Miniature armored acanthomorph teleosts from the Albian/Cenomanian (Cretaceous) of Mexico

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Abstract

Small, armoured teleosts in the Albian/Cenomanian of the Muhi Quarry near Zimapán, State of Hidalgo, Mexico, are described as "monocentrid-like" (beryciforms) and acanthomorph incertae sedis. Two new genera and species, †*Handuichthys interopercularis* gen. et sp. nov. and †*Pseudomonocentris microspinosus* gen. et sp. nov., are established. The two species are distinct from the acanthomorph incertae sedis †*Dalgoichthys tropicalis* gen. et sp. nov. by having a large interopercle, differences in shape of subopercle and infraorbitals 2 and 3, and arrangement of the body shields (irregular in †*Handuichthys* and †*Pseudomonocentris*, but distributed in characteristic longitudinal rows in †*Dalgoichthys*). †*Handuichthys interopercularis* gen. et sp. nov. and †*Pseudomonocentris microspinosus* gen. et sp. nov. are placed in a new family, †Pseudomonocentrididae. Members of the family †Pseudomonocentrididae are small fishes less than 6 cm maximum length, with large head, balloon-like body, and short and narrow caudal peduncle resembling extant pinecone fishes or monocentrids. †Pseudomonocentrids have a large opercle, a small and narrow subopercle posteroventral to the opercle, and a large interopercle, which is longer than the ventral margin of the preopercle. Strong pelvic and anal spines are present, whereas dorsal spines are absent. Head bones and body shields are ornamented with tubercles and bony ridges, and the body is covered with heavily ossified, overlapping shields, which are not arranged in well-defined horizontal or vertical rows. In contrast, the body of †*Dalgoichthys* gen. nov. is covered with heavily ossified, overlapping shields ordered in rows in similar fashion as extant agonids. †*Dalgoichthys* gen. nov. presents a curious mosaic of cottiform and scorpaeniform features such as a parietal [= postparietal] bone fused with the extrascapula that makes its identification problematic; therefore, the fish is interpreted as an acanthomorph incertae sedis, an assigment that should be revised when more specimens become available.

Introduction

Fossil fishes were first discovered in the Muhi quarry (Fig. 1) near Zimapán, State of Hidalgo, Mexico in 1998; the first specimen of a new "agonid-like" teleost described here was found in 2007. The fish was first identified as a "semionotid", a primitive neopterygian, by a semionotiform expert based on photographs. Nevertheless, the fish lacks the ganoid scales of semionotids, but has overlapping bony shields arranged in well-defined rows. After realizing the uniqueness of this small fossil fish in 2009, the authors started to identify the group of teleosts to which the fish belongs, by comparing it with fossil and extant teleosts. With continuing research the authors realized that the fish is important for many reasons, e.g. the timing of occurrence and its environment. After first identification in 2009, the authors worked separately and met in Mexico several times to compare their results and to return to the locality in search of more specimens.

A second specimen of a "monocentrid-like" teleost, but a different taxon, was discovered among unprepared material in the UAHMP collection in December 2010 by Rocío BAÑOS RODRÍGUEZ during the search of material for her project on the taphonomy of specimens from the Muhi quarry. The authors, together with another student, Citlalli HERNÁNDEZ-GUERRERO, visited the quarry in January 2012 and recovered seven additional "monocentrid-like" specimens with the assistance of the quarry workers. Another additional, unprepared specimen was found in the collection and two more in the most recent
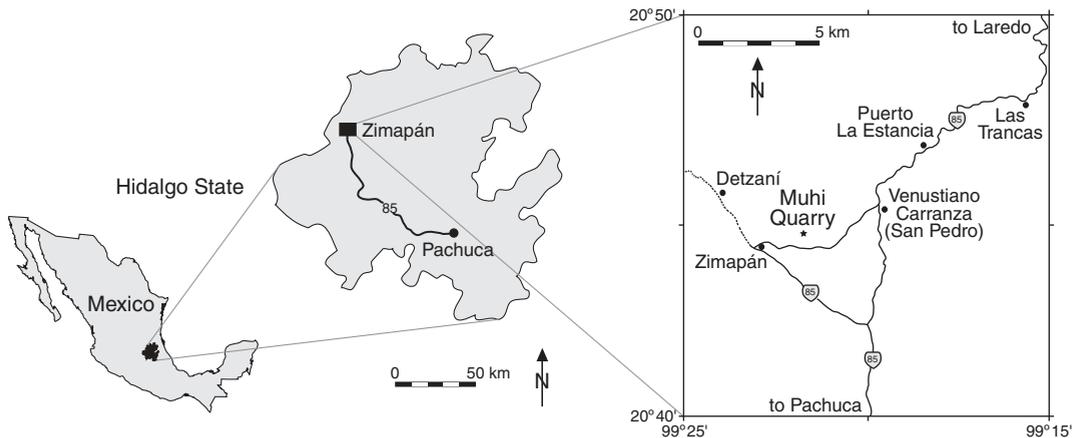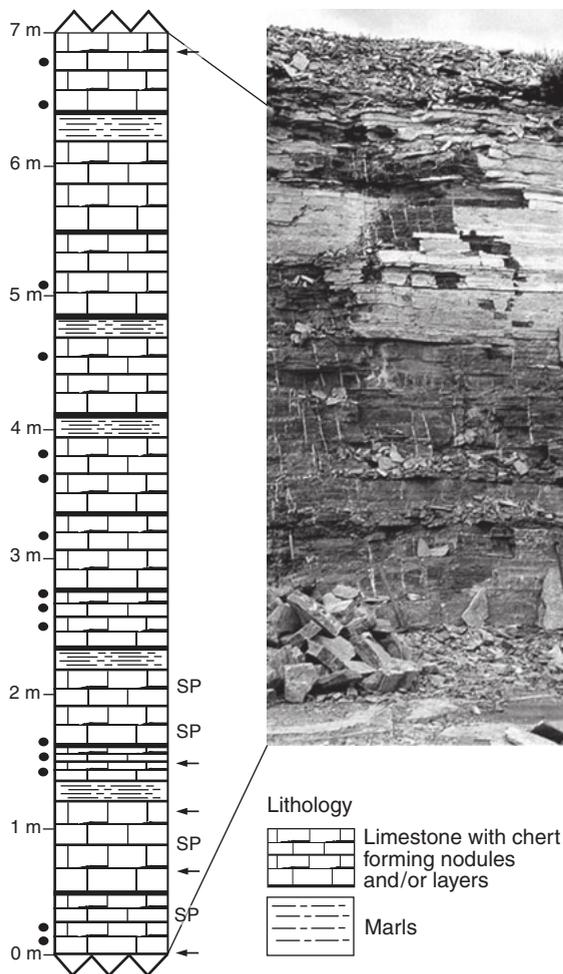
Fig. 1.
Geographic position of Muhi quarry, State of Hidalgo, Mexico.

Lithology

Limestone with chert forming nodules and/or layers

Marls

visits to the quarry. Thus one "agonid-like" and nine small "monocentrid-like" fishes have been recovered up to June 2012. Most of these specimens are described here; five small specimens, mostly impressions (UAHMP-3722, -3725, -3730, -3731, and -3732), could not be assigned with certainty to either of the two "monocentrid-like" species.

The small acanthomorphs described here are difficult to interpret since all of them preserve their body armors; therefore, postcranial characters concerning vertebral column and associated bones, as well the endoskeletal elements of the unpaired fins, cannot be observed. The three groups (two †pseudomonocentrids and one "agonid-like") cannot be assigned with certainty to any extant family. These shortcomings are discussed here since they clearly illustrate some problems that identification of fossils may have.

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Fig. 2.
Stratigraphic sequence in Muhi quarry, State of Hidalgo, Mexico. **A,** stratigraphic sequence with indications of samples taken for thin sections of rocks (dots) and of levels of fish fossils (arrows); **B,** lithofacies example from the quarry sequence. **SP**, stylolitic suture plane (BRAVO-CUEVAS et al. 2009).

Locality and its fossiliferous content

The Muhi quarry is located in the Zimapán area, in the northwest of the Mexican state of Hidalgo, between 20°40'–20°50'N Lat and 99°15'–99°25'W Long. The outcrop represents the La Negra Facies of the El Doctor Formation of Albian–Cenomanian age and consists of a sequence of gray to light gray, thin bedded biomicritic and micritic limestones and gray yellowish and white bluish, moderately indurated marls set in thin-bedded strata. The limestones frequently bear chert nodules and/or 3–10 cm thick chert bands. Scarce stylolitic suture planes are present (BRAVO-CUEVAS et al. 2009). The quarry sequence (Fig. 2) is a mudstone-biomicrite with abundant calcispheres and nannoplankton, as well as globigerinids and †*Gyroidinoides* specimens, and the black chert layers are formed by recrystallized radiolarians. The lithology and microfossil record are indicative of open shelf to deep shelf-margin environments (BRAVO-CUEVAS et al. 2009). The foraminifers *Cuneolina* sp. (Cretaceous), *Valvulammina picardi* (Albian and Late Cretaceous), ?*Orbitoides* (Late Cretaceous), *Carnuloculina* sp., *Nummoloculina heimi* (Albian–Cenomanian), *N.* sp., and *Quinqueloculina* sp. (Early Cretaceous–Recent), along with the rudist *Toucasia* sp. (Cretaceous) are recorded for the El Doctor Formation (HERNÁNDEZ-AVELINO 2008). These fossils are consistent with an Albian/Cenomanian assignment of the formation, but they do not allow a more precise age determination.

The Muhi quarry has produced more than one thousand invertebrate and vertebrate fossils. Invertebrates include foraminifers, radiolarians, planktonic crinoids (comatulids), spines of echinoderms, ammonites (†*Mortoniceras* sp.; ESQUIVEL-MACÍAS 2009), and crustaceans (†*Aeger hidalguensis* and †*Palinurus* sp.; FELDMAN et al. 2007). The ammonite genus †*Mortoniceras* occurs in the middle and upper Albian of Africa, Europe, North and South America. Vertebrates are represented by rare sharks (†*Squalicorax* sp., †*Ptychodus* sp.), and a rich, mostly undescribed actinopterygian fauna (aspidorhynchiforms, crossognathiforms [pachyrhizodontids], ichthyodectiforms, elopiforms, clupeiforms, tselfatiiforms, basal euteleosts, aulopiforms [ichthyotringids, dercetids, halecids, enchodontids], and acanthomorphs here described) and a recently collected reptile (GONZÁLEZ-RODRÍGUEZ & BRAVO-CUEVAS 2005; GONZÁLEZ-RODRÍGUEZ & FIELITZ 2005, 2008, 2009; FIELITZ & GONZÁLEZ-RODRÍGUEZ 2008, 2010; BRAVO-CUEVAS et al. 2009, 2012). The identification of the ammonite *Mortoniceras* (Albian) was verified by G. SCHWEIGERT, Stuttgart, and J. LEHMANN, Bremen.

Material and methods

The fossil specimens of the Muhi quarry were mechanically prepared using different fine needles under a stereomicroscope, but only slightly due to their delicate nature. The impression-preserved specimens of the "monocentrid-like" form were not prepared; casts were done of the latter forms with Cavex Stabisil impression material. Photographs were taken with a Nikon Coolpix P4 digital camera and drawings were made using Wild M5A and Leica MZ6 stereomicroscopes, both with camera lucida attachment. The catalogue numbers of the fossil specimens are presented in the descriptive sections of each form.

A broad survey of fossil and extant teleosts with modified scales and body shields, as well as a broad survey of the literature concerning possible related groups of fishes, was conducted. However, only the material that is relevant to the assignments given here is listed below. The material includes one fossil taxon and a number of extant taxa represented by specimens (sp.) preserved in alcohol (alc), and specimens cleared and stained (c&s) for both cartilage and bone, and dry skeletons.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, New York, USA; **FMNH**, Field Museum of Natural History, Department of Ichthyology, Chicago, Illinois, USA; **KUNHM**, Division of Ichthyology, Natural History Museum, The University of Kansas, Lawrence, Kansas, USA; **KUVP**, Division of Vertebrate Paleontology, Natural History Museum, The University of Kansas, Lawrence, Kansas, USA; **SIO**, Scripps Institution of Oceanography, University of California San Diego, USA; **UAHMP**, Museo de Paleontología Universidad Autónoma del Estado de Hidalgo, Pachuca, State of Hidalgo, Mexico; **USNM**, United States National Museum, Smithsonian Institution, Washington, D.C., USA.

Material used in comparisons

Basal teleosts

Order †Crossognathiformes
    †Crossognathidae
        †*Apsopelix anglicus*: KUVP 309 (fossil: holotype of †*Leptolepis agilis*)

Acanthomorphata
    Division Berycacea
        Order Beryciformes
            Monocentrididae
                Cleidopus gloriamaris: AMNH 0961338D, about 44.24 SL (dry skeleton, partially dissected).
                Monocentris japonica: AMNH 2141538D (dry skeleton, shields in position), USNM 307587, 54.82 mm SL (1 c&s sp.) and 3 alcohol specimens of 94.43, 73.55 and 79.14 mm SL.
                Monocentris reedi: FMNH 107283, 76.52 and 83.10 mm SL (2 sp.).
            Trachichthyidae
                Gephyroberyx darwini: FMNH 67021, 107 mm SL (1 c&s sp.).
            Holocentridae
                Holocentrus diadema: FMNH 44130 (3 c&s sp.).

Division Percomorphacea
    Order Dactylopteriformes
        Dactylopteridae
            Dactylopterus volitans: FMNH 46612, 91 mm SL (1 c&s sp.).

Order Cottiformes
    Suborder Cottoidei
        Agonidae
            Agoninae
                Podothecus acipenserinus: KUNHM 18126 (3 c&s sp.).
                Agonopsis vulsa: KUNHM 10016, 73–128 mm SL (3 c&s sp.).
            Anaplagoninae
                Xenertmus latifrons: KUNHM 12975, 108–128 mm SL (4 c&s sp.). *Bathyagonus pentacanthus*: KUNHM 28256 (2 alc. sp.).
            Percininae
                Hypsagonus quadricornis: KUNHM 10012 (3 alc sp.); KUNHM 27943 (1 alc sp.); KUNHM 28207 (1 c&s sp.).
        Cottidae
            Cottus bairdi: KUNHM 15228, 22.5, 25.1, 26.3, 26.5 and 37 mm SL (5 c&s sp.).
            Icelus spiniger: USNM 208352, 75 mm SL (1 c&s sp.).
        Rhamphocottidae
            Rhamphocottus richardsoni: SIO uncat., 67 mm SL (1 c&s sp.).

Order Scorpaeniformes
    Suborder Scorpaenoidei
        Aploactinidae
            Erisphex potti: SIO 80-214, 72 mm SL (1 c&s sp.).
        Scorpaenidae
            Setarches guentheri: FMNH 73380, 112.2 mm and 113 mm SL (2 c&s sp.).
    Suborder Platycephaloidei
        Peristediidae
            Peristedion mihimum: FMNH 66548, 137 mm SL (1 c&s sp.).
    Suborder Normanichthyoidei
        Normanichthyidae
            Normanichthys crockeri: SIO 01-78, 64 mm SL (1 c&s sp.).

Order Tetraodontiformes
    Suborder Balistoidei
        Balistidae
            Balistes caprisus: FMNH 113474, 66.7 mm SL (1 c&s sp.).
            Canthidermis sufflamen: KUNHM uncat. (Teaching collection), 51 mm SL (1 c&s sp.).

Monacanthidae
    Aluterus scriptus: KUNHM 30391, 24 mm, 28.5 mm, 29 mm, and 86 mm SL (4 c&s sp.).
Suborder Tetraodontoidei
  Tetraodontidae
    Arothron hispidus: FMNH 47879, 49 mm and 52 mm SL (2 c&s sp.).
    Tetraodon fluviatilis: KUNHM 23539, 51 mm SL (1 c&s sp.).
  Diodontidae
    Diodon holacanthus: AMNH 45083, 73 mm SL (1 c&s sp.).
  Molidae
    Masturus lanceolatus: SIO 8-128, 2 disarticulated c&s specimens.

Terminology

Skull roof bones. We use here the traditional terminology for skull roof bones and give in brackets the correct homology for actinopterygians, e.g., frontal bone [= parietal] and parietal bone [= postparietal] (see SCHULTZE 2008 for discussion), in text as well as in illustrations.

The bone named tabular by KANAYAMA (1991: 156, figs. 76A, 77A, 81A,B,H,J, 82A; table 15) and described as attached to the pterosphenoid anteriorly and parietal [= postparietal] is identified here as the lateral extrascapula by comparison to other teleosts. According to IMAMURA & YABE (2002) the parietal bone [= postparietal] including a sensory canal is not homologous for scorpaeniforms and cottiforms; and the presence or absence of spines associated with the extrascapular canal (supratemporal commissure) is used to justify such interpretation. However the presence of the canal indicates an early fusion of the parietal [= postparietal] with the medial extrascapular bone, a condition seen in other unrelated teleostean lineages (e.g., Clupeiformes). The fusion is a condition found in scorpaeniforms and cottiforms. The difference lies in the dermal cover of the extrascapular canal (supratemporal commissure) that may involve spines (in scorpaeniforms) or not (in cottiforms).

Extrascapular bones may involve one or more elements on each side in teleosts; the most lateral one lies usually just posterior to the pterotic and is the bone where otic, extrascapular canals (supratemporal commissure) and main lateral line join. The medial extrascapula may extend above the parietal [= postparietal] or parietal and epiotic. The medial extrascapula bears the extrascapular canal (supratemporal commissure), which has been called "parietal canal" in some percomorphs (e.g., WILEY & JOHNSON 2010) or simple "sensory canal" by IMAMURA & YABE (2002). One or more lateral extrascapulae may be present in cottiforms and in agonids, for instance in some members of the subfamily Percininae *(Hypsagonus*, *Percis)*, Agoninae *(Agonopsis)* and Anoplagoninae *(Bathyagonus*, *Xenertmus*, *Odontopyxis)*, and apparently in all Brachyopeinae. The scorpaeniform/cottiform synapomorphy involves a fusion of the parietal [= postparietal] and the medial extrascapular bones.

Circumorbital series. The circumorbital series of basal teleosts commonly includes supraorbital(s) dorsally, antorbital antero-dorsally, five or six infraorbitals ventrally and postero-dorsally, and the dermosphenotic (or dorsal-most element of the postero-dorsal infraorbitals where the junction of supra- and infraorbital and otic canals may occur) (ARRATIA 1984, 1997). The first infraorbital represents the lacrimal. The third infraorbital borders the postero-ventral corner of the orbit. The posterior border of the orbit may be formed by infraorbital 4, 5 and 6, or 4 and 5, or a fusion of elements may occur in different teleostean groups. Beryciforms have a complete series of infraorbital bones (lacrimal plus four infraorbitals) in most cases.

Scorpaeniforms have in common infraorbitals 1 to 3, but the postero-dorsal infraorbitals vary in number and appearance. Five to six infraorbitals may be present in cottiforms (e.g., YABE 1985: figs. 3, 4), whereas only four infraorbital bones are found in agonids (KANAYAMA (1991: figs. 55, 56). According to KANAYAMA (1991) agonids have only a lacrimal [= infraorbital 1], and three infraorbitals [= four independent infraorbital bones herein]. Within modern agonids, only one infraorbital follows dorsal to the third one. This bone can be ossicle-like (e.g., *Hypsagonus*, *Percis*; KANAYAMA 1991: fig. 55A–D; pers. observ.) or a more enlarged bone (e.g., *Leptagonus*, *Xenertmus*; KANAYAMA 1991: fig. 56A,C; pers. observ.). We use here the terminology "infraorbital 4/5" in the acanthomorph incerta sedis described herein to indicate that we don't know if this last infraorbital is homologous to infraorbital 4 or 5 or to 4, 5 or 6 in cottiforms and scorpaeniforms, or if it represents a fusion of elements. In contrast, the dorsal-most posterior element was interpreted as infraorbital 5 in agonids [= infraorbital 4/5] by KANAYAMA (1991: 125), a questionable homology based only on position of elements.

An independent dermosphenotic is the plesiomorphic condition in teleosts; however, the bone can be fused with the underlying autosphenotic (e.g., in the fossil †pseudomonocentrids here described and in certain genera of the trachichthyoid Diretmidae; ZEHREN 1979, KOTLYAR 1990), or the bone may be absent (e.g., Monocentrididae). According to our observations and based also on published illustrations, cottoids and agonids do not have a dermosphenotic. In extant agonids that we examined, the junction of the three canals is not bone-enclosed, but occurs just at the point where the autosphenotic, frontal [= parietal], and pterotic bones meet.
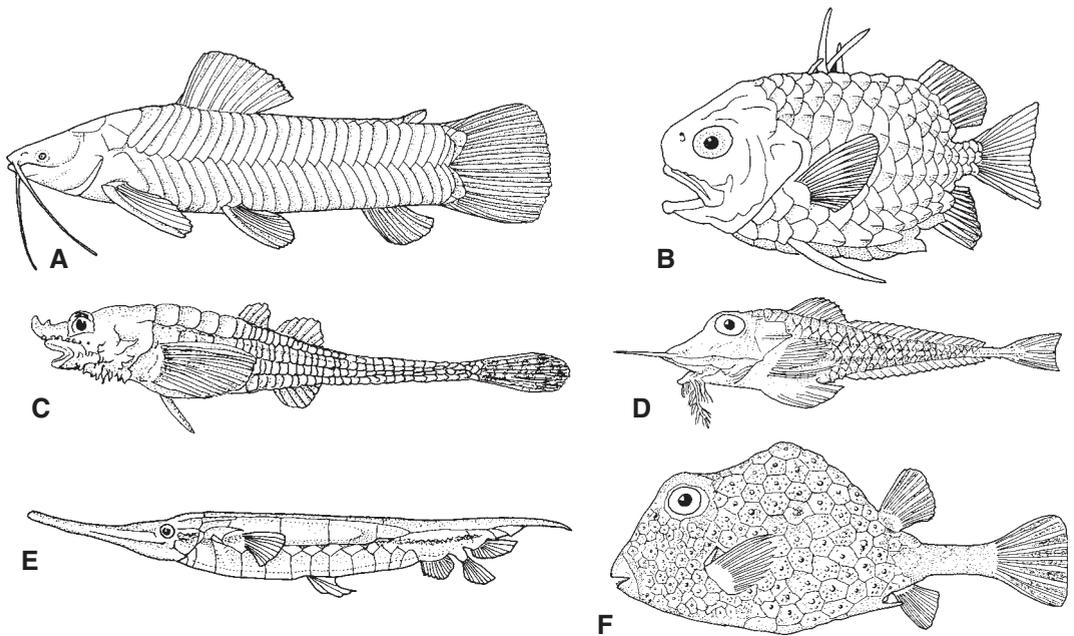
Fig. 3.
Semidiagrammatic illustrations of armored teleosts with skin ossifications as overlapping shields: **A**, Siluriformes, Callichthyidae: *Hoplosternum littorale*; **B**, Beryciformes, Monocentrididae: *Monocentris japonicus*; **C**, Cottiformes, Agonidae: *Agonus cataphractus*; **D**, Scorpaeniformes, Triglidae: *Peristidion longispatha*. Armored teleosts with skin ossifications as plates: **E**, Gasterosteiformes, Centriscidae: *Aeoliscus strigatus*; **F**, Tetraodontiformes, Otraciidae: *Lactophrys trigonus*.

Bony shields, plates, and spines. The acanthomorph taxa dealt with herein have strong skin ossifications or bony shields and plates. These ossifications (shields) overlap each other like scales in armored siluriforms and agonids, whereas they (plates) are sutured in armored tetraodontiforms (HERTWIG 1876, 1882; RAUTHER 1929). Shields and plates form first as small units, scales or scale-like structures.

We deal here with small armored teleosts. The body is fully covered by massive dermal ossifications, not with scales or developing ossifications, indicating an adult or at least subadult stage (see below, description of fossils). The ossifications are different in these three fossil taxa from those of tetraodontiforms. The tetraodontiforms have a firm armor of hexagonal plates (Fig. 3F), whereas the ossifications overlap each other in the three taxa from Muhi quarry. There is no clear definition for these ossifications available in extant teleosts. The terms, scutes, plates and shields and even tesserae are used interchangeably. RAUTHER (1929) and FRANCILLON-VIEILLOT et al. (1990) gave a comprehensive presentation of dermal structures in fishes. The replacement of cycloid or ctenoid scales by dermal ossifications occurred independently in different taxa of teleosts. The dermal ossifications are new formations. They do not show any similarity to cycloid scales in their development. Naked forms occur in closely related taxa.

Systematic distribution of armored teleosts (Fig. 3). The distribution of shields and plates in fossil and extant teleosts is presented below following the classification proposed by WILEY & JOHNSON (2010). According to their distribution, armored teleosts are rare and their shields or plates are not homologous, e.g., the shields of catfishes versus shields of beryciform monocentrids (see below).

Basal teleosts
        Order †Crossognathiformes
            †Crossognathidae (fossil): **shields**, †*Apsopelix*
Cohort Otomorpha
  Subcohort Ostariophysi
    Section Otophysa
      Order Siluriformes
        Doradidae: one row of deep epaxial lateral **shields**, many genera, but not in *Liosomadoras*
        Loricariidae: **shields**, *Loricaria* and other genera in six subfamilies
        Callichthyidae: two rows of overlapping deep **shields**, *Hoplosternum* (Fig. 3A) and eight genera
          in two subfamilies
Cohort Euteleosteomorpha
  Subcohort Neoteleostei
    Infracohort Eurypterygia
      Section Ctenosquamata
        Subsection Acanthomorphata
          Division Berycacea
            Order Beryciformes
              Monocentrididae: platelike scales (= overlapping **shields**), *Monocentris* (Figs. 3B, 4), *Cleidopus*
          Division Percomorphacea
            Series Smegmamorpharia incertae sedis
            Order Gasterosteiformes: **plates**
              Suborder Gasterosteoidei: **plates** (Fig. 3E) covering part of body
                Gasterosteidae (sticklebacks): *Gasterosteus* (one row of plates)
                Indostomidae (armored sticklebacks): *Indostomus*
              Suborder Syngnathoidei: **plates** enclosing the whole body, except Aulostomidae *(Aulostomus)*
              Pegasidae: *Pegasus*
              Syngnathidae: *Syngnathus* and other genera, *Hippocampus*
              Solenostomidae: *Solenostomus*
              Fistulariidae: *Fistularia*
              Macroramphosidae: *Centriscops*, *Macroramphus*, *Notogon*
              Centriscidae: *Aeoliscus* (Fig. 3E), *Centriscus*
         Percomorphacea incertae sedis
          Order Cottiformes
            Agonidae: overlapping **shields** (Figs. 3C, 5A,B), many genera in six subfamilies
          Order Dactylopteriformes
            Dactylopteridae: scute-like scales = shields, *Dactylopterus*, *Dactyloptena*
          Order Scorpaeniformes
            Suborder Scorpaenidae
              Triglidae
                Subfamily Peristediinae: heavy spine-bearing **plates** (Fig. 3D), *Peristidion* and three genera
          Order Tetraodontiformes: shields with spines or **plates**
            Balistidae: *Balistes* and ten genera with overlapping plate-like scales = shields
            Monacanthidae: ossifications with spines
            Triacanthidae: ossifications with spines
            Ostraciidae: *Caprichthys*, *Lactophrys*, *Ostracion* and other genera with body encased in **plates**
            Diodontidae: isolated plates with spines, *Diodon* and five genera

RAUTHER (1929) described the ossifications in agonids as shields (p. 253: "Knochenschilder") and in tetraodontiforms as plates (p. 249: "Panzer aus hexagonalen, dicht aneinanderschließenden verkalkten Platten"). FRANCILLON-VIEILLOT et al. (1990: 486) used the general term "scutes" (= bony plates, transformed scales). TYLER & SORBINI (1996) used the term "plates" for the skin ossification in tetraodontiforms as RAUTHER (1929) did. We follow here RAUTHER (1929), who distinguished shields, as overlapping ossifications, from plates or ossifications, which border each other by straight or digitating sutures.

    Overlapping shields occur in the members of three siluriform families (Doradidae, Loricariidae, Callichthyidae). Different overlapping shields occur in the crossognathiform †*Apsopelix* and the beryciform Monocentrididae (Figs. 3B, 4A), the Peristediidae within the Scorpaeniformes (Fig. 3D), and the cottiform Agonidae (Fig. 3C). The two modern genera of Monocentrididae have shields scarcely overlapping, so that it appears in dried specimens as if plates suturing to each other are present, but this is an artifact of preparation in the illustrated specimen

Fig. 4.
Lateral view of a dried specimen of the monocentrid *Monocentris japonica* (AMNH 2141538D). **A,** distribution of bony shields on the body. **B,** enlargement of head bones illustrating fine ridges covered with minuscule spines (arrowed). Abbreviation: **ll,** bony shields carrying the lateral line canal.

Fig. 5.

Agonid *Hypsagonus quadricornis* (KUNHM 28207). **A,** mid flank body shields. **B,** spiny plates on the dorsal fin rays. The open region on the sphenotic where the supraorbital, infraorbital and otic canals join each other is indicated by a small black arrow. **C,** additional bone dorsal to the preopercle. Abbreviations: **abp**, spine-like bony plate; **DLR**, dorso-lateral row of shields; **ILR**, infralateral row of shields; **Io4/5**, infraobital 4/5; **LLR**, lateral line row of shields; **SLR**, supralateral row of shields; **VLR**, ventro-lateral row of shields.

(see Fig. 3). In contrast, the shields overlap clearly in agonids and are ordered in rows as they are in the crosso-gnathiform †*Apsopelix* and peristediids.

Plates are typical for Gasterosteiformes (e.g., Fig. 3E; Gasterosteidae, Syngnathidae, Solenostomidae, Fistu-lariidae, Centriscidae), and for families (e.g., Ostraciidae) within Tetraodontiformes (Fig. 3F).

The small fossil teleosts from the Muhi quarry can only be compared with armored acanthomorphs; there is no similarity to armored siluriforms. Strong skin ossifications in the form of shields are presented in the fossils. The fossil specimens with shields fall in two taxonomic groups. (1) We compare the one group including most of the small teleosts with the pinecone fishes, Monocentrididae, because of the body shape (deep body followed by a short low caudal peduncle) and the irregularity of the shields, which become more scale-like towards the caudal peduncle. In recent monocentrids, the shields (Fig. 4B) slightly overlap each other and they are arranged in irregular rows and not in well-defined longitudinal rows, with the exception of the row carrying the lateral line canal. (2) In contrast, we compare the shields broadly overlapping each other and arranged in well-defined longitudinal rows in the one specimen of †*Dalgoichthys tropicalis* sp. nov. with the shields in modern agonids (additional similarities in the head) (see below).

Additional shields. Comparing the fossils described here with extant monocentrids and agonids, we discovered additional shields not described by KANAYAMA (1991) for agonids. Some of these occur in the here described fossils also. There is an extra bony plate dorsal to the preopercle (Fig. 5C: abp) just in front of the dorsal of the opercle in some agonids such as *Hypsagonus quadricornis*, and also in monocentrids (e.g., *Monocentris japonica*). This opercular plate does not carry the preopercular canal, so that it cannot be considered as a suprapreopercle. However, a plate carrying the preopercular canal is found in scorpaeniforms such as the peristediid *Peristedion mihimum*, in the same position as the so-called suprapreopercle in other teleosts where the bone occurs. Additionally, small spine-like bony plates may lie on the lateral surface of the opercular bones. These plates are identified here as additional opercular plates in *Hypsagonus* as well as in the fossil described here (see below).

Additional bony plates are placed between infraorbital 3 and the preopercle in *Monocentris japonica* so that no space is left between bones (Fig. 4A).

Minuscule spine-like bony plates develop on the external surfaces of the dorsal and pectoral fin-rays in *Hypsagonus* (Fig. 5B). Fin-ray plates are unknown in the pectoral and dorsal fins of the fossils due to condition of preservation (see below). They should not be confused with the spine or spiny processes on the bony shields or cranial bones. The minuscule spine-like bony plates are attached to the surface of the bones; nevertheless they are not part of the bone itself. We identified these plates as spiny fin-ray plates.

Two bones, here named postcleithro-pectoral plates, are present in both fossil species, the "monocentrid-like" and the "agonid-like". They occur in front of the pectoral fin just posterior to the posterior margin of the cleithrum. Such bones are not known from extant agonids, other cottiforms, or scorpaeniforms in general. They exhibit ridges and tuberculation similar to that of skull bones or body shields (see below).

Both "monocentrid-like" and the "agonid-like" forms dealt with here have strong skin ossifications or bony shields. These ossifications (shields) overlap each other as do scales in monocentrids and agonids, whereas the plates of tetraodontiforms are sutured to each other.

Systematic paleontology

Infraclass Teleostei MÜLLER, 1845
Subsection Acanthomorphata ROSEN, 1973
Division Berycacea WILEY & JOHNSON, 2010
Order Beryciformes GÜNTHER, 1880

†Pseudomonocentrididae new family

Diagnosis (based on a unique combination of characters)**.** Small fishes about 50 mm maximum length, with peculiarly shaped, balloon-like body ending in a markedly narrow peduncle. Head large, about 30 % in SL. Ossified sclerotic bones absent. Supramaxillary bone absent. Ornamented dermosphenotic fused with the underlying autosphenotic (sphenotic). Very large opercular bone sutured with a small, narrow subopercle positioned postero-ventral to the opercle. Large interopercle, even longer than ventral margin of the preopercle. Pectoral fin inserted in middle region of the flank. Pelvic fin inserted anteriorly, just below or anterior to pectoral fin insertion. Pelvic fin with a strong spine ornamented with longitudinal ridges and/or small spines. Dorsal spine(s) absent. Anal fin with a strong spine ornamented with longitudinal ridges, and almost as long as pelvic spine. Head bones and body shields ornamented with tubercles and

bony ridges. Body covered by overlapping, strong, heavily ossified shields, not arranged in well-defined horizontal or vertical rows.

Content: Two genera, †*Handuichthys* gen. nov. and †*Pseudomonocentris* gen. nov.

†*Handuichthys* gen. nov.

Diagnosis. "Monocentrid-like" teleost with gentle, slightly rounded profile. Large, round orbit present. Infraorbital 2 the largest infraorbital, partially occupying the position of infraorbital 2 and 3 in other teleosts. Dorsalmost infraorbital 4/5 somewhat rectangular ventrally and expanded postero-dorsally. Pre-opercular and infraorbital canals meeting on infraorbital 4/5. Large, narrow opercle ending in a smooth tip ventrally, and producing a markedly oblique suture with a subopercle. Narrow subopercle contained about 8 times in opercle depth. Long and expanded interopercle, even longer than ventral arm of pre-opercle and reaching cleithrum posteriorly.

Type species: †*Handuichthys interopercularis* gen. et sp. nov.

Etymology. The generic name refers to the Otomí (a native Mexican language) name "handu" meaning fossil, combined with "ichthys" (Greek) meaning fish.

†*Handuichthys interopercularis* gen. et sp. nov.
(Figs. 6A,B, 7, 8, 9)

Holotype: UAHMP-1389 (Fig. 6A) is represented by head and anterior body; the preserved length is 25 mm.

Paratype: UAHMP-690 (about 44.24 mm SL) is a nearly complete specimen (Fig. 7), missing anterior most tip of the snout and the soft fin rays that seem to be very thin as illustrated by two incompletely preserved pectoral rays; the dorsal, anal and caudal fin rays are missing.

Additional specimens: UAHMP-3736, head and anterior part of body. The heavily ornamented surfaces of both the head bones and body shields are weathered away. ?UAHMP-3731, visible as a "ghost" behind a covering of limestone.

Diagnosis: As for genus.

Etymology: The species name refers to the large interopercle, the most outstanding element of the opercular series of the species.

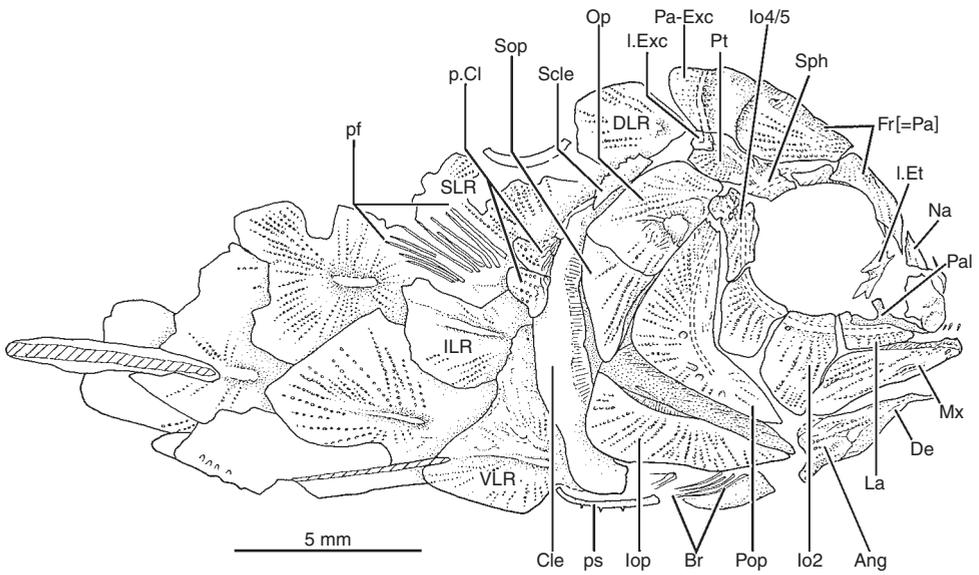**Locality:** Muhi quarry, Zimapán, State of Hidalgo, Mexico.

Age: El Doctor Formation, Albian/Cenomanian, Cretaceous.

Description

General features. The holotype specimen is not complete; head and shields of the anterior ventral body are preserved (Fig. 6A,B). The posterior part of the body including dorsal, anal and caudal fins is missing. It is characterized by a large, round orbit, which occupies about 32 % of the length of the head. The paratype specimen is preserved on its left side. It has an almost ovoid body tapering into a reduced caudal peduncle and an apparently small caudal fin. The small specimen is about 44 mm SL. The head is large, about 33 % of SL. The deepest region of the head is at its posterior margin. The narrow caudal peduncle is about 80 % of SL and about 18 % in the maximum depth of the body (close to the level of the insertion of the anal fin). According to its imprint, the pelvic spine (about 9 mm length) is slightly longer than the anal spine (about 7.4 mm length). The pelvic fin has an anterior insertion, slightly anterior to the pectoral fin. The anal fin is positioned posterior to the mid-point of the SL, closer to the pelvic spine than to the caudal fin. The skull bones and the bony shields on the body are ornamented with tubercles and tiny crests arranged in radiating ridges; they are denser on the shields than on the cranial bones in general. The surface of some bones as well as of some shields is weathered away.
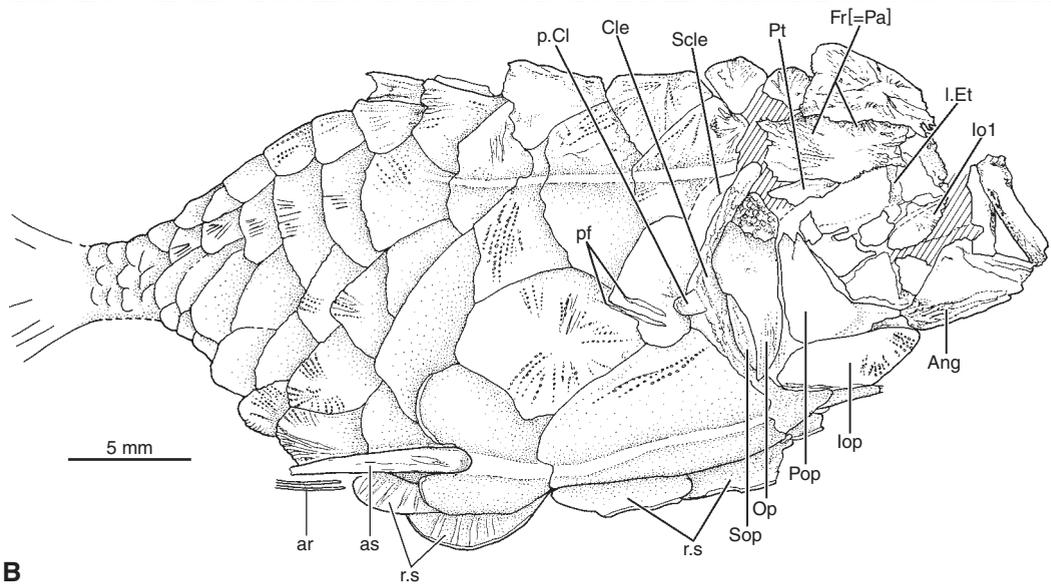
Fig. 6.

†*Handuichthys interopercularis* gen. et sp. nov. in lateral view (UAHMP-1389, holotype). El Doctor Formation, Albian/Cenomanian, Cretaceous; Muhi quarry, Zimapán, State of Hidalgo, Mexico. **A,** photograph; **B,** drawing. Abbreviations: **Ang**, angular; **Br**, branchiostegal rays; **Cle**, cleithrum; **De**, dentary; **DLR**, dorso-lateral row of shields; **Fr[=Pa]**, frontal [= parietal] bone; **ILR**, infralateral row of shields; **Io2, 3, 4/5**, infraobital 2, 3, 4/5; **Iop**, interopercle; **La**, lacrimal or infraorbital 1; **l.Et**, lateral ethmoid; **l.Exc**, lateral extrascapula; **Mx**, maxilla; **Na**, nasal bone; **Op**, opercle; **Pa-Exc**, parieto-extrascapula; **Pal**, palatine; **p.Cl**, postcleithro-pectoral plates; **pf**, pectoral rays; **ps**, broken pelvic spine; **Pop**, preopercle; **Pt**, pterotic; **Scle**, supracleithrum; **Sop**, subopercle; **Sph**, sphenotic; **SLR**, supralateral row of shields; **VLR**, ventro-lateral row of shields.

Fig 7.

†*Handuichthys interopercularis* gen. et sp. nov. in lateral view (UAHMP-690, paratype). El Doctor Formation, Albian/Cenomanian, Cretaceous; Muhi quarry, Zimapán, State of Hidalgo, Mexico. **A,** photograph; **B,** drawing. Abbreviations: **Ang**, angular; **ar**, anal rays; **as**, anal spine; **Cle**, cleithrum; **Fr[=Pa]**, frontal bone [= parietal]; **Iop**, interopercle; **l.Et**, lateral ethmoid; **Op**, opercle; **p.Cl**, postcleithro-pectoral plate; **pf**, pectoral fin; **Pop**, propercle; **Pt**, pterotic; **Scle**, supracleithrum; **Sop**, subopercle; **r.s**, shields of the right side preserved in medial view.

Skull roof. A large and long frontal [= parietal] bone (Fig. 6A,B), broken in three pieces, lies in front of the parieto-extrascapula; it forms most of the skull roof in the holotype. The bone is expanded posteriorly, narrows considerably at the level of the orbit, and curves down anteriorly. The bone bears sharp, spiny processes (Fig. 6B) laterally and anteriorly at its anterior end. Both frontal [= parietal] bones are displaced in the paratype (Fig. 7), and broken anteriorly; however, their size indicates that the skull roof may be very broad. The orbital margin of the frontal [= parietal] bone is finely serrated.

The frontal bone [= parietal] in the holotype sutures with the sphenotic at the posterior corner of the orbit, postero-laterally with the pterotic, and posteriorly with the parieto-extrascapula. The sphenotic (a fusion between the dermosphenotic and the underlying autosphenotic) forms the postero-lateral corner of the orbit.

The junction of the otic canal with the single canal resulting from the confluence of both the infraorbital and preopercular canals occurs in the sphenotic (Fig. 8). The lateral ethmoid is placed antero-ventral to the frontal bone [= parietal]. The lateral ethmoid of the holotype presents a sharp, spine-like lateral process about its mid-length and another sharp process distally. Anterior to the frontal bone [= parietal], the nasal bone is broken in the holotype, and the region is not preserved in the paratype. Its dorsal margin is composed of a few serrations, and an anterior spine-like projection is associated to the nasal bone. The nasal bone, as preserved in specimen UAHMP-3736, is triangular and has a large, round opening anteriorly.

A broad, rectangular pterotic sutures anteriorly with the sphenotic, antero-medially with the frontal bone [= parietal] and postero-medially

Fig. 8.

†*Handuichthys interopercularis* gen. et sp. nov. (UAHMP-1389, holotype). Enlargement of the opercle and dorsal most infraorbitals illustrating the join of the preopercular and infraorbital canals (indicated by an arrow). El Doctor Formation, Albian/Cenomanian, Cretaceous; Muhi quarry, Zimapán, State of Hidalgo, Mexico. Abbreviations: **abp**, additional bony plate; **Io3, 4/5**, infraorbital bones 3 and 4/5; **Op**, opercle; **Pop**, preopercle; **Sop**, subopercle; **Sph**, sphenotic.

with the parieto-extrascapula. It bears a spiny process in the holotype. It is unclear whether more spiny processes were present and could have been lost either during preparation or due to weathering of the bony surfaces. The broad parieto-extrascapula forms the posterior part of the skull roof. The extrascapular commissure runs closer to the posterior margin of the bone than to the anterior margin; it is just placed posterior to a small crest on the bone surface.

A section of the supraorbital canal runs close to the orbital margin of the frontal bone [= parietal] in the holotype. Evidence of the trajectory of the supraorbital canal has not been observed in other specimens, possibly due to the ornamentation of the skull roof bones. Neither a parietal branch of the supraorbital canal nor any other sensory tubule is observed. The otic canal, as well as other cephalic sensory canals, runs in a narrow tube that is exposed as a groove in places where the external surface of the bone is damaged.

Circumorbital bones. The circumorbital series (Figs. 6, 8) is incomplete antero-dorsally. Apparently, an antorbital is not present because the bone or its remnants have not been observed. There are four independent infraorbital bones. The lacrimal (or infraorbital 1) is a narrow, slightly rectangular bone, which carries the anterior part of the infraorbital canal. An elongated chondral bone with a dorsal process appears medial to the lacrimal. It may be the autopalatine.

The second infraorbital bone is the largest and deepest infraorbital and extends ventrally between infraorbital 3 and the maxilla. It reaches with its lower triangular portion to the anterior end of the preopercle and the most posterior tip of the maxilla. This bone occupies, partially, the position of infraorbitals 2 and 3 in other teleosts. Due to conditions of preservation it is not possible to observe the medial side of the bone to check if a shelf was present or not. The infraorbital sensory canal runs close to the orbital margin of the bone.

Infraorbital 3 is rhomboidal, and the second largest bone of the series. Its posterior margin slightly overlaps the anterior margin of the preopercle. It bears one sensory canal pore close to the orbital margin.
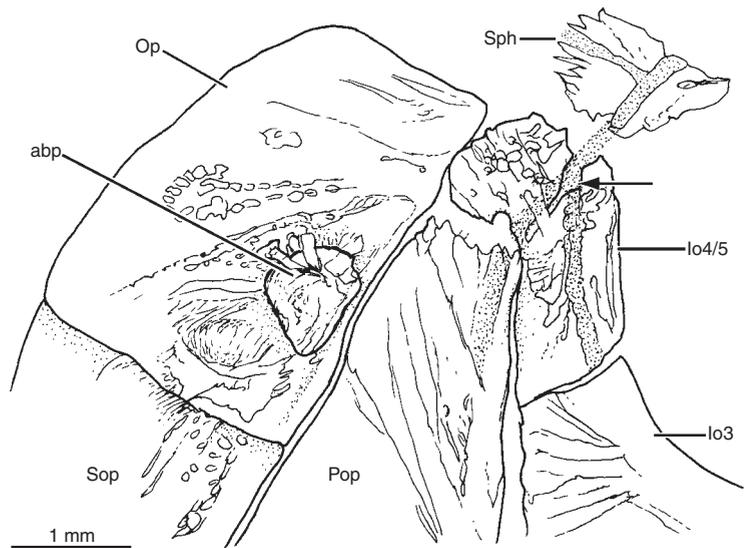
The bone that we interpret as a possible infraorbital 4/5 (Figs. 6, 8) is a flat, almost rectangular bone in its ventral portion, whereas it is broad dorsally and extending onto the opercular region. It is in contact with infraorbital 3 ventrally. There is no separate dermosphenotic.

Upper jaw. The maxilla is preserved, whereas the premaxilla cannot be identified in the holotype and paratype (Figs. 6, 7B). The maxilla forms an elongated plate that narrows anteriorly; its anterior articular region is not preserved. It has a straight, horizontal dorsal margin and an oblique ventral margin without teeth. The maxilla reaches posteriad to the ventral extension of infraorbital 2, whereas it borders the lacrimal dorsally. The maxilla is broken in the paratype and does not provide additional information. A supramaxilla has not been observed in the available material.

Lower jaw. The lower jaw (Fig. 6A,B) of the holotype is curiously shaped, and probably part of its anterior oral border is missing. The dentary expands from a low, spoon-like anterior portion (without teeth) to a deeper middle and posterior part. The small angular forms the postero-lateral part of the lower jaw with an unornamented postero-ventral extension. It connects by an irregular suture with the dentary. The lower jaw of the paratype, although missing its anterior tip, is better preserved than that in the holotype, being more triangular shaped, with a high coronoid process (Fig. 7B). The ventral region of the bone and the posterior part of the angular are ornamented with thin, horizontal ridges. A retroarticular is not exposed laterally.

The lower jaw-quadrate articulation (Figs. 6A,B, 7B) is placed below the posterior half of the orbit or slightly anteriorly.

Opercular series. The large preopercle (Figs. 6A,B, 7B) makes a rounded right angle, with its dorsal arm larger than the narrower ventral one in the holotype. Its posterior border, as well as its surface, do not show indications of spines; if they were present they were very small. The preopercular sensory canal runs in a groove closer to the anterior margin of the bone, and in addition its trajectory is marked by four large pores opening ventral to the main canal. The preopercle (Fig. 7A,B) of the paratype does not add significant information; in addition, its external surface has lost its ornamentation. The preopercular canal joins the infraorbital canal (Fig. 8) before reaching the skull roof, a condition present in some psychrolutid cottoids, but not observed in extant monocentrids such as *Monocentris* and *Cleidopus*.

The opercle (Figs. 6A,B, 8) is a narrow, elongate bone forming most of the posterior part of the opercular apparatus. It is almost square dorsally; its anterior margin is almost straight, whereas the posterior one is gently curved and narrowing ventrally, ending in a narrow, slightly rounded corner. The ventral region of the opercle is markedly ornamented with vertical ridges in the paratype (Fig. 7). A small additional plate lies on the lateral surface of the opercle and attaches to the opercular surface by projections of different lengths (Fig. 8); this additional bony plate protrudes laterally, but it is not so large as to be defined as a lateral spine.

The subopercle (Fig. 6A,B) is a small, triangular bone firmly articulated to the postero-ventral margin of the opercle. The surface of the bone is completely covered with fine ridges. The dorsal margin is wide and the bone narrows strongly ventrally.

The unusually large interopercle (Figs. 6A,B, 7A,B) is an elongated subtriangular bone that tapers anteriorly; the dorsal margin is straight and the postero-ventral border is rounded in the holotype, and slightly acute in the paratype. It rests along the length of the ventral margin of the preopercle extending anteriorly, close to the posterior margin of the lower jaw, and posteriorly extends below the subopercle reaching the cleithrum. A broad unornamented surface lies alongside the dorsal margin in the holotype. We assume that this area corresponds to the region where the preopercle lies. According to this arrangement, the branchiostegal rays lie below the interopercle, not the subopercle as commonly seen in teleosts.

Girdles and paired fins. The pectoral girdle (Fig. 6A,B) is best preserved in the holotype. It is represented by the supracleithrum, cleithrum and two postcleithro-pectoral plates. The posttemporal is not preserved, but the space where the bone was placed is observed between the pterotic and the supracleithrum.

The supracleithrum is a small, flat bone with irregularly serrated posterior border in the holotype. Only an impression of a bone at the postero-dorsal margin of the cleithrum could correspond to the supracleithrum in the paratype. The lateral line canal is not observed running in the bone. The cleithrum is a long bone, almost straight but recurved antero-dorsally as in the holotype. There is no clear distinction between dorsal and ventral limbs, but apparently it broadens in its lower half as shown by the paratype (Fig. 7B). A broad, extensive unornamented region at the anterior margin of the bone corresponds to the region where the posterior margins of the opercle, subopercle, interopercle and branchiostegals rays lie.

Fig. 9.
†*Handuichthys interopercularis* gen. et sp. nov. (UAHMP-690, paratype). El Doctor Formation, Albian/Cenomanian, Cretaceous; Muhi quarry, Zimapán, State of Hidalgo, Mexico. Broken pelvic spine with tiny spines indicated by small arrows. Scale bar = 5 mm.

Elongate vertical ridges and some small tubercles form the ornament of the exposed surface of the cleithrum.

Two small and slightly rounded postcleithro-pectoral plates (Fig. 6A,B) are placed on the mid flank together with the pectoral fin in the holotype. This region is not well preserved in the paratype, and only a displaced element is observed lying off the posterior margin of the cleithrum.

The pectoral fin lies above the second row of shields counting from the ventral margin in the holotype. The fin is composed of 11 unbranched and unsegmented fin rays, which are narrow and thin. Remnants of only two fine, thin rays are preserved in the paratype.

A piece of a triangular, broad and massive pelvic basipterygium is present in the paratype, just in front of the insertion of the pelvic fin. The pelvic fin in the holotype (Fig. 6A) is represented only by a short piece of the incomplete spine that bears three small spinules. A broken spine (Fig. 9), bearing numerous minuscule spines at its dorsolateral margin is found in the paratype.

Unpaired fins. No dorsal spines or soft rays are present in the available specimens.

One strong anal spine (Figs. 7) is present. Soft anal rays are not preserved in the holotype, but remnants of two thin rays are displaced in the paratype (Fig. 7). The external surface of the spine is ornamented with irregular ridges.

Body shields. The anterior half of the body of the holotype is covered by four series of bony, elongate, leaf-like shields (Fig. 6A,B) on each side, each shield extensively overlapping the next more posterior one. The shields have different sizes and shapes and are not arranged in well-defined longitudinal rows like in the "agonid-like" fish described in this contribution or in extant agonids (KANAYAMA 1991). A series of lateral line shields is absent, and we assume that the lateral line runs enclosed within the wall of the shields

as observed in extant monocentrid fishes studied here. All dorsal shields are damaged in the holotype, but they are present in the paratype (Fig. 7A,B). As shown by the paratype, the size of some ventral shields in the anterior half of the body seems to be larger than the dorsal ones, and their size and number decrease caudally. The fish seems to have about 15 vertical rows of shields along the dorsal body region.

The ornamentation consists of ridges of tubercles originating from an anterior, elongate growth center of the shields in the anterior half of the body (Figs. 6A,B, 7A,B). Such growth center protrudes from the lateral surface of the shields but apparently they were not spine-like. The external surfaces of the posterior shields are damaged so that the ornamentation is preserved only in certain areas and consists mainly of tiny tubercles arranged in fine ridges.

†*Pseudomonocentris* gen. nov.

Diagnosis. A miniature †pseudomonocentrid with gentle, slightly triangular profile of the head. Skull roof with bony ridges covered with minuscule spines. Narrow, oval orbit. Ventral margin and lateral surface of lacrimal (or infraorbital 1) covered with minuscule spines. Premaxilla longer than maxilla and main element of the oral dorsal border. Preopercular bones triangular, lacking a distinct ventral arm. Additional, ornamented bony plates covering cheek region. Large, broad opercle, with a straight dorsal margin, slightly rounded anterior and posterior margins, and an acute tip ventrally. Subopercle very narrow, small, and triangular. Large, heavily ossified overlapping shields covering the anterior half of the body and numerous small shields, irregularly arranged, covering the posterior half, including the caudal peduncle.

Etymology. The generic name refers to the overall similarity in shape with members of the extant family Monocentrididae.

Type species: †*Pseudomonocentris microspinosus* gen. et sp. nov.

†*Pseudomonocentris microspinosus* gen. et sp. nov.
(Figs. 10, 11)

Holotype. UAHMP-3721is represented by an almost complete specimen (Fig. 10A); the preserved standard length is 37.30 mm. Thus the total length was about 40−41 mm. There are remnants of very delicate and thin caudal rays.

Diagnosis: As for genus.

Etymology. The species name refers to the minuscule spines present on the lacrimal and on bony ridges in the skull roof.

Locality: Muhi quarry, Zimapán, State of Hidalgo, Mexico.

Age: El Doctor Formation, Albian/Cenomanian, Cretaceous.

Description

General features. The holotype specimen (Fig. 10A,B) is almost complete; head and shields of the body are preserved. The specimen is preserved with its left side visible and the head is slightly twisted to the left. The orbit is oval, with its maximum diameter at the horizontal plane.

The fish has an almost ovoid body tapering into a narrow caudal peduncle and an apparently small caudal fin. The specimen is small, about 37.3 mm in SL. The head is relatively moderately large, making up about 20 % of the SL. The short caudal peduncle is about 9 % of the SL, and its depth about 22 % of the maximum depth of the body (measured close to the level of insertion of the anal fin). The pelvic spine (about 9.5 mm long) is slightly longer than the anal spine (about 7.3 mm long). The pelvic fin has an anterior insertion, slightly anterior to the pectoral fin. The anal fin is positioned posterior to the middle of the SL, closer to the pelvic spine than to the caudal fin. The skull bones and the bony shields are ornamented with tubercles and tiny crests arranged in radiating ridges. The surface of some head bones as well as of most shields is weathered away.

Skull roof. The anterior part of the head is not well preserved, but a small bone placed anterior to both of the frontal [= parietal] bones could be the mesethmoid. Two broad and long frontal [= parietal] (Fig. 11A,B)

bones form most of the skull roof. The right nasal bone partially lies on the anterior margin of the frontal bone [= parietal]. Its dorso-lateral margin bears minuscule spines (Fig. 11C). The right frontal [= parietal] is partially lying on the left one, and both bones are broken anteriorly. The suture between them is achieved by smooth articulating surfaces. No serrations or identations are observed. As revealed by its borders, the frontal bone [= parietal] is markedly thick and well ossified. The orbital margin is slightly concave, and the bone produces a groove at the inner region of the orbital margin that bears a delicate bony ridge with minuscule spines. The spiny bony ridge extends anteriorly, but its complete path is unknown because of incomplete preservation.

An approximately triangular bone at the postero-dorsal margin of the orbit is interpreted as the sphenotic (Fig. 11B). The exposed surface, projecting ventro-laterally, is covered with tubercles and small, irregularly distributed minuscule spines. The bone sutures with the frontal [= parietal] medially and with the pterotic along its posterior margin. The external surface of the pterotic is worn away so that its ornamentation and the trajectory of the otic canal cannot be described. The pterotic (Fig. 11B) is partially broken caudad, and additionally, the anterior shields with their ornamentation make it difficult to separate the limits of the bones. This problem also can be extended to the parietal [= postparietal] and extrascapular bones because we cannot identify them properly. Additionally, the region where the parietal [= postparietal] would be is worn away, and the external surface of the bone is not preserved. An incomplete right extrascapular bone bears two large pores of the extrascapular commissure. It is unclear whether parietal [= postparietal] and extrascapular bones are fused with each other or not, but there is a continuity between both bones where they are not broken. The presence of shields abutting the posterior region of the skull roof makes it impossible to observe the supraoccipital, epiotic, and posttemporal bones.

Evidence of the trajectory of the supraorbital and otic canals has not been observed, possibly due to the thickness of the bones and their ornamentation.

Circumorbital bones. The circumorbital series is incomplete antero-dorsally (Fig. 11B). There are no supraorbital and antorbital bones. Remnants of sclerotic bones have not been observed. There are four independent infraorbital bones with thickened, heavily ossified orbital borders. The lacrimal or infraorbital 1 is a moderately large bone that has a rounded ventral margin covered with minuscule spines (Fig. 11A,B). Scattered minuscule spines cover the lateral surface of the bone. Dorso-medially the bone has a well-developed process to articulate with the autopalatine and/or lateral ethmoid.

The ventral margin of the second infraorbital bone is difficult to determine, but the bone seems to be large. Because of poor preservation, it is not possible to observe the medial side of the bone and to check whether a shelf was present or not. The infraorbital sensory canal runs close to the orbital margin of the bone.

Infraorbital 3 is rhomboidal; it is the second largest bone of the series. Its posterior margin slightly overlaps the anterior margin of the preopercle. It bears three sensory canal pores close to the orbital margin. The bone interpreted as a possible infraorbital 4+5 is incompletely preserved. It is narrow in its ventral portion but it is broken dorso-laterally, so that its complete shape is unknown. It is in contact with infraorbital 3 ventrally. There is not a separate dermosphenotic.

It is unclear whether the infraorbital canal runs partially protected by the thick orbital margin, or if the canal was partially protected by some bony ridges. We believe that the latter is unlikely due to the rest of ornamentation partially covering the exposed surfaces.

Additional bony plates (Fig. 11B), heavily ornamented with small tubercles, lie between infraorbital 2, maxilla and preopercle, completely closing the check region.

Upper jaw. The upper oral border is formed only by the premaxilla. The premaxilla is slightly longer than the maxilla. The anterior region of the premaxilla (Fig. 11B) is incompletely preserved, but it seems to have a small process that protrudes laterally, and more anteriorly a narrow and short ascending process. The premaxillary blade is narrow anteriorly and becomes broader posteriorly. As consequence, the maxillary oral border is slightly concave. The lateral surface of the bone is partially covered with elongate bony ridges.

The maxilla (Fig. 11B) slightly expands anteriorly in a modest articular region. The maxillary blade is narrow and of the same depth along its length; it has straight dorsal and ventral margins. The maxilla borders the lacrimal (or infraorbital 1) dorsally.

Premaxillary teeth have not been observed.

Lower jaw. The lower jaw (Fig. 11B) is curiously shaped: it is expanded anteriorly and ventrally at the mandibular symphysis. The ventral margin of the jaw is almost straight posteriorly, and the dorsal margin

ascends gently. However, most of the jaw is obscured by the premaxilla and maxilla so that its complete shape is unknown. The dentary forms most of the lower jaw. A large round space appears on the lateral surface of the dentary close to the symphysis. The small angular forms the postero-lateral part of the lower jaw, and a postarticular process seems to be absent. A retroarticular is not exposed laterally. Dentary teeth have not been observed.

The mandibular sensory canal runs in an open groove bordered by thicker bone. The groove is partially covered anteriorly by arch-like, thin bone framing two large openings.

The lower jaw articulation (Fig. 11A,B) is placed below the anterior half of the orbit, close to its anterior margin.

Opercular series. The preopercle (Figs. 10, 11B) has an unusual shape. It is triangular and projects anteriorly in a short ventral arm. The bone shows an incompletely preserved but thickly ossified anterior margin. Its posterior border, as well as its surface, does not show indications of spines; if any were present they were very small. The surface of the bone is weathered away so that the trajectory of the preopercular sensory canal is not observed.

The opercle (Figs. 10, 11B) is large, with an expanded upper half and a narrowed lower half ending in an acute ventral region. The ventral region ends in a spine that is slightly curved caudad. Its anterior margin, below the articulation with the hyomandibula, is slightly rounded. Its posterior margin is gently rounded as well. The dorso-lateral surface of the opercle has a lateral ridge starting close to the hyomandibular articulation and extending posteriorly. A spine is not associated with this ridge. Vertical ridges and grooves are observed in the posterior half of the bone.

The subopercle (Figs. 10, 11B) is a very small bone, firmly articulated to the postero-ventral margin of the opercle through a markedly oblique joint.

The interopercle (Figs. 10, 11B) is a massive bone extending below the preopercle and probably reaching posteriorly to the cleithum as in †*Handuichthys interopercularis* gen. et sp. nov. The posterior part of the interopercle is covered by shields that also cover the base of the pelvic spine.

Branchiostegal rays have not been observed because the presence of shields abutting the ventral region of the body obscures them.

Girdles and paired fins. Only a section of the cleithrum (Figs. 10, 11B) can be seen because the opercular bones cover some of its ventral part. Apparently, postcleithro-pectoral plates are not present. We could not identify them between the ornamented shields.

The pectoral fin is represented by remnants of four very thin and delicate rays. The rays are oriented at a postero-dorsal angle.

The pelvic spine (Figs. 10, 11A,B) has an insertion that is slightly in front of that of the pectoral fin. The spine is massive, heavily ossified, and covered at its proximal region by at least two overlapping shields.
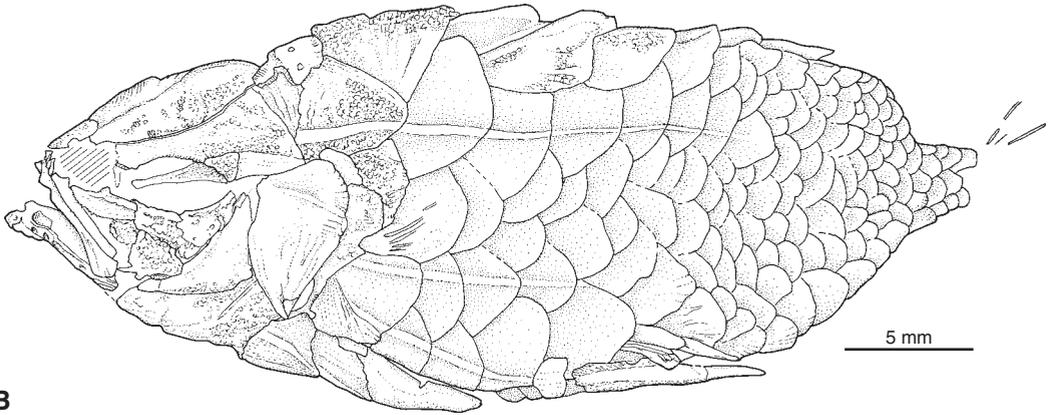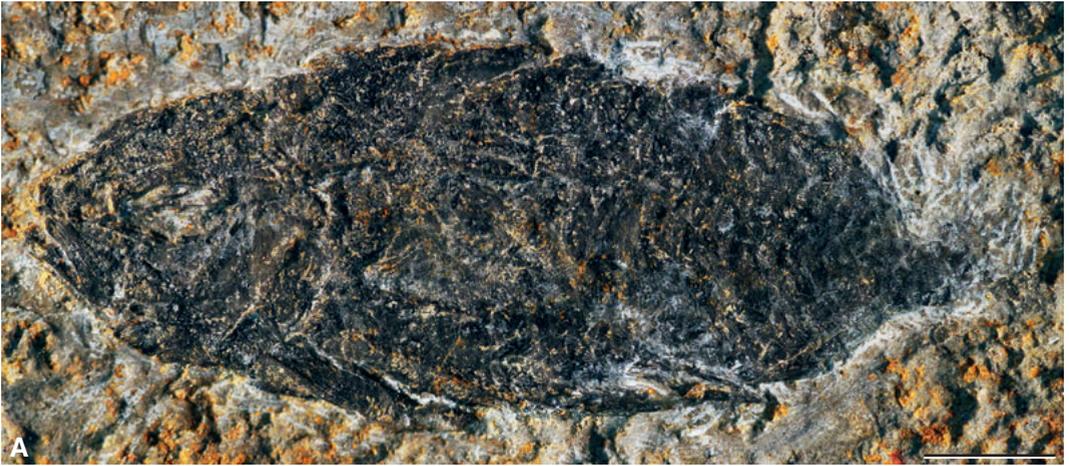
Unpaired fins. No dorsal spines or soft rays are present in the available specimens.

One strong anal spine (Fig. 10A,B), slightly thinner than the pelvic one, is present. The external surface of the spine is ornamented with irregular ridges. Soft anal rays are not preserved.

Body shields. The anterior half of the body is covered by three or four vertical rows of large bony shields (Figs. 10A,B, 11B), each extensively overlapping the next one, and with rounded or slightly acute posterior margins. The large shields positioned in the rows close to the dorsal margin of the anterior half of the body have mainly rounded free margins, whereas the margins can be rounded or acute in the shields found in the ventral region of the anterior half of the body. The shields found in this species do not follow a precise row pattern, have different sizes and shapes, and are not arranged in well-defined rows like those of extant agonids (KANAYAMA 1991) or in the "agonid-like" fish described in this contribution. A series of specialized lateral line shields is absent, and we assume that the lateral line runs enclosed in the wall of the shields as observed in extant monocentrid fishes studied here.

The size of the dorsal shields in the anterior half of the body seems to be larger than that of the ventral ones (see Figs. 10, 11). The sizes of the shields decrease caudally, being very small in the caudal peduncle, where the shields adopt rounded or oval shapes. As a consequence of the decreasing size, numerous vertical and horizontal rows of heavily ossified and overlapping shields form the armored cover of the posterior half of the body.

In general, the ornamentation of the shields is worn away, but some remnants are observed in some

Fig. 10.
†*Pseudomonocentris microspinosus* gen. et sp. nov., in lateral view (UAHMP-3721, holotype). El Doctor Formation, Albian/Cenomanian, Cretaceous; Muhi quarry, Zimapán, State of Hidalgo, Mexico. **A,** photograph; **B,** drawing.
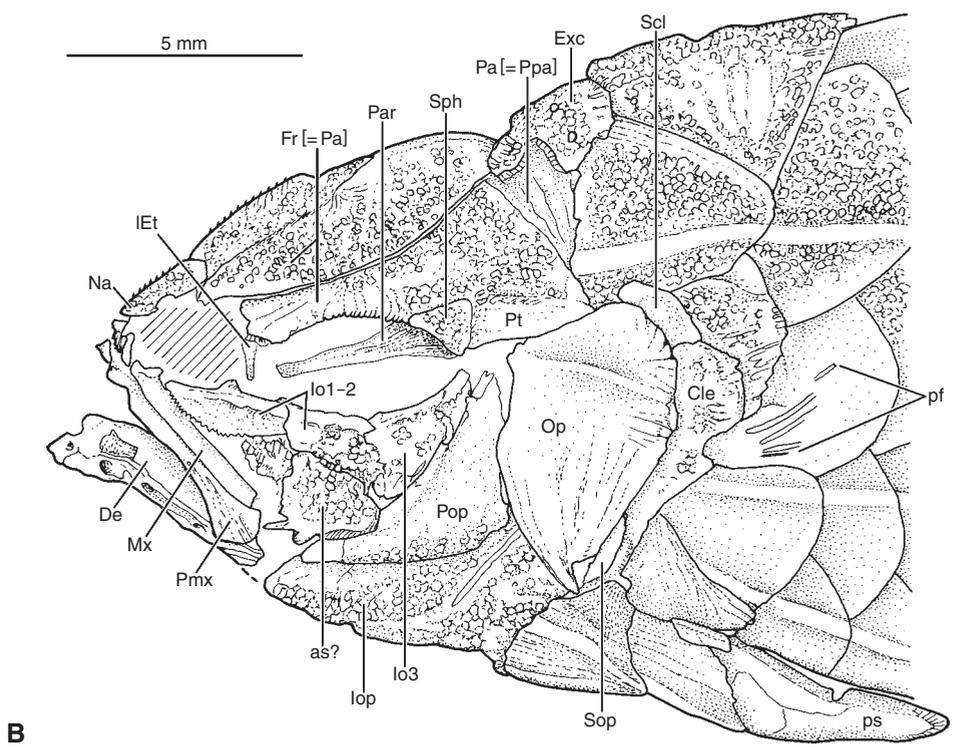
shields. It consists of fine ridges and tubercles. It is unclear whether the small but thick shields of the posterior half of the body, especially in the caudal peduncle, have ornamentation or smooth surfaces.

Comments

Our survey of the distribution of overlapping shields and the peculiar body shape of the fossil fishes narrows the scope of the groups to which our †Pseudomonocentrididae fam. nov. can be assigned. Certainly, the head morphology of the fossil fishes does not correspond to that of armored catfishes (e.g., Fig. 3A), so that the options are restricted to the groups of advanced teleosts bearing overlapping shields. As shown in the section of Terminology, the possible candidates are among neoteleosts. However, currently the Neo-

Fig. 11.   ▷
†*Pseudomonocentris microspinosus* gen. et sp. nov. Anterior part of body lateral view (UAHMP-3721, holotype). El Doctor Formation, Albian/Cenomanian, Cretaceous; Muhi quarry, Zimapán, State of Hidalgo, Mexico. **A,** photograph; **B,** drawing; broken area is represented with oblique lines. **C,** enlargement of the spiny ridge on nasal bone. Abbreviations: **as**, additional shields or bony plates; **Cle**, cleithrum; **De**, dentary; **Exc**, extrascapula; **Io1–3**, infraorbital bones 1–3; **Iop**, interopercle; **Fr[=Pa]**, frontal bone [= parietal]; **l.Et**, lateral ethmoid; **Mx**, maxilla; **Na**, nasal bone; **Op**, opercle; **Pa[=Ppa]**, parietal bone [= postparietal]; **Par** parasphenoid; **pf**, pectoral fin; **Pmx**, premaxilla; **Pop**, preopercle; **Pt**, pterotic; **Scle**, supracleithrum; **Sop**, subopercle; **Sph**, sphenotic.

A

B

C

teleostei are supported by five synapomorphies (WILEY & JOHNSON 2010: 143), four of which are soft anatomical characters (e. g., muscles and some particular kinds of insertions) and one corresponds to type 4 tooth attachment. The fishes studied here do not have teeth in the jaws, so this character is inapplicable. Assuming that these synapomorphies were present in the studied †pseudomonocentrids, even though we do not see them because of conditions of preservation, we next checked the synapomorphies that have been proposed for ctenosquamates and acanthomorphs (see WILEY & JOHNSON 2010: 146−147). Again we face the problem that most of these synapomorphies are soft or internal anatomical characters that are obscured by the shields in the studied fossils. At minimum, the new family †Pseudomonocentrididae fam. shares with ctenosquamates the absence of supraorbital bones.

Despite the major problems that we face trying to identify incompletely known fossils, the presence of certain morphological structures can be helpful. The possession of thickly ossified, overlapping bony shields together with a balloon-like body, a very narrow caudal peduncle, and pelvic spine is a combination of features shared with "pinecone fishes" (the monocentrid trachichthyoids) among extant neoteleosts. Members of the Monocentrididae also are characterized by the possession of dorsal spines, the lack of anal spines, and the presence of bacterial light organs on the dentary (MOORE 1993). The fossil fishes described herein do not appear to have dorsal spines, but they have a well-developed anal spine contrary to monocentrids. It is possible, but not certain, that the fossa present in the dentary in †*Pseudomonocentris* gen. nov. may have been associated with a bacterial light organ.

Another character that supports a relationship of the †Pseudomonocentrididae fam. nov. with trachichthyoids is the absence of ossified sclerotic bones (MOORE 1993). Two ossified sclerotic bones are commonly found in acanthomorphs and in more basal teleosts.

The presence of two supramaxillary bones is the plesiomorphic condition in teleosts. Most trachichthyoids have only one supramaxillary bone, a feature also found in other acanthomorph lineages. However, among trachichthyoids the genus *Scopelogadus* has lost supramaxillary bones (EBELING & WEED 1963, 1973, MOORE 1993), a feature also present in †Pseudomonocentrididae here described.

Trachichthyoids have a distinctive pattern of ridges on the frontal [= parietal] bones consisting of a modified X pattern (ZEHREN 1979). The ridges all meet at a point over the eye and from there, two anteriorly directed ridges extend to the antero-medial and antero-lateral corners of the frontal [= parietal]. Three ridges are posteriorly directed towards the supraoccipital, parietal [= postparietal] and pterotic (MOORE 1993). This pattern was illustrated for *Monocentris* and *Hoplostethus* by PATTERSON (1964: figs. 63, 65). We have not observed a pattern like this in †*Handuichthys interopercularis* gen. et sp. nov., but the skull roof of †*Pseudomonocentris microspinosus* gen. nov. reveals thin ridges covered by minuscule spines when it is observed under high magnification.

Monocentrids have complete bony arches over the infraorbital sensory canal (ROSEN 1973, MOORE 1993). Enclosed tube-like infraorbital canals represent the plesiomorphic condition in teleosts (ARRATIA 1997) and this feature is present in †*Handuichthys interopercularis* gen. et sp. nov.; however, the condition of the infraorbital canal is unclear in †*Pseudomonocentris microspinosus* gen. et sp. nov.

Trachichthyoids can have five independent infraorbital bones (including the lacrimal) as in the trachichthyid *Hoplostethus* (MOORE 1993: fig. 2). We have observed five infraorbitals (including the lacrimal) in *Monocentris* and *Cleidopus*. The fossil described here has three or four independent infraorbitals (including the lacrimal), a reduction that seems to be autapomorphic.

The two extant monocentrid genera, *Monocentris* and *Cleidopus*, lack anal spines unlike other trachichthyoids. In contrast, the fossils described herein have an anal spine. Other trachichthyoids may have two or three anal spines (Trachichthyidae; NELSON 2006); one or more anal spines are usually found in acanthomorphs and percomorphs.

Summarizing the evidence, the new fossils described herein – †*Handuichthys interopercularis* and †*Pseudomonocentris microspinosus* – share with the extant family Monocentrididae most of its synapomorphies, except the absence of an anal spine. Notwithstanding these shared synapomorphies, the fossil species present major differences from the extant family Monocentrididae in several morphological characters, such as the absence of a supramaxilla, the presence of a reduced number of independent infraorbitals, a dermosphenotic fused with the underlying autosphenotic, a large interopercle, an anal spine, and the apparent absence of dorsal spines.

Due to these major differences with the extant representatives, we assign the two new fossil genera to a new extinct family, †Pseudomonocentrididae.

Extant monocentrids are currently included within the Beryciformes sensu WILEY & JOHNSON (2010). Beryciformes are supported by two synapomorphies (presence of Jakubowski's organ and absence of

pharyngobranchial 4) according to WILEY & JOHNSON. Neither of these synapomorphies can be observed in the fossils described herein due to conditions of preservation.

The family Monocentrididae includes two genera and four species; they occur today at depths of 30 to 300 meters in the tropical and subtropical Indian and Pacific Oceans (NELSON 2006) over ledges, rocky reefs and in caves. The Cretaceous †pseudomonocentrids inhabited a similar environment.

Acanthomorpha incertae sedis

†*Dalgoichthys* gen. nov.

Diagnosis. Acanthomorph teleost with dorsal margin of orbit convex and predorsal margin of body moderately elevated. Infraorbital 2 the largest infraorbital; infraorbital 2 with well-developed medial shelf; dorsal-most infraorbital (4/5) tubular in its ventral part and expanded in its upper half; small, triangular interopercle positioned at the postero-ventral corner of the preopercle. Two, flat, well-developed, subtriangular postcleithro-pectoral plates antero-dorsal to base of pectoral fin. Heavily ossified, large body shields overlapping each other and arranged in longitudinal rows; few vertical rows; supralateral and infralateral shields wide and deep. Lateral line canal running in a row of rectangular-shaped shields placed next to each other (= lateral line shields).

Type species: †*Dalgoichthys tropicalis* gen. et sp. nov.

Etymology. The generic name refers to the Otomí (a native Mexican language) name "Dalgo" meaning Hidalgo, the Mexican state where it was discovered, combined with "ichthys" (Greek) meaning fish.

†*Dalgoichthys tropicalis* sp. nov.
(Figs. 12, 13B, 14)

Holotype. UAHMP-1387 is represented by head and anterior body (Fig. 12A). The preserved length is 23 mm. C. FIELITZ (Emory and Henry College, Virginia, USA) collected the specimen during a field trip organized by the University of Hidalgo, Mexico, in 2007.

Diagnosis: As for genus.

Etymology. The species name refers to the presence of the fish in Late Cretaceous tropical waters.

Locality: Muhi quarry, Zimapán, State of Hidalgo, Mexico.

Age: El Doctor Formation, Albian/Cenomanian, Cretaceous [about 100 My].

Description

General features. The holotype, even though incomplete, is a well-preserved specimen. It is exposed on its left side. The rostral region, including mainly the nasal bone and premaxilla, is separated from the main portion of the head by a fracture (Figs. 12). A lower jaw is not preserved. The branchiostegal rays are dislocated and partially broken. Remnants of pectoral, dorsal and anal fins are preserved. The skull bones and the bony shields on the body are heavily ornamented with tubercles arranged in radiating ridges.
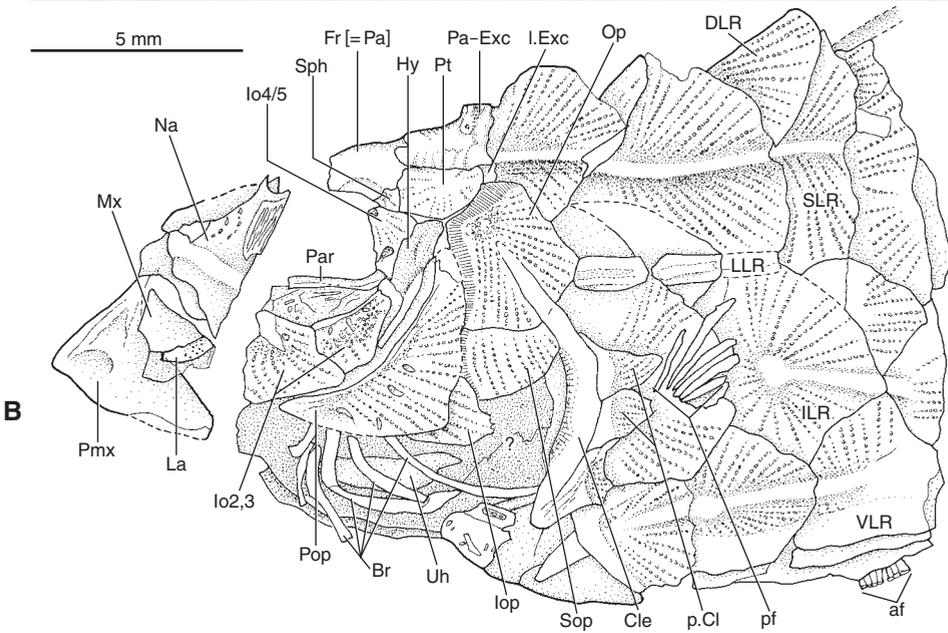
Skull roof and parasphenoid. The skull is preserved in lateral view. The rostral portion consists of the deep premaxilla and the nasal bone that together produce a slightly rounded anterior profile of the head, not a projecting one as found in some cottiforms.

The nasal bone (Figs. 12B, 13B), with the typical shape of agonids, presents a spine-like process dorsally; behind this process the nasal bears a deep groove like the one present in extant agonids (Fig. 13A; KANAYAMA 1991: figs. 73, 74). The nasal spine sits on the joint between the ridge to the antero-medial projection and a dorsal ridge, as in extant agonids (Fig. 13A; KANAYAMA 1991: fig. 73). An antero-medial projection connects the bone with its opposite in the fossil in a similar pattern to that of extant agonids. That is a situation similar to hypsagonids, whereas both sides are sutured in more advanced agonids. The anterior free nasal margin is smooth, and a rostral plate is not observed.

The frontal [= parietal] bone (Figs. 12A,B, 14A,B) is broken and only its posterior part is observed, dorsally in front of the parieto-extrascapula and postero-ventrally next to the autosphenotic. The parietal

Fig. 12.

†*Dalgoichthys tropicalis* gen. et sp. nov., holotype UAHMP-1387, whole specimen; El Doctor Formation, Albian/Cenomanian, Cretaceous; Muhi quarry, Zimapán, State of Hidalgo, Mexico. **A,** photograph; **B,** drawings. Abbreviations: **af,** anal fin; **br,** branchiostegal rays; **Cle,** cleithrum; **p.Cl,** postcleithro-pectoral plates; **DLR,** dorso-lateral row of shields; **F[=Pa],** frontal [= parietal] bone; **Hy,** hyomandibula; **ILR,** infralateral row of shields; **Io2,3,4/5,** infraorbital 2, 3, 4/5; **Iop,** interopercle; **La,** lacrimal (or infraorbital 1); **l.Exc,** lateral extrascapula; **LLR,** lateral line row of shields; **Mx,** maxilla; **Na,** nasal bone; **Op,** opercle; **Pa-Exs,** parieto-extrascapula; **pf,** pectoral fin; **Pmx,** premaxilla; **Pop,** preopercle; **Pasp,** parasphenoid; **Pt,** pterotic; **SLR,** supralateral row of shields; **Sop,** subopercle; **Sph,** sphenotic; **Uh,** urohyal; **VLR,** ventro-lateral row of shields.

[= postparietal] bone is fused with the medial extras-capula forming a slightly rectangular bone (Figs. 14B) that projects a kind of broad crest or protrusion where the extrascapular canal runs. This crest is higher closer to the midline, similar to the condition illustrated for some agonids (e. g., *Hypsagonus* by KANAYAMA 1991: figs. 4–9; pers. observ.). The almost rectangular pterotic is as long as the whole length of the parieto-extrascapula. Both bones join with each other through a smooth su-ture. The pterotic exhibits anteriorly a foramen of the otic canal; the opening for the preopercular canal is not observed, because apparently it is covered by the lateral ornamentation of the bone surface. A small, slightly squarish bone lies posterior to the pterotic. This small element is interpreted as a lateral extrascapula because of its structure and position. Other bones, such as as the epiotic and the supraoccipital, are not observed because the first most dorsal shield is closely attached to the posterior margin of the parieto-extrascapular bone.

A portion of the parasphenoid is visible in the or-bit medial to the infraorbital bones and entopterygoid (Fig. 12A,B). The bone is stout and curves upwards posteriorly.

Fig. 13.
Left nasal bone of **A,** *Hypsagonus quadricornis* (after KANAYAMA 1991: fig. 72A) and of **B,** †*Dalgoichthys tropicalis* gen. et sp. nov., holotype UAHMP-1387. Horizontal arrows point to median process and the vertical arrows to the deep groove in the margin part of the bone.
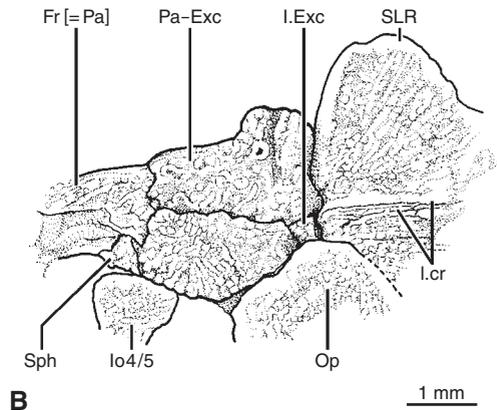
Circumorbital bones. The circumorbital series is incomplete antero-dorsally. Circumorbital bones consist of one lacrimal [= infraorbital 1] and three infraorbital bones (Fig. 12A,B). A small portion of the lacrimal is preserved above the broken maxilla. Its shape and size are unclear, but at least two rows of tubercles are observed on its lateral surface. Ossified sclerotic bones or their remnants are not present, as in †pseu-domonocentrids, extant monocentrids and agonids.

The second infraorbital bone (broken at its anterior margin) is the deepest infraorbital and produces a postero-ventral projection that is tightly attached to infraorbital 3 and extends to the anterior margin of the preopercle. A well-ossified shelf projects medially from the inner wall of infraorbital 2, but due to condi-tions of preservation it is unclear whether the medial tip of the shelf is directed anteriorly or posteriorly. Because of the angle of the preserved section, probably it is directed anteriorly.

Fig. 14.
†*Dalgoichthys tropicalis* gen. et sp. nov., fused parieto[= postparietal]-extrascapula (UAHMP-1387, holotype). El Doctor Formation, Albian/Cenomanian, Cretaceous; Muhi quarry, Zimapán, State of Hidalgo, Mexico. **A,** pho-tograph; **B,** drawing. Abbreviations: **Pt,** pterotic; **Dsph,** dermosphenotic; **Io4/5,** infraorbital 4/5; **Op,** opercle; **Pa-Exs,** parieto-extrascapula; **SLR,** supralateral row of shields; **l.Exc,** lateral extrascapula.

Infraorbital 3 (partially broken posteriorly) is triangular and narrows dorsally. It is the second largest bone of the series. Parts of the bone lie posteriorly on the broad articular surface of the preopercle as in other agonids. A posterior extension or so-called suborbital stay is not present in infraorbital 3. Additional bony plates positioned between infraorbital 3 and preopercle, like those present in †*Pseudomonocentris* gen. nov., are not present. The bone interpreted here as infraorbital 4/5 is tubular ventrally and expanded dorsally. It is barely attached to infraorbital 3. The bone-enclosed infraorbital sensory canal runs close to the orbital margin of the bone and opens by one pore in infraorbital 2 and three pores near the orbital margin in infraorbital 3.

The orbit is small and dorso-laterally placed. Because of its position, it is assumed here that it was slightly protruding above the lateral margins of the skull roof.

Upper jaw. The premaxilla (Fig. 12A,B) is broad and slightly L-shaped in lateral view. The ascending process is long and tapers dorsally, but an articular process is not observed in the new fossil. It is unclear if the process is missing or it is not observed because the broken maxilla lies on this region. The oral border lacks teeth as in some extant agonids. A piece of the anterior portion of the maxilla is preserved, but its extension is not observed.

Lower jaw. The lower jaw is not preserved.

Suspensorium and opercular series. The hyomandibula is partly covered by the dorsalmost infraorbital 4/5. The lateral exposed region of the hyomandibula is slightly rectangular with an expanded dorsal portion, which articulates posteriorly with the opercle. A sharp bony crest extends along the lateral surface of the bone.

The preopercle (Fig. 12A,B) is crescentic in shape; along the upper portion of the anterior margin it shows a notch where the hyomandibula partially abuts. It bears little indication of spines on its posterior margin, only as extensions of the ornamented bony ridges covering the lateral surface of the bone. The preopercle bears anteriorly a broad, unornamented articular surface for the hyomandibula, and infraorbital bones 2 and 3. Its posterior margin overlaps the opercle and subopercle, and postero-ventrally it overlaps the interopercle. The sensory canal is marked by four large pores.

The preserved opercle (Fig. 12A,B) is slightly rectangular, but its posterior margin is broken; the ventral portion is wider than the dorsal portion and is slightly undulated. An elevated spiny tubercle projects laterally close to the dorsal, middle region of the bone. The opercle presents broad unornamented surfaces dorsally and anteriorly. The subopercle (Fig. 12A,B) is a slightly rectangular bone tightly attached to the ventral margin of the opercle. The posterior region is not observed due to the displacement of the cleithrum. The interopercle (Fig. 12B) is a small, subtriangular bone placed at the postero-ventral corner of the preopercle. A few small spiny projections are observed at the posterior margin, in continuation with the ornamented bony ridges covering the surface of the bone. The size of the bone and its relationships to surrounding bones is a major difference with the †pseudomonocentrids described above.

Hyoid region. The urohyal and six broken branchiostegal rays (Fig. 12A,B) are the only bones that we are able to identify in this region. The urohyal is a laterally flattened, long bone with a wide and triangular posterior blade. It is preserved medial to the branchiostegal rays, which are curved, rod-like bones.

Girdles and paired fins. The only elements of the pectoral girdle that we are able to observe are the cleithrum and two postcleithro-pectoral plates (Fig. 12A,B). The posttemporal and the supracleithrum are hidden by the opercle.

The cleithrum (Fig. 12A,B) is a narrow, elongate bone slightly recurved antero-dorsally, like the cleithrum present in modern agonids (KANAYAMA 1991: 156). A well-defined angle between dorsal and ventral limbs is missing and the ventral portion of the bone is almost straight. The ventral portion has a peculiar posterior extension that is partially ornamented. This extension forms the rostral postcleithro-pectoral plates. A broad unornamented surface at the anterior margin of the bone indicates the region where the opercle, subopercle and branchiostegal rays lie. The posterior margin of the cleithrum joins two postcleithro-pectoral plates, which are small, flat, subtriangular bones and are partially ornamented.

The incomplete pectoral fin does not have a high position on the flank, but lies at the midlevel of the second row of body shields. The body shield surrounding the place of attachment of the fin rays lacks ornamentation. The fin consists of six or seven unbranched and unsegmented rays that extend to the limit of the second lateral shield. There is an impression behind the dorsal-most fin rays that may indicate the

extent of the pectoral fin web (dotted line in Fig. 12B). The bases of the rays have a small fin web, so that they were not free.

A piece of heavily ossified bone lying in front of the antero-ventral tip of the cleithrum is interpreted here as part of the basipterygium, extending anteriorly to the insertion of the pectoral fin.

Unpaired fins. The dorsal fin is not preserved; however, the impression of the base of one dorsal ray (Fig. 12B) is seen at the level of the third vertical row of body shields. Due to its thickness the bone may correspond to a spine.

The poorly preserved anal fin (Fig. 12B) is positioned in the anterior part of the body at the level of the third bony shield row behind the head. The bases of seven very thin fin rays (and no spine) are preserved.

Body shields. The body of †*Dalgoichthys tropicalis* sp. nov. is covered with four series of bony shields (Fig. 12A,B) arranged in well-defined rows. The dorso-lateral series of shields (DLR) forms the border of a flat to depressed dorsal region and is composed of shields half the size of the supralateral (SLR) and infralateral (ILR) rows, which are similar to each other in dimensions. Two lateral line shields (LLR) are observed between the two lateral rows; they are rectangular and exhibit the lateral line canal and some pores along their length. Remnants of a third lateral line shield are partially preserved. The lateral line shields lie above a surface lacking ornament. The ventro-lateral row (VLR) is slightly smaller than the one above. All series, except LLR, bear tubercles arranged in radiating ridges, similar to those covering the cranial bones.

Each shield overlaps the next one posteriorly for approximately one third of its length. They are spineless, except that the middle ridge of the first ILR shield behind the pectoral fin bears a spine-like protrusion in the center of the shield that continues posteriorly in a low crest. It is unclear whether other protrusions are found in the ventro-lateral row (VLR). The shields of the supralateral row (SLR) bear a sharp and continuous lateral ridge. A dense ornamentation composed of bony tubercles of different sizes and shapes (some round, others oval, others elongate), usually arranged in radiating lines, covers usually the surface of the shields, except for the overlapped regions, lateral line plates, and around the region of insertion of the pelvic fin.

Extant agonids exhibit two narrow vertical rows of shields per segment, whereas one wide row seems to be a unique character of the fossil here described.

Comments

Based on our investigations of the available literature and on actual observation on specimens as well, we believe that the fish described above more closely resembles members of the family Agonidae than any other teleost. According to KANAYAMA (1991: 192), the family Agonidae is characterized by 16 characters (his so-called "synapomorphies") that are not uniquely derived characters because they are not restricted to agonids. They can be found in other cottiforms and scorpaeniforms. Only four characters of KANAYAMA can be recognized in the fossil described here: four circumorbital bones [= lacrimal plus three infraorbitals]; six branchiostegal rays; absence of anal spine; and presence of overlapping bony shields covering the body, and arranged in rows. However, with the exception of the last character, some of the features present in †*Dalgoichthys tropicalis* are currently interpreted as synapomorphies of Cottiformes. For instance: the presence of six branchiostegal rays, lack of spines on the extrascapular canal (= supratemporal or so-called parietal canal of other teleosts), and the presence of two lateral extrascapulae (however, one or two lateral extrascapulae are found in Agonidae; see KANAYAMA 1991: his 'tabular', p. 156, figs. 76A, 77A, 81A,B,H,J, 82A, table 15). Cottiformes present other homoplasious characters (also found in Scorpaeniformes) such as the fusion of the parietal bone [of traditional terminology] with the medial extrascapula. This feature is also found in the fossil here described (see Fig. 14A,B).

The Peristediidae, another family in the Scorpaeniformes, carries three rows of heavy spine-bearing shields on the flank in an arrangement somewhat comparable to the body cover of agonids. Peristediids have an inferior mouth like some advanced agonids. That is not the case in primitive agonids nor in the new fossil fish, †*Dalgoichthys tropicalis*. Characteristic for peristediids are lacrimals (most times called "preorbitals", e.g., HEEMSTRA & HEEMSTRA 2004, MCEACHRAN & FECHHELM 2005) with forward projections (see GREGORY 1933: figs. 220 + 221B, called "lacrymal"), a feature not found in any agonid and quite different from the new fossil. There are no free and enlarged rays in the pectoral fin in agonids and the new fossil in contrast to peristediids (NELSON 2006).

The suborder Cottoidei is characterized by two synapomorphies according to WILEY & JOHNSON (2010: 161), e. g., suborbital stay originating from the third infraorbital (IMAMURA & YABE 2002; homoplasious by parsimony with suborbital stay in other groups). The second synapomorphy is a soft anatomical feature related to muscles. Although the suborbital stay is proposed as a synapomorphy of Cottoidei, the suborbital stay is not present in all members of the suborder because agonids do not have a stay or projection on the third infraorbital bone (KANAYAMA 1991; pers. observ.).

Certainly, the current uncertainties about characters, and consequently of the classification and content of the orders Cottiformes and Scorpaeniformes, are not the most promising scenario when someone is trying to identify some new and unusual fossil fish with all limitations derived from conditions of preservation. In addition to searching for all potential synapomorphies available in the fossils, we also searched for all possible similarities that we could find and could help to assign the miniature, "agonid-like" fish to a major clade. Considering the unusual combination of morphological characters of †*Dalgoichthys tropicalis*, we interpret it as an acanthomorph incertae sedis until more specimens are available for study.

Ecological importance of the miniature armored teleosts

The Muhi quarry has been extensively compared with other Cretaceous Mexican localities such as the Tlayúa quarry, the Vallecillos quarry and the El Rosario quarries among others, as well as Eastern Tethys localities in Lebanon, Morocco, and Ein-Yabrud (Palestine) because of the fish fauna and the paleoenvironment they present (GONZÁLEZ-RODRÍGUEZ & BRAVO-CUEVAS 2005; BRAVO-CUEVAS et al. 2009, 2012). Teleosts with well-ossified bony shields, such as those listed in page 463, may be more likely than others to be preserved as fossils. The monocentrids have a good fossil record going back to the Cenomanian (e. g., PATTERSON 1993a,b). The beryciform Trachichthyoidea (e. g., †*Hoplopteryx*, †*Judeoberyx*, †*Libanoberyx*, †*Lissoberyx*, †*Stichopteryx*) and Holocentroidei (e. g., †*Stichoberyx*, †*Stichocentrus*, †*Trachichthoides*) are already represented by many genera in the Cenomanian. Basal acanthomorphs have also been discovered in the Cenomanian, including †Aipichthyidae (†*Aipichthys*, †*Aipichthoides*, †*Paraipichthys*), †Dinopterygiidae (†*Dinopteryx*), †Pharmacichthyidae (†*Pharmacichthys*), †Pycnosteroididae (†*Pycnosteroides*), Polymixiiformes (e.*g.* †*Berycopsis*, †*Homonotichthys*, †*Omosoma*) and †*Muhichthys* from the Muhi quarry. Nevertheless, none of these sites contain taxa related to the fishes here described. The Muhi quarry not only presents "agonid-like" and †pseudomonocentrid fishes never reported before in Cretaceous deposits of the Americas, it has also yielded the first confirmed report of Ichthyotringoidea (FIELITZ & GONZÁLEZ-RODRÍGUEZ 2008). These new records not only increase the geochronological ranges of the acanthomorphs but their worldwide distribution and the ecological conditions they inhabited.

Recently, BRAVO-CUEVAS et al. (2012) proposed the Muhi quarry as a fossil concentration Lagerstätte because of its fossil richness. The fossil concentration of the quarry represents a mixed assemblage by parautochthonous-allochthonous association that was deposited in an outer shelf setting with warm waters of the western Tethys, which received periodic pulses of pelagic waters, and occasional influxes of near-shore waters maybe during storms (BRAVO-CUEVAS et al. 2009, 2012). The fishes here described could be demersal inhabitants of the continental shelf, like their possible recent relatives.

Monocentrids are tropical fish living on the continental shelf. Thus there is no change in environmental preference if we accept that the †pseudomonocentrids from Muhi quarry are close relatives of monocentrids. In contrast, the presence of the "agonid-like" Acanthomorphata incertae sedis in the Muhi quarry suggests that the group was warm-water adapted during that time, whereas extant agonids are mainly Arctic fishes, only one species occurring on the Chilean and Patagonian coast east as far as the Falkland islands – also in cold water. Most species live in the northern Pacific from Korea and Japan, east to Alaska, and south to California. Three species occur in the North Atlantic (KASCHNER et al. 2008).

Conclusions

Based on the evidence presented and discussed here we conclude that:

1. The fossils here described represent an early record of advanced acanthomorphs (like that published by WILSON & MURRAY 1996), "monocentrid-like" fishes of the order Beryciformes and "agonid-like" fishes, if our comparison with fossil and extant armored teleosts is correct.

2. The new family †Pseudomonocentrididae, interpreted as a group of acanthomorphs, is created to include two new genera, †*Handuichthys* and †*Pseudomonocentris*.

3. †Pseudomonocentrids share an unusually shaped body resembling that of extant monocentrids, but they differ in some major features such as the presence of both pelvic and anal spines, whereas only the pelvic spine is present in extant monocentrids. The latter has dorsal spines, which appear to be lacking in †pseudomonocentrids. The †pseudomonocentrids have heavily ornamented and thick cranial bones and bony shields in contrast to extant monocentrids.

4. †Pseudomonocentrids have a large opercular bone articulated with a very small, narrow subopercle positioned postero-ventral to the opercle. A large interopercle, even longer than the ventral margin of the preopercle, is present in both new fossil genera. The pectoral fin is inserted in the middle region of the flank. The pelvic fin is inserted anteriorly, just below or in front of the pectoral fin insertion. The pelvic fin has a strong spine ornamented with longitudinal ridges and/or small spines. The body is covered with overlapping strong, heavily ossified shields, not arranged in well-defined horizontal or vertical rows.

5. †Pseudomonocentrids and monocentrids share the presence of additional bony shields in the cheek region.

6. The incompletely preserved fish interpreted here as an Acanthomorphata incertae sedis resembles extant agonids in the type of bony shields and their distribution in ordered longitudinal rows in the preserved part of the body. It shares with cottiforms and agonids some of their putative synapomorphies, but due to its incomplete preservation and therefore incomplete morphological knowledge, it cannot be assigned to any of the known acanthomorph groups.

7. The new miniature fossils, †pseudomonocentrids and the acanthomorph incertae sedis, share with other acanthomorphs the absence of supraorbital and ossified sclerotic bones.

8. Finally, the fishes recovered in the Muhi Quarry represent the first discovery of such miniature armored acanthomorphs in the Cretaceous. Cretaceous and Eocene and extant monocentrids, like the †pseudomonocentrid teleosts of Muhi quarry, occur in tropical waters, indicating no change in environmental preference for both groups.

Acknowledgements

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