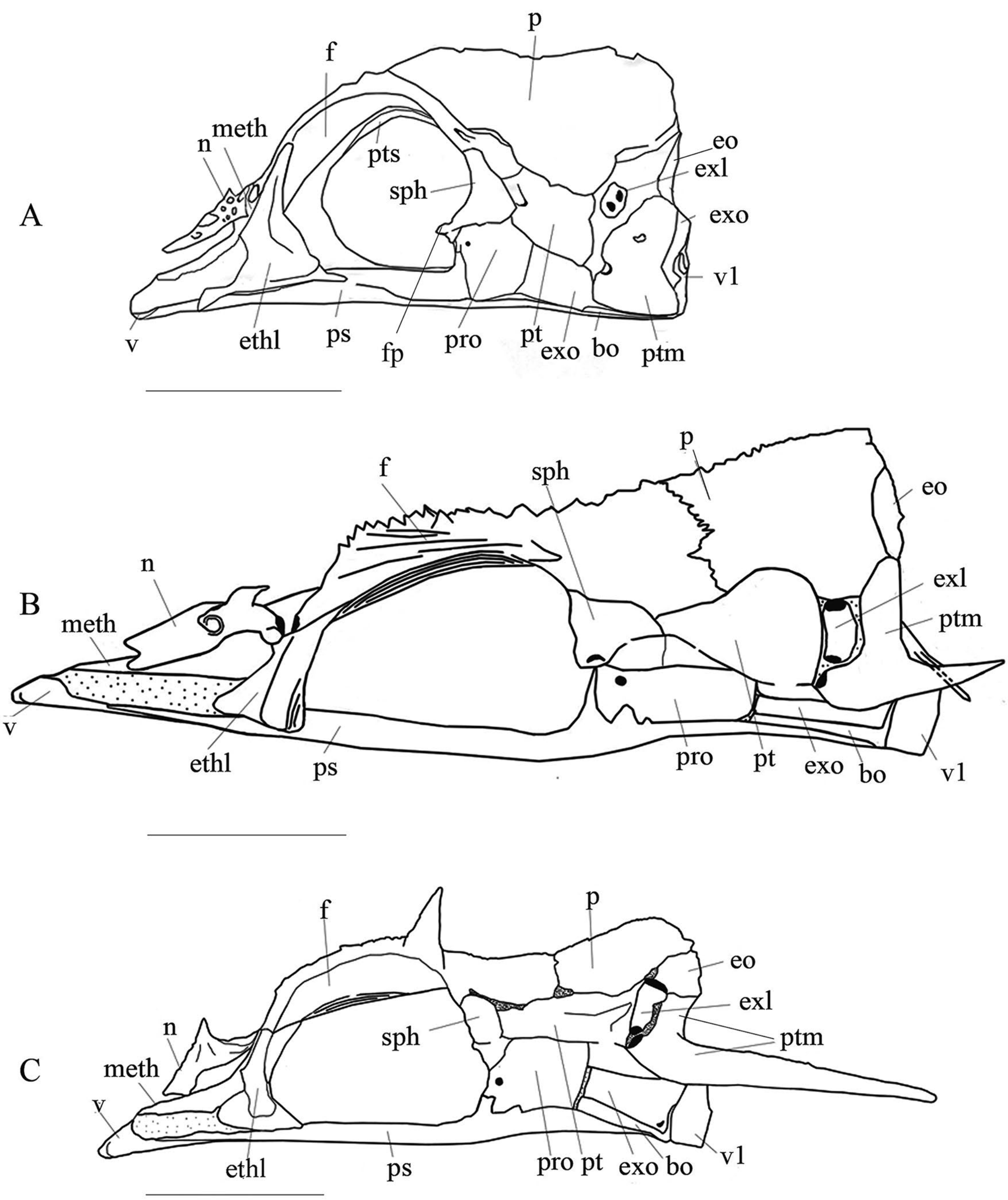

Fig. 3 Neurocranium (lateral view). *Congiopodus coriaceus* ZIN 50281-24 (**A**), *Alertichthys blacki* ZIN 45669-31 (**B**), *Zanclorhynchus spinifer spinifer* ZIN 45691-26 (**C**); *bo* basioccipital, *en* epineural, *ethl* lateral ethmoid, *eo* epioccipital, *exl* lateral extrascapula, *exo* exoccipital, *f* frontal, *fp* flexion point for articulation with infraorbital 3, *ic* intercalar, *lex* lateral extrascapular, *meth* mesethmoid, *n* nasal, *p* parietal, *pro* prootic, *ps* parasphenoid, *pt* pterotic, *ptm* posttemporal, *sph* sphenotic, *v* vomer, *v1* first vertebrae

spine. The parietal structure of *Alertichthys* differs from that of *Zanclorhynchus*; the parietals of the right and left sides are connected throughout, displacing the supraoccipital to the posterior surface of the cranium. Each parietal posteriorly forms a small vertical ridge, forming a notch similar to the supraoccipital fossa (Figs. 1A–C, 2A–C).

Ethmoid region (Figs. 1A–C, 3A–C)

Congiopodus has an elongated lateral ethmoid and mesethmoid. The anterior plate of the lateral ethmoid laterally overlaps the ethmoid cartilage by almost 3/4, but does not reach the posterior margin of the vomer. The mesethmoid anteriorly reaches the posterior margin of the vomer, but does not connect it. In *Zanclorhynchus*, the horizontal plate of the lateral ethmoid is much shorter—it laterally covers no more than a quarter of the posterior portion of the ethmoidal cartilage; the mesethmoid anteriorly reaches the vomer. The horizontal plate of the lateral ethmoid in *Alertichthys* is even shorter; it is almost undeveloped and does not extend beyond the vertical plate of the bone. Dorsally, part of the ethmoid region is covered with the nasal, the last one is firmly attached behind the anteriormost of the frontal and to the upper portion of the lateral ethmoid. In *Congiopodus*, the nasal overlaps about 2/3 of the ethmoid region. *Zanclorhynchus* has a relatively short nasal that dorsally covers half of the ethmoidal region of the cranium. In *Alertichthys*, this bone almost completely covers the ethmoidal region.

Base of the neurocranium **(Fig. 2A–C)**

The vomer lacks teeth in all three genera and forms a rather long handle, which penetrates posteriorly between the anterior processes of the parasphenoid, reaching the level of the vertical plate of the lateral ethmoid. As mentioned above, in *Congiopodus*, the anterior portion of the parasphenoid forms a downward bend (about 20°) at the level of the vertical plates of the lateral ethmoid. In *Zanclorhynchus* and *Alertichthys*, the parasphenoid is straight throughout. The ascending process of the parasphenoid in *Congiopodus* is located mainly along the orbital surface of the prootic, not reaching the lower margin of the pterosphenoid dorsally—a large elongated oval bone, which is located below the ventral margin of the frontal in the orbital region of the skull. The pterosphenoid of *Zanclorhynchus* is a small rounded bone located in the posterior corner of the orbit and connects with the frontal dorsally, posterodorsally with the sphenotic, and ventrally with the prootic. In *Alertichthys*, along the dorsal edge of the pterosphenoid, a vertical orbital process of the parasphenoid meets this bone. In *Zanclorhynchus*, the ascending process of the parasphenoid is forked, where the ventral process of the prootic is inserted. Its shorter anterior process is located along the orbital surface of the prootic, but also does not reach the lower margin of the pterosphenoid. In *Congiopodus*, the basisphenoid is absent, but it is present in both other genera and ventrally borders the anterior opening of the skull, without forming the ventral myodome.

Otic region **(Fig. 3A–C)**

In *Congiopodus*, the prootic forms a large, rounded plate on the anteroventral portion of the lateral surface of the cranium. Anteriorly, the upper portion of the prootic bends inward, forming an oval, obliquely located, projecting articular surface at the flexion point for articulation with infraorbital 3. The anterior portion of the bone forms the posterior margin of the orbit, ventrally forming the dorsal border of the foramen for n. trigeminus. Ventrally, this foramen is bordered by the ascending process of the parasphenoid, associated with the internal section of the prootic anteriorly to that foramen. The foramen for n. facialis is located in the lateral plate of the prootic posterior to the articular surface for infraorbital 3. The posterodorsal margin of the lateral plate of the prootic is sutured with the ventral margin of the pterotic. The articular surface for infraorbital 3 in *Zanclorhynchus* and *Alertichthys* is smoothed and expanded. The dorsal margin of the prootic in *Zanclorhynchus* forms posteriorly an elongated triangular process overlapping the lateral surface of the pterotic (Fig. 3C). This process is absent in *Alertichthys*.

In *Congiopodus*, the sphenotic bears a lateral prominence on the dorsal surface, which is almost hidden in dorsal view and, apparently, is a dermosphenotic fused with it. In *Zanclorhynchus* and *Alertichthys*, the dorsolateral margin of the sphenotic is flat. The pterotic in *Congiopodus* forms a rather extensive plate on the lateral surface of the cranium, being smaller on the dorsal surface. In *Zanclorhynchus*, the pterotic forms posteriorly a small, pointed spine, directed backward. The same spine is found in *Alertichthys*, in which the ventral margin of the pterotic forms a very large oval plate that does not suture with the posterior margin of the prootic. In all three genera the intercalar is similar in shape and location and is situated at the posterior margin of the lateral surface of the cranium on a small area of the posterior surface of the skull. It is a small rounded bone, posteriorly narrowed and in *Congiopodus* its small dorsal process is sutured with the ventral limb of the posttemporal. In *Zanclorhynshus*, the suture is essentially absent (there is one small denticle), and in *Alertichthys*, its dorsal margin is plain and also does not form a suture with the ventral end of the posttemporal. In the point of transition to the posterior surface of the cranium, the intercalar of *Congiopodus* forms a posterior process for articulation with the supracleitrum, just below which the ventralmost end of the intercalar inserts into the exoccipital notch. On the posterior surface of the cranium, the intercalar grows upward along the posterior margin of the posttemporal and the lateral margin of the exoccipital. It meets dorsally the ventral margin of the epioccipital. A similar structure was found in the other two genera. There is a small area of the epioccipital, situated on the dorsal surface of the cranium, that meets the parietal dorsally, posttemporal ventrally and lateral extrascapular anteriorly. The epioccipital bends onto the posterior surface of the cranium and forms its dorsal lateral region, connecting dorsally with the medial process of the posttemporal, medially with supraoccipital, and ventrally with neural process of the first vertebra and with the intercalar. In both genera, the epioccipital of the right and left sides are not articulated with each other: in *Congiopodus*, they are separated by the neural process of the first vertebra, and in *Zanclorhynchus* by the connective tissue membrane. In *Alertichthys*, the epioccipitals are closest to each other, but not directly articulated.

Occipital region (Figs. 4, 5)

In *Congiopodus*, the supraoccipital is a large, flat, non-tubercular oval bone, meeting anteriorly with the posterior margin of the frontal. Laterally, the supraoccipital is connected along its entire length with a narrow horizontal portion of the parietal on the dorsal surface of the cranium, and the posterior, relatively short edge of the bone is laterally bounded by the epioccipitals. In *Zanclorhynchus*, the supraorbital is rudimentary and much smaller and is located posteriorly in the pit that is formed by the medial margins of the parietals, being a small, narrow, elongated triangle, not reaching the posterior margin of the frontal anteriorly. On the posterior surface of the cranium, the supraoccipital forms a small oval prominence, the dorsal surface of which is covered with small tubercles. In *Alertichthys*, the supraoccipital does not extend to the dorsal surface of the cranium and is completely located in the upper sector of its posterior surface, where it divides the upper thirds of the medial margins of the epioccipitals. It is not tubercular.

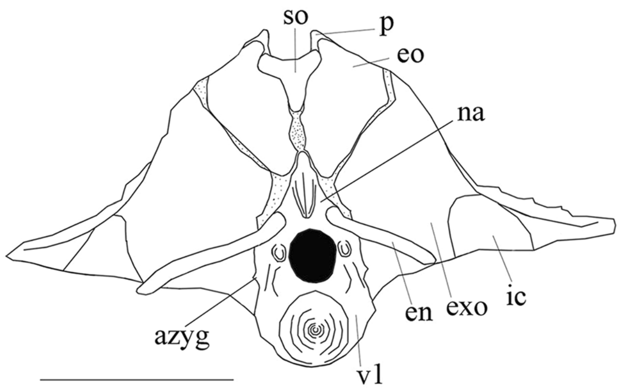

Fig. 4 Neurocranium *Alertichthys blacki* ZIN 45669-31. Posterior view. *azyg* anterior zygapophysis of the first vertebra, *en* epineural, *eo* epioccipital, *exo* exoccipital, *ic* intercalar, *p* parietal, *so* supraoccipital, *v* vertebrae

The anterior portion of the exoccipital is located along the posterior half of the lateral surface of the cranium in all three genera. Posteriorly, the upper margin of the bone forms a rather deep notch, curving inward in this narrow area and forming here a small plate that covers part of the posterior wall of the skull. In *Congiopodus*, this plate overlaps medially the centrum of the first vertebra and forms with it a small rounded articulation In *Zanclorhynchus* and *Alertichthys*, the exoccipital plate is less developed on the posterior surface of the cranium than in *Congiopodus*. Despite the fact that it also overlaps medially the centrum of the first vertebra, it does not extend deep into the cranium as in *Congiopodus*. The basioccipital is located dorsal to the posteriormost

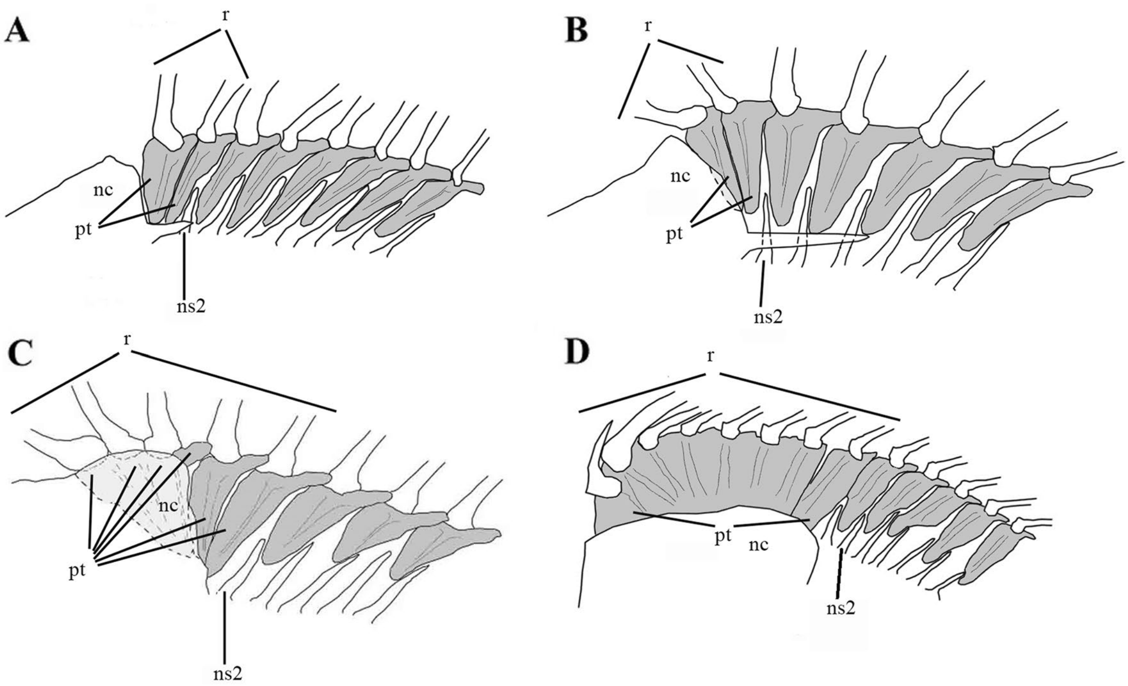

Fig. 5 Schematic view of the first dorsal pterigiophore position in *Alertichthys blacki* (A), *Zanclorhynchus spinifer* (B), *Congiopodus coriaceus* (C), *Pataecus fronto* (D). *nc* neurocranium, *ns2* second neural spine, *pt* pterygiophres (position of the bones behind is shown with a dotted line, pterigiophores filled grey), *r* rays

tip of the parasphenoid, and its posterior surface forms a joint with the anterior surface of the first vertebra. The most dense joint with first vertebra was noted in *Congiopodus*, which is almost indistinguishable in lateral view.

The first vertebra of the Congiopodidae is tightly attached to the posterior surface of the neurocranium, and its central foramen takes on the role of the foramen magnum. Ventrally, in all three genera, the joint of the first vertebra with the posterior facet of the basioccipital is clearly visible, but on the lateral and posterior walls of the neurocranium, traces of its articulation with the exoccipital can be seen with great difficulty. In this case, the anterior zygapophys of the first vertebra is displaced to its lateral surface and here it meets the medially curved articular surface of the exoccipital. Dorsal to the first vertebral centrum there is a neural arch, medially articulating with the exoccipitals. Its dorsal tips join to form a neural spine, which meets the medial margins of the epioccipitals and separates their ventral margins. Well-developed epineurals are laterally attached to the neural arch. In *Congiopodus*, the first vertebra is firmly attached to the bones of the posterior wall of the skull; in *Zanclorhynchus* and *Alertichthys*, it shows some mobility.

Temporal region

The temporal region comprises two ossifications—lateral extrascapular and posttemporal. The first one is located on the dorsal surface of the cranium between the pterotic, parietal and posttemporal being a small oval bone that dorsally forms a canal for the lateral segment of the temporal canal of the seismosensory system. The posttemporal borders the posterior lateral section of the cranium and anteriorly is firmly attached to the pterotic, anterodorsally to the parietal, and meets the intercalar on the lateral surface of the skull, and the exoocipital posteriorly. At the line of a connection with the intercalar, both bones anteriorly form a large notch. The posterodorsal portion of the posttemporal bears a large and very long spine in *Zanclorhynchus* and a shorter spine in *Alertichthys*. Posteriorly, the supracleithrum articulates with the posttemporal.

Pectoral and pelvic girdles (Figs. 6, 7)

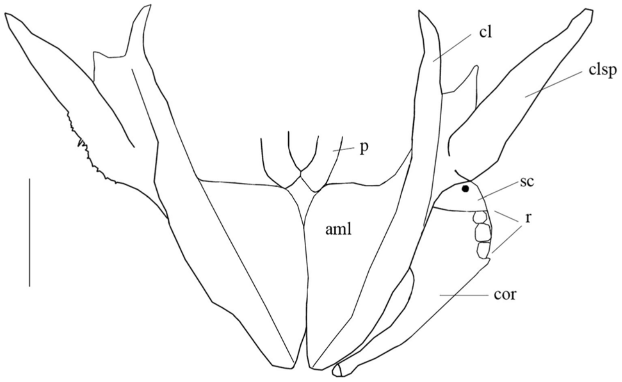

Fig. 6 Pelvic girdle *Alertichthys blacki* ZIN 45669-31. Anterior view. *cl* cleithrum, *clsp* cleithrum spine, *cor* coracoid, *mr* medial ridge, *p* pelvis, *r* radial, *sc* scapula

In *Zanclorhynchus* and *Alertichthys* the supracleithrum is a flattened triangular bone, dorsally articulated with the posttemporal, intercalar, and epioccipital. In *Congiopodus*, the cleithrum dorsally forms a high process, which bears a deep notch in the middle. The supracleithrum is connected dorsally to its anterior plate, and an oval-shaped proximal postcleithrum articulates with the base of its posterior plate. A rather long distal postcleithrum articulates with its posterior margin. The cleithrum forms a high ridge along its outer edge, the ventral section of which bends medially, forming a wide plate here and is firmly attached to the medial plate of the bone of the opposite side. The anterior tip of the pelvis comes anteriorly to the dorsal surface of the medial plate of the cleithrum, where it inserts in the small notch. A shorter ridge extends along the lower margin of the cleithrum, articulating with that of the opposite side. Laterally, the anterior edge of the coracoid connects this ridge. The anterior portion of the coracoid bends inward at an almost right angle and attaches internally to the inner border of the cleithrum and its inferior crest. The narrow and elongated precoracoid foramen in Zanclorhynchynae opens on the inner surface of the cleithrum, unlike Congiopodinae and other Scorpaenoidei. The ventral portion of precoracoid process of the coracoid extends to the lowermost tip of the cleithrum. As a result, the cleithrum and coracoid form a very complex volumetric structure for the attachment of the muscles of the pectoral girdle. The rectangular scapula is pierced by a foramen in its center. *Congiopodus* has four free small radials the two other genera have only three (the upper one is fused with the scapula). The coracoid is a medium-sized flat bone, articulated dorsally with the posterior inner surface of the cleithrum and the scapula. Ventrally, the coracoid in *Congiopodus* bears a long precoracoid process that connects the ventralmost tip of the cleithrum and forms a large piercing precoracoid foramen. The postcoracoid process is small in *Congiopodus* and *Alertichthys* and some longer in *Zanclorhinchus.* The length of the pelvis in *Congiopodus* is slightly less than the height of the cleithrum. In this species, the pelvis is relatively wide; the bones of the right and left sides are connected along the midline almost along the entire length of the anterior processes. The lateral ridge of the bone is absent. In *Zanclorhynchus* and *Alertichthys*, the cleithrum also forms a high dorsal process, the anterior and posterior lobes of which are divided with a small notch. The anterior lobe is high, while the posterior lobe is almost reduced. The base of the dorsal process of the cleithrum bears a long,

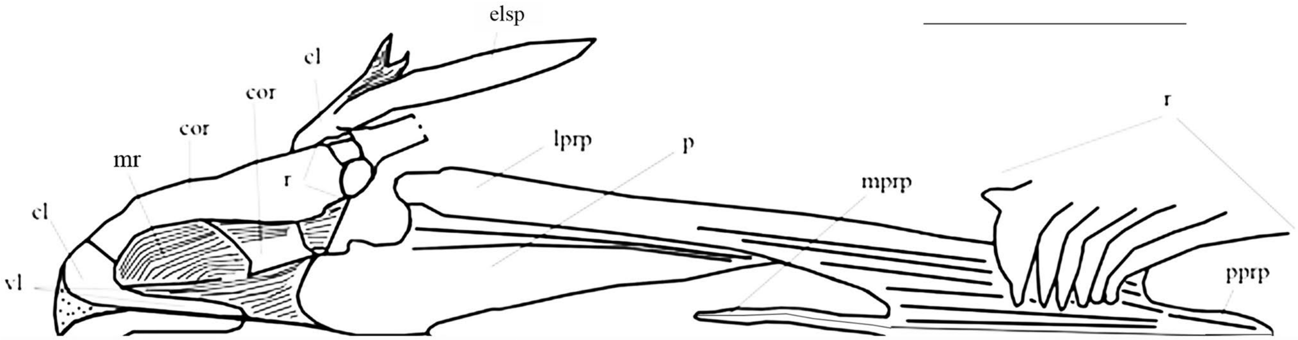

Fig. 7 Pelvic girdle and pelvis *Alertichthys blacki* ZIN 45669-31 (left side). Ventral view. *cl* cleithrum, *clsp* cleithrum spine, *cor* coracoid, *lprp* lateral ridge on pelvis, *mr* medial ridge on cleithrum, *mprp* medial process on pelvis, *p* pelvis, *pprp* posterior process on pelvis, *r* radials, *Vl* ventral ligament of cleithra

sharp spine with a wide base; medially, the dorsalmost of the postcleithrums articulates with the cleithrum. Medially, the ventral expanded tips of the contralateral cleithra are connected to each other with a broad ligament and form a shallow medial notch (Fig. 6). Medially, the posterior ridge of the bone forms a large rounded plate directed backward and connected to the same plate on the opposite side over the its entire surface. The anterior process of the pelvis is attached to the central notch of this medial cleithral plate posteriorly (Fig. 7). In *Zanclorhynchus*, the coracoid is centrally pierced by a large foramen. The posterior process on the coracoid is small and forms a surface to articulate with the ventralmost radial. In *Alertichthys*, the posterior process of the coracoid does not articulate with the ventralmost radial. The precoracoid process of the coracoid in *Zanclorhynchus* and *Alertichthys* is elongated and enlarged, located parallel to the cleithrum and connected with it only at the ventralmost tip of this bone. The dorsal portion of the coracoid is longitudinally bent inward along its entire length, and its narrow dorsal tip articulates with the inner surface of the cleithrum. The precoracoid foramen of a narrow and elongated shape located between these bones. In *Zanclorhynchus* and *Alertichthys*, the pelvis is elongated and in the posterior third bears a thin, central, anteriorly directed process, firmly connected to the process of the opposite side. The anterior processes of the pelvis are widely separated from each other. Laterally, on the posterior half of the pelvis, there is a longitudinal ridge, ending in a small, anteriorly directed spinous process. The pelvis in *Zanclorhynchus* and *Alertichthys* is slightly longer than the cleithrum.

Cladistic analysis

To clarify the position and taxonomic rank of the family Congiopodidae in the suborder Scorpaenoidei, a cladistic analysis of genera from clade 14A of Imamura (2004) was performed. Congiopodidae was included in that clade by that author based on a study of Scorpaenoidei relationships. As a basis for the character matrix, we took the morphological parameters characters of the seismosensory system and the skeleton characters (including fin rays) from Imamura (2004) (Fig. 8), excluding those that had the same state in all representatives of clade 14A and outgroups. Characters nos. 2, 3, 4, 6, 15, 17, 22, 26, 28, 32, 35, 44, 52–53, 57, 64, 65, 68, 69, 71 are excluded. Character no. 5 is excluded, because of the absence of the fifth infraorbital in Congiopodidae. Some characters from Imamura (2004) were modified in accordance with the data obtained in the present study of the skeleton and of the structure of the seismosensory system of the head in Congiopodidae from Zhukov (2019). The following characters from the manuscript of Imamura (2004) were modified (Table 1): 12—infraorbital canal ventral to dermosphenotic: (0) continuous, (1) interrupted; 14—nasal attached to neurocranium: (0) loosely, (1) firmly; 21—suture between intercalar and posttemporal: (0) absent, (1) present (found in *Congiopodus* only); 24—presence of a spine

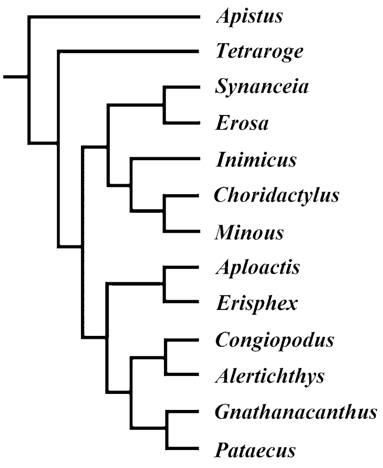

Fig. 8 Clade 14A on Imamura (2004) with changes

Table 1 Character matrix of a newly described characters of the skeleton and seismosensory system of Scorpaenoidei in taxa from clade 14A (Imamura 2004)

Taxon/character*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Sebastes	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Scorpaena	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Scorpaenodes	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Apistus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tetraroge	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Synancea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Erosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inimicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Choridactylus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Minous	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aploactis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Erisphex	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Congiopodus	1	1	2	1	0	1	1	1	0	1	0	0	0	1	1
Alertichthys	0	1	1	0	1	1	1	1	1	0	1	1	1	1	2
Zanclorhynchus	0	1	1	0	1	1	1	1	1	0	1	1	1	1	2
Gnatanacanthus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pataecus	0	2	0	0	0	0	0	0	0	0	?	?	?	1	?

*Characters. 1. Vertical ridge on parietal: absent (0), present (1). 2. Anterior pterygiophores attached: second and third neural processes (0), between first and second neural processes (1), on the head (2). 3. The number of pterygiophores D1 between first and second neural processes: absent (0), 2 (1), 5 (2). 4. Supraoccipital and frontal: connected (0), separated (1). 5. Supraoccipital located: both on dorsal and posterior surfaces of the cranium or only on posterior (0), distinctly on dorsal surface (1). 6. Epiotics connection medially: absent (0), present (1). 7. First vertebra: separated (0), included into posterior wall of the cranium (1). 8. Posttemporal: loosely attached to neurocranium (0), firmly attached to neurocranium (1). 9. Spines on frontal, pterotic, and posttemporal: absent (0), present (1). 10. Posteroventral and ventromedial ridges on cleithrum: absent (0), present (1). 11. Precoracoid foramen: piercing (0), appeared only on inner surface of the cleithrum (1). 12. Notch between anterior processes of pelvis: absent (0), present (1). 13. Infraorbital canal on infraorbital 2: continuous (0), interrupted (1). 14. Connection of the preoperculomandibular and temporal canals: present (0), absent (1). 15. Supratemporal commissure: continuous (0), interrupted once (1), interrupted thrice (2)

associated with the seismosensory canal on the parietal: (0) present, (1) absent; 25—Baudelot's ligament: (0) attached to basioccipital and first vertebra, (1) attached to first vertebra only, (2) absent; 46—connection of posteroventral margin of cleithrum and ventralmost tip of the coracoid is present in Congiopodidae (1); 48—Imamura's value (2) in *Pataecus* was changed to (1) as all other taxa have a value of (0). The characters from Imamura (2004) were supplemented by several characters of the structure of the neurocranium and the skeleton of the pectoral and pelvic girdles, which are described for the first time and which further separate Congiopodidae from other Scorpaenoidei (Table 1). Our matrix contains 76 characters of equal weight and 17 terminal taxa, 3 of which there are out groups (*Sebastes*, *Scorpaena*, and *Scorpaenodes*); as well as *Zanclorhynchus* is included in the matrix for the first time. Because most of the characters are taken from the Imamura's (2004) matrix, we present the resulting cladogram without publishing here the complete character matrix. Using the heuristic algorithm in the NONA and WinClada software package, a single tree with a length of 163 steps, consistency index (CI) 58, retention index (RI) 68 (Fig. 9) was obtained. The resulting cladogram shows the isolated position of the Congiopodidae in clade 14a of Imamura (2004), with the exception of *Apistus* from the family Apistidae. Congiopodidae s.l. uniquely share seven apomorphies: absence of fourth and fifth infraorbitals; dermosphenotic fused with the sphenotic; epioccipitals connected in midline; first vertebra incorporated into posterior wall of cranium; posttemporal firmly attached to skull; presence of posteroventral and ventromedial ridges on cleithrum, palatine and ectopterygoide widely spaced.

Discussion

Comparison of our results with the data of previous studies shows that the characters of the structure of the neurocranium and skeleton of the pectoral girdle of the Congiopodidae that we found were not noted in previous studies. In addition, there are certain inconsistencies between our data and the data published by other authors about the structure of these skeleton regions. The most noticeable differences

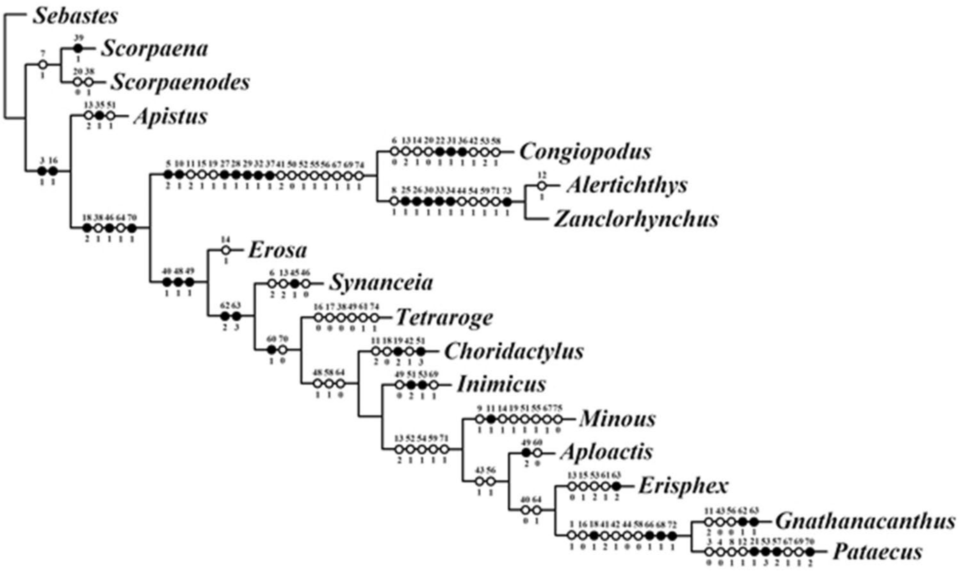

Fig. 9 Phylogenetic relationships of the Congiopodidae s.l

between species *Congiopodus* and *Zanclorhynchus* plus *Alertichthys*, published here for the first time are: structure of the parietals, location, shape and size of the supraoccipital, and the position of these bones in relation to the anterior pterygiophores D1. The parietals in *Congiopodus* have high medial ridges that form the lateral walls of a deep cavity, ventrally formed by the posterior edges of the frontals and a large oval supraoccipital. There are five (in *C. coriaceus*) anterior proximal pterygiophores D1 in the center of this cavity, making it possible for the anteriormost portion of D1 to be placed forward so that it lies at the posterior edge of the orbit of the eye. As described in previous studies (e.g., Mandritsa 2001; Fig. 218), the proximal tips of the pterygiophores come close to each other and insert in the space between the first and second vertebrae. In the described cavity at the posterior part of the neurocranium, branches of the m. rectus dorsalis pass laterally along both sides of the pterygiophores D1 and attach to the posterior margins of the frontals. In *Zanclorhynchus* and *Alertichthys*, similar medial ridges of the parietals occur only in the latter genus. In these genera, the contralateral parietals articulate along the midline up to the posterior margin of the cranium, displacing the supraoccipital to the posterior wall of the skull. As a result, the size of the supraoccipital is significantly reduced, and it only dorsally separates the upper tips of the epioccipitals. The ventralmost tips of the epioccipitals are close to each other medially, but do not connect, as noted by other authors (Regan 1913; Ishida 1994; Mandritsa 2001). The uniqueness of the structure described for *Congiopodus* is confirmed by the study of radiographs of a sister clade sensu Imamura (2004) (*Pataecus fronto*, *Gnathanacanthus goetzeei*), in which D1 also extends onto the head. In the latter species, the anterior pterygiophores are shortened and attached directly to the bones of the skull. An additional, previously undescribed character Congiopodidae s.l is the articulation of the first vertebra with the neurocranium, involving the location of the dorsalmost tips of the anterior pterygiophores of D1 between the neural spines of the first and second vertebrae in. Mandritsa (2001) noted that the lowermost tips of the anterior pterygiophores of D1 are attached to the first vertebra, but this is not confirmed by our observations. As far as is known from the past studies (Mandritsa 2001; Ishii and Imamura 2008; and others), in all other taxa of the Scorpaenoidei, the neural processes of the first and second vertebrae This led Ishii and Imamura (2008) to suggest a complete reduction of the first vertebra in Congiopodidae. We think that such an assumption is invalid, because of the complex origin of the vertebra in teleost fishes; traces of such a structure as a neural process of the reduced vertebra should remain, after the centrums are fused or after reduction of the vertebra (Voskoboinikova 2010; and others). Moreover, the first ray of the dorsal fin is supernumerary in Congiopodidae, as in most Scorpaenoidei, which might indicate a reduction in the corresponding pterygiophore, but not evidence of a reduction of the corresponding vertebra due to the relative independence of these parts of the axial skeleton (Voskoboinikova 2010; and others).

Among other differences between Congiopodinae and Zanclorhynchynae which we noted for the first time, are the stronger development of the horizontal plate of the lateral ethmoid in *Congiopodus* in comparison with the other two genera; anterior portion of the parasphenoid in *Congiopodus* bends downward, while in Zanclorhynchynae, this bone is straight throughout; the presence of a rather deep groove in the midline of the interorbital space in Zanclorhynchinae, formed by the high lateral ridges of the frontals above the orbit; the absence of the basisphenoid in *Congiopodus*, which contrary to Ishida (1994) are present in both genera of Zanclorhynchinae. Ishii and Imamura (2008) noted the difference between *Congiopodus* and the genera Zanclorhynchinae in the presence of a spine on the parietal in the latter taxa. However, according to our data, a very reduced spine on the parietal, if present, occurs only on one side, or it is absent at all in all representatives of Congiopodidae s.l., apparently due to the absence of a medial extrascapular with which this spine is associated. The study of other structural characters of the neurocranium revealed a discrepancy between our data and that of the previously established synapomorphies of Congiopodidae s.l. by Imamura (2004) and Ishii and Imamura (2008). These authors described suturing of the intercalar with the ventralmost margin of the posttemporal in fishes of this group. In our materials of Congiopodidae, we found such a suture only in *Congiopodus*, so that it can be considered as an apomorphy of Congiopodinae. In Zanclorhynchinae, there is no suture between these bones. That does not make it possible to use it as a diagnostic character of Congiopodidae s.l.

Studying the structure of the pectoral girdle and pelvis of Congiopodidae s.l., we noticed that only few of its characters were used previously to describe Congiopodidae s.l. or its subfamilies. Herein, we found several synapomorphies of Congiopodidae s.l., which are not found otherwise among all Scorpaeniformes. The primary character is the highly complex structure of the cleithrum. Nazarkin and Voskoboinikova (2000) described an unusual structure of the ventralmost tip of the cleithrum in Trichodontidae which was later considered as a superfamily in Cottoidei by Imamura et al. (2005). In these fishes, the cleithrum expands ventrally, where it firmly attaches to the cleithrum of the opposite side. Nazarkin and Voskoboinikova (2000) considered such an unusual structure of cleithrum as a diagnostic characters of these groups. We believe that the unusual complex formed by the cleithrum and coracoid in Congiopodidae s.l. supports its higher taxonomic rank.

Study of the structure of the neurocranium and the skeleton of the pectoral and pelvic girdles, revealed previously undescribed apomorphic characters of the Congiopodidae s.l. and its constituent subfamilies the cladistic analysis with the addition of these characters show a derived position of Congiopodidae s.l. among the Scorpaenoidei families in clade 14A of Imamura (2004) (except for *Apistus*). According to the results of this analysis, based on the distinctive structure of the skeleton, we recommend elevation of the Congiopodidae s.l. to superfamily, and of the subfamilies Congiopodinae and Zanclorinchinae to the rank of families. This conclusion confirms the opinion of a number of previous researchers (Regan 1913; Mandritsa 2001; and others). Accordingly, we recognize the validity of the superfamily Congiopodoidea comprising the families Congiopodidae and Zanclorynchidae in the suborder Scorpaenoidei.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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