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NEW ACROPOMATIFORM FOSSILS FROM THE UPPER KUEICHULIN FORMATION (LOWER PLIOCENE), NORTHERN TAIWAN

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Abstract. The Indo-West Pacific is home to a diverse array of modern fish species, and the study of their fossils can provide valuable insights into the origins and evolution of this biodiversity. This report presents rare remains of five individuals of acropomatiform fish, including a semi-articulated skeleton, recovered from the Upper Kueichulin Formation (Lower Pliocene) in northern Taiwan. The fossils are preserved in the form of nodules discovered at the locality known for abundant marine crustaceans and echinoderms. These specimens can be assigned to the family Stereolepididae, based on morphology of the opercle with the presence of two spines, a preopercle characterized by serrations on the posterior margin and denticulations on the ventral margin, and a distinctive skull architecture. Differences in skull morphology distinguish these specimens from other species within the genus and thus are described as *Stereolepis arcanum* n. sp. Significantly, the species represents the oldest known record of the family globally and stands as the second known fossil representative. This discovery not only enhances our understanding of the palaeobiodiversity of fish fauna in the Indo-West Pacific during the Neogene, but also highlights the importance of further research efforts in this area.

INTRODUCTION

In contrast to the extensive diversity observed in the contemporary fish fauna, the records of fish fossils in the tropical-subtropical West Pacific region are notably limited and elusive. Despite ongoing efforts and the accumulation of knowledge related to some taxa, such as elasmobranchs (e.g., Marramà et al. 2018; Kocsis et al. 2019; Lin et al. 2022b), the overall understanding of palaeoichthyology in this region remains conspicuously sparse. As a result, significant portions of this vast expanse continue to be *terra incognita* in the field of palaeoichthyology.

The island of Taiwan is situated within the Sino-Japanese Province (Toonen et al. 2016), a position shaped by a complex convergent boundary. The fossil fish remains found on the island are represented by teeth, otoliths, isolated bones, and very rarely, by articulated and semi-articulated skeletons

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(Lin et al. 2021, 2022a; Lin & Chien 2022). Noteworthy among these finds are fish skeletons from the Lower Pliocene deposits of the Kueichulin Formation in northern Taiwan, as mentioned in Lin et al. (2021: fig. 3A). Specifically, this study focuses on the investigation of five individuals discovered from this formation, aiming to elucidate their significance within the broader context of palaeoichthyofauna.

The extant members of the order Acropomatiformes exhibit a widespread distribution across both shallow and deeper waters in tropical and subtropical regions worldwide. Several species within this order possess light-emitting organs on their ventral sides (Okamoto & Gon 2018; Ghedotti et al. 2018; Smith et al. 2022). Notably, the formal recognition of the order Acropomatiformes is a relatively recent development, primarily established based on molecular analysis (see Smith et al. 2022 for details). Consequently, the composition and relationships among the families within this order have become a focal point of discussion (e.g., Davis et al. 2016; Mirande 2016; Ghedotti et al. 2018; Smith et al. 2022). Based on the latest findings, the order is now recognised to comprise 20 families (Smith et al. 2022). Furthermore, the ongoing taxonomic exploration has led to the continuous discovery of new species within this extensive group (e.g., Yamanoue 2016; Schwarzhans & Prokofiev 2017; Mediodia et al. 2024).

For the fossil record of the order Acropomatiformes, pertinent otolith evidence appears to be widely distributed, with early putative acropomatid otoliths such as "Acropomatida" *bagassiana* Nolf, 2003 from the Santonian of Spain (Nolf 2003), and *Plesiopoma otiosa* Schwarzhans, 2010 from the Maastrichtian Bavaria, Germany (Schwarzhans 2010). However, it is not until the Late Palaeogene that the otoliths exhibit a closer affinity to those of their extant counterparts. In the West Pacific, acropomatiform otoliths are predominantly represented by the genus *Parascombrops* (see Schwarzhans & Prokofiev 2017), including *Parascombrops schwarzhansi* van Hinsbergh & Helwerda, 2019 from the northwest Philippines (van Hinsbergh & Helwerda 2019) and *Parascombrops ohei* Schwarzhans & Prokofiev, 2017 from eastern Japan (Mitsui et al. 2021). Otoliths of *Acropoma* are also commonly found in the Lower Pleistocene deposits in southwestern Taiwan (Lin et al. 2018). More recently, Lin et al. (2023) reported otoliths of *Malakichthys*, *Synagrops*, and *Acropoma* from a Lower Pliocene deep-sea assemblage in southern Taiwan.

Nevertheless, the skeletal fossil record of Acropomatiformes is not significant worldwide, with only a handful of records primarily originating from families Acropomatidae and Stereolepididae (for details, see Discussion). The studied specimens represent a noteworthy addition to the fossil record of the Stereolepididae. Consequently, the main purpose of this paper is to document, discuss, and evaluate the acropomatiform specimens discovered from the Tachi site (Kueichulin Formation; northern Taiwan).

Geological setting

The sampling site (Tachi) is situated within the Upper Kueichulin Formation (locally also recognized as the Erchiu Formation), which is Early Pliocene in age (Fig. 1). The formation is widely exposed along the upstream of the Dahan River and it primarily consists of intensely bioturbated muddy sandstone with thick-bedded mudstone and interbedded layers of sandstone and mudstone (Pan et al. 2015; Chen 2016). In addition to abundant trace fossils and shell fragments (Wang 1983 1984b; Chen 1986), articulated marine fossils, exceptionally well-preserved within nodules, are also commonly found in the strata (Chen 2016).

These fossiliferous nodules often are encapsulating in situ marine fossils, predominantly crustaceans (Hu & Tao 1996). The fish skeletons described in the present paper are from such nodules. The locality also yields other marine fossils not being encased in nodules, such as echinoids (Wang 1984a, 1985; Hsu et al. in review), mollusks (Hu 1992), cuttlebones (Lee unpublished data), and fish otoliths (Lin unpublished data). In summary, based on both sedimentology and ichnology, the sedimentary environment of this locality indicates relatively shallow water depths, positioned above the shoreface-offshore transition zone (Chen 1986; Pan et al. 2015; Chen 2016).

Material and methods

The fossils were discovered by local amateur fossil collectors in the 2010s in Tachi, Taoyuan, northern Taiwan. These specimens collectively represent five individuals, with four encased within two nodules and one isolated skull. These fossils are deposited in the Na-

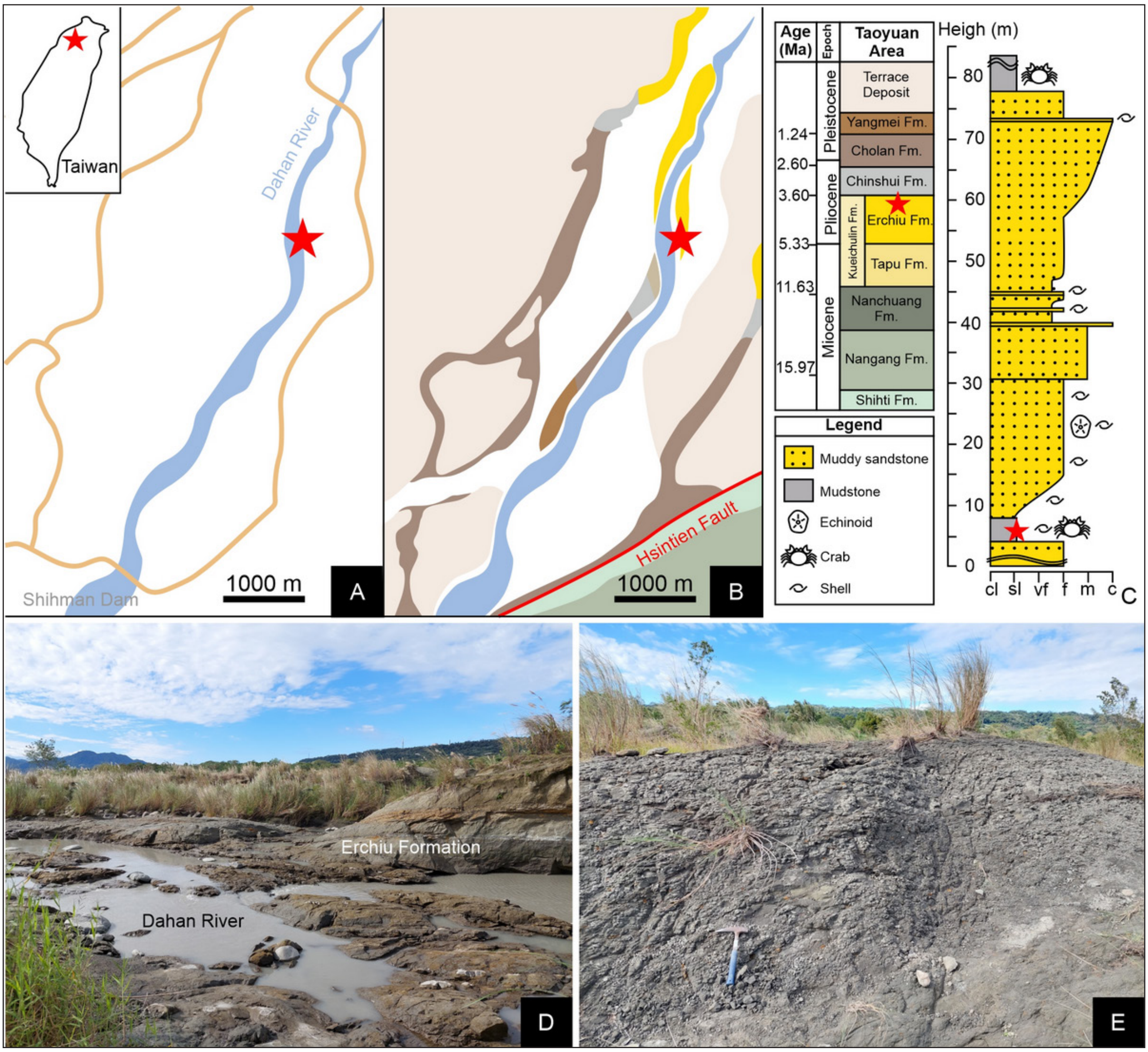


Fig. 1 - The geological setting of the acropomatid fossils. A) Location of the study area; B) geological map of the study area; C) geological column and stratigraphy of the study area (modified from Pan et al. 2015; Chen 2016); D) photograph of the locality; E) exposure where the fossil nodules were found. Red stars represent the sampling site.

tional Museum of Marine Science and Technology, Keelung, Taiwan (under the registration code NMMST) and the Biodiversity Research Museum, Academia Sinica, Taiwan (ASIZF).

The first nodule, designated as NMMST 20190-3001 (Fig. 2), preserves the semi-articulated remains of a single fish with a measurable length of 101 mm. The head length is approximately 25 mm, with the neurocranium measuring around 23 mm in length. The second nodule, NMMST 20190-3005 (Fig. 3A, B), contains the remains of three individuals, especially partially preserved skulls. Two neurocrania are more or less complete, with a complete neurocranium measuring about 30 mm in length, along with fragments of the postcranial skeletons. Besides these two nodules, there is yet another partially preserved skull (ASIZF0100722, Fig. 3C). Despite the fragmented nature of the specimens, all individuals are considered to be monospecific due to morphological similarities of the available parts of the skulls. The dislocation of scales, together with disarticulation of vertebral column, abrasion of some bones, and partial loss of the fin spines and rays, suggest potential post-mortal transport and/or alternations to the original positioning of the body. Therefore, it is reasonable to expect that the body proportions and certain meristic characters might have been different in their original state than is currently observed.

Data for comparative osteological analysis were drawn from the following references and specimens. The standard length (SL) and total length (TL) of the fish are used to describe the size of the fish. Acropomatidae: *Acropoma hanedai* Matsubara, 1953: unnumbered specimen (dry semi-articulated skull; 110 mm estimated SL; sex unknown; Taiwan); *Acropoma japonicum* Günther, 1859: unnumbered specimen (dry semi-articulated skull; 100 mm estimated SL; sex unknown; Taiwan); *Doederleinia berycoides* (Hilgendorf, 1879): GLU-

Fig. 2 - Holotype specimen (NMMST 20190-3001) of *Stereolepis arcanum* n. sp.

2023-0099 (dry semi-articulated skeleton; 270 mm SL; female; Daxi, NE Taiwan), GLU-2023-0124 (dry semi-articulated skeleton; 237 mm SL; female; Daxi, NE Taiwan). Lateolabracidae: *Lateolabrax japonicus* (Cuvier, 1828): GLU-2023-0101 (dry semi-articulated skeleton; 399 mm SL; sex unknown; Dongyin Island), GLU-2023-0126 (dry semi-articulated skeleton; 271 mm SL; male; Daxi, NE Taiwan). Moronidae: *Dicentrarchus labrax* (Linnaeus, 1758): unnumbered specimen (dry semi-articulated skeleton; 390 mm estimated SL; sex unknown; Spain), unnumbered specimen (dry semi-articulated skeleton; 290 mm estimated SL; sex unknown; France); *Morone chrysops* (Rafinesque, 1820): unnumbered specimen (dry semi-articulated skeleton; 260 mm SL; sex unknown; North America). Stereolepididae: *Stereolepis gigas* Ayres, 1859: CAS-ICH 66626 (photo of dry semi-articulated skull; 1460 mm SL; sex unknown; California, USA); *Stereolepis doederleini* Krasyukova, 1969: NMMB-P32813 (X-ray of the head of the complete specimen in alcohol; 385 mm SL; sex unknown; southeastern Taiwan). Symphysanodontidae: *Symphysanodon typus* Bleeker, 1877: GLU-2022-0026 (cleared and stained specimen; 165 mm SL; sex unknown; Donggang, SW Taiwan).

The clear and stain method followed Taylor & van Dyke (1985). The micro-computed tomography (µCT) scanning was carried out at the Taiwan Mouse Clinic, Academia Sinica and Taiwan Animal Consortium, Taipei, Taiwan. The specimens were scanned using a desktop µCT scanner (SkyScan 1276, Bruker microCT, Kontich, Belgium). The voltage, current, and scan resolution of X-ray source were set to 100 kV, 200 µA, and 10.3–41.1 µm, respectively. The filters Al and Cu were used. The µCT projections were back reconstructed using NRecon software (Bruker, MicroCT, Kontich, Belgium) and visualised and exported with CTVox software (Bruker, MicroCT, Kontich, Belgium).

Institutional abbreviations: ASIZF – Biodiversity Research Museum, Academia Sinica, Taiwan; CAS-ICH – California academy of Sciences, Ichthyology Collection; GLU – Institute of Geology of the Czech Academy of Sciences in Prague, the Czech Republic; MNHN.F – fossil fish collection, Muséum National d'Histoire Naturelle, Paris, France; NMMB – National Museum of Marine Biology and Aquarium, Pingtung, Taiwan; NMMST – National Museum of Marine Science and Technology, Keelung, Taiwan.

Systematic Palaeontology

ACANTHOMORPHA Rosen, 1973
Acropomatiformes Smith & Wheeler, 2006 *sensu* Smith et al., 2022
Stereolepididae Smith, Ghedotti & Davis, 2022
Stereolepis Ayres,1859

Stereolepis arcanum Přikryl & Lin, n. sp.

Fig. 2–10

Holotype: The nodule preserving a partially complete individual NMMST 20190-3001 (Fig. 2).

Type horizon and locality: Lower Pliocene, Upper Kueichulin Formation, Tachi (northern Taiwan).

Paratypes: NMMST 20190-3005 preserving remains of three individuals and ASIZF0100722 preserving a single individual. All specimens are from the type locality.

Etymology: The species name refers to "secret" in Latin, reflecting incomplete and mysterious nature of these fossils.

Diagnosis: The new species differs from other species of the genus by having a significantly shorter ethmoidal area of the skull (less than 50% of the orbital area), strongly developed sphenotics with their depth in lateral view representing approximately half of the ethmoidal depth, and the strongly developed "pit and ridges" ornamentation in most of the dorsal surface of the frontal bones.

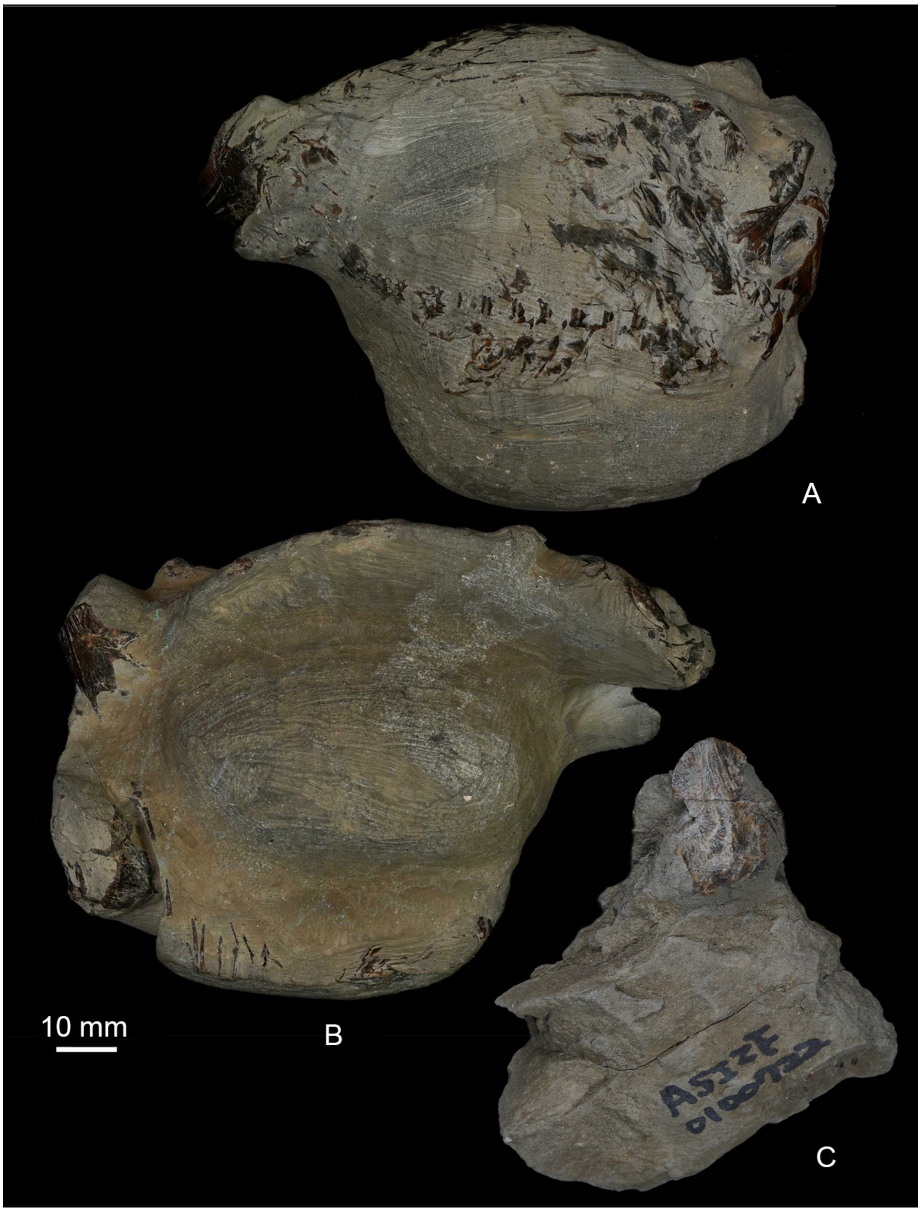


Fig. 3 - Paratype specimens of *Stereolepis arcanum* n. sp. A, B) NMMST 20190-3005; C) ASIZF0100722.

Description. The fossils under examination contain remains of small fish with partially preserved skeletons (Figs 2–4). The estimated SL (based on the measurable length of NMMST 20190-3001) is about 110 mm.

The neurocranium. The neurocrania (Figs 5–7) exhibit dorsal surface dermal ornamentation characterised by numerous ridges and pits. This distinctive ornamentation is predominantly observed on the frontals, extending partly to other elements, such as parietals, sphenotics, parts of pterotics, and supraoccipital. The frontals are about one and a half times longer than their width, and their maximal width occur just in the postorbital section, precisely at the level of articulation with the sphenotic. The anterior margin of the frontals is convex, with a parabolic shape. Positioned anteriorly to the frontals is a recognizable short, but deep triangle-shaped mesethmoid, accompanied by laterally articulated lateral ethmoids, showing a concave anterior surface of the bone. The ethmoid area is short (representing maximally half the length of the orbit) and relatively deep (approximately the same as the orbit length). The frontals articulate posteriorly with the supraoccipital, parietals and pterotics. Posteriorly to the frontals, in the mid-line of the neurocranium, a clearly recognizable supraoccipital is present. The antero-dorsal part of the supraoccipital bears typical dermal structures, while the posterior half is thin and forms the dorsal margin of a short and very low supraoccipital crest. Laterally to anterior section of the supraoccipital are rhomboid-shaped

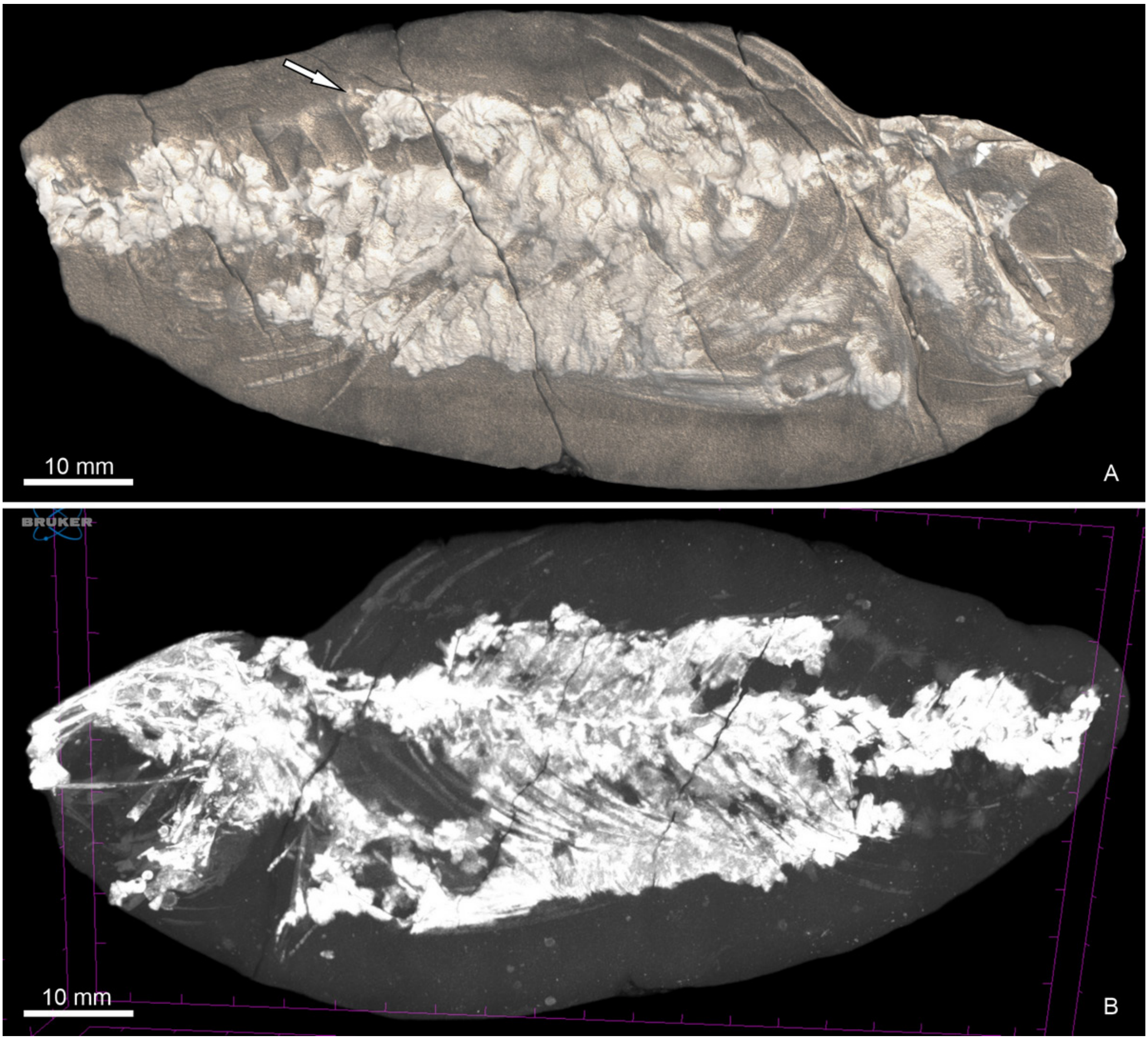


Fig. 4 - CT examination of the holotype specimen of *Stereolepis arcanum* n. sp. NMMST 20190-3001. A) Right external surface of the body showing partly preserved skull, surface of the body, fins, and scales of the body. The arrow marks start of the soft part of the dorsal fin; B) left scan showing the inner space of the nodule and covered side of the skeleton.

parietals that do not meet each other in the midline. The parietals articulate anteriorly with the frontals and extend laterally and postero-laterally with the pterotics. The pterotics bear posteriorly oriented fossae to accommodate the anterior-most part of the epaxial musculature. Slightly bifurcating ventro-laterally, the sphenotics are massive and short bones that join the lateral margin of the frontals and antero-lateral margins of the pterotics. The otic part of the skull (Fig. 5C) is much larger than the ethmoid one, measuring about three times the length and twice the depth. Other details are not recognizable due to insufficient preservation. There are recognizable neural canals within several skull elements, including the frontal (starting in the antero-medial corner of the bone and extending postero-laterally), sphenotic, pterotic, and parietals. The basicranium is bent (Fig. 8).

Other skull elements. The opercle is trapezoid shape characterised by two postero-dorsaly directed spines. The upper spine is markedly shorter than the lower one and is oriented at an angle of approximately 20°. Both spines are separated by a deep notch. The spines themselves are sup-

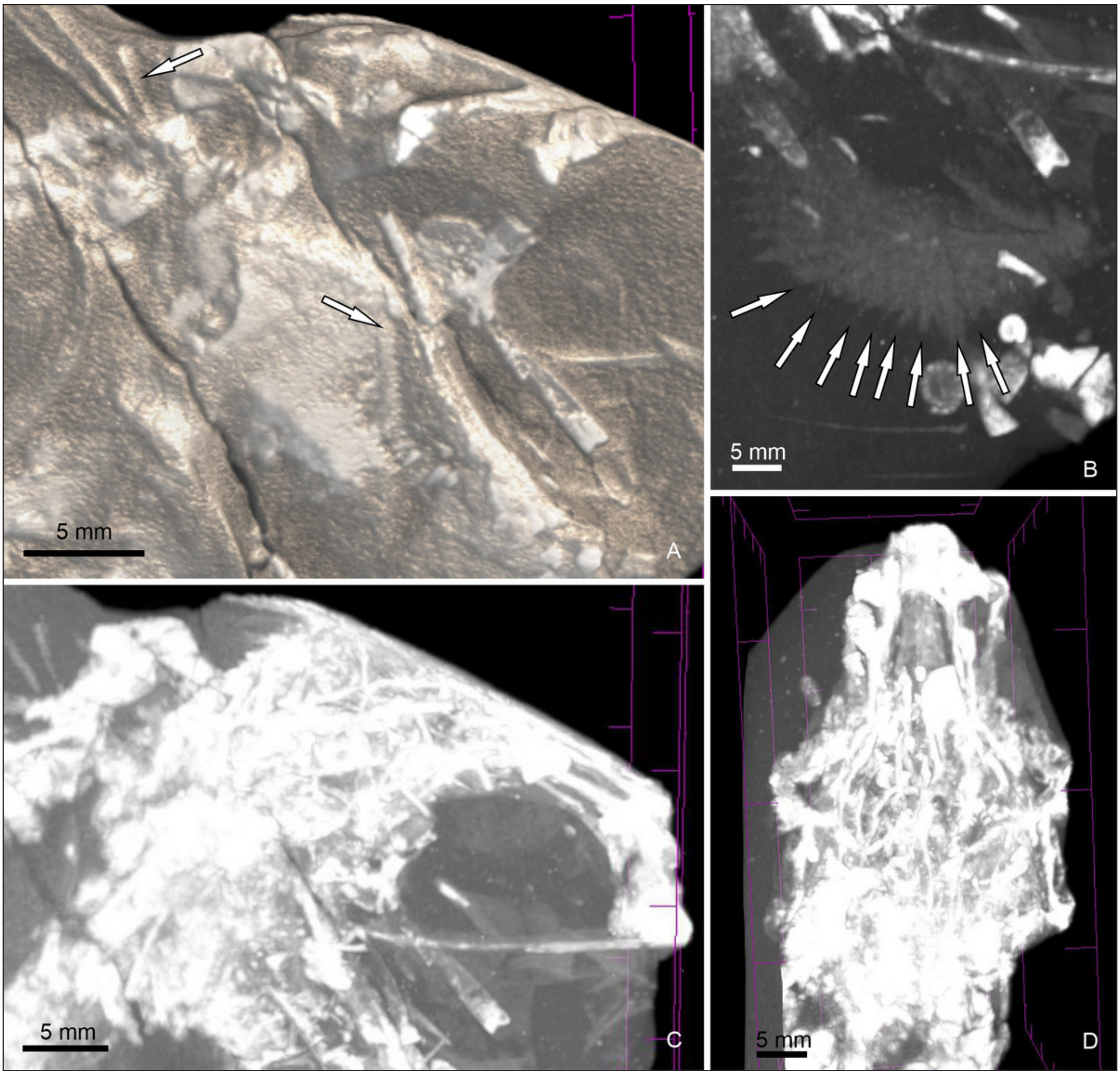


Fig. 5 - Detail CT examination of holotype specimen of *Stereolepis arcanum* n. sp. NMMST 20190-3001. A) Right external surface of the skull showing spinulation of the preopercle and preserved supraneural (marked by arrows); B) right inner scan showing the spinulation of the lower part of the preopercle bone (individual spines marked by arrows); C) right inner scan showing the general shape of the neurocranium in lateral view; D) inner scan showing the general shape of the neurocranium in dorsal view.

ported by robust skeletal tissue (i.e. creating "rib-like" thorns). Similarly, the anterior margin of the opercle is enforced by thickened bonny tissue—the opercle is therefore all together reinforced by three axes, which are located on the anterior edge and in the axes of the spines. The upper spine is dorsally completed by bony lamina with a convex dorsal margin. Notably, one of the opercles preserved in NMMST20190-3005 has undergone taphonomic reduction, retaining only the most ossified parts of the bone (see Fig. 8B).

The preopercle is sickle-shaped, with the vertical ramus much longer than its horizontal part (about four times as long). While spinulation and serration are not macroscopically visible, micro-CT examination (Fig. 5) reveals these structures along the posterior and ventral margins of the bone. The posterior section in the dorsal part of the preopercle is relatively finely serrated and spines become slightly larger in the corner of the bone and along the ventral margin of the horizontal limb (Fig. 5A, B).

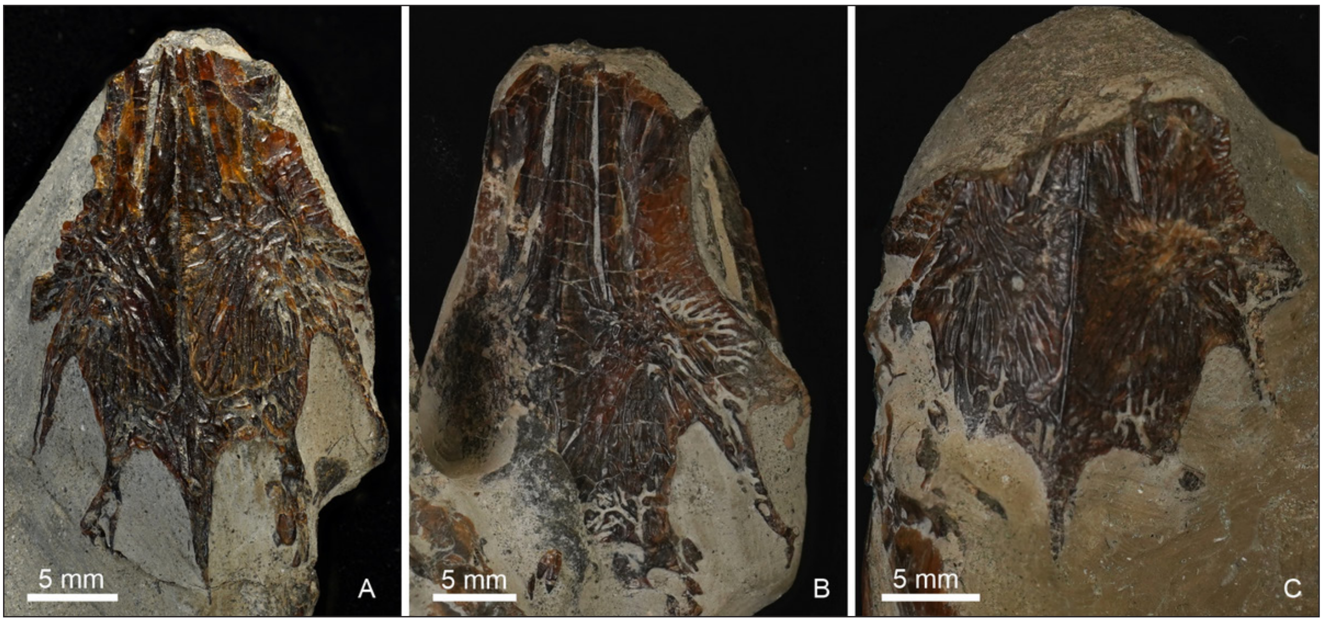


Fig. 6 - Neurocrania of *Stereolepis arcanum* n. sp. All specimens are in dorsal view. A) Holotype specimen NMMST 20190-3001; B, C) paratype specimen NMMST 20190-3005. Note the third neurocranium preserved in NMMST 20190-3005 and the isolated skull in ASIZF0100722 are too incomplete to provide any visual information and are not figured here.

Posteriorly to the corner of preopercle, there is an articulated interopercle, but the details of its morphology is not clear. A rod-like element preserved in the specimen NMMST20190-3001, showing an antero-dorsally expanded part, is interpreted as a partially preserved hyomandibula, but this bone is incompletely preserved. Other parts of the skull are not determinable due to insufficient preservation.

The axial skeleton. The vertebral column is not completely preserved in any of the available specimens. Disarticulated remains preserved in NMMST 20190-3001 allow for the recognition of 8 abdominal and 10 caudal vertebral centrae, but the actual number of vertebrae was unequivocally higher. The vertebral centrae do not bear recognizable growth rings. The fossil also preserves the remains of a single predorsal bone, although the postcranial section is not sufficiently preserved, it is reasonable to expect other predorsals were presented. Approximately seven or eight moderately-developed large ribs are discernible. The caudal skeleton and caudal fin are not preserved.

The dorsal fin. The dorsal fin exhibits remains of ten spines, with the preservation suggesting that this count is either original or only slightly higher. Additionally, about 6 rays are recognizable. The base of the spinous part of the dorsal fin is much longer than its soft part. The articulation of the last spinous dorsal element is in the level just in front of the start of the anal fin. Length proportions of individual spines and rays are not determinable.

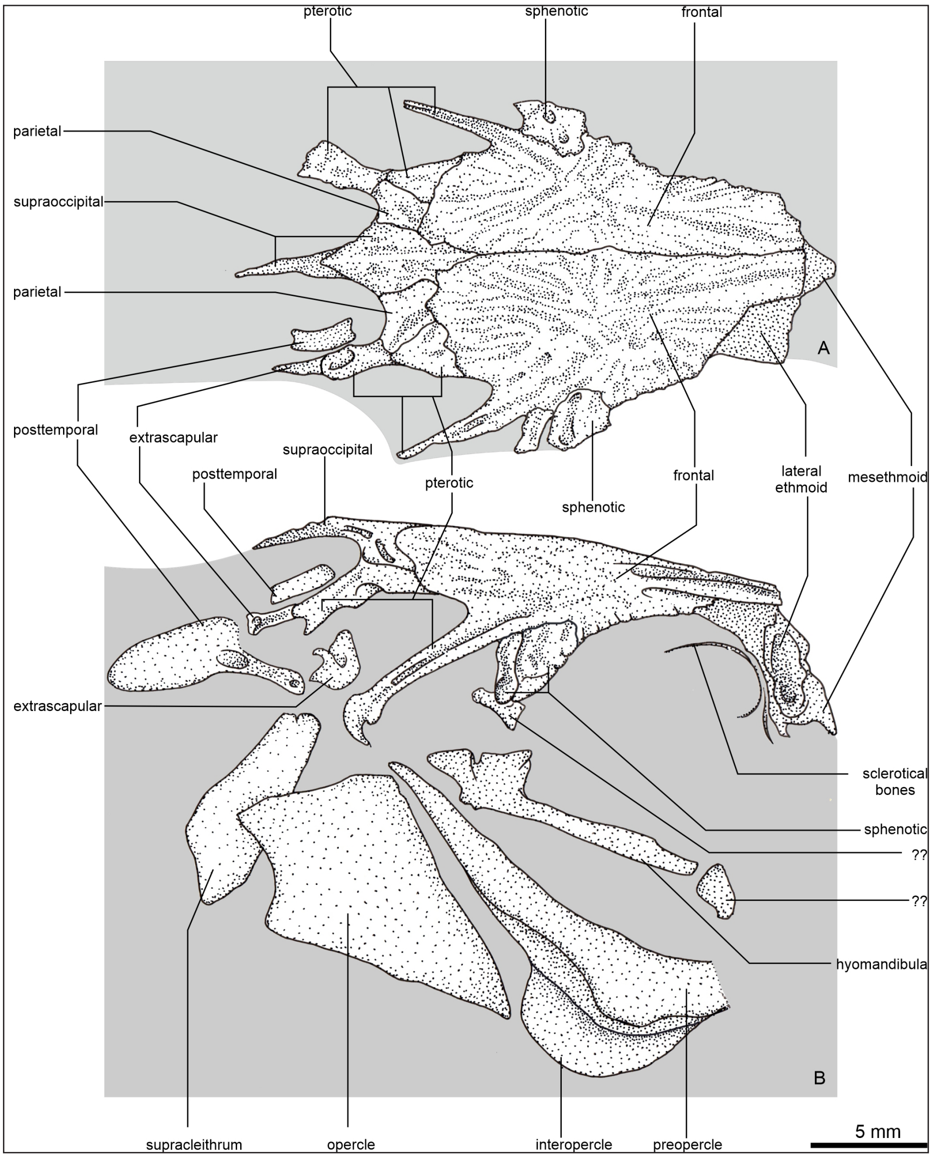
The anal fin. The anal fin is characterized by a short base. The fin itself is developed in the posterior-most third of the body, just below the soft part of the dorsal fin. It consists of three spines and seven or eight rays. The first spine is shortest than the second and third ones (see Table 1 for details of proportions).

The pectoral girdle and fin. The cleithrum is stick-like, more or less straight, dorsally enlarged to plate-like. The scapula is trapezoid, with a large central foramen. The supracleithrum widens postero-ventrally, with a length more or less the same as the maximal antero-posterior length of the opercle. Posteriorly to the right pterotic of the specimen NMMST 20190-3001, a plate lake posttemporal is recognizable. This posttemporal has two anteriorly oriented rami. The dorsal posttemporal ramus continues towards the epioccipital, although the articu-

Anal fin spine	**Length (mm)**	**% of the 2nd spine length**
First	6.9	67,6
Second	10.2	--
Third (incomplete – the distal-most tip is missing)	9.2	90,2

Tab. 1 - Length of anal fin spines in the holotype of *Stereolepis arcanum* n. sp. (NMMST 20190-3001).

Fig. 7 - Interpretative drawings of *Stereolepis arcanum* n. sp. holotype specimen NMMST 20190-3001 in dorsal (A) and lateral (B) views.



lation is covered by sediment in all specimens. The ventral ramus extends towards the lateral extension of the pterotic. The pectoral fin is preserved only as fragments of its base, with recognizable remains of 16 or 17 rays. The shape of the fin itself is not determinable.

The pelvic fin and girdle. The position of the pelvic fin is just below the pectoral girdle. The basal plate has the shape of a strongly elongated triangle, with a well-developed post-pelvic process. The pelvic fins consist of one spine and five elongated rays, with their posterior-most tips reaching approximately half of the body length.

Scales. The body is covered by very small cycloid scales, with an approximate diameter ranging from 2 to 3 mm. These scales are preserved in larger areas of the body. The original scale formula is not recognizable.

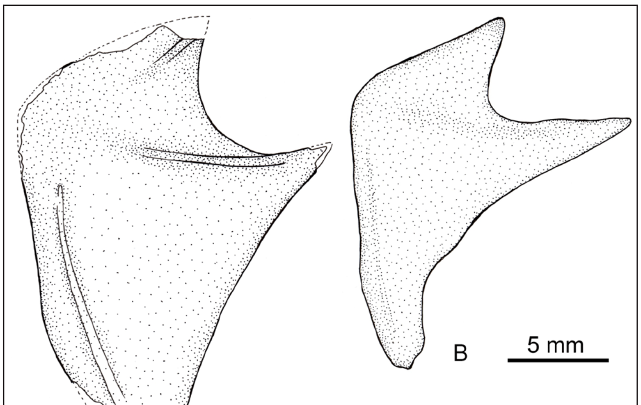


Fig. 8 - Interpretative drawings of the opercles preserved in NMMST 20190-3005. A) Reversed; B) opercle showing strong abrasion of the marginal parts of the bone.

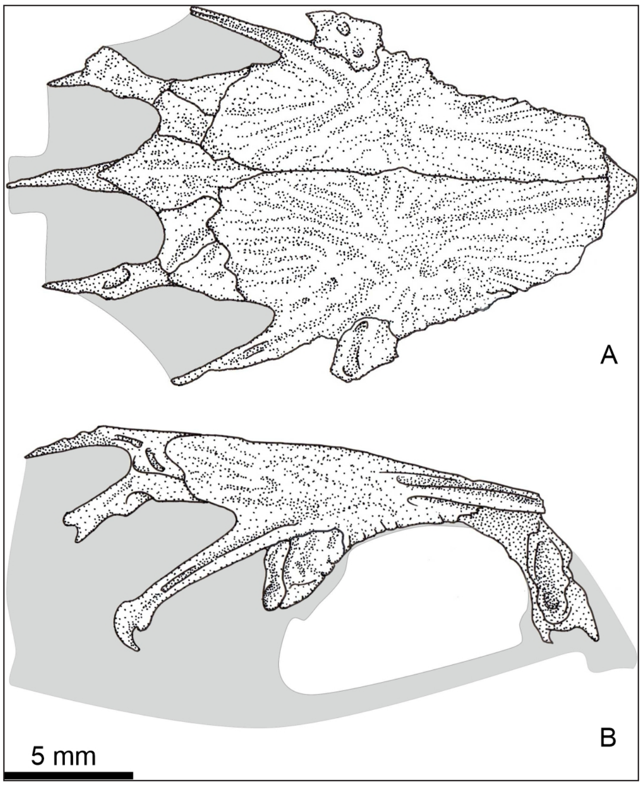


Fig. 9 - Reconstruction of the nurocranium of *Stereolepis arcanum* n. sp. in dorsal (A) and lateral (B) views.

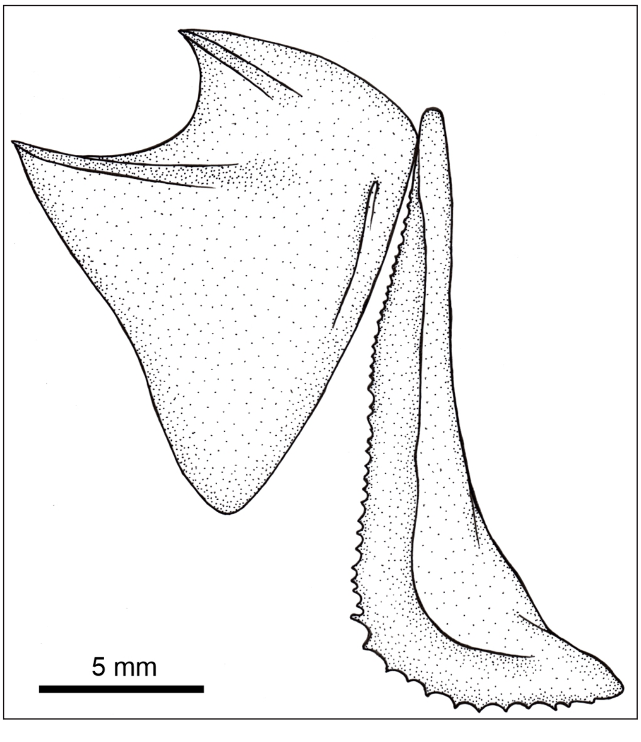


Fig. 10 - Reconstruction of the opercle and preopecle of *Stereolepis arcanum* n. sp. in lateral view.

Discussion

The general habitus of the studied fossils, together with the presence of dorsal limb of posttemporal firmly bound to the epioccipital (although this character is inferred based on superficial conditions and not directly observed), the ossification of the medial pelvic process distally, and the presence of true spines in the dorsal and anal fins, allows us to classify the fossils into the subsection Acanthomorpha Rosen, 1973 (see Willey & Johnson 2010). This enormously diversified Teleostei crown group is in constant center of interest (e. g. Johnson & Patterson 1993; Willey et al. 2000; Davesne et al. 2016). Even after extensive research activities, a number of issues are not fully solved until today.

We are aware of the problems associated with the classification of fossil percoidei fishes, and these issues have been summarised with main points and references by Bannikov & Carnevale (2005). While the fossils at hand lack any direct characters that can be unequivocally used for classification into any of the acanthomorph orders, such as precise meristic characters or the distribution of predorsals or caudal skeleton, we applied a procedure based on the utilization of the maximal number of available characters. This procedure involves considering not only phylogenetically significant characters but also maximizing the use of available morphological features for a more comprehensive understanding of the fossils (Murray & Stewart 1999).

Familial and subfamilial classification of the fossils

The morphology of the opercle with two spines allows for the exclusion of certain groups characterised by a different number of opercular spines. For example, Serranidae possesses three opercular spines (Gosline 1966; Johnson 1983) and Latidae has a single opercular spine (Otero 2004). The opercle with two spines observed in the fossil specimens shares at least partial morphological similarity with opercles of some taxa from various families, including Percilidae (*Percilia*: Arratia 1982: figs 102, 103), Howellidae (*Bathysphyraenops*: Prokofiev 2007b: fig. 3; partly also *Howella*: Prokofiev 2007a: fig. 2), Acropomatidae (*Acropoma*: Katayama 1959: fig. 6A; *Doederleinia*: Katayama 1959: fig. 6A), Polyprionidae (*Polyprion*: Arratia 1982: fig. 48), Lateolabracidae (*Lateolabrax*: Katayama 1959: fig. 6D; Fig. 11a) Percich-

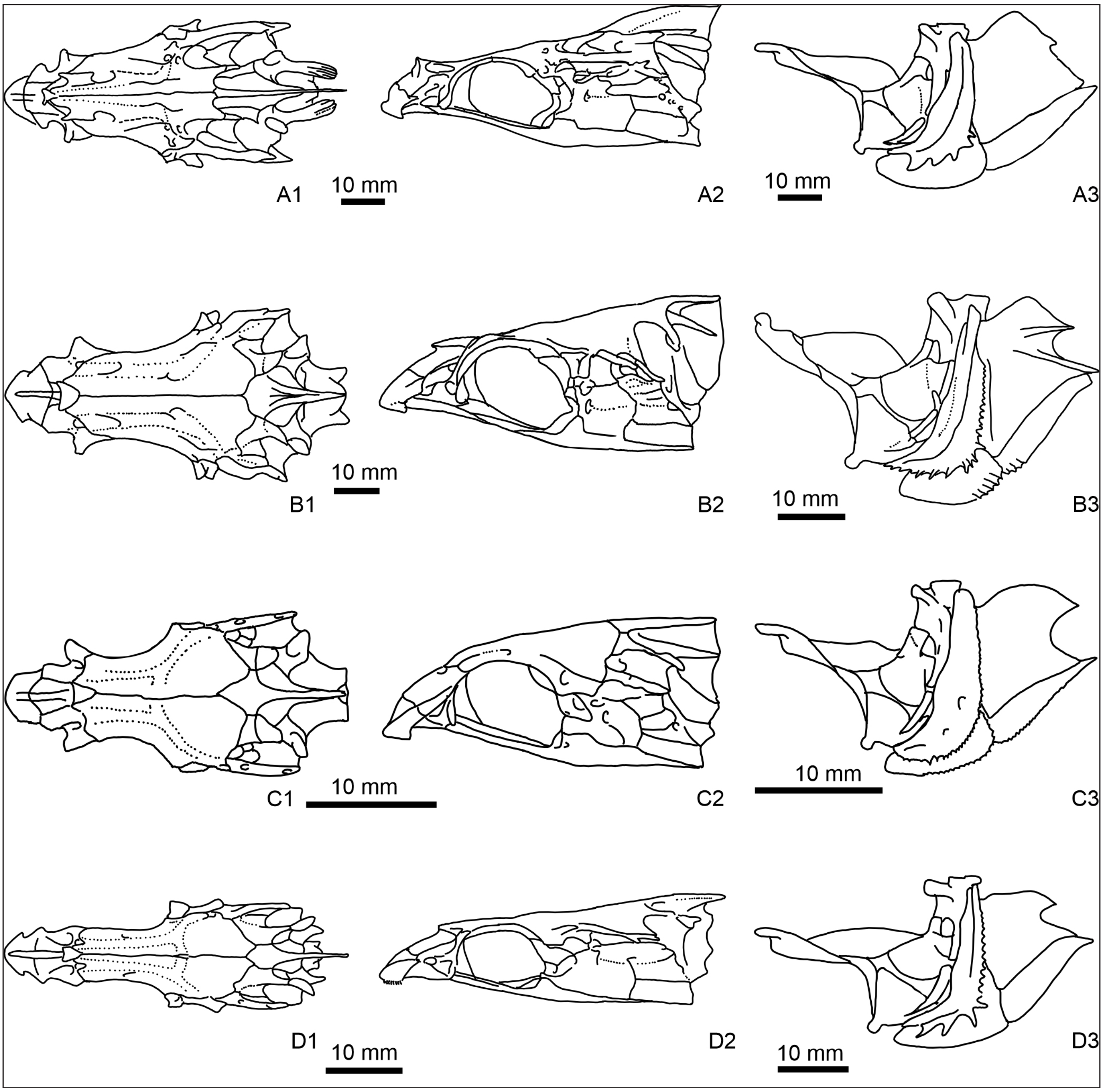


Fig. 11 - Neurocrania in dorsal (1) and lateral (2) views and part of viscerocrania (3) of selected potential classification candidates (adopted from Katayama 1959). A) *Lateolabrax japonicus* (Cuvier, 1828); B) *Stereolepis gigas* Ayres, 1859 (listed as *Stereolepis ischinagi*); C) *Coreoperca kawamebari* Temminck & Schlegel, 1843; D) *Siniperca chuatsi* (Basilewsky, 1855).

thyidae (*Percichthys*: Arratia 1982: figs 47, 49; *Macquaria*: MacDonald 1978: fig. 2; *Macculochella:* MacDonald 1978: fig. 2), Sinipercidae (*Siniperca*: Katayama 1959: fig. 6E, Fig. 11D; *Coreoperca*: Katayama 1959: fig. 6F, Fig. 11C), Stereolepididae (*Stereolepis*: Katayama 1959: fig. 6C, Fig. 11B), Symphysanodontidae (*Symphysanodon*: personal observation) or Moronidae (*Morone*: Sutton 1913: fig. 6; personal observation). In the following paragraphs, these families are commented in details in terms of similarities and differences of the characters.

The family **Percilidae**, represented by two species within the single genus *Percilia*, is restricted to freshwater environments in South America and was formerly included in the family Percichthyidae (Nelson et al. 2016). Although the morphology of the opercle in Percilidae is superficially similar to that of our fossils, the upper spine of percilid opercle is not supported by thickened skeletal tissue, the ventral margin of the preopercular horizontal limb is smooth (with small spines developed in its corner), the cranial roof is smooth, and the construction of the neurocranium in dorsal view is significantly different (for details see Arratia 1982: fig. 95). Therefore, based on these distinctive features, Percilidae can be confidently excluded.

The family **Howellidae** comprises marine fish distributed in the Atlantic, Indian, and Pacific oceans, with 9 species in three genera (Nelson et al. 2016). Prokofiev's detail osteological studies (2007a, b) have revealed different morphological characters in opercle and preopercle bones compared to our fossils. For example, in *Bathysphyraenops* the shape of the dorsal lamina and the absence of concave notch in between dorsal and ventral spine and in *Howella*, the shape of dorsal lamina, multiple spinulation in the distal part of the ventral opercular spine, and the significantly smaller concave notch in between dorsal and ventral spines. Additionally, the spinulation is in different rate and restricted to the corner of the bone in both *Bathysphyraenops* and *Howella*. Furthermore, the neurocranium in dorsal view shows differences in construction (Prokofiev 2007a: fig. 1; Prokofiev 2007b: fig. 1). All these characters prevent unifying the fossils with the family Howellidae.

The family **Acropomatidae** encompasses marine fish distributed in Atlantic, Indian, and Pacific oceans, classified with 31 species in seven genera (Nelson et al. 2016). However, *Synagrops*, *Parascombrops*, *Caraibops*, and *Kaperangus* have been more recently classified within a separate family Synagropidae (Fricke et al. 2020; Smith et al. 2022). The opercles of Acropomatidae possess a more or less thickened lower opercular spine, but the upper spine and the anterior margin of the bone are not reinforced by bonny tissue, or are reinforced to a much lesser degree than observed in the studied fossils (Katayama 1952: figs 1 and 2, 1959: figs 6, 9; personal observation). Further, the preopercle spinulation is developed in a different size and distribution pattern than those in the studied fossils. The most significant difference is in the morphology of the dorsal surface of the neurocrania—the shape of some bones and their configuration is not fully comparable, dorsal surfaces of the cranium lack any sculptation, and neural canals are expanded and largely opened (Katayama 1952: figs 1 and 2, 1959: fig. 15; personal observation).

The skeletal fossil record of this family is limited, with *Acropoma lepidotum* (Agassiz, 1836) described from the Eocene deposits of Bolca, Italy (Sorbini 1975; Bannikov 2014; Carnevale et al. 2014), the genus *Cottopsis* Priem, 1908 from the middle Eocene of Caucasus (synonymum *Synagropoides*; see Bannikov 2002; Prokofiev 2007b), and the late Eocene of Iran (synonymum *Gobiopsis*; see Priem 1908; Arambourg 1967). There is also a possible Acropomatidae gen et sp. indet (originally described as *Epigonus* (?), see Bannikov 2000). *Acropoma lepidotum* differs from the studied fossils for reasons described for Recent representatives (see above). The genus *Cottopsis* can be excluded due to its opercle, featuring one dominant spine, the absence of concave notch, fine serration around the corner of the preopercle, and distinct details of the frontal morphology (Bannikov 2002; TP, personal observation of the Iranian specimens in the MNHN.F).

The family **Polyprionidae** is a group of marine fish recorded in the Atlantic, Indian, and Pacific oceans. Historically, the genus *Stereolepis* was also included in this family (e.g. Nelson et al. 2016). We herein follow Smith et al. (2022), which separate the genus *Stereolepis* into a distinct family (see below). The opercular apparatus of the genus *Polyprion* was figured by Arratia (1982: fig. 48), which shows certain degree of similarity with the studied fossils. However, key differences are evident, as only the lower opercular spine in *Polyprion* is supported by a thorn, and the preopercular denticulation is clearly different. Furthermore, *Polyprion* has a smooth cranial roof (Arratia 1982).

The family **Stereolepididae** includes two species within a single genus, which was previously classified within Polyprionidae but is now recognised as a separate group with a different phylogenetic position (Smith et al. 2022). The opercle of Stereolepididae, characterised by two spines supported by thorns, a deep concave notch, and an enforced anterior margin, is fully comparable with the studied fossils (see Katayama 1959: fig. 6C, Fig. 11B). The general shape of the preopercle and its denticulation also align with the studied fossils. The dorsal side of the neurocranium is relatively flat, with a low and short supraoccipital crest. The anterior margin of the frontals creates a parabolic shape, and the sphenotics are relatively well developed and ventro-laterally bifurcated. The relative articulation of the individual bones is fully comparable with the studied fossils (compare Figures 9 and 11B). Although dermal sculptation is not explicitly mentioned by any authors, at least partial presence of the same type of dermal ornamentation was recognised in some adult specimens (see Ho et al. 2021: fig. 2; personal observation in CAS-ICH 66626). The fossil record of the family is restricted to a single remain of an angular bone determined as *Stereolepis* sp., collected in the Pleistocene deposits of Atsumi group in Japan (Ohe & Moriwaki 1996). Due to lack of respective remains, a direct comparison with the studied fossil is not possible.

The family **Lateolabracidae**, represented by the single genus *Lateolabrax*, is restricted to inshore waters of Western Pacific (Nelson et al. 2016). It exhibits a generally similar morphology of the opercle with our fossils (although the complete bone is surprisingly thick), but the horizontal arm of the preopercle in *Lateolabrax* is ventrally ornamented by several large spines (rather than average denticulation observed in the studied fossils). Additionally, the neurocranium in Lateolabracidae is smooth, generally elongated and differs from the studied fossils in other details (see Katayama 1959; personal observation).

The fish from the family **Percichthyidae** are primarily distributed in freshwater (rarely brackish) environments in Australia and South America. This family is diverse, consisting of nine genera and 24 species (Nelson et al. 2016). Furthermore, several Eocene (genera *Properca* Sauvage, 1880, *Amphiperca* Weitzel, 1933, *Bilinia* Obrhelová, 1971 and most probably *Tretoperca* Sytchevskaya, 1986 too) and Oligocene (genus *Dapaloides* Gaudant, 1985) percichthyids were described from freshwater deposits of Europe. The percichthyid opercle has a thickened anterior margin, and the lower spine is supported by a thorn, but not the upper one (MacDonald 1978: fig. 2; Arratia 1982: figs 47, 49). Compared to our fossils, the preopercle shows a different pattern in spinulation and/or serration (MacDonald 1978: fig. 8; Arratia 1982: figs 47, 49) and the neurocranium in dorsal view has a completely different structure (Arratia 1982: figs 93; MacDonald 1978: fig. 7). The fossil percichthyds may be excluded due to reasons mentioned for contemporary taxa (for details about osteology and other comments see especially Obrhelová 1971, 1976; Gaudant 1979; Micklich 1987, 1988; Gaudant & Micklich 1990; Dykan et al. 2018 – for alternative taxonomic attitude see Gaudant 2000).

The family **Sinipercidae** is a group of mainly freshwater fish found in Eastern Asia, with two Recent genera and 12 species (Fang & Chong 1932; Nelson et al. 2016). Several fossil taxa (one extinct genus) of this family have been described from the Lower Miocene freshwater deposits of Korean Peninsula (Nam et al. 2023) and China (Chen et al. 1999), Middle Miocene of Japan (Yabumoto 2020; Yabumoto & Uyeno 2009), and Middle Miocene marine deposits of Japan (Yabumoto & Uyeno 2000). The fossils under consideration share relatively high similarity with sinipercids, but *Siniperca* can be excluded due to the lack of support for the opercular spines, large spines at the ventral margin of the horizontal preopercular ramus (in some respects reminding preopercle of *Lateolabrax* – compare figs 6E and 6D in Katayama 1959), and a generally elongated neurocranium (Katayama 1959: fig. 17C). Similar arguments are valid for the exclusion of the extinct genus *Inabaperca* (Yabumoto & Uyeno 2000). The genus *Coreoperca* shows a generally very similar opercle, but it lacks support for opercular spines, with both spines being more or less the same size (Katayama 1959: fig. 6F; Chen et al. 1999: fig. 5; Yabumoto & Uyeno 2009: figs 2, 3; Nam et al. 2023: fig. 5), and a short neurocranium with a rather narrow anterior portion of the frontal bones (more concave in the studied fossils; Katayama 1959: fig. 17C). Finally, the dorsal surfaces of the neurocrania are obviously smooth.

The family **Symphysanodontidae**, with two genera, is distributed in tropical and subtropical parts of the Pacific, Indian and Atlantic oceans (Kimura et al. 2017). The opercle with two spines (e.g. Johnson 1981; Kimura et al. 2017) is generally similar, but not supported in the same way as in the studied fossils (the lower spine is supported by an axis thorn, but not the upper one, and the distal part of both spines is thickened by stronger ossification). The preopercle is serrated in a different way, and the dorsicranium lacks typical sculptation (personal observation).

The family **Moronidae**, with six Recent species within two genera, inhabits brackish, freshwater, and marine coastal areas of North America and Europe (Nelson et al. 2016). The opercle is highly similar, with both spines more or less supported by thorns, but the preopercle shows significant differences (in Moronidae, the horizontal ramus is somehow longer and some larger spines are distally bifurcated; Micklich 1988: fig. 14a; personal observation), and the dorsal side of the neurocranium is proportionally different, and its surface is smooth (personal observation). Two opercular spines in the extinct

Oligocene genus *Beaumontoperca* Gaudant, 2000 lack thorny supports, and preopercular spines in the ventral section of the bone are bifurcated similarly as in other moronids (Gaudant 2000: fig. 6).

The studied specimens were also compared with Eocene European **percomorphs of uncertain systematic position** possessing similar morphology of the opercle with two spines. These are: *Anthracoperca* Voigt, 1934, *Rhenanoperca* Gaudant & Micklich, 1990, *Palaeoperca* Micklich, 1978, and *Pararhenanoperca* Micklich & Wuttke, 1988 (the number of opercular spines is not entirely clear in the latter genus, but noted below too). The results are as follows: 1. Two opercular spines in the genus *Anthracoperca* are in obviously different condition than in studied fossils (Micklich & Gaudant 1989: fig. 9), and neither a smooth preopercle nor dorsicranium is associable with studied specimens. 2. Similarly, the genus *Rhenanoperca* also showed different morphology (Gaudant & Micklich 1990). 3. The genus *Palaeoperca* possesses a preopercle with a completely different morphology of posterior spinulation of the vertical preopercular ramus (Micklich 1978; 2205). 4. The number of opercular spines is not clear in the genus *Pararhenanoperca* Micklich & Wuttke, 1988, but the preopercle is smooth, same as the neurocranium surface (Micklich & Wuttke 1988).

The provided brief overview, based on the comparison of available parts of the opercular apparatus (opercle and preopercle) and the dorsal side of the neurocranium, suggests a similarity with the family Stereolepididae, the group recently established by Smith et al. (2022). This family includes two species combined in a single genus—*Stereolepis gigas* Ayres, 1859 and *S. doederleini* Lindberg & Krasyukova, 1969—both inhabiting the subtropical part of the Pacific Ocean (Froese & Pauly 2023). Boulenger (1895) initially included *Stereolepis* in his Serranidae, and his diagnostic section for the genus included various characteristics that align with the studied fossil. For instance, the very small scales, a serrated preopercle with few strong antrorse spines on the lower border (which disappears in larger individuals), an opercle with two spines, a spinous portion of the dorsal fin much longer than the soft one (with XI+10), a short-based anal fin with III+8, and a pectoral fin with 18 to 19 rays. Boulenger (1895) also mentioned strong anal spines, with the first shortest, second and third equal and about as long as the second dorsal fin spine for *S. gigas*.

Although there are some differences, such as in meristic counts of some fin rays, these are interpreted as resulting from inadequate preservation rather than reflecting the natural anatomical state. Further details that could confirm the classification, such as the precise predorsal formula, dorsal fin formula (see also Katayama 1960a, b), and other features, are challenging to determine due to insufficient preservation. The number of vertebrae (12+14), together with 9 to 12 dorsal fin spines and the presence of supramaxilla, would be crucial for confirming our classification within the family Stereolepididae (see family diagnosis in Smith et al. 2022).

Due to the absence of most parts of the viscerocranium and an articulated postcranial skeleton, the comparison of *Stereolepis arcanum* with its congeners is limited to the neurocranium. *Stereolepis arcanum* shows a shorter ethmoidal region, representing maximally 50% of the orbital length (in contrast to *S. gigas* and *S. doederleini*, where the ethmoidal and orbital areas are practically equal; personal observation) and much better-developed sphenotics, with the depth of this bone in lateral view approximately half of the ethmoidal depth (this bone is significantly smaller in both other species; personal observation). Particularly noteworthy is the strongly developed "pit and ridges" ornamentation on the dorsal surface of the frontal bones in *S. arcanum*, while this structure is only poorly developed in both other species (Ho et al. 2021: fig. 2B; personal observation).

Palaeobiological notes on the studied specimens

The stereolepids, particularly *S. gigas*, are known for their large size and are often sought-after catches by fishermen. Although their size might suggest that they can live up to a hundred years, recent studies based on *S. gigas* have revealed slightly lower ages, with the maximal recorded age being about 76 years (Allen & Andrews 2012; Hawk & Allen 2014). Data for *S. doederleini* are practically missing (noted in the latter publication). Given the size of the fossil specimens, it is reasonable to infer that they do not belong to fully grown and most probably non-adult individuals. Consequently, it seems reasonable to expect that some morphological characters and proportions may be different from those recorded for large, fully grown individuals. Such ontogenetic condition is recorded in various groups (see e.g. Cloutier 2010; Přikryl 2017).

Any morphological data for non-adults of *Stereolepis* are anecdotal and restricted to larval and early post-larval developmental stages (Shane et al. 1996; Ladin 2022 and references therein). However, Coufer (2017) and Benseman & Allen (2018) presented three phases of young-of-the-year *Stereolepis gigas*, which include black (10–21 mm TL), brown (23–33 mm TL) and orange (41–186 mm TL) phases. Based on the estimated SL of the studied specimens, it seems reasonable to compare them with individuals in the orange phase. However, the figures provided by Benseman & Allen (2018: figs 1, 2C) do not allow for the verification of details, and they certainly do not enable the evaluation of skeletal characters. Nevertheless, the available information suggests comparable proportions of spinous and soft parts of the dorsal fin, as well as proportions of individual spines in the anal fin. Such an assumption would lead us to the interpretation of the fossil specimens as individuals younger than one year. This interpretation is also supported by the absence of the growth rings at the vertebral centrae and opercle bone.

Noichi et al. (1990) and Benseman et al. (2019) documented the behavior of juvenile *Stereolepis*, particularly their distribution in shallow and soft-bottomed habitats immediately below the wave base. Benseman & Allen (2018) mentioned that individuals in the orange phase were distributed "almost exclusively" at depths of 6 to 10 meters. These observations are valuable for contextualizing the environment in which the studied fossils might have lived. However, it is essential to consider the sedimentology and the accompanying fossils. The relatively high degree of disarticulation, incompleteness, and partial abrasion observed in the fossils may indicate a highly dynamic environment rather than re-deposition.

The genus *Stereolepis*, which is currently restricted to the Eastern and Northwestern Pacific (Froese & Pauly 2023), has a notable southern extension with the recent discovery of *Stereolepis doederleini* in Taiwan by Ho et al. (2021). It is necessary to mention that such southern occurrence is considered relatively exceptional in the present-day context. Although data on climate change in this region during the Pliocene are scarce, the past occurrence of *Stereolepis* in southern regions is foreseeable, especially considering the prevailing oceanic currents and the topography of the ocean floor around Taiwan (Jan et al. 2002).

The contrast between the fossil and modern distribution of *Stereolepis* in Taiwan during the Early Pliocene adds an intriguing insight into our understanding of the historical biogeography of this genus. These palaeobiological findings highlight the importance of continued palaeontological exploration in the underrepresented tropical-subtropical West Pacific.

CONCLUSIONS

The semi-articulated specimens from the Lower Pliocene deposits of the Upper Kueichulin Formation in northern Taiwan are identified as a new species of the family Stereolepididae, *Stereolepis arcanum* n. sp., based on the morphology of the neurocranium. While some characters are partially incomplete, they are consistent with the features observed in the family Stereolepididae. However, they also distinctly differentiate the specimens from previously described species. The estimated age of the specimens is less than one year, based on comparisons with the size of *Stereolepis gigas*. The discovery of the specimens represents the second record of this group globally and highlights the importance of ongoing fossil exploration to enhance our understanding of fish palaeobiodiversity and evolutionary history in the Indo-West Pacific region, particularly during the Neogene.

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References

Agassiz L. (1833–1844) - Recherches sur les Poissons Fossiles. Petitpierre, Neuchâtel et Soleure, 1420 pp.

Allen L. G. & Andrews A. H. (2012) - Bomb radiocarbon dating and estimated longevity of Giant Sea Bass (*Stereolepis gigas*). *Bulletin Southern California Academy of Sciences*, 111: 1-14. https://doi.org/10.3160/0038-3872-111.1.1

Arambourg C. (1967) - Les Poissons oligocenes de l'Iran. *Notes et mémoires sur le Moyen-Orient*, 8: 9-247.

Arratia G. (1982) - A review of freshwater percoids from South America (Pisces, Osteichthyes, Perciformes, Percichthyidae and Perciliidae). *Abhandlungen der Senckenberg Gessellschaft fuer Naturforschung*, 540: 1-52.

Ayres W. O. (1859) - [On new fishes of the Californian coast.]. *Proceedings of the California Academy of Sciences (Series 1)*, 2: 25-32.

Bannikov A. F. (2000) - New data on Late Paleocene marine percoids (Perciformes) of Turkmenistan. *Journal of Ichthyology*, 40: 564-570.

Bannikov A. F. (2002) - A new Middle-Eocene marine percoid (Perciformes, Percoidei) from the Northern Caucasus. *Journal of Ichthyology*, 42: 695-700.

Bannikov A. F. (2014) - The systematic composition of the Eocene actinopterygian fish fauna from Monte Bolca, northern Italy, as known to date. *Studi e ricerche sui giacimenti terziari di Bolca, XV - Miscellanea paleontologica*, 12: 23-34.

Bannikov A. F. & Carnevale G. (2007) - The Eocene *"Dules" temnopterus* Agassiz, 1836 from Monte Bolca, and the problem of classifying fossil percoid fishes. *Palaeontographia Italica*, 91: 69-84.

Basilewsky S. (1855) - Ichthyographia Chinae Borealis. *Nouveaux mémoires de la Société impériale des naturalistes de Moscou*, 10: 215-263.

Benseman S. A. & Allen L. G. (2018) - Distribution and recruitment of Young-of-the-Year Giant Sea Bass, *Stereolepis gigas*, off Southern California. *Copeia*, 106: 312-320. https://doi.org/10.1643/CE-18-021

Benseman S. A., Couffer M. C. & Allen L. G. (2019) - Behavior of Young-of-the-Year Giant Sea Bass, *Stereolepis gigas*, off the Sandy Beaches of Southern California. *Bulletin Southern California Academy of Sciences*, 118: 79-86. https://doi.org/10.3160/0038-3872-118.2.79

Boulenger G. A. (1895) - Catalogue of the fishes in the British Museum. Catalogue of the perciform fishes in the British Museum. Second edition. Volume I. British Museum (Natural History), London, i-xix + 1-394pp, Pls. 1-15.

Carnevale G., Bannikov A. F., Marramà G., Tyler J. C. & Zorzin R. (2014) - The Pesciara-Monte Postale Fossil Lagerstatte: 2. Fishes and other vertebrates. In: Papazzoni C. A., Giusberti L., Carnevale G., Roghi G., Bassi D & Zorzin R. (Eds) - The Bolca Fossil-Lagerstätte: A window into the Eocene World. Rendiconti della Società Paleontologica Italiana 4: 37-63. Società Paleontologica Italiana, Milano.

Chen W.-S. (1986) - Trace fossils and depositional environment of the lower Pitou Formation, northeastern coast, Taiwan. *Ti-Chih*, 7: 65-81. [In Mandarin]

Chen W.-S. (2016) - An introduction to the geology in Taiwan. Geological Society of Taiwan, Taipei, 204 pp. [In Mandarin]

Chen P.-F., Liu H.-Z., Yan J.-X. (1999) - Discovery of fossil *Coreoperca* (Perciformes) in China. *Vertebrata PalAsiatica*, 37: 212-227. [in Chinese with English summary]

Couffer M. C. (2017) - Individually unique spot patterns of young of the year Giant sea bass, *Stereolepis gigas* in captive-raised fish. *Bulletin of the Southern California Academy of Sciences*, 116: 98-109. https://doi.org/10.3160/soca-116-02-98-109.1

Cloutier R. (2010) - The fossil record of fish ontogenies: Insights into developmental patterns and processes. *Seminars in Cell and Developmental Biology*, 21: 400-413. https://doi.org/10.1016/j.semcdb.2009.11.004

Cuvier G. & Valenciennes A. (1828) - Histoire naturelle des poissons. Tome second. Livre Troisième. Des poissons de la famille des perches, ou des percoïdes. Chez F. G. Levrault, Paris, 2: i-xxi + 2 pp. + 1-490 pp., Pls. 9-40.

Davesne D., Gallut C., Barriel V., Janvier P., Lecointre G. & Otero O. (2016) - The phylogenetic intrarelationships of spiny-rayed fishes (Acanthomorpha, Teleostei, Actinopterygii): fossil taxa increase the congruence of morphology with molecular data. *Frontiers in Ecology and Evolution*, 4: 129. https://doi.org/10.3389/fevo.2016.00129

Davis M. P., Sparks J. S. & Smith W. L. (2016) - Repeated and widespread evolution of bioluminescence in marine fishes. *PLoS ONE*, 11: e0155154. https://doi.org/10.1371/journal.pone.0155154

Dykan N., Kovalchuk O., Dykan K., Gurov E., Dašková J. & Přikryl T. (2018) - New data on Paleocene-Eocene fauna (gastropods, ostracods, fishes) and palynoflora of the Boltysh impact structure (Ukraine) with biostratigraphical and paleoecological inferences. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 287: 213-239.

Fang P.-W. & Chong L. T. (1932) - Study on the fishes referring to *Siniperca* of China. *Sinensia*, 2: 137-200.

Fricke R., Eschmeyer W. N. & Van der Laan R. (Eds) (2020) - Eschmeyer's catalog of fishes: Genera, species, references. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. Electroninc version.

Froese R. & Pauly D. (Eds) (2023) - FishBase. World Wide Web electronic publication. www.fishbase.org, version (10/2023).

Gaudant J. (1979) - Mise au point sur l'ichthyofaune paléocene de Menat (Puy-de-Dôme). *Comptes Rendus de l'Académie des Sciences, Paris, D*, 288: 1461-1464.

Gaudant J. (1985) - Mise au point sur les Vertébrés inférieurs de l'Oligocène de Sieblos (Hesse, Allemagne). *Comptes rendus de l'Académie des Sciences Série IIA, Sciences de la Terre et des planets*, 300: 185-188.

Gaudant J. (2000) - Nouvelles observations sur quelques Percoidei (Poissons téléostéens) des eaux douces et saumatres du Cénozoique européen. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 217: 199-244.

Gaudant J. & Micklich N. (1990) - *Rhenanoperca minuta* nov.

gen., nov. sp., ein neuer Percoide (Pisces, Perciformes) aus der Messel-Formation (Mittel-Eozän, Unteres Geiseltalium). *Paläontologische zeitschrift*, 64: 269-286.

Ghedotti M. J., Gruber J. N., Barton R. W., Davis M. P. & Smith W. L. (2018) - Morphology and evolution of bioluminescent organs in the glowbellies (Percomorpha: Acropomatidae) with comments on the taxonomy and phylogeny of Acropomatiformes. *Journal of Morphology*, 279: 1640-1653. https://doi. org/10.1002/jmor.20894

Gosline W. A. (1966) - The limits of the fish family Serranidae, with notes on other lower percoids. *Proceedings of the California Academy of Sciences, 4th series*, 33: 91-111.

Hawk H. A. & Allen L. G. (2014) - Age and growth of the giant sea bass, *Stereolepis gigas*. *California Cooperative Oceanic Fisheries Investigations Reports*, 55: 128-134.

Ho H.-C., Tang C.-N. & Cheng C.-M. (2021) - A southward range extension of a wreckfish, *Stereolepis doederleini* (Actinopterygii: Acropomatiformes: Polyprionidae), to tropical water off eastern Taiwan. *Acta Ichthyologica et Piscatoria*, 51: 365-370. https://doi.org/10.3897/aiep.51.e73207

Hu C.-H. (1992) - Taiwan shellfish fossil record. *Taichung National Museum of Natural Science*, 3: 1013–1074. [In Mandarin]

Hu C.-H. & Tao H.-J. (1996) - *Crustacean fossils of Taiwan*. San-Ming Book Co. Ltd., Taipei, 228 pp. [In Mandarin]

Jan S., Wang J., Chern Ch.-S. & Chao S.-Y. (2002): Seasonal variation of the circulation in the Taiwan Strait. *Journal of Marine Systems*, 35: 249–268.

Johnson G. D. (1981) - Limits and relationships of the Lutjanidae and associated families. *Bulletin of the Scripps Institution of Oceanography*, 24: 1-114.

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

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

Katayama M. (1952) - Systematic position of *Döderleinia berycoides* (HILGENDORF) and *Synagrops japonicus* (STEINDACHNER et DÖDERLEIN). *Japanese Journal of Ichthyology*, 2: 104-110.

Katayama M. (1959) - Studies on the Serranid Fishes of Japan (I). *Bulletin of the Faculty of Education, Yamaguchi University*, 8: 103-180.

Katayama M. (1960a) - Fauna Japonica, Serranidae. Biogeographical Society of Japan, Tokyo, viii+189 pp.

Katayama M. (1960b) - Studies of the serranid fishes of Japan (II). *Bulletin of the Faculty of Education, Yamaguchi University*, 9: 63-96.

Kimura S., Johnson G. D., Peristiwady T. & Matsuura K. (2017) - A new genus and species of the family Symphysanodontidae, *Cymatognathus aureolateralis* (Actinopterygii: Perciformes) from Indonesia. *Zootaxa*, 4277: 51-66. https://doi.org/10.11646/zootaxa.4277.1.4

Kocsis L., Razak H., Briguglio A. & Szabo M. (2019) - First report on a diverse Neogene cartilaginous fish fauna from Borneo (Ambug Hill, Brunei Darussalam). *Journal of Systematic Palaeontology*, 17: 791-819. https://doi.org/10.1080/14772019.2018.1468830

Ladin E. S. (2022) - Developmental osteology of young of the year Giant Sea Bass, *Stereolepis gigas*. Master thesis, California State University, Northridge, 67 pp. https://scholarworks.calstate.edu/concern/theses/hd76s6356

Lin C.-H., Chien C.-W., Lee S.-W. & Chang C.-W. (2021) - Fossil fishes of Taiwan: a review and prospection. *Historical Biology*, 33: 1362-1372. https://doi.org/10.1080/08912963.2019.1698563

Lin C.-H., Wang L.-C., Wang C.-H. & Chang C.-W. (2018) - Common early Pleistocene fish otoliths from Niubu in Chia-Yi County, southwestern Taiwan. *Journal of the National Taiwan Museum*, 71: 47-68. https://doi.org/10.6532/JNTM.201809_71(3).04

Lin C.-H., Ou H.-Y., Lin C.-Y. & Chen H.-M. (2022a) - First skeletal fossil record of the red seabream *Pagrus major* (Sparidae, Perciformes) from the Late Pleistocene of subtropical West Pacific, southern Taiwan. *Zoological Studies*, 61: 10. https://doi.org/10.6620/ZS.2022.61-10

Lin C.-H., Wu S.-M., Lin C.-Y. & Chien C.-W. (2023) - Early Pliocene otolith assemblages from the outer-shelf environment reveal the establishment of mesopelagic fish fauna over 3 million years ago in southwestern Taiwan. *Swiss Journal of Palaeontology*, 142: 23. https://doi.org/10.1186/s13358-023-00288-0

Lin C.-Y., Lin C.-H. & Shimada K. (2022b) - A previously overlooked, highly diverse early Pleistocene elasmobranch assemblage from southern Taiwan. *PeerJ*, 10: e14190. https://doi.org/10.7717/peerj.14190

Lindberg G. U. & Krasyukova Z. V. (1969) - Fishes of the Sea of Japan and of adjacent areas of the Sea of Okhotsk and the Yellow Seas. Part 3. Teleostomi XXIX Perciformes. *Opredeliteli Faune SSSR*, 99: 1-479. [In Russian]

MacDonald C. M. (1978) - Morphological and Biochemical Systematics of Australian Freashwater and Estuarine Percichthyid Fishes. *Australian Journal of Marine and Freshwater Research*, 29: 667-698.

Marramà, G., Klug, S., de Vos, J., Kriwet, J. (2018) - Anatomy, relationships and palaeobiogeographic implications of the first Neogene holomorphic stingray (Myliobatiformes: 29 Dasyatidae) from the Early Miocene of Sulawesi, Indonesia, SE Asia. *Zoological Journal of the Linnean Society*, 184, 1142-1168.

Mediodia, D. P., Chang C.-H., Ho H.-C., Přikryl T. & Lin C.-H. (2024) - A new cryptic species of splitfin fish from Taiwan with revision of the genus *Synagrops* (Acropomatiformes: Synagropidae). *Zoological Studies*, 63: 20.

Micklich N. (1978) - *Palaeoperca proxima*, ein neuer Knochenfisch aus dem Mittel-Eozän von Messel bei Darmstadt. *Senckenbergiana lethaea*, 59: 483-501.

Micklich N. (1987) - Neue Beiträge zur Morphologie, Ökologie und Systematik Messeler Knochenfische: 1, Die Gattung *Amphiperca* Weitzel 1933 (Perciformes, Percoidei). *Courier Forschungsinstitut Senckenberg*, 91: 35-106.

Micklich N. (1988) - Ergänzungen zur Morphologie und Systematik der Gattung *Bilinia* Obrhelova 1971 (Pisces, Percoidei). *Paläontologische Zeitschrift*, 62: 297-317.

Micklich N. & Gaudant J. (1989) - *Anthracoperca siebergi* Voigt 1934 (Pisces, Perciformes). *Ergebnisse einer Neuuntersuchung. Zeitschrift für Geologische Wissenschaften*, 17: 503-521.

Micklich N. & Wuttke M. (1988) - Weitere Fischfunde aus dem Eozän von Eckfeld bei Manderscheid (SW-Eifel, Bundesrepublik Deutschland). *Mainzer naturwissenschaftliches archiv*, 26: 107-149.

Mirande J. M. (2016) - Combined phylogeny of rayfinned fishes (Actinopterygii) and the use of morphological characters in large-scale analyses. *Cladistics*, 33: 333–350. https://doi.org/10.1111/cla.12171

Mitsui S., Taru H., Ohe F., Lin C.-H. & Strüssmann C. A.

(2021) - Fossil fish otoliths from the Chibanian Miyata Formation, Kanagawa Prefecture, Japan, with comments on the paleoenvironment. *Geobios*, 64: 47-63. https://doi.org/10.1016/j.geobios.2020.11.003

Murray A. M. & Stewart K. M. (1999) - A new species of tilapiine cichlid from the Pliocene, Middle Awash, Ethiopia. *Journal of Vertebrate Paleontology*, 19: 293-301.

Nam G.-S., Nazarkin, M. V. & Bannikov, A. F. (2023) - A new Chinese perch (Perciformes, Sinipercidae) from the early Miocene of South Korea. *Historical Biology*, 35: 615-622. https://doi.org/10.1080/08912963.2022.2056842

Nelson J. S., Grande T. C. & Wilson M. V. H. (2016) - Fishes of the world, 5th edition. John Wiley and Sons, Hoboken, 752 pp.

Noichi T., Kanbara T., Mito T., Sakamoto F., Kimura M. & Senta T. (1990) - Occurrence and ecology of juvenile striped jewfish *Stereolepis doederleini* (Family Percichthyidae) in Yanagihama beach, Nagasaki Prefecture. *Bulletin of the Faculty of Fisheries of Nagasaki University*, 68: 29-34. [In Japanese]

Nolf D. (2003) - Fish otoliths from the Santonian of the Pyrenean faunal province, and an overview of all otolith-documented North Atlantic Late Cretaceous teleosts. *Bulletin de l'Institut Royal des Sciences Neturelles de Belgique, Sciences de la Terre*, 73: 155-173.

Obrhelová N. (1971) - Über einen Serranid (Pisces) aus dem nordböhmischen Süßwassertertiär. Časopis pro mineralogii a geologii, 16: 371-387.

Obrhelová N. (1976) - Eine neue Percoiden-Art (Pisces) aus dem nordböhmischen Süßwassertertiär. Bemerkungen zur Gattung *Bilinia* Obrhelova, 1971. Časopis pro mineralogii a geologii, 21: 233-256.

Ohe F. & Moriwaki T. (1996) - A fossil angular of *Stereolepis* sp. (Percichthyidae) from the Pleistocene Atsumi Group, Atsumi Peninsula. *Kaseki no Tomo*, 43: 29-34.

Okamoto M & Gon O. (2018) - A review of the deepwater cardinalfish genus *Epigonus* (Perciformes: Epigonidae) of the Western Indian Ocean, with description of two new species. *Zootaxa*, 4382: 261-291. https://doi.org/10.11646/zootaxa.4382.2.3.

Otero O. (2004) - Anatomy, systematics and phylogeny of both Recent and fossil latid fishes (Teleostei, Perciformes, Latidae). *Zoological Journal of the Linnean Society*, 141: 81-133. https://doi.org/10.1111/j.1096-3642.2004.00111.x

Pan T.-Y., Lin A. T.-S. & Chi W.-R. (2015) - Paleoenvironments of the evolving Pliocene to early Pleistocene foreland basin in northwestern Taiwan: An example from the Dahan River section. *Island Arc*, 24: 281-378.

Priem F. (1908) - Poisson fossiles de Perse. (Mission Morgan). *Annales d'Histoire naturelle, Paléontologie*, 1: 1–25.

Přikryl T. (2017) - Notes on development of the Oligocene trachinid *Trachinus minutus* (JONET, 1958). *Palaeontographica Abteilung A*, 308: 69-87.

Prokofiev A. M. (2007a) - Osteology and some other morphological characters of *Howella sherborni*, with a discussion of the systematic position of the genus (Perciformes, Percoidei). *Journal of Ichthyology*, 47: 413–426.

Prokofiev A. M. (2007b) - The osteology of *Bathysphyraenops symplex* and the diagnosis of the Howellidae (Perciformes: Percoidei) family. *Journal of Ichtyology*, 47: 566–578.

Rosen D. E. (1973) - Interrelationships of higher euteleostean fishes, In: Greenwood P. H., Miles R. S. & Patterson C. (Eds) Interrelationships of Fishes: 397-513. Academic Press, London.

Sauvage M. H. E. (1880) - Notes sur les Poissons fossiles. *Bulletin de la Société géologique de France, Serie 3*, 8: 451-462.

Schwarzhans W. W. (2010) - Otolithen aus den Gerhartsreiter Schichten (Oberkreide: Maastricht) des Grehartsreiter Grabens (Oberbayern). *Palaeo Ichthyologica*, 4: 1–100.

Schwarzhans W. W. & Prokofiev A. M. (2017) - Reappraisal of *Synagrops* Günther, 1887 with rehabilitation and revision of *Parascombrops* Alcock, 1889 including description of seven new species and two new genera (Perciformes: Acropomatidae). *Zootaxa*, 4260: 1-74. https://doi.org/10.11646/ zootaxa.4260.1.1.

Shane M. A., Watson W. & Moser H. G. (1996) - Polyprionidae: Giant sea basses and wreckfishes, In: Moser H. G. (Ed.), The Early Stages of Fishes in the California Current Region. California Cooperative Oceanic Fisheries Investigations (CalCOFI) Atlas 33: 873-875. CalCOFI, La Jolla.

Smith W. L., Ghedotti M. J., Domínguez-Domínguez O., McMahan C. D., Espinoza E., Martin R. P., Girard M. G. & Davis M. P. (2022) - Investigations into the ancestry of the Grape-eye Seabass (*Hemilutjanus macrophthalmos*) reveal novel limits and relationships for the Acropomatiformes (Teleostei: Percomorpha). *Neotropical Ichthyology*, 20: e210160. https://doi.org/10.1590/1982-0224-2021-0160

Smith W. L. & Wheeler W. C. (2006) - Venom evolution widespread in fishes: a phylogenetic road map for the bioprospecting of piscine venoms. *Journal of Heredity*, 97: 206–217. https://doi.org/10.1093/jhered/esj034

Sorbini L. (1975) - Studio paleontologico di *Acropoma lepidotus* (Agassiz) Pisces, Acropomidae. *Miscellanea Paleontologica. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 2: 177-203.

Sutton A. C. (1913) - On an abnormal specimen of *Roccus lineatus* with especial reference to the position of the eyes. *The Anatomical Record*, 6: 195-201. https://doi.org/10.1002/ar.1090070603

Sytchevskaya E. K. (1986) - Freshwater Palaeogene ichthyofauna of the USSR and Mongolia. *Proceedings of the Joint Soviet-Mongolian Paleontological Expedition*, 29: 1-157. [In Russian]

Taylor W. R. & Van Dyke G. C. (1985) - Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9: 107-119.

Temminck C. J. & Schlegel H. (1843) - Pisces, In: Siebold P. F. de (Ed.) - Fauna Japonica, sive descriptio animalium, quae in itinere per Japoniam ... suscepto annis 1823-1830 collegit, notis, observationibus et adumbrationibus illustravit Ph. Fr. de Siebold. Lugduni Batavorum [Leiden] (A. Arnz et soc.). Part 1: 1-20 pp. Apud Auctorem, Lugduni Batavorum.

Toonen R., Bowen B., Iacchei M. & Briggs J. (2016) - Biogeography, Marine, In: Kliman, R. M. (Ed.) Encyclopedia of Evolutionary Biology: 166-178. Academic Press, London. https://doi.org/10.1016/B978-0-12-800049-6.00120-7

van Hinsbergh V. W. M., & Helwerda R. A. (2019) - Fish otoliths from the Cabarruyan Piacenzian-Gelasian fauna found in the Philippines. *Zootaxa*, 4563: 401-443. https://doi.org/10.11646/zootaxa.4563.3.1

Voigt E. (1934) - Die Fische aus der mitteleozéinen Braunkohle des Geiseltales, mit besonderer Beriicksichtigung der erhaltenen Weichteile. *Nova Acta Leopoldina, neue folge*, 2: 21-146.

Wang C.-C. (1983) - Note on faecal pellets from Pliocene Erhchiu Formation of Pitou-Chiao, north Taiwan. *Ti-Chih*, 4: 45-50. [In Mandarin]

Wang C.-C. (1984a) - New classification of clypeasteroid echinoids. *Proceedings of the Geological Society of China*, 27: 119-152.

Wang C.-C. (1984b) - Three star-like trace fossils from Neogene of Taiwan. *Ti-Chih*, 5: 7-10. [In Mandarin]

Wang C.-C. (1985) - Fossil clypeasterid echinoids from Taiwan. *Proceedings of the Geological Society of China*, 28: 143-176.

Weitzel K. (1933) - *Amphiperca multiformis* n. g. n. sp. und *Thaumaturus intermedius* n. sp., Knochenfische aus dem Mittel-Eozän von Messel. *Notizblatt des Vereins für Erdkunde und der Hessischen Geologischen Landesanstalt zu Darmstadt*, 5: 89-97.

Wiley E. O., Johnson G. D. & Dimmick W. W. (2000) - The interrelationships of Acanthomorph fishes: a total evidence approach using molecular and morphological data. *Biochemical Systematics and Ecology*, 28: 319-350. https://doi.org/10.1016/S0305-1978(99)00069-1

Wiley E. O. & Johnson G. D. (2010) - A teleost classification based on monophyletic groups, In: Nelson J. S., Schultze H.-P. & Wilson M. V. H. (Eds) - Origin and Phylogenetic Interrelationships of Teleosts: 123-182. Verlag Dr. Friedrich Pfeil, München

Yabumoto Y. (2020) - *Siniperca ikikoku*, a new species of freshwater percoid fish from the Miocene of Iki Island, Nagasaki, Japan. *Paleontological Research*, 24: 226-237. https://doi.org/10.2517/2019PR016.

Yabumoto Y. & Uyeno T. (2000) - *Inabaperca taniurai*, a new genus and species of Miocene percoid fish from Tottori Prefecture, Japan. *Bulletin of the National Science Museum. Series C, Geology & Paleontology*, 26: 93-106.

Yabumoto Y. & Uyeno T. (2009) - *Coreoperca maruoi*, a new species of freshwater percoid fish from the Miocene of Iki Island, Nagasaki, Japan. *Bulletin of the Kitakyushu Museum of Natural History, Series A*, 7:103-112. https://doi.org/10.34522/kmnh.7.0_103

Yamanoue Y. (2016) - Revision of the genus *Verilus* (Perciformes: Acropomatidae) with a description of a new species. *Journal of fish biology*, 89: 2375-2398. https://doi.org/10.1111/jfb.13124