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A Turonian pycnodontiform fish from the San José de Gracia Quarry, Puebla, Mexico

Un pez pycnodontiforme turoniano de la Cantera San José de Gracia, Puebla, México

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ABSTRACT

We report the presence of pycnodontiform fishes in the Turonian marine deposits of the Mexcala Formation, exposed in the San José de Gracia Quarry in the Municipality of Molcaxac, Puebla, central Mexico. This report includes a complete, articulated, and superficially poorly preserved specimen. This specimen has some peculiar osteological features for example: the supraorbital skull region is peculiarly prominent and rounded; its neural and hemal arcocentra have long, sharp lateral flanges that interlock with those of the contiguous arcocentra, forming tight and complex zigzagging suture; and its vomerine and pre-articular teeth have a flat and concave medial surface and lateral edges with aligned serrations and cusps. These along with other features are sufficient to allow us to conclusively identify this fish as a member of the order Pycnodontiformes, suborder Pycnodontoidei, family Pycnodontidae, and subfamily Nursalliinae. Comparison of the species within the subfamily allows us to identify the specimen of San José de Gracia as *Paranursallia gutturosa*, previously only known from northwestern Africa. In Addition, similar fossil fishes of the Agua Nueva Formation, previously recovered at sites such as the Vallecillo quarries in Nuevo León, Huehuetla in Puebla, and Xilitla in San Luis Potosí, suggest that these represent the same species.

Keywords: Turonian, Pycnodontiformes, *Paranursallia gutturosa*, Cantera San José de Gracia, Puebla.

RESUMEN

Se reporta la presencia de peces picnodontiformes en los depósitos marinos del Turoniense de la Formación Mexcala, expuestos en la Cantera San José de Gracia en el Municipio de Molcaxac, Puebla, centro de México. Este reporte incluye un espécimen completo, articulado y superficialmente mal preservado. Este espécimen tiene algunas características osteológicas peculiares, por ejemplo: la región supraorbitaria del cráneo es peculiarmente prominente y redondeada; sus arcocentros neurales y hemales tienen bridas laterales largas y afiladas que se entrelazan con las de los arcocentros contiguos, formando una sutura en zigzag apretada y compleja; y sus dientes vomerianos y prearticulares tienen una superficie medial plana y cóncava y bordes laterales con serraciones y cúspides alineadas. Estas, junto con otras características, son suficientes para permitirnos identificar de manera concluyente a este pez como miembro del orden Pycnodontiformes, suborden Pycnodontoidei, familia Pycnodontidae y subfamilia Nursalliinae. La comparación de las especies dentro de la subfamilia permite identificar el ejemplar de San José de Gracia como Paranursallia gutturosa, anteriormente solo conocido en el noroeste de África. Además, peces fósiles similares de la Formación Agua Nueva, recuperados previamente en sitios como las canteras de Vallecillo en Nuevo León, Huehuetla en Puebla y Xilitla en San Luis Potosí, sugieren que representan la misma especie.

Palabras clave: Turoniano, Pycnodontiformes, Paranursallia gutturosa, Cantera San José de Gracia, Puebla.

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1. Introduction

The San José de Gracia Quarry is a recently reported Mexican Turonian paleontological site (Alvarado-Ortega *et al.*, 2009, 2020a). The cream-brown colored marly flagstones extracted here exhibit a peculiar fossil marine biota mainly represented by different fish taxa.

The site is on the southeast side of the Cacique Creek, near the homonymous town of the Municipality of Molcaxac, State of Puebla, central Mexico (Figure 1). Here, the strata excavated represent about 20 meters thick, which in some places are remarkably folded, whose lower and upper contacts are still unknown.

Before discovering these fossils, the lithostratigraphic sequence of the San José de Gracia Quarry was unidentified; however, its extent is still unknown. Despite this, some geological and paleontological data suggested that this Turonian age marine sequence tentatively represents part of the Mexcala Formation. Quaternary continental deposits entirely cover this sequence; however, this is younger than the massive Cenomanian limestones of the Morelos Formation and the Aptian fossil-lacking dolomites of the Miahuatepec Formation, respectively exposed to the south and the west of the paleontological site.

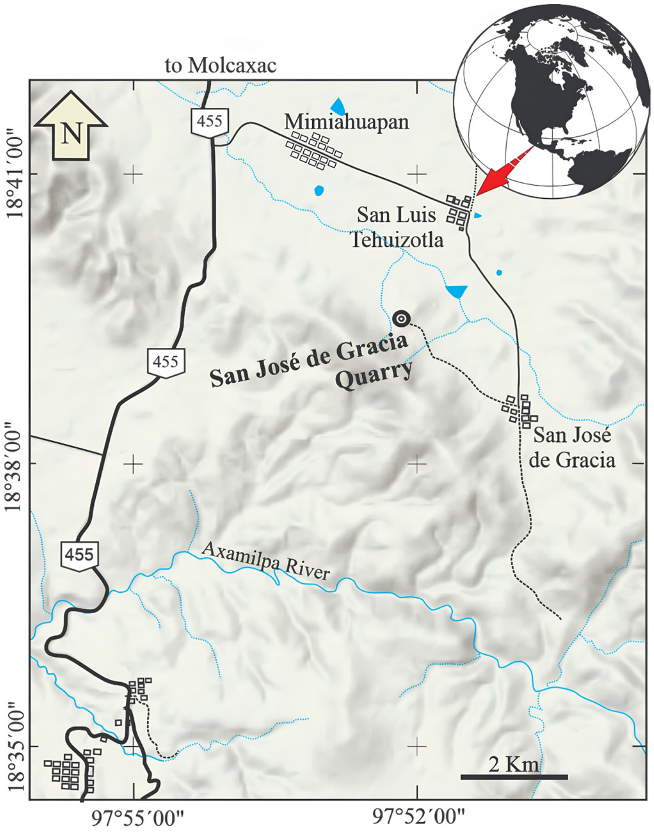

Figure 1 Map of the San José de Gracia Quarry, Puebla, Mexico.

Until now, the fossil assemblage of San José de Gracia Quarry represents a few plant remains, as well as ammonites, belemnites, gastropods, bivalves, crabs, fish, and reptiles. The invertebrates include the Turonian bivalve index fossil *Inoceramus* (Mityloides) *labiatus* Schlotheim (1813), as well as possible members of the amonite families Hamitidae and Anisoceratidae. The vertebrates are represented by undeterminate species of the Aulopiformes *Dercetis* Agassiz, 1833, and *Enchodus* Agassiz, 1833; undeterminate fossil herring belonging to the family Clupeidae; possible allies to *Laminospodylus transversus* Springer, 1957, and members of the order Crossognatiformes; a possible Acanthomorphata species of *Xenyllion* Wilson and Murra, 1996; and remians of a Mosasauroidea representing the Subfamily Yaguarasaurinae (Alvarado-Ortega *et al.*, 2009, 2020a; Pulido-González, 2011; Romero-García, 2013; Zavaleta-Villareal, 2015; Villeda Ruiz, 2022; Medina Castañeda, 2013). This contribution aims to describe and determine the taxonomic identity of the first pycnodontifom fish representative of the subfamily Nursalliinae collected from the San José de Gracia Quarry.

Pycnodontiformes is a diverse order of highly specialized Late Triassic-Eocene neopterygian fishes (Berg, 1937). The deep-bodied species of this widely distributed group inhabited the coastal environments of tropical and subtropical seas (Nursall, 1996; Martín-Abad and Poyato-Ariza, 2013; Ebert and Kölbl-Ebert, 2018). In the first monographic study of this order, Poyato-Ariza and Wenz (2002, p. 216, 223-224, and fig. 43) named the subfamily Nursalliinae to include the species of *Nursallia* Blot, 1987, *Abdobalistum* Poyato-Ariza and Wenz, 2002 and *Palaeobalistum* Blainville,

1818. At the same time, the last authors identified Nusalliinae and its sister group Pycnodontinae, forming the clade most derived from the family Pycnodontidae, which today is the most diverse amongst the five families recognized by them. In such hypothesis, *Palaeobalistum gutturosum* Arambourg, 1954, from the Moroccan Cenomanian marine deposits of the Jebel Tselfat, is considered as a possible member of *Nursallia*; so, this was reported as *Nursallia? gutturosum*.

Later, Capasso (2007) recorded *N. gutturosum* from Cenomanian marine sites in Italy. Then, *Nursallia tethysensis* Capasso et al, 2009, was erected based on Cenomanian specimens from Lebanon, which the authors noted was more closely related to *N. gutturosum* than to other species of the genus. However, a few years later, *N. gutturosum* was renamed *Paranursallia gutturosa* by Amalfitano *et al.* (2020) to include it in the genus *Paranursallia*, erected by Taverne *et al.* (2015) with their species, *P. spinosa*, from the Cenomanian of Dir Oulad Yahia, Jebel Bargou, Tunisia as the type species and part of Nursalliinae. The newest member of *Nursallia*, *N. fenestrata* Capasso, 2023a, was recently described from the Turonian of the Akrabou Formation, Morocco. Previously, Taverne and Capasso (2018) reranked and renamed this *Nursallia*-group as the tribe Nursallini. More recently, Taverne and Capasso (2020) claimed that *Flagellipinna rhomboides* Cawley and Kriwet, 2019, belongs to this group. Another monospecific genus, *Njoerdichthys dyckerhoffi* Cawley *et al.* 2020, from the Turonian deposits of the Hesseltal Formation, Westphalia, Germany, is a pycnodontid recently described that surprisingly exhibits some of the most peculiar features present in Nursalliinae. Capasso (2023b) concluded that the tribe Nursaliini (here, subfamily Nursalliinae) also includes *Haqelpycnodus picteti* Taverne and Capasso, 2018, from the Cenomanian deposits of Haqel, Lebanon, firstly described as part of Pycnodontidae. Finally, Neomesturus asflaensis Cooper and Martill, 2020, from Turonian deposits of the Akrabou Formation in Asfla, Morocco, was described as part of Nursallinae based on isolated jaw bones.

Soon, after the establishment of the Nursaliinae in the monographic study on the Pycnodontiformes of Poyato-Ariza and Wenz (2002), Late Cretaceous specimens attributable to this subfamily began to be recognized in Mexico; however, such reports present certain inconsistencies that lead to an imprecise knowledge of the taxonomic diversity of Nursaliinae in Mexico. The first of these fossils, recovered in the Turonian deposits of the Vallecillo Quarry, Nuevo León, was vaguely referred to and illustrated as a Pycnodontoidea by Blanco-Piñón (1998, p. 52, lam. VII).

Later, together with other specimens from the same locality were erroneously identified as part of the family “Nursallidae” previously erected by Blot, 1987 (Blanco *et al.*, 2001, p. 188, lam. VII). Finally, more accurately, these were identified as “*Nursallia?* cf. *gutturossum* Arambourg, 1954” (Blanco, 2001, p. 66-94; Blanco-Piñón, 2003), indeterminate species of “*Nursallia* Blot, 1987” (Blanco-Piñón *et al.*, 2002, p. 45, fig. 3.b), “*Nursallia* cf. *N. gutturosum* (Arambourg, 1954)” (in Ifrim, 2006, p. 60, fig. 7.15), “*Nursallia gutturosum* (Arambourg, 1954)” (in Giersch, 2014, p. 57-64), and simply as “*Nursallia gutturosum*” (Stinnesbeck *et al.*, 2019). Giesrch *et al.* (2008, p. 44) reported other specimens of “*Nursallia gutturosum*” from the Cenomanian-Turonian deposits of the Sierra de Arteaga site, Coahuila, Mexico. Recently, a headless specimen from the Turonian deposits of the Huehuetla Quarry, Puebla, was recognized as *Nursallia tethysensis* Capasso *et al.*, 2009 (Alvarado-Ortega *et al.*, 2019, p. 4, fig. 2), and an incomplete and strongly disarticulated specimen from the Campanian marine deposits of the Tizimol Quarry, Chiapas, was identified as an indeterminate species of *Nursallia* (Alvarado-Ortega *et al.*, 2020b, p. 6-7, fig. 5).

In addition, specimens that may represent *Paranursallia gutturosa*, from the Turonian deposits of the Xilitla Quarry, San Luis Potosi, have been vaguely reported as Pycnodontiformes by Galavíz Hernández and Alvarado Valdez (2022). To conclude, Capasso (2023b) recognized that the referred pycnodontids from the Vallecillo Quarry

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belong to *Paranursallia gutturosa*. Given this scenario, this study also reviews the taxonomic status of these Mexican fossils.

2. Materials and methods

Preparation methods. The fossil studied here was prepared mechanically with needles and odontological scavengers under a stereoscopic microscope and hardened with a weak solution of plexigum PQ 611 diluted in methacrylate acetate applied with a fine brush. The specimen was observed and photographed under different illumination conditions, including white, natural, and long-wave UV (254 nm) light. The magnesium-coated specimen made it possible to obtain high-resolution gray-tone photographs.

Institutional abbreviations. The fossil studied here and other specimens from the San José de Gracia are deposited and cataloged under the acronym IGM, which corresponds to the Colección Nacional de Paleontología, housed in the Instituto de Geología, UNAM. Here, the San José de Gracia Quarry is recorded as IGM-loc 3876 in the catalog of paleontological sites of IGM. The Colección de Paleontología of the Benemérita Universidad Autónoma de Puebla houses a similar collection. The acronyms of other pycnodontiform specimens referred here include: CPC, Colección Paleontológica de Coahuila, Museo de Desierto (MUDE), Coahuila, Mexico.

Anatomical terminology and abbreviations. The anatomical terminology and abbreviations used in this contribution are based on those considered in similar previous publications works dealing with the anatomy of the Pycnodontiformes (*e.g.*, Nursall, 1996; Poyato-Ariza and Wenz, 2002; Ebert, 2020; Taverne *et al.*, 2015).

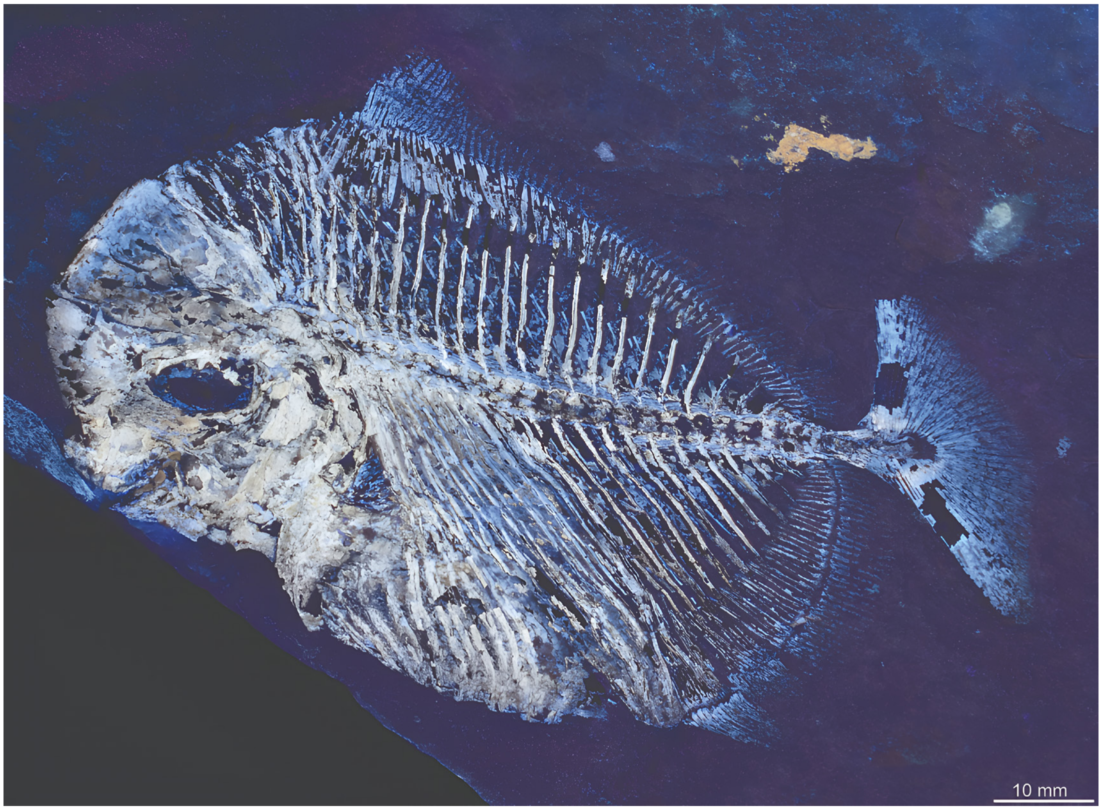

Figure 2 IGM 13950 observed under UV light, a representative of *Paranursallia gutturosa* (Arambourg, 1954), from the Turonian marine deposits of the San José de Gracias quarry, Molcaxac Municipality, Puebla, Mexico.

3. Results

3.1. SYSTEMATIC PALEONTOLOGY

Orden Pycnodontiformes Berg, 1937
Suborden Pycnodontoidei *sensu* Nursall, 1996
Familie Pycnodontidae *sensu* Nursall, 1996
Subfamily Nursalliinae *sensu* Poyato-Ariza & Wenz, 2002
Genus *Paranursallia* Taverne *et al.*, 2015
Paranursallia gutturosa (Arambourg, 1954)

Referred material. IGM 13950, a nearly complete specimen exposing the left side of the body, recovered in the San José de Gracia Quarry, Molcaxac Municipality, Puebla Central Mexico (Figure 2).

Sinonimous. *Paranursallia gutturosa* Arambourg, 1954.

3.2. DESCRIPTION

General measurements and proportions. Table 1 and Figure 3 summarize the measurements and body proportions of IGM 13950. Considering that the longitudinal axis of the body is a horizontal line that crosses the anteroventral end of the skull ethmoid region and the most distal end of the caudal fin, the estimated total (LT) and standard (LS) lengths of this fish are 101.2 and 83.5 mm, respectively. This fish has an oval body, slightly tilted anterodorsally and strongly laterally compressed, in which the maximum body height is 77.3 % of the SL. The head is broad, wide-fronted, anterodorsally rounded, and slightly projected anteriorly, in which the height and length of the head are 48.3 and 39.8 % of the SL. In the skull, the preorbital region is barely longer than the orbital longitudinal axis (12.8 % *versus* 12.4 % of the SL). The postorbital region of the skull is short, and its length is just 3.3. % of the SL. The unpaired fins are long-based, falcate, and display an acuminate anterior lobe. The dorsal fin is long, rises in the anterior half (38.2% of SL), and occupies more than one-half of the body (55.3 of the SL). The anal fin is comparatively short, rises in the

Table 1. Body measurements and proportions of IGM 13950. See the abbreviation in Figure 3.

Feature	In mm.	As % of SL
Total length (TL)	101.2	—
Standard length (SL)	83.5	1
Head length (HL)	29.2	39.8
Head height (HH)	40.4	48.3
Prorbital length (PoL)	10.4	12.4
Longitudinal orbital diameter (LOD)	10.7	12.8
Postorbital length of the skull (PoLS)	2.8	3.3
Maximum body heigh (MBH)	64.6	77.3
Predorsal length (PDL)	31.9	38.2
Dorsal fin length (DFL)	46.2	55.3
Prepelvic length (PPL)	52.4	62.7
Preanal length (PAL)	63.4	75.9

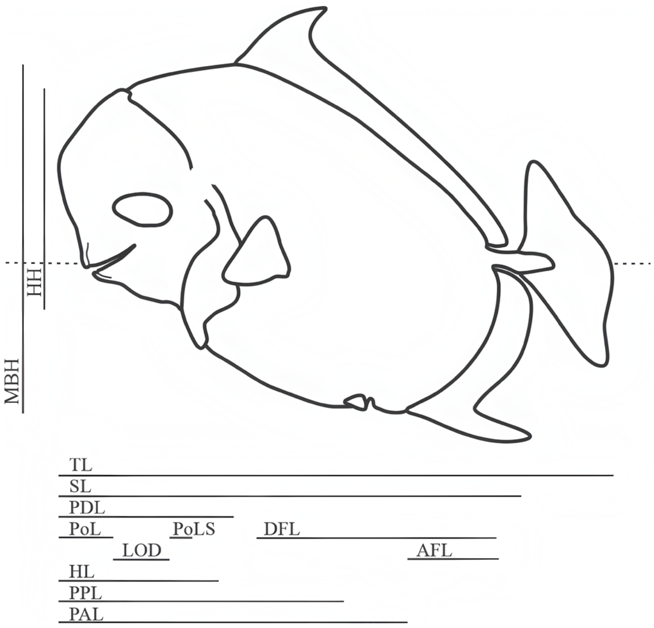

Figure 3 Sketch of IGM 13950 showing the body measurements considered in this work. See Table 1. The dotted line represents the longitudinal axis of the body.

posterior quarter (75.9 % of the SL), and extends just one-fifth of the body (20.8 % of the SL). The unpaired fins are fan-shaped and rounded posteriorly; the pelvic fin is small, close to the abdominal border, and rises in the posterior half of the body (at 62.7 % of SL); in contrast, the pectoral fin is expanded, located in the mid-distance between the vertebral column and the abdominal border, and rise behind the head. The caudal peduncle is shallow and short. The rear edges of the anal and dorsal fins reach the anterior edge of the caudal fin.

Skull. In lateral view, the head has a high and short oval profile, in which the orbit is at mid-height, the snout is short and slightly inclined anteroventrally, and the ventral head margin and the anterior margin of the cleithrum form an acute "V"-shaped notch (Figure 4). The frontal-occipital region expands remarkably, occupying about half of the lateral surface of the head, showing a dorsal edge slightly convex and inclined anteroventrally, as well as a slightly concave and vertical anterior border. Here, the preorbital length and horizontal orbital diameter are similar (10.4 and 10.7 mm,

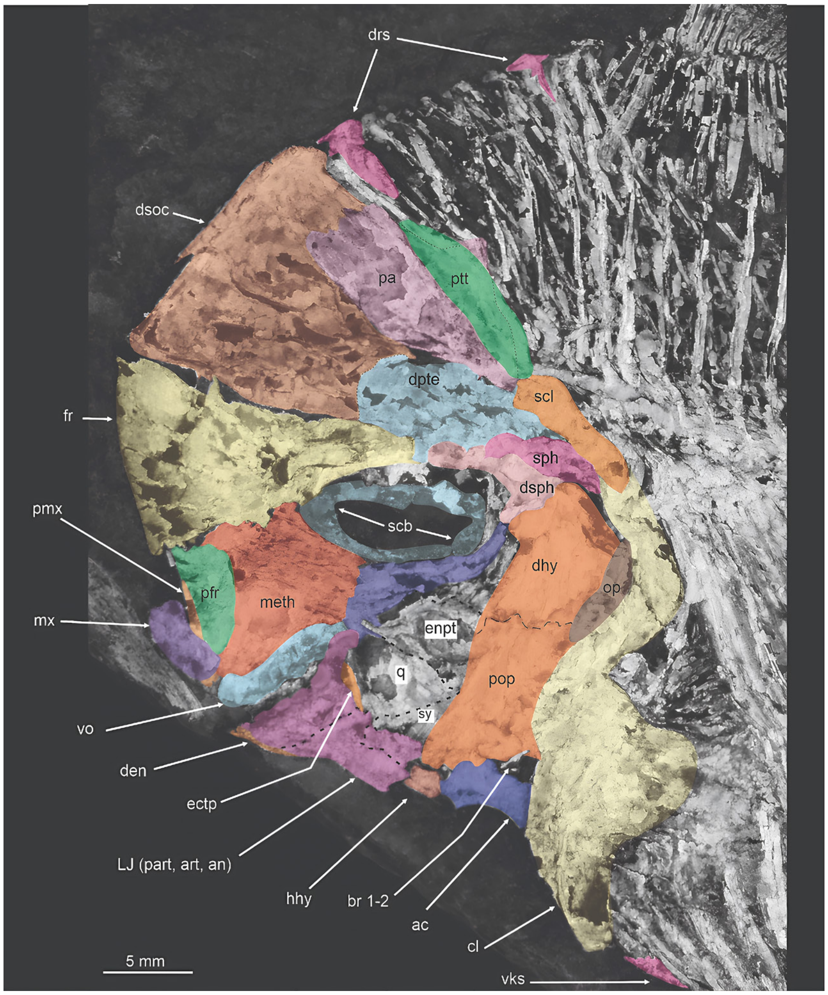

Figure 4 Head of IGM 13950. Abbreviations: ac, anterior ceratohyal; br 1-2, branchiostegal rays 1 and 2; cl, cleithrum; den, dentary; dhy, dermohyomandibular; dsoc, dermosupraoccipital; dsph, demosphenotic; drs, dorsal ridge scale; ecpt, ectpterygoid; enpt, entopterygoid; fr, frontal; hhy, hypohyals ventral and dorsal; LJ, lower jaw in which the suture between the prearticular (part), articular (art), and angular (an) are unclear; meth, mesethmoid; mx, maxilla; op, opercle; pa, parietal; pfr, prefrontal; pmx, premaxilla; pop, preopercle; ptt, posttemporal; q, quadrate; scb, sclerotic bones; scl, supracleithrum; sph; sphenotic; sy, symplectic; vks, ventral keel scute; vo, vomer.

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respectively), while the postorbital length is just 2.3 mm.

The frontal-occipital region of the skull consists of the dermosupraoccipital and the pair of frontals, parietals, and dermopterotics (Figure 4). The frontal is a slice-shaped bone extended to the middle of the orbit, anteriorly broad and with a curved and smooth edge, sharp posteriorly, and sutured to dermosupraoccipital and dermopterotic dorsally and to the mesethmoid anteroventrally. The dermosupraoccipital is an axe-shaped bone with a curved and smooth dorsal border, a posteroventral notch suturing the parietal, and a dorsoposterior process reaching the upper part of the nape. The parietal is a narrow and inverted triangular bone located in the back of the skull, suturing the dermosupraoccipital anterodorsally and the dermopterotic anteroventrally, which is as high as two-thirds of the posterior part of the dermosupraoccipital and displays a short postparietal process not branched distally. The sphenotic and dermosphenotic cover the postorbital part of the skull; the first borders the orbit posteriorly, and the last extends to the nape.

The ventral part of the skull involves the parasphenoid and mesethmoid bones that join below the middle of the orbit (Figure 4). The parasphenoid is a sigmoid bone only partially exposed, slightly ventrally tilted in its posterior part, and strongly inflected ventrally in its anterior end. The mesethmoid is a semi-oval bone, somewhat concave at its anterior, which attaches the vomer ventrally, the parasphenoid posteriorly, and the frontal dorsally. A pair of thick and broad prefrontal bones overlie the anterior part of the mesethmoid. A couple of broken sclerotic bones occupy the orbit; these are narrow, laminar, and curved bones that join each other dorsally and ventrally in the middle of the orbit. There are no circumorbital bones preserved.

The vomer exposes its left labial surface in part (Figure 5). As in other Pycnodontiforms, this bone bears molariform or massive oval teeth. Although

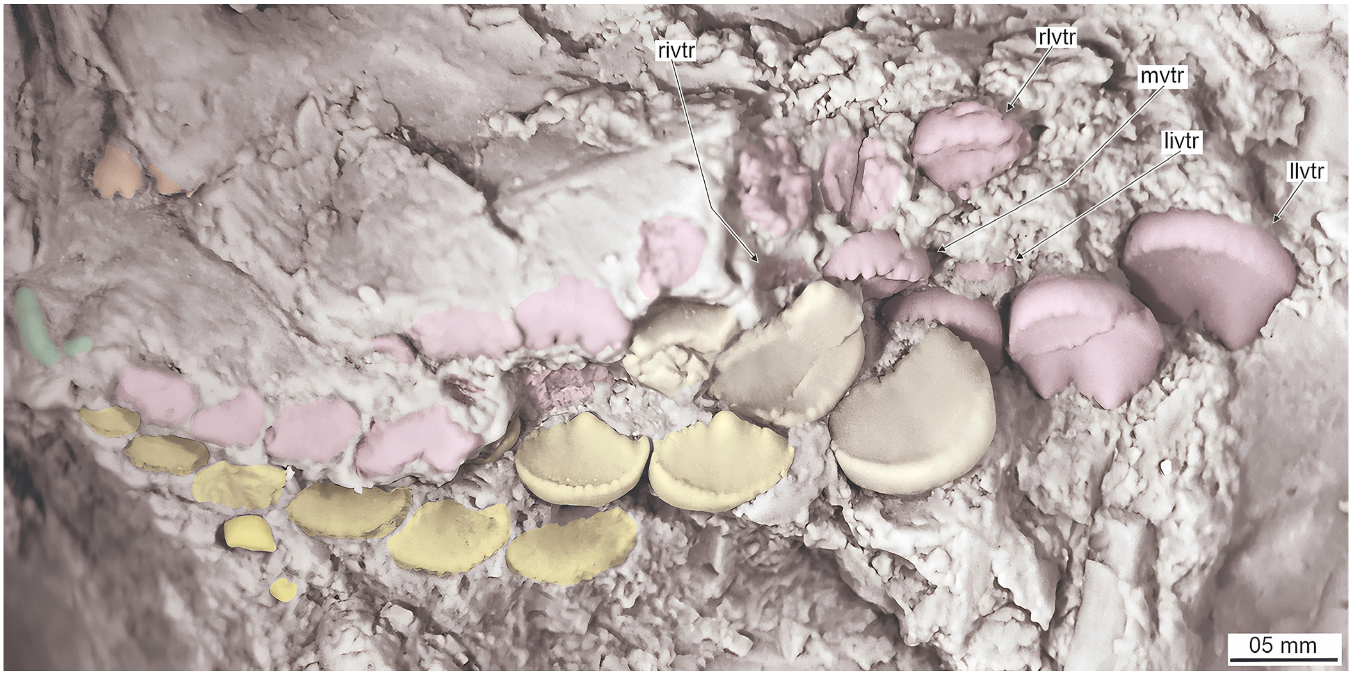

Figure 5 Teeth of IGM 13950 with the specimen coated with magnesium. Abbreviations. livtr: left intermedial vomerine tooth row; llvtr: left lateral vomerine tooth row; mvtr: medium vomerine tooth row; rivtr: right intermedial vomerine tooth row; rlvtr: right lateral vomerine tooth row; green color: dentary teeth; orange color: premaxillary teeth; pink color: vomerine teeth; yellow color: prearticular teeth (here, the decreased intensity of the color shows the presence of four tooth rows).

these teeth are undefined in number, they increase in size in anterior-posterior order and form five rows. Although adjacent lateral vomerine teeth have similar sizes, most lateral teeth seem slightly more prominent. Medially, these teeth are concave and smooth, showing lateral cutting borders with sharp ridges aligned lingual and labially. On the lateral teeth, the labial cutting edge also shows two conspicuous acute cusps.

Jaws. IGM 13950 shows a tripartite occlusion between two ventral elements (lower mandibles) and one dorsal element (vomer plus both premaxillae), excluding the maxilla and including the vomer (Figures 4 and 5). The upper jaw consists of a large oval and toothless maxilla plus a slender and straight stick-like premaxilla that bears two small incisor teeth and is nearly as high as three-quarters of the mesethmoid.

The lower jaw is a complex structure triangular-shaped, equally long as high, with no postarticular process, and composed of the dentary, prearticular, angular, and articular tightly sutured (Figure 4).

The dentary is a slender curved bone that forms the anterior end of the jaw and bears two small incisiform teeth (Figures 4 and 5). The prearticular is a roughly rectangular bone in lateral view and the principal carrier of teeth in the lower jaw, which has a straight alveolar border and a coronoid process with a rounded tip that is short

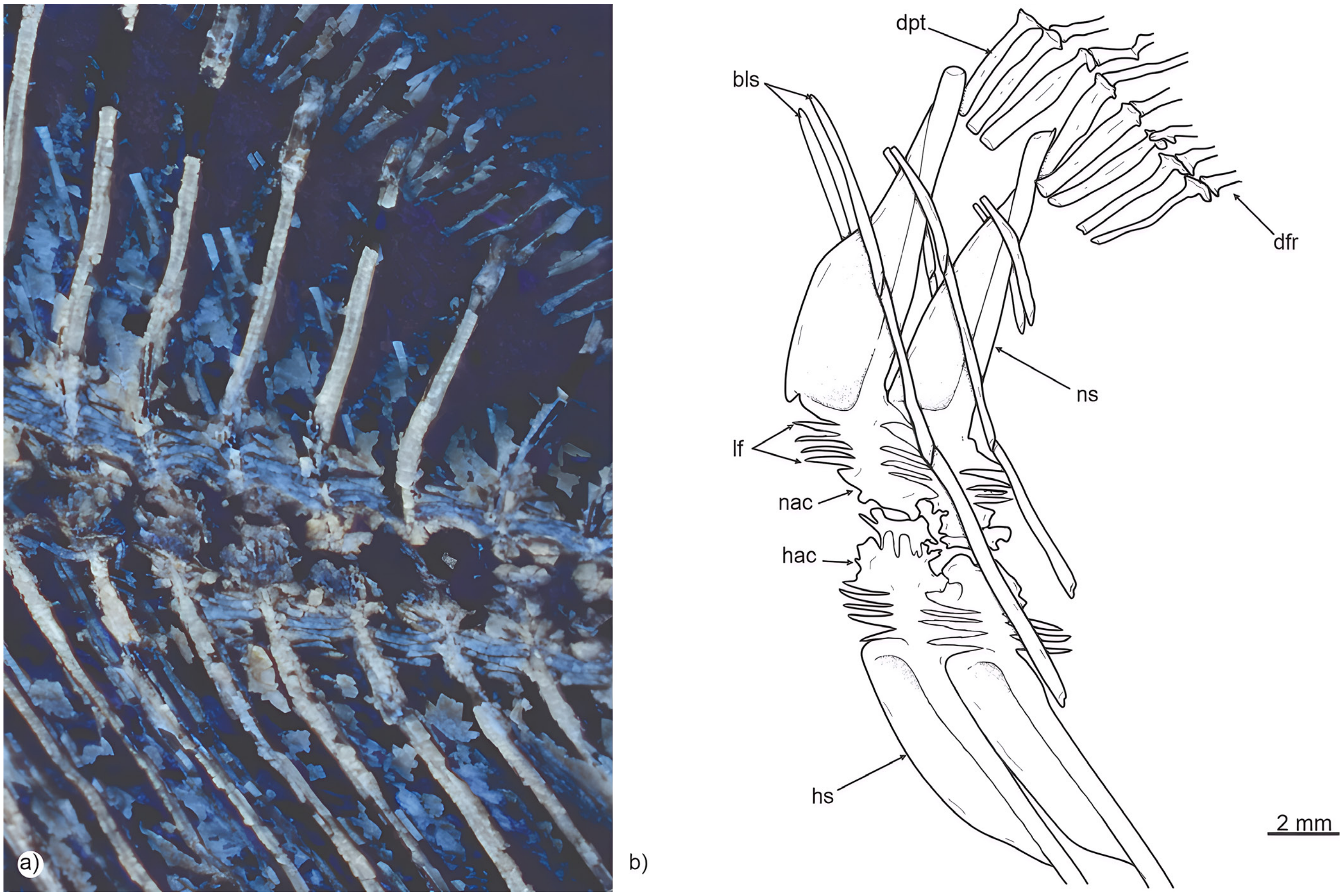

Figure 6 Dorsal and ventral arcocentra of the caudal trunk region of IGM 13950. a) Photography under UV light. b) Idealized reconstruction of two arcocentra and associated skeletal elements. Abbreviations. bls: modified bar-like scale; dfr: dorsal fin ray; dpt: dorsal pterygiophore; hac: hemal arcocentrum; hs: hemal spine; lf: lateral flanges of arcocentrum; nac: neural arcocentrum; ns: neural spine.

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and tilted posterodorsally. The articular and angular bones are robust bones that project, forming the posteroventral end of the lower jaw. Despite being covered, it is possible to recognize that the lingual surface of the prearticular bone shows four rows of oval molariform teeth of increasing size in anteroposterior and ventral-dorsal orders. Among these prearticular teeth, those of the three dorsal rows are remarkable for being somewhat concave and smooth in the middle surface and have acute conspicuous labial cusps plus lingual and labially cutting edges formed by aligned sharp serrated ridges. The labial cusp rises in the posterior half of each tooth of the first and third rows, while in the second row, such cusp is medial.

Opercular bones. This series lacks the infraopercle and subopercle bones (Figure 4). The opercle is a small and narrow crescent-shaped bone located at the anterior apex of the cleithrum. The preopercle is a rectangular bone fused to the ventral edge of the hyomandibular.

Suspensorium and hyoid arch. The exposed part of the suspensorium includes a robust quadrate bone with an inconspicuous articular head, a thick oblong robust symplectic, a curved and slender ectopterygoid, as well as a subrectangular ectopterygoid and a high triangular metapterygoid (Figure 4). The dermohyomandibular is somewhat rectangular, has a curved articular head, and its dermal part is similar in size to the preopercle.

The ventral and dorsal hypohyials are long and thick rectangular bones joining the anterior edge of the anterior ceratohyal (Figure 4). The anterior ceratohyal is a roughly rectangular bone, about twice as long as high and dorsoventrally constrained in the middle. Two elongated and curved branchiostegals are present.

Axial skeleton. Practically, the vertebral axis is straight and posteroventrally inclined.

The notochordal canal is partially empty because the chordocentra or autocentra are unossified (Figures 2 and 6). The arcocentra have neural and haemal arches irregularly expanded with dissimilar radial projections, which often are in contact, surrounding the notochord partially or totally. Regardless of the epichordal and hypochordal elements of the caudal skeleton, the axial skeleton consists of 27 paired archocentra, including 14 caudals and 13 abdominals.

The anterior six neural arcocentra are fused, forming a large synarcual. The anterior seven neural spines are autogenous (Figure 2). In both series, the neural and hemal spines are straight and thin structures harmoniously enlarged and tilted backward. In the predorsal region, the neural spines 5 to 6 are the longest, support the dorsal apex of the trunk, and project dorsally, forming an angle nearly straight. Other neural spines become progressively shorter; those in anterior positions project anterodorsally, generating obtuse angles close to 100°, while the inclination of those occupying posterior positions increases progressively between nearly 80° to 10°. The size and inclination of the hemal spines are nearly symmetrically opposite to that shown by the corresponding hemal spines; however, in general, the hemal spines are slightly larger and a little more inclined posteroventrally.

The neural and hemal spines have a thin and long anterior sagittal wing except for the anterior seven neural spines and the four haemal spines ahead of the caudal skeleton. All hemal and neural arcocentra have deep zigzagging anterior and edges, in which there are 2 to 7 long triangular projections or flanges that interlock with the corresponding neighboring arches, allowing tightly suture (Figure 6). There are no intermuscular bones. At least ten long and slightly curved ribs surround most of the abdominal cavity. The postcoelomic is a long bone extended between the vertebral axis and the ventral margin of the body, with a triangular ventral part projected rostrally and an acute and long dorsal part.

Paired fins. Unfortunately, the bones that form the dorsal part of the pectoral girdle are partially preserved (Figures 2 and 7). Here, the posttemporal is an oblong bone, small, narrow, and tilted anterodorsally against the upper half of the parietal rear. The supracleithrum is another oblong and tilted bone located behind the basicranium. The cleithrum is a high sinuous bone in which the lower half is conspicuous, broad, and ventrally projected beyond the head; in contrast, its dorsal half is relatively narrow and extends up to the vertebral column. The ventral edge of the head and the anterior edge of the cleithrum form a deep and acute angle. The cleithrum shows a deep posterior notch in which the pectoral fin arises. The shape of the pectoral fin is not determinable; however, it preserves at least 12 rays.

The pelvic girdle and fin are not well preserved in IGM 13950 (Figure 7); only a few incomplete rays reveal the small size of this fin and its position near the abdominal edge. The scales entirely cover the pelvic bones. The pelvic rays are short, thin, segmented, and distally branched. At least six twisted forward rays of the left pelvic fin are present, and at least three small robust radials joint the proximal ends of such rays. Otherwise, at least five rays of the right pelvic fin are below the impression of the postcloacal ventral keel scutes.

Unpaired fin. In both unpaired fins, the anterior distal part is partially missing; however, it is possible to note that these fins are falcate to acuminate shaped (type C, in Poyato-Ariza and Wenz, 2002, fig. 34) (Figure 7).

The dorsal fin consists of 71 rays, arises before the middle of the trunk, and extends along 55.3 % of the SL, between 38.2 and 93.5 % of the SL. Here, five short rays of increasing size precede the dorsal lobe, including the subsequent and notice-

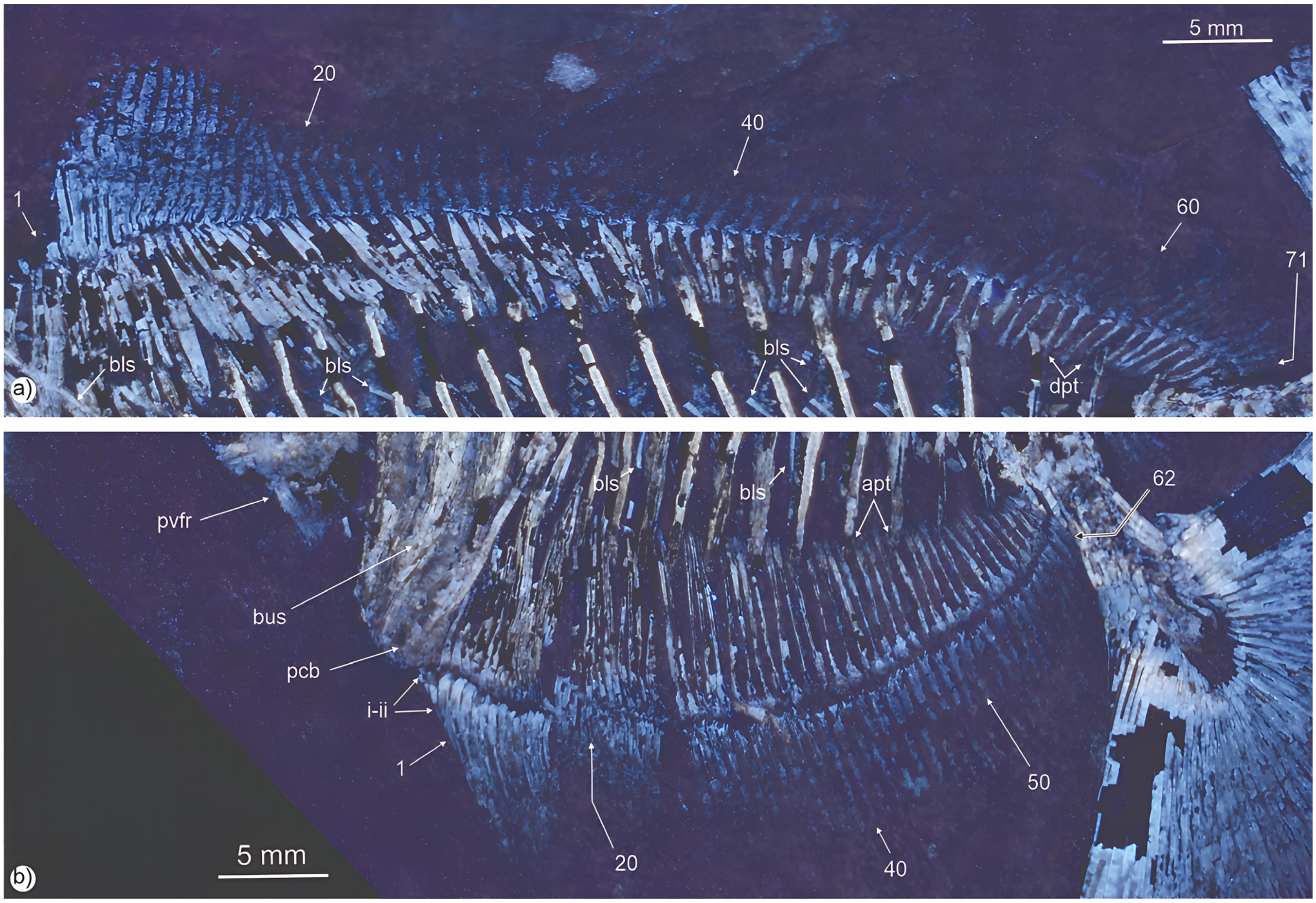

Figure 7 Unpaired fins of IGM 13950 contrasted with UV light. a) Dorsal fin. b) Anal fin. Abbreviations. apt: anal pterygiophore; bls: modified bar-like scales; bus: unmodified broad scales in the abdominal region; dpt: dosal pterygiophore; i-ii: procurrent rays in anal fin; pcb: potcoelomic bone; pvfr: pelvic fin rays; 1-71, principal rays on the dorsal (in a) and anal (in b) fins.

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ably larger eleven rays (Figure 7). The remaining dorsal rays are noticeably smaller and more evenly sized. Among dorsal fin rays, the anterior three are probably unsegmented and unbranched; the rest have distal ends evenly segmented, and at least the rays 13-70 are also distally branched. A series of 70 dorsal proximal pterygiophores support the dorsal fin; these bones are flat, evenly spaced side-by-side, harmoniously decreasing in size in the anteroposterior direction, and penetrate only the most distal part of the inter-neural spaces,

The anal fin is relatively shorter and only consists of 64 rays (Figure 7), represents 20.8 % of the SL, and extends in the posterior half of the body, between 75.9 and 96.7 % of the SL. Here, there are two procurrent rays plus 62 principal rays. These procurrent rays and the anterior four principal rays are short and precede the anal lobe, which comprises the ten subsequent 10-12 enlarged rays. The posterior anal rays become short. All anal rays are distally segmented and branched except for the procurrent rays and the anterior two principals. A series of 58 anal proximal pterygiophores support the principal anal rays. These flat and stick-like bones are evenly spaced side-by-side, harmoniously decreasing in size in the anteroposterior order, penetrating only the most distal part of the inter-hemal spaces. The postcoelomic bone supports the two procurrent rays (Figure 7).

Caudal fin. The caudal peduncle is short and shallow and involves two centra, in which the hemal and neural spines are relatively small and nearly horizontal (Figures 7 and 8). This peduncle is dorsal and ventrally enclosed by the last rays of the dorsal and anal fins.

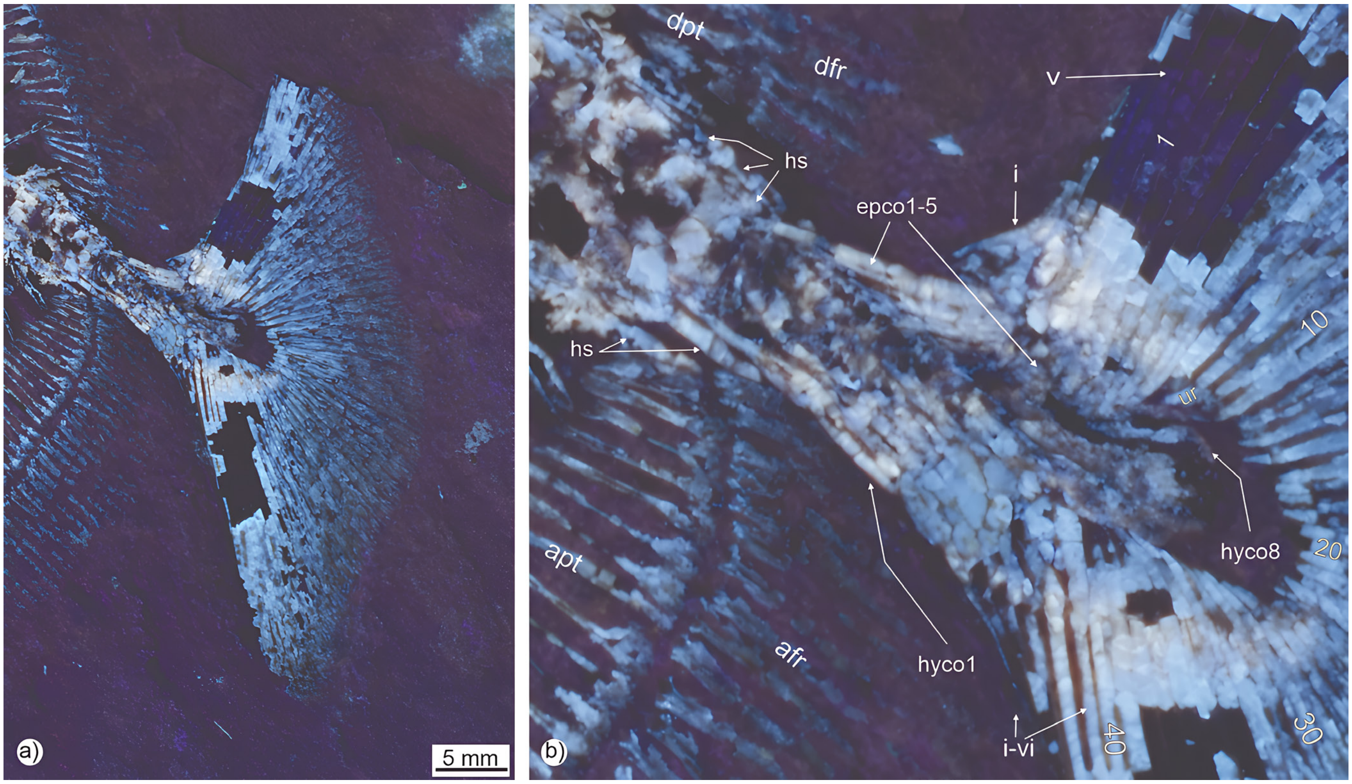

Figure 8 Caudal fin of IGM 13950. a) View under UV light. b) Close-up showing caudal skeleton and adjacent bones. Abbreviations. afe: anal fin ray; apt: anal pterygiophore; dfr: dorsal fin ray; dpt: dosal pterygiophore; epco: epicordal; hs: hemal spines; hyco: hypocordal; i-vi: procurrent rays in both dorsal and ventral caudal lobes; ns: neural spine; ur: urodermal; 1-40, principal caudal rays.

The caudal endoskeleton consists of 9 epichordal and 11 hypochordal elements, supporting the proximal ends of the caudal fin rays (Figure 8). In this series, the hypocordals 8-11 are noticeable for being paddle-shaped, triangular, and rounded posteriorly, and becoming smaller and thinner from the hypocorsal 10. Concerning the most posterior dorsal and hemal spines, the epicordal 1 and hypocordal 1 are more robust, at least twice longer, and less inclined posteriorly; subsequently, the remaining epi and hyporcordal elements are progressively shorter and thinner. At least one small comma-shaped urodermal is present. The caudal fin is vertical (= type F in Poyato-Ariza and Wenz, 2002, fig. 36) and has 54 total rays, including 43 principals plus 6 and 5 ventral and dorsal procurrent rays, respectively. The posterior edge of this fin is sinuous and has a convex protruding central part.

Scales and scutes. Scales extensively cover the abdominal and caudal regions of the trunk. The abdominal region shows about 18 rows of high, expanded ovoid scales articulated together and poorly ornamented with small and scarce tubercles (Figure 4). Most ventral abdominal scales are acicular, higher, and have sharp ends. Fourteen of these abdominal scale rows are precloacal, and four are post-cloacal. At least 21 rows of modified scales, rod-like and anterodorsally tilted, cover the predorsal and caudal regions of the trunk. In the caudal region, these scale rows extend in the region between the anal and dorsal pteryogiophores, while in the back or predorsal region, these project between the abdominal scales and the dorsal ridge scales. Three acicular scales border the cloacal vestibule, two similarly sized in the posterior edge and one elongated in the anterior one. There is no bifid cloacal scale. A series of at least 12 dorsal ridge scales border the predorsal part of the trunk, between the occiput and the dorsal fin (Figure 4). In contrast, about ten ventral keel scutes frame the abdomen, including eight precloacal and two postcloacal scutes. In both series, these triangular structures have external borders that are slightly convex, smooth, and hardly in contact.

4. Discussion

Considering the diagnostic features of the different pycnodontiform clades defined in the monographic study of Poyato-Ariza and Wenz (2002), it is possible to conclude that IGM 13950 belongs to the order Pycnodontiformes, suborder Pycnodontoidea, family Pycnodontidae, and subfamily Nursaliinae. Like other members of the order Pycnodontiformes, this fish has a skull with a hypertrophied ethmoid region, in which the mesethmoid is comparatively large (probably also T-shaped in a longitudinal section); the parasphenoid is elongated, edentulous, and inflected downwards; the opercle is small; the maxilla is edentulous and loosely attached; the vomerine and prearticular have rows of massive teeth; the dentary is small; long, stout mandibular symphysis; and modified scales named dorsal ridge and ventral keel scutes border the trunk. Besides, IGM 13950 and other members of Pycnodontoidei share the presence of large sagittal flanges only on the anterior part of the neural and haemal spines, and the body is partially nude because the scales do not cover the supporting bones (pterygiophores) of unpaired fins. As in the Pycnodontidae, IGM 13950 shows the panniculus-like process in the rear of the parietals; the maxilla is oval to reniform; the first ten or fewer anterior neural spines are autogenous; and the scales are incompletely ossified, at least in the dorsal abdominal region. And finally, as in Nursalliinae fishes, IGM 13950 exhibits the notochord partially surrounded by the expansions of the corresponding neural and haemal arcocentra; the complex to hyper-complex zigzagging contact between the adjacent neural and haemal arcocentra; the hypochordal elements of the caudal endoskeleton are enlarged or hypertrophied; and there are scales in the abdominal and caudal regions of the trunk.

Table 2 shows the valid nominal species similar to *Nursallia*, including those firstly identified as part of Nursalliinae by Poyato-Ariza and Wenz (2002, p. 216, 223-224, and fig. 43) that belong to *Nursallia* Blot, 1987; *Abdobalistum* Poyato-Ariza

Table 2. Valid nominal species resembling Nursallia, including those gathered into Nursalliinae plus *Flagellipinna rhomboides* and *Njoerdichthys dyckerhoffi* (based on Poyato-Ariza and Wenz, 2002; Amalfitano *et al*., 2020; Capasso, 2020, 2023a, b; Capasso *et al*., 2009; Taverne and Capasso, 2020; Cawley and Kriwet 2019; Cawley *et al*., 2020; and Taverne *et al*., 2015).

Species	Synonymous	Distribution
Abdobalistum thyrsus Poyato-Ariza and Wenz, 2002.	*Palaeobalistum orbiculatum* Blainville, 1818 (in part).	Ypresian, Eocene. Monte Bolca, Italy.
Flagellipinna rhomboides Cawley and Kriwet, 2019.	—	Cenomanian. Haqel, Lebanon.
Haqelpycnodus picteti Taverne and Capasso, 2018	—	Cenomanian. Haqel, Lebanon.
Njoerdichthys dyckerhoffi Cawley, Lehmann, Wiese, and Kriwet, 2020.	—	Turonian. Westphalia, Germany.
Neomesturus asflaensis Cooper and Martill, 2020	—	Turonian. Asfla, Morocco.
Nursallia veronae Blot, 1987.	—	Ypresian, Eocene. Monte Bolca, Italy.
Nursallia flabellatum (Cope, 1886).	*Pycnodus flabellatus* Cope, 1886.	Aptian-Albian, Santana Fm. Brazil.
Nursallia tethysensis, Capasso, Abi Saad, and Taverne, 2009.	—	Cenomanian. Nammoura and Hgula, Lebanon.
Nursallia fenestrata Capasso, 2023a.	—	Turonian. Akrabou Formation, Morocco.
Palaeobalistum orbiculatum Blainville, 1818.	*Palaeobalistum zignoi* Blot, 1987.	Ypresian, Eocene. Monte Bolca, Italy.
Palaeobalistum geiseri Thurmond,1974.	—	Aptian. Twin Mountain Fm., Texas, USA.
Palaeobalistum goedeli (Heckel, 1854).	*Palaeobalistum goedelii* Heckel, 1854. *Palaeobalistum ventralis* Davis, 1887.	Cenomanian, Haqel, Lebanon.
Palaeobalistum rectidens Thurmond,1974.	—	Aptian. Twin Mountain Fm., Texas, USA.
Palaeobalistum dossantosi Maury, 1930.	—	Maastrichtian. Parahyba do Norte, Brazil.
Palaeobalistum libanicum Kramberger, 1895.	—	Cenomanian, Lebanon.
Paranursallia spinosa Taverne, Layeb, Layeb-Tounsi, and Gaudant, 2015.	*Paranursallia gutturosa* (Arambourg, 1954) (in part).	Cenomanian. Jabel Bargous, Tunisia. Floresta, Italy.
Paranursallia gutturosa (Arambourg, 1954).	*Palaeobalistum gutturosum* Arambourg, 1954. *Nursallia gutturosum* (Arambourg, 1954).	Cenomanian and Turonian. Jabel Tselfat and Gara Sbaa, Morocco. Vallecillo, Mexico. Furlo and Cinto Euganeo, Italy?
Paranursallia cavani Cooper and Martill, 2020	—	Turonian. Asfla, Morocco.

and Wenz, 2002; *Palaeobalistum* Blainville, 1818; *Paranursallia* Taverne *et al.*, 2015; and *Neomesturus* Cooper and Martill, 2020. This table also includes fishes previously referred to as other suprageneric clades, such as *Flagellipinna rhomboides* Cawley and Kriwet, 2019, and *Haqelpycnodus picteti* Taverne and Capasso, 2018. Since *Njoerdichthys dyckerhoffi* Cawley *et al.*, 2020, and such *Nursallia*-like fishes share some peculiar features of Nursaliinae, Table 2 also includes it.

The osteological features of some of these *Nursallia*-group genera are distinctive. *Haqelpycnodus* has a fenestra temporalis and a relatively elongated *panniculus parietalis* with a brush-like distal end, which are absent in other members of our *Nursallia*-group (Table 2). In *Abdobalistum*, the ventral keel scutes are scutellum-shaped, and all the scales are incompletely ossified and reduced to bar scales (Poyato-Ariza and Wenz, 2002). In *Palaeobalistum*, unmodified expanded scales cover the trunk, and the ventral keel scutes have spines (Poyato-Ariza and Wenz, 2002). In *Flagellipinna*, the frontal-occipital region of the head is relatively small, the anterior head edge is anteroventrally tilted, and the ventral keel scutes and dorsal ridge scales have spines (Cawley and Kriwet, 2019, figs. 1-3, 6).

Njoerdichthys has a double emarginated caudal fin and a frontal-occipital skull region not- prominent because the orbit is in the dorsal half of the head (Cawley *et al.*, 2020, fig. 3). IGM 13950 differs from each of these genera because it has ventral keel scutes and dorsal ridge scales smooth, as well as bar-like modified scales in the predorsal and caudal regions, unmodified scales on the abdomen, a prominent frontal-occipital skull region, a vertical caudal fin, and a vertical anterior head edge. IGM 13950 differs from *Neomesturus* in the shape of teeth in the primary (dorsal) of predentary tooth row; in this Mexican fish, such teeth are large and have a medial concave cavity plus lateral edges with serrations and cusps aligned; on the contrary, in *Neomesturus* such teeth are small, rounded, and unornamented.

The comparison of IGM 13950 with *Nursallia* and *Paranursallia* is somewhat complicated because these genera are very similar. Additionally, when "*Nursallia gutturosum*" was moved to *Paranursallia*, the diagnosis of *Nursallia* was not emended. However, comparing the species of these two genera provides elements that allow the accurate taxonomical determination of IGM 13950 . Table 3 shows a list of 19 comparative features of these fishes. These features are:

1) *Nursallia fenestrata*, in which its author described a huge parietal fenestrate (Capasso, 2023a, p. 46). IGM 13950 and species of *Nursallia* and *Paranursallia*, the skull devoid of any lateral fenestra but

2) *Nursallia tethyensis* and *Paranursallia spinosa* have spines in the posterior part of the dorsal skull border that corresponds to dermosupraoccipital (Capasso *et al.*, 2009, figs, 3, 4; Taverne *et al.*, 2015, figs. 3, 4). On the contrary, the dorsal skull edge has no spines in IGM 13950 and other species of *Nursallia* and *Paranursallia*.

3) *Paranursallia gutturosa*, *P. spinosa*, and IGM 13950 show an outstanding diagnostic *Paranursallia* feature (Taverne *et al.*, 2015, p. 218), the presence of wide prefrontal bones in front of the mesethmoid. These paired bones are absent in *Nursallia* veronae and *N. tethyensis*, whereas their presence in other species of *Nursallia* and *Paranursallia* is not confirmed yet. Actually, and simply for topological reasons, the prefrontal could be hypertrophied anterior lateral wings of the mesethmoid, thickened and posteriorly widened, covering the anterolateral flanks of the large and longitudinal medial part of the mesethmoid.

4) According to its authors, in *Paranursallia spinosa*, the frontal and parietal bones are in contact (Taverne *et al.*, 2015). On the contrary, the species of *Nursallia* and others of *Paranursallia*, in which this part of the skull is well known, separate these bones.

5) Taverne *et al.* (2015, p. 224) noted that the ventral part of the head (= ventral edge of the preopercle) and the anterior edge of the cleithrum form a deep acute angle in *Paranursallia spinosa*, *P. gutturosa*, *Nursallia* veronae, and *N. tethyensis*. This

feature is also present in IGM. This angle is less acute in *N. fenestrata* (Capasso, 2023a).

6) The species of *Paranursallia* and *Nursallia* fenestrate show a triangular robust lower jaw that is relatively short and has similar height and length; on the contrary, in *Nursallia veronae* and *N. tethyensis* this jaw is longer than high (Copper and Martill, 2023; Capasso, 2023a). IGM 13950 displays the first of these conditions.

7) There are three kinds of dorsal ridge scales in the species of *Nursallia* and *Paranursallia*. As in *P. gutturosa* and *N. fenestrate*, these scales are smooth in IGM 13950; in contrast, these are scutellum-like in N. veronae and dorsally serrated in N, tethyensis and *P. spinosa* (Capasso *et al.*, , 2009; Capasso, 2023a; Taverne *et al.*, 2015).

8) The poor preservation of IGM 13950 allows us to recognize at least 12 dorsal ridge scales. These scales are eight in *Nursallia* tethyensis and *Paranursallia spinosa*, and 16 in *P. gutturosa* (Taverne *et al.*, 2015; Capasso *et al.*, 2009; Capasso, 2023a).

9) The ventral keel scutes are variable in the species of *Nursallia* and *Paranursallia*. These are scutellum-like in *N. veronae*, dorsally smooth in *P. gutturosa*, all have spines in *P. spinosa*, and in *N. tethyensis*, the anterior three have spines, and the rest are ventrally smooth (Capasso *et al.*, 2009; Capasso, 2023a; Taverne *et al.*, 2015). IGM 13950 also shows smooth ventral keel scutes.

10) As in the case of the dorsal ridge scales, the number of ventral-keel scutes in the species of *Nursallia* and *Paranursallia* are somewhat imprecisely known; however, this feature seems to be poorly variable. IGM 13950 has at least 10 of these scutes, like those counted in *Nursallia spinosa* (Capasso *et al.*, 2009) and close to the 11 recorded in *P. gutturosa* (Taverne *et al.*, 2015; Capasso *et al.*, 2009; Capasso *et al.*, 2023a).

11) The number of prearticular tooth rows is not well-known in most species of *Nursallia* and *Paranursallia*; however, as far as is known, this number is specific diagnostic. The prearticular tooth rows are six in *P. cavani*, four in *P. gutturosa*, and two in *N. tethyensis* (Capasso *et al.*, 2009; Cooper and Martill, 2020). In this case, IGM 13950 resembles *P. gutturosa*.

12) Although the number of vomerine tooth rows is not a well-known feature in the species of *Nursallia*, according to Cooper and Martill (2020), *Paranursallia gutturosa* and *P. cavani* have five of these rows, including large teeth in the laterals and medial rows and small teeth in the intermedial and somewhat discontinuous rows. The teeth of the medial row are slightly smaller than those of lateral rows in *Paranursallia gutturosa*, while in *P. cavani*, the medial teeth are noticeably the largest in the vomer. In this case, IGM 13950 resembles *P. gutturosa*.

13) In *Paranursallia gutturosa* and IGM 13950, the ventral extremity of the cleithrum is long and broad, while in the other species considered here, this structure is elongated but noticeably narrower (compare Fig. 3 in this work; Taverne *et al.* 2015, fig. 4, 9-11; and Capasso *et al.*, 2009, figs. 3-4).

14) Except for a slight overlap, the total number of anal rays in the species of *Nursallia* is overall less than in those of *Paranursallia*. According to the data collected and estimated by different authors, these rays are 24-62 in the former and 56-70 in the last. The total 64 anal rays of IGM 0001 place it into the *Paranursallia*-range.

15) Although by a slim margin, the number of dorsal rays of the species most complete of *Nursallia* and *Paranursallia* differs, from 53-67 in the former to at least 70 in the last. In this case, IGM 0001 has 71 and resembles *Paranursallia*,

16) The number of principal caudal fin rays is highly variable, between 29-43 in the species *Nursallia* and *Paranursallia*; however, in some cases, specific diagnostics (*e.g.*, *P. spinosa* has only 29). The 40 of these rays observed in IGM 0001 fall within the range observed in *Nursallia tethyensis* (38-44) and close to those reported in *P. gutturosa* (≈40) and *N. flabellatum* (40).

17) Taverne *et al.* (2015) identified the presence of a bifid cloacal scale in *Nursallia* veronae and *N. Tethuyensis*. Although it is uncertain in African specimens of *Paranursallia gutturosa*, *P. cavani*, and other species of *Nursallia*, this trait is absent in *Paranursallia tethyensis* and IGM 13950.

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Table 3. Comparison of IGM 13950 and species of *Nursallia* and *Paranursallia*.

Feature/taxa	*N. flavelatum*	*N. fenestrata*	*N. veronae*	*N. tethyensis*	*P. spinosa*	IGM 00001	*P. gutturosa*	*P. cavani*
1. Fenestra temporal	?	Yes	No					?
2. Spines in the skull dorsal edge.	?	No		Yes		No		?
3. Broad prefrontal bone	?		No		Yes			?
4. Frontal contacts the parietal	?	No	?	No	Yes	No		?
5. Cleithrum-head contact.	?	Nearly straight	Acute and deep V-shaped.					?
6. Lower jaw	?	As long as high	Longer than high		As long as high			?
7. Kind of dorsal ridge scales	?	Smooth	Scutellum-like	With spines		Smooth		?
8. Number of dorsal ridge scales	?			8		12?	16	?
9. Kind of ventral keel scutes	?		Scutellum-like	With spines	Spiny and smooth	Smooth		?
10. Number of ventral keel scutes	?			7	10	10?	11	?
11. Prearticular tooth rows	?			2	?	4		6
12. Vomerine tooth rows	?	3	3?	?		5		
13. Ventral limb of the cleithrum	?	Long and narrow.				Long and broad.		?
14. Anal fin rays (totals)	24	?	≈62?	≈52-54	≈70	64	≈54	?
15. Dorsal fin rays	53	?	≈67?	≈58-60	≈70	71	≈68	?
16. Caudal principal rays	40	?	35-36	38-44	29	40	≈40	?
17. Cloacal bifid scale	?		Yes		No		?	

As a result of the comparative exercise above, it is possible to point out that given the identification of 13 shared features (1-7, 9, and 11-14, 17 in Table 3), IGM 13950 is identified as part of the species *Paranursallia gutturosa*, previously identified and limited to Cenomanian-Turonian deposits of northwestern Africa (Taverne *et al.*, 2015; Capasso *et al.*, 2009; Capasso *et al.*, 2023b). Among these common features, five are exclusive of *Paranursallia* — the broad prefrontal bones (3), four or more prearticular tooth rows (11), five vomerine tooth rows (12), at least 70 dorsal total rays (15), and the absence of cloacal bifid scale (17) — and other three are diagnostic of *P. gutturosa* — the smooth ventral keel scutes (9), four prearticular tooth rows (11), and the vertical limb of the cleithrum long and broad (13). Unfortunately, the accurate number of elements that make up the series of dorsal ridge scales and ventral keel scutes in IGM 13950 is unknown, and the values reported are just estimated. Soon, we hope to have more pycnodont specimens from the San José de Gracia quarry to clarify these apparent inconsistencies. Concerning the other Mexican pycnodontiforms fishes, like IGM 13950, previously reported by different authors, it is noticeable that most of them come from various sites of the Turonian deposits of the Agua Nueva Formation, from the Vallecillo Quarry in Nuevo León, Huehuetla Quarry in Puebla, and Xilitla Quarry in San Luis Potosí.

Among the pycnodontiforms mentioned above of the Agua Nueva Formation, those from the Xilitla Quarry are the least studied, and there are not enough arguments to discuss their taxonomic identity. On the contrary, most specimens and reports on these fishes are from the Vallecillo Quarry; unfortunately, none of the available publications has a detailed description and identification of the generic or specific diagnostic features that support an accurate taxonomic determination. In addition, especially the latest of these reports have ignored the different nomenclatural changes in the name of the species today known as *Paranursallia gutturosa*, previously known as *Paleobalistum gutturosum* and *Nursallia gutturosum* (*e.g.*, Taverne *et al.*, 2015; Amalfitano *et al.*, 2020, p. 270; Table 2).

Thus, throughout history these fossils were recognized as "Pycnodontoidea" (Blanco-Piñón, 1998), "Nursallidae" (Blanco *et al.*, 2001), "*Nursallia*? cf. *gutturossum*" (Blanco et al,, 2001; Blanco-Piñón, 2003), "*Nursallia*" (Blanco-Piñón *et al.*, 2002), "*Nursallia* cf. *N. gutturosum*" (in Ifrim, 2006), and "*Nursallia gutturosum*" (Giersch, 2014; Stinnesbeck *et al.*, 2019). A quick review of the published images of some of the Valleciclo specimens allows us to recognize that they also belong to *Paranursallia gutturosa*. For example, the specimens FCT 195 (in Blanco-Piñon, 2003, fig. 8.5), as well as CPC 3012 and CPC 521 (in Giersch, 2014, fig. 4.30; Stinnesbeck *et al.*, 2019, fig. 5), are undoubtedly fishes of the subfamily Nursalliinae because they have rounded and prominent skulls, but they also show smooth ventral keel and a long and long broad vertical limb in the cleithrum, here identified as exclusive of *Paranursallia gutturosa*.

Otherwise, the report of *Nursallia tethysensis* in the Huehuetla Quarry is based on IGM 6618, a headless specimen exhibiting feature that supports its inclusion in *Nursallia* or *Paranursallia* (Alvarado-Ortega *et al.*, 2019, p. 4, fig. 2, Tab. 1). These features include the presence of a vertical caudal fin, modified bar-like scales in the abdominal part of the trunk, and complex zigzaging inter-arcocentra sutures. The specific identification of such specimen is based on the count of pterygiophores in the anal (70) set in the diagnosis of *Paranursallia*, including *P. gutturosa* (Taverne *et al.*, 2015, p. 2018). Given that the relation of pterygiophores and rays is 1 to 1 in members of Nursaliinae, it is possible to conclude that this diagnosis may include 70 rays instead of 70 pterygiophores. However, more recently, Capasso (2020, p. 5) redefined the number of rays in these fins based on the study of Moroccan specimens of *Paranursallia gutturosa* (see Table 3). Given these numbers, the inclusion of IGM 6618 as *N. tethyensis* loses support because the nearly 55 anal rays of this specimen are practically indistinguishable from those anal rays recorded in *N. tethyensis* as well as in *P. gutturosa*. Thus, it is possible to recognize that IGM 6618 must referred to as an indeterminate Nursallinae.

In Mexico, another single and isolated report of *Nursallia* includes an incomplete disarticulated specimen, IGM 11401, recovered from the marine Campanian deposits of the Angostura Formation exploited in the Tzimol Quarry, Chiapas, southeastern Mexico (Alvarado-Ortega *et al.*, 2020b, fig. 5). This nursalliin fish shows two peculiar features, three premaxillary teeth and a complex zigzaging inter-arcocentra suture including 7 or 8 lateral flanges in each laterally adjacent arcocentra plus 3 or 4 ventrodorsal flanges in each adjacent neural and hemal arcocentra. The first of these features is unique within the subfamily and suggests that this specimen may represent a new species. The second feature has already been observed in *Nursallia veronae* (Poyato-Ariza and Wenz, 2002, fig. 26). Based on the evidence presented here, IGM 11401 is identified as an indeterminate species of *Nursallia*. The occurrence of *Paranursallia* and *Nursallia* in the Cenomanian-Turonian of Mexico is consistent with the distribution of Nursalliinae, recently drawn by Capasso (2023b) in a taxonomical and geographical review of the group.

According to this author, these fishes had a wide distribution throughout and near the domains of the Tethys Sea, including North and South America, the Middle East, northern Africa, and Europe, from the end of the Early Cretaceous to the Eocene, with a notable diversification in the Cenomanian and Turonian. In this scenario, *Paranursallia* inhabited the western region, from Italy to Mexico, during a relatively short time between the Cenomanian and Turonian, while *Nursallia* survived longer between the Cenomanian to Eocene, in the region to the west, from Morocco to the Midwest. On the other hand, the presence of *Nursallia* sp. in the Campanian of Chiapas is evidence that this fish reached this territory in a post-Turonian biogeographic event or could be the remnant of the previous presence of the genus in Mexico. In any case, more paleontological data are necessary to understand better the evolutionary and biogeographic history of Nursallinae throughout the Americas.

5. Conclusions

This work confirms that the first and, so far, only pycnodontiform fossil recovered in the San José de Gracia Quarry, Puebla, Mexico, belongs to the subfamily Nursalliinae and the species *Paranursallia gutturosa*. The taxonomic and morphological review of the fishes today included in this subfamily allows us to recognize that different fossils recovered in sites of the Agua Nueva Formation and somehow previously referred to as *Nursallia gutturosum* represent the species *P. gutturosa*. It is possible to have other Nursalliinae species in the Agua Nueva Formation; however, here, we recommend that any new report should be supported by the conjunction of a detailed osteological study of the fossils involved, the review of the composition of the genus to which these may be attributed, and the execution of a comprehensive comparative anatomic exercise.

In this paper, we discard the report of a Mexican fossil of the species *Nursallia* tethyensis, recovered in the Turonian of the Huehuetla Quarry; it is advisable to recognize it simply as an indeterminate Nursalliinae species.

Here, we also identify a potentially new species of the genus *Nursallia* in the Campanian deposits of the Tzimol Quarry, Chiapas, whose formal description awaits the recovery of additional and better-preserved specimens.

Contributions of authors

The authors participated equally in the conceptualization, preparation, and study of the fossil described here, as well as in the graphic design and preparation of the present manuscript.

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Conflicts of interest

The authors declare no conflict of interest.

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