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OLDEST STEM TELEOSTEI FROM THE LATE LADINIAN (MIDDLE TRIASSIC) OF SOUTHERN CHINA

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Abstract. The origin of the largest modern vertebrate group, the Teleostei, saw major refinements in the last decades, thanks to newly discovered and stratigraphically closely spaced Triassic Lagerstätten. Here we report the oldest Pholidophoriformes (stem teleosts) that were collected during a large scale yet detailed excavation of Upper Ladinian (Middle Triassic) marine deposits in Xingyi City, Guizhou Province, China. Taxonomic comparisons support the erection of a new pholidophorid genus, *Malingichthys* gen. nov., with two species. The new genus shows a partially fused skull roof, a preopercular bone with a hockey-stick shape and, for the first time in Pholidophoridae, supraneural elements.

Most Triassic marine vertebrate clades (fishes and reptiles, *Malingichthys* included) first emerged in the South China Block, with Late Ladinian showing an important faunal transformation that was strengthened by our last findings. The material here described is about 2 million years older than the previous records for pholidophorids.

Introduction

The Teleostei is the dominant group of ray-finned fish (Actinopterygii) that holds the largest diversity among extant vertebrates (Nelson 2006). Teleostei with Holostei (gars and bowfins) and many fossil stem taxa, form the clade Neopterygii. Interrelationships of Teleostei to other neopterygian clades, including fossil groups, have thoroughly been discussed in the recent past, though in some cases fossil taxa were not properly considered (Patterson 1973; Grande & Bemis 1998; Arratia 1999, 2000, 2001, 2004; Hurley et al. 2007; Grande 2010; Taverne 2011; Near et al. 2012; Sallan 2014). As recently pointed out (López-Arbarello 2012; Friedman 2015), notwithstanding a significant amount of new information collected in the last years, still the advance in the study of Middle Triassic actinopterygians is not enough to build a firm foundation for future systematic and evolutionary studies. This is mostly due to the enormous diversity of the group.

Pholidophoridae is a clade of fossil actinopterygians related to the crown-group Teleostei. It has traditionally been considered the most basal member of the Teleostei despite its position outside the crown group ("true" Teleostei sensu Arratia 2013). This traditional and inclusive definition of Teleostei is employed hereafter. So far, pholidophorids have been known only in the western Tethys, corresponding to the today's Alps, in Upper Triassic units mostly cropping out in Northern Italy (Arratia 2013; Zambelli 1986, 1990). Here, we report for the first time two species of pholidophorid fishes from southern China that, besides being new taxa, represent the oldest fossil record along the teleostean branch of the neopterygian phylogenetic tree (Teleostomorpha), narrowing the gap between fossil age and molecular estimates. We also aim to contribute in both stratigraphy and anatomy of these two earliest species

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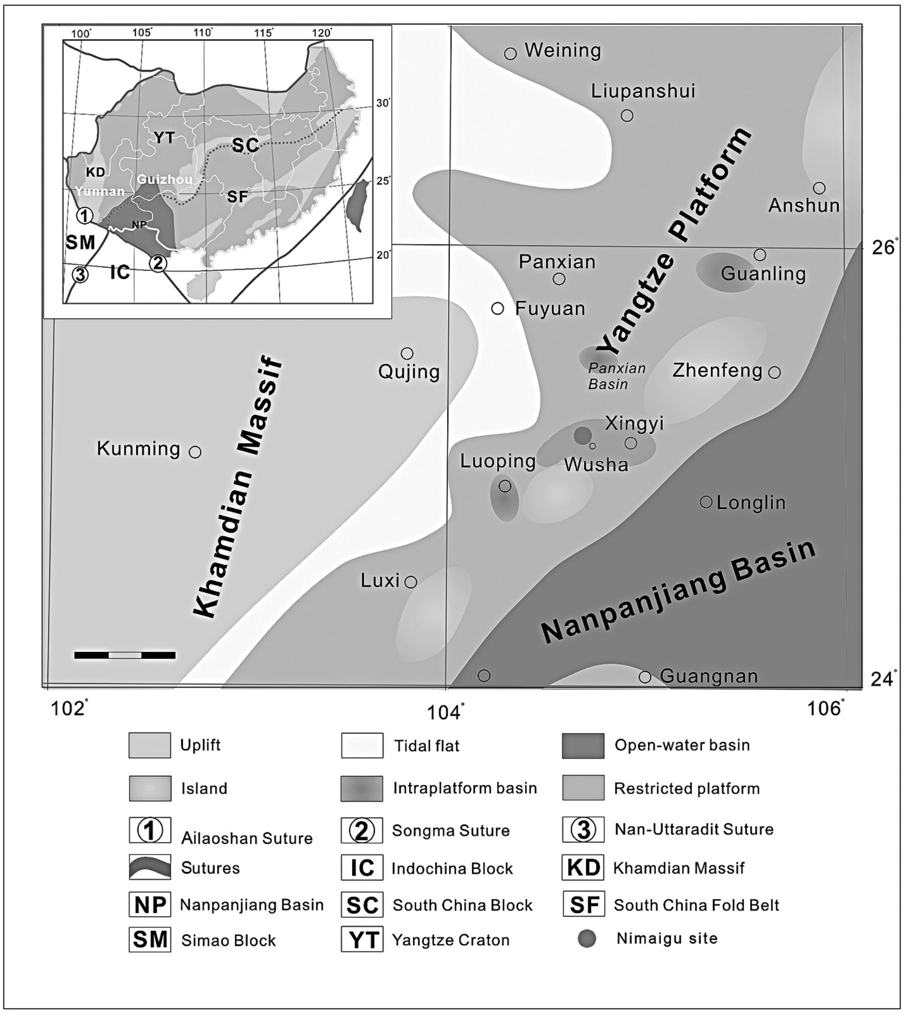

Fig. 1 - Geological setting. Paleogeographic map of southern China during the Middle Triassic (modified after Liu et al. 2013). Intra-platform basins yielding the different Vertebrate Faunas are marked: from bottom to top, Panxian (Middle Anisian), Luoping (Late Anisian), Xingyi (Late Ladinian) and Guanling (Early Carnian).

of pholidophorids, shedding new light to the very early evolution of teleostean fishes.

Geological setting

The new findings are the result of detailed fossil excavations in the Late Ladinian (Middle Triassic) of Xingyi City, Guizhou Province, southern China, between 2011 and 2013 (Figs 1, 2). Many of the vertebrate specimens that we found are still under preparation, but some have already been described (e.g., *Thoracopterus*, Tintori et al. 2012; *Nothosaurus*, Ji et al. 2014). This fossiliferous site opens a window on the Xingyi Fauna (Jiang et al. 2009), which is mainly famous for the pachypleurosaur (small sauropterygian) *Keichousaurus*, the first marine reptile described in China (Young 1958).

Fossil fishes had been known from this region before (Su 1959; Liu et al. 2003; Lin et al. 2011; Hu et al. 2011), but the field works of 2011-13 revealed a much higher diversity than previously recognized. In particular, based on bed-by-bed excavation, two different vertebrate assemblages (Lower and Upper assemblages) have been recognized near Nimaigu village, Wusha District, Xingyi City, Guizhou Province (N 25° 09' 53", E 104° 47' 18"), across the 5.5 m thick interval yielding vertebrate. The Lower assemblage is dominated by *Keichousaurus,* together with the fishes *Asialepidotus* and *Habroichthys*, while the upper one yields large ichthyosaurs associated to *Marcopoloichthys*, the oldest species of the flying fish *Thoracopterus* and several small peltopleuriforms (Tintori et al. 2014). The new taxa described herein belong to the Lower assemblage.

The age of the Xingyi Fauna has been controversial, but a recent study presented new evidence for a middle Late Ladinian age (Zou et al. 2015), based on the ammonoids collected from the Falang Formation at Nimaigu (Wusha) near Xingyi.

Materials and Methods

Specimens described herein were collected during a bed-by-bed excavation started in August 2011 and ended in May 2013, near Nimaigu village, Wusha District, Xingyi City, Guizhou Province, China (Figs 1, 2). This is the first exhaustive excavation that conforms to the scien-

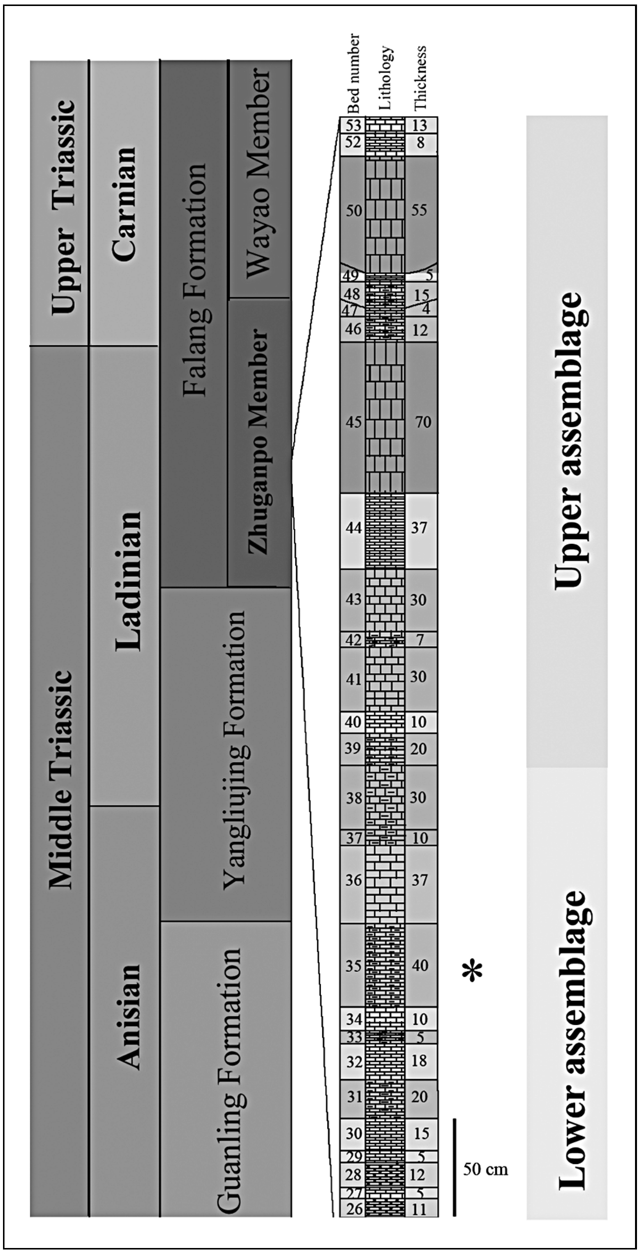

Fig. 2 - Middle-Upper Triassic stratigraphic units from Southern China. The detailed log represents the part of Zhuganpo Member of the Falang Formation containing the Lower and Upper assemblages. The asterisk points to the bed 35 where *Malingichthys* gen. nov. has been found.

tific standards in the fossiliferous areas near Wusha, yielding the Xingyi Fauna.

The vertebrate horizon has been carefully checked for both vertebrate and invertebrate specimens. Thicker non-laminated beds have been removed by means of pneumatic drill while laminated beds, yielding most of the specimens, have been processed with hammers and different kinds of chisels. After having been collected, specimens were stored in the temporary building on-site, where a small preparation laboratory was available. Preparations were completed mechanically, both in the Nimaigu and PKU labs, by mean of very fine sharpened steel needles under binocular microscopes.

The matrix containing the fossil specimens is a light grey mudstone with very low or absent carbonate content. Consequently, chemical preparations using acids were not suitable, but diluted formic acid was sometimes used during the final part of the work.

Drawings were realized by camera-lucida device mounted on a binocular microscope and later compiled by the software Photoshop CS or were done based on photos aided by constant examinations of the specimens under a Nikon SMZ 645 binocular. Pictures were taken by Nikon D3100 with Nikkor 60mm Micro lens. Use of graphic program such as Adobe Photoshop CS5 was limited to improvement of the contrast.

Abbreviations

Anatomical abbreviations: Ang, angular; Ant, antorbital; B.fu, basal fulcra; Br, branchiostegal rays; Cl, cleithrum; Clv, clavicle; De, dentary; Dpt, dermopterotic; Dsph, dermosphenotic; Exsc, extrascapular; F.fu, fringing fulcra; Fr, frontal; Io3-5, infraorbitals; Iop, interopercle; Mx, maxilla; Na, nasal; Op, opercle; Pa, parietal; Pax.p, pelvic axillary process; Pcl, dorsal and ventral postcleithrum; Pel.r, pelvic rays; pl, anterior, middle and posterior pit lines; Pop, preopercle; Pt, posttemporal; Ro, rostral; Sob, suborbital; Sc, scales; Scl, supracleithrum; Scler, sclerotics; Smx, supramaxilla; So, supraorbital; Sop, subopercle.

Institutional abbreviations: GMPKU-P, Geological Museum Peking University, paleontological collection; XNGM-WS, Xingyi National Geological Park Museum-Wusha excavation collections.

Systematic Paleontology

Actinopterygii Cope, 1887

Neopterygii Regan, 1923

Teleostei sensu Arratia, 1999

Pholidophoriformes sensu Arratia, 2013

Pholidophoridae sensu Arratia, 2013

Malingichthys gen. nov.

Type species: *Malingichthys nimaiguensis* gen. et sp. nov.

Etymology: From the Maling Gorge, a famous deep canyon near Xingyi City, Guizhou Province, China, recalling the deepest part of pholidophorid history represented by the new genus.

Diagnosis (based on a unique combination of characters,*apomorphies): Small Pholidophoridae up to 65 mm in standard length (SL); *dermal skull roof bones (frontals, parietals, dermopterotics) independent or partially fused; dermal bones and scales covered by a smooth thin layer of ganoine except the jaw bones which are ornamented by longitudinal ganoine ridges; supramaxilla 1 very small, lying below the anteroventral process of supramaxilla 2; rostral triangular with somewhat notched anterior margin; *preopercle 'hockey-stick' shaped; posterior edge of scales serrated.

Stratigraphic and geographic distribution: So far known only from bed 35 of the vertebrate horizon yielding the Lower Assemblage of the Xingyi Fauna, in the Zhuganpo Member of the Falang Formation, at the excavation site of Nimaigu village, Wusha District, Xingyi City, Guizhou Province, China.

Zoobank register: http://zoobank.org/ urn:lsid:zoobank.org:act:4201A021-33AD-4497-9B8F-C62457E34317

Fig. 3 - *Malingichthys nimaiguensis* gen. et sp. nov. The single slab with the holotype GMPKU-P-3163 (in the upper position) and paratype GMPKU-P-3162 (in the lower position). Scale bar equals 5 mm.

Malingichthys nimaiguensis gen. et sp. nov.

Figs 3-7

Etymology: From Nimaigu village, where the excavation site is located.

Holotype: GMPKU-P-3163.

Paratypes: GMPKU-P- 3160/2, 3180, 3187, XNGM WS-35-F31, 33, 37, 45.

Type locality: Nimaigu village, Wusha District, Xingyi City, Guizhou Province, China.

Diagnosis (*apomorphies): *Jaws edentulous; left and right frontals and parietals fused to each other; *ventral blade of the preopercle expanded anteriorly, not showing sensory pores and tubules; *dorsal body lobe ending with a row of nine elongate scales.

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Description. Specimens are of small size, up to 65 mm in SL. They have a fusiform body, with body depth approximately 30% of SL. The head length is about 30% of SL and the orbit is moderately large, with its diameter about 25% of the head length (Figs 3, 4a, b). The depth of the caudal peduncle is about 17% of SL.

Skull. The snout is short and broad, consisting of a small, triangular rostral with somewhat embayed anterior margin and paired broad nasals that are sutured with each other for most of their length. The lateral margin of the nasals is notched to frame the posterior nostril opening. The supraorbital sensory canal is marked by three or four large pores (Fig. 4a, b).

The skull roof is rather broad. Frontals and parietals are fused to each other but the dermopterotics are independent. The fused frontals display a broad bell shape, with its maximum width just behind the orbit; anteriorly a stout triangular area slots in the region outlined by the posterior margin of the nasals (Fig. 4a). The supraorbital canal enters the frontal at its anterolateral corner, detectable by large pores (up to seven-eight) on the surface of the bone. The parietal plate is small and rectangular, with its width being about half the fused frontals. Pit-lines are usually well visible, the middle one extending also in the dermopterotic. The dermopterotic is a boot-like plate. The otic sensory canal ran along the lateral margin as detectable by one or two pores on the surface of the element. The large triangular extrascapula has a straight anterior margin, extending from the medial region of the parietal to the posterolateral margin of the dermopterotic, whereas its posterior margin shows a few denticulations. The supratemporal commissure run in the medial part of the element (Fig. 4a, b).

The circumorbital ring consists of antorbital, probably five infraorbitals and the dermosphenotic. The number of infraorbitals is inferred, being the elements Io1 and Io2 not visible on specimens. The antorbital is an antero-posteriorly, slightly bent, elongated bone, lying against the anterior arm of the maxilla and contacting the rostral bone at its anterior end. Infraorbital 3 is a large irregular element at the posteroventral corner of the orbit, slightly overlapping the anterior margin of the preopercle (Fig. 4a, b). An almost horizontal pit-line groove is present, making the anterior division of the supramaxillary pit-line, being usually coupled by a vertical groove on the preopercle (the posterior division) (Fig. 4b). Dorsally, Io3 contacts both the small squarish Io4 and the large suborbital. Infraorbitals 4 and 5, posteriorly bordering the orbit, are almost equal in size. Their posterior margins commonly

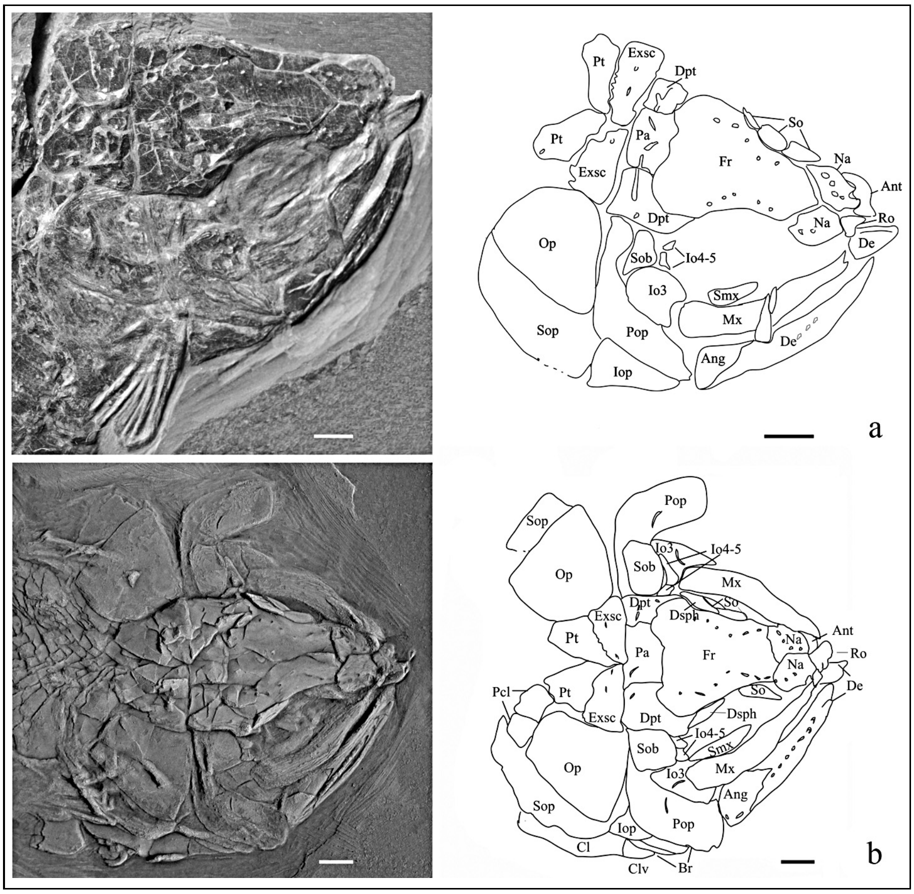

Fig. 4 - *Malingichthys nimaiguensis* gen. et sp. nov. a) Skull and corresponding camera-lucida drawing of GMPKU-P-3162; b) skull and corresponding camera-lucida drawing of GMPKU-P-3160. Scale bars equal 2 mm.

have one or two sparsely placed serrations that overlap the suborbital (not shown in Fig. 4b). Tubules or pores of the infraorbital sensory canal are not visible. A large single suborbital lays dorsal to Io3 and shows a few concentric thin ridges of ganoine.

Jaws. The maxilla and at least one supramaxilla are preserved. The gently curved maxilla is as long as the lower jaw or slightly longer, extending to the posterior half of the orbit. Posterior to the straight and narrow anterior region, the dorsal margin of the bone is slightly concave, to contain the elongate posterior supramaxilla (Fig. 4a, b). Anterior to this, there is a small space for a possible very small anterior supramaxilla. The posterior margin of the maxilla is gently oblique. The oral margin is edentulous. The external surface of the maxilla and supramaxillae is ornamented with longitudinal ganoine ridges. The lower jaw shows an almost straight oral margin in its anterior half, while the coronoid process is never visible. Dentary and angular are detectable, the dentary extending well below the angular. A short vertical pit-line lies at the posteroventral corner of the angular (Fig. 4b). A series of large pores indicates the course of the mandibular canal. As for the maxilla, longitudinal ridges of ganoine ornament the dentary.

Opercular region. The opercle is a broad, roughly shield-like bone, almost as long as deep. The subopercle is smaller, half the depth of the opercle, its anteroventral margin being oblique and sutured to the large triangular interopercle (Fig. 4a). The anterior tip of the latter extends below the anteroventral margin of the preopercle, close to the posterior margin of the lower jaw.

The preopercle is hockey stick-shaped, its anterior region projecting anteriorly to the far end of the mandible. Its anteroventral margin is smooth, without a notch at the entrance of the sensory canal. The dorsal portion of the preopercle is largely covered by the suborbital (Fig. 4b). The path of the preopercular sensory canal cannot be easily followed as no pore is present, however, it appear as it ran along the midline of the bone A groove housing the posterior division of the supramaxillary pit-line is visible in some specimens (GMPKU-P-3162, Fig. 4b).

There are at least seven branchiostegal rays. They are elongate, ribbon-like in shape, and with thick smooth ganoine on the surface.

Vertebral column. Though scarcely ever visible as in most fishes covered by ganoid scales, the endoskeletal post-cranial elements are visible in two specimens (XNGM WS-35-F31-37) as the exposed flank shows some gaps in the covering, due to taphonomic events. However, the preservation of the axial skeleton is quite poor as if all the structures were not well ossified (e.g.,

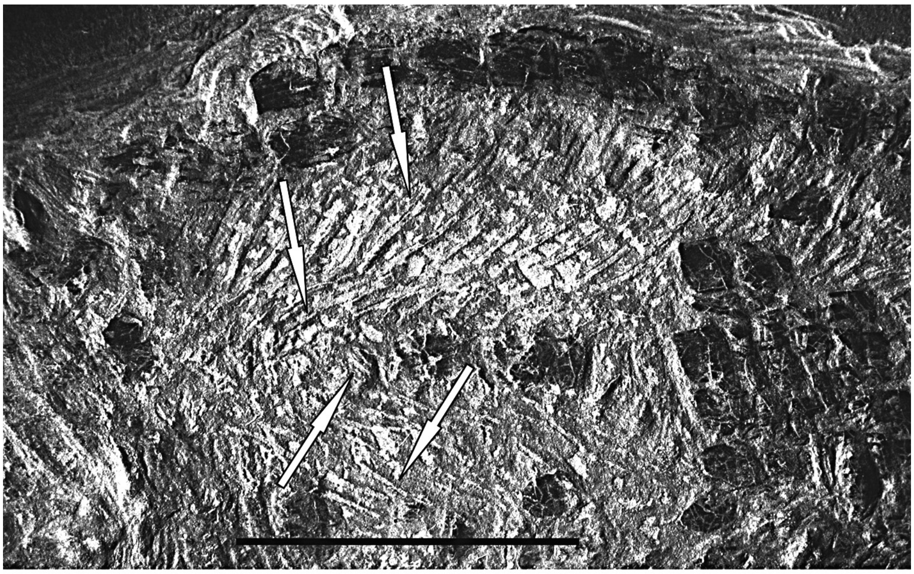

Fig. 5 - *Malingichthys nimaiguensis* gen. et sp. nov. Specimen XNGM WS-35-F31, partially disarticulated specimen, lacking the abdominal left scale covering. Arrows point to: upper left, neural arches; upper right, supraneurals; lower left, hemichordacentra; lower right, ribs. Scale bar equals 10 mm.

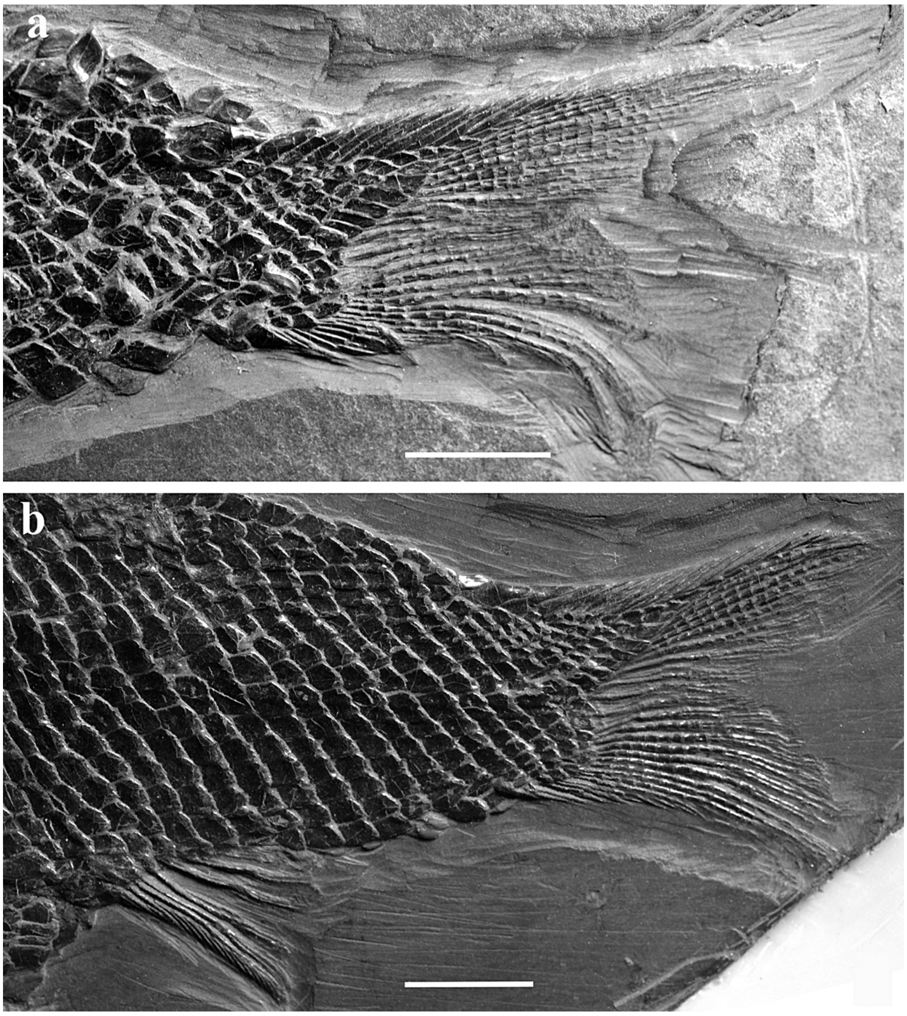

Fig. 6 - *Malingichthys nimaiguensis* gen et sp. nov. a) Specimen GMPKU-P-3161, caudal fin; b) the holotype, specimen GMPKU-P-3163, caudal region showing anal and caudal fin.

neural arches and spines, ribs) or mineralized (e.g., chordacentra). This is true especially for the hemichordacentra which are identifiable by their semicircular shape when they are preserved in axial view. For the first time elongate abdominal ribs and supraneurals are recorded in Pholidophoriformes (Fig. 5), though their exact shape, histology and distribution cannot be achieved in detail owing to the preservation.

Paired fins. Some dermal elements of the pectoral girdle are poorly visible on most of specimens. The paired shield-like posttemporals meet each other and are partially overlapped by the posterior margin of the

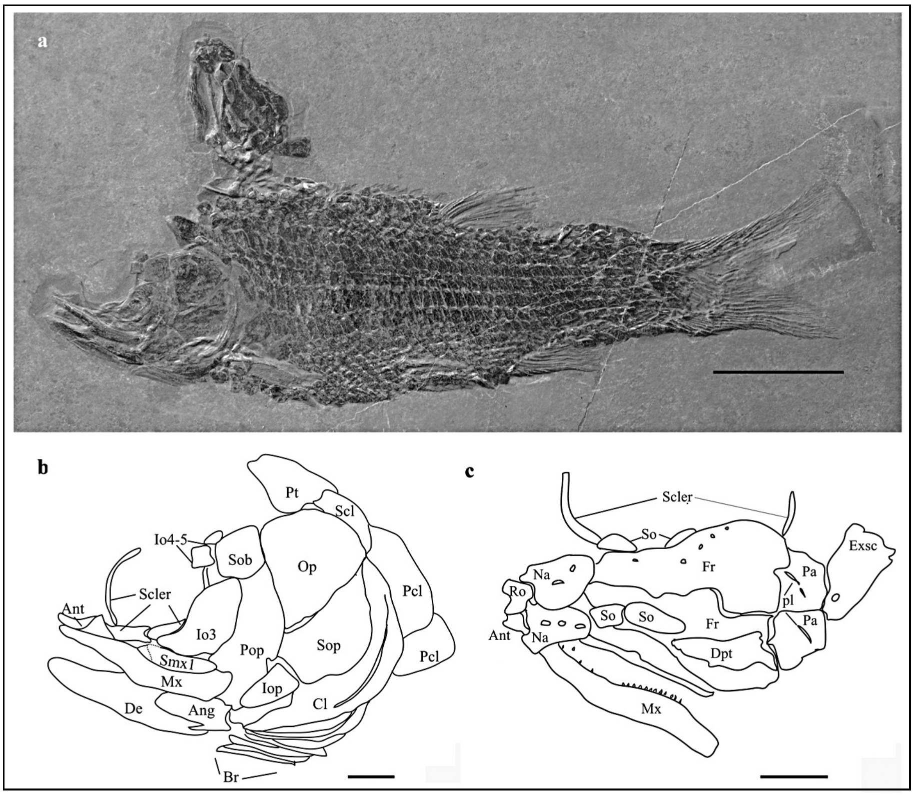

Fig. 7 - *Malingichthys wanfenglinensis* gen. et sp. nov. The holotype GMPKU-P-3181. a) The complete specimen showing the partially disarticulated skull. Scale bar equals 5 mm; b-c) camera lucida drawings of the splitted skull; b - mostly lateral view of the skull still attached to the body; c - detached skull roof, note reversed position of the scattered maxilla.

extrascapulars. The cleithrum is only partially exposed, since most of its anteromedial region is overlapped by adjacent dermal bones in the available specimens. Only the ventral ramus of the cleithrum is well visible in specimen GMPKU-P-3160, showing its suture with the small triangular clavicle. Two rather small, quadrangular postcleithra are present.

The pectoral fins have a low position, as illustrated by the few remnants of fin rays, of which the first fin ray is a compound element (sensu Arratia 2013) made by the fusion of a large basal fulcrum and a few fringing fulcra. Owing to the dorso-ventrally flattened preservation, as with most specimens, the pelvic fins are not visible in the available specimens.

Median fins. The triangular dorsal fin is placed at the level of 22nd scale row. There are about 10 principal rays. Four basal fulcra and a series of well-developed fringing fulcra lie on the first ray. Between the 3rd and 4th basal fulcra, there is one fringing fulcrum.

The insertion of the small anal fin is at the level of the 19th or 20th vertical row of scales. Three basal fulcra and a series of elongate fringing fulcra are associated with the first ray.

The caudal fin is of abbreviate heterocercal type, deeply forked (Fig. 6a, b). The dorsal margin has nine or 10 large basal fulcra followed by a series of elongate fringing fulcra. Lepidotrichia are robust and 21 or 22 principal rays follow an epaxial rudimentary ray (see Arratia 2013). Along the ventral margin, fringing fulcra are present; some of them lie between the procurrent rays.

Scales. The body is covered by ganoid scales. All scales are serrated posteriorly and have a smooth surface. Serrations decrease in number posteriad, and in the caudal peduncle only two or three serrae are still present on each scale. In the abdominal region, four horizontal rows of scales are much deeper than long, comprising one dorsal and two ventral to the lateral line one. In the caudal peduncle, the scales are of approximately uniform size and rhombic. The axial body lobe is rather short: the last row is made of nine longer than deep scales above the last lateral line scale. Approximately 37 scales carried the lateral line canal: these scales show a small posterior slit and accessory pores are also present at the center of very few of them.

$$\text{Pterygial formula: } \frac{D23}{P?A18C34}T38$$

Malingichthys wanfenglinensis gen. et sp. nov.

Figs 7- 9

Etymology: From Wanfenglin, translated as "Forest of Ten Thousand Peaks", a karst region nearby Xingyi City characterized by pointed rocky hills giving rise to a toothed skyline, remembering the teeth of this new species.

Holotype: GMPKU-P-3181, the only known specimen.

Type locality: Nimaigu village, Wusha District, Xingyi City, Guizhou Province, China.

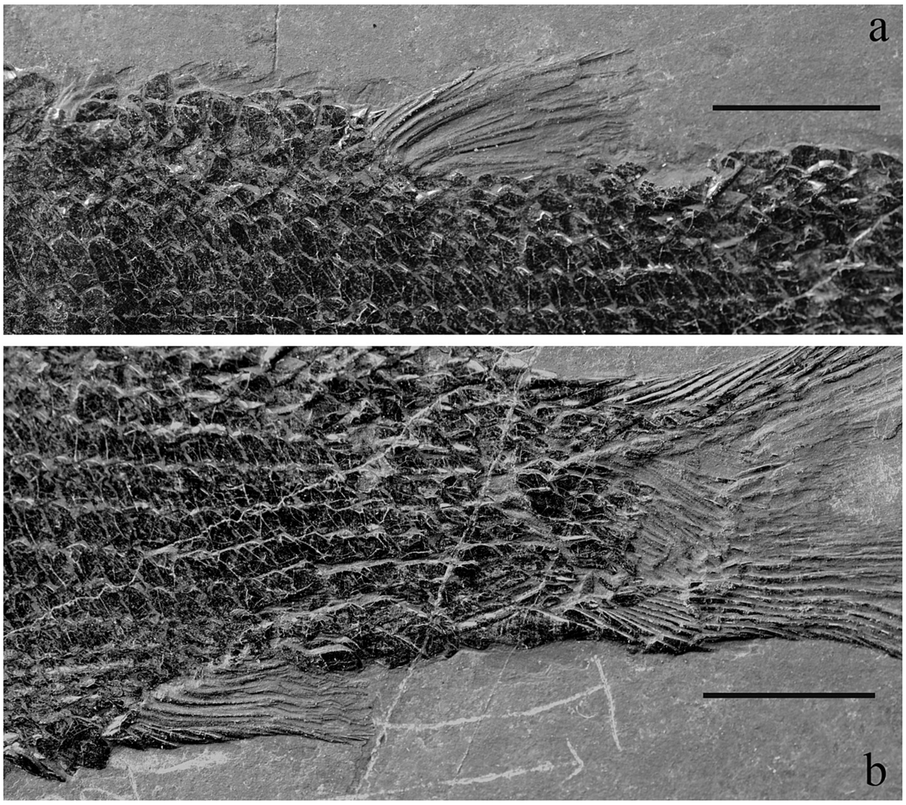

Fig. 8 - *Malingichthys wanfenlingensis* gen. et sp. nov., the holotype specimen GMPKU-P-3181. a) The dorsal fin; b) the anal fin. Scale bars equal 5 mm.

Diagnosis (*apomorphies): *Malingichthys* with *dermal skull bones still completely separated; *conical teeth well developed along oral margin of jaws; ventral blade of the preopercle not very expanded; sclerotic ring made by two sclerotic bones, anterior and posterior to the eye.

Zoobank register: http://zoobank.org/ urn:lsid:zoobank.org:act:628C6B33-9A8C-4AE8-A996-49A2A1937A72

Description. The holotype, and only known specimen, is 48 mm in SL (Fig. 7) and about 58 in total length. Head is about 32% of the SL. The following description will concentrate on features that hitherto differentiate this species from the type species.

The frontals and the parietals are not fused to each other or with other skull bones. The interfrontal suture is sinuous, mainly posteriorly, where a remarkable indentation is present. The paired parietals are small, squarish in shape, with evident pit-lines. The maxilla is rather slender and it bears a complete series of conical teeth all along the oral margin. In addition, the maxilla shows a marked curvature, with a supramaxillary process more developed than in *M. nimaiguensis*. The supramaxilla 1 lies below the anterior process of the supramaxilla 2, being less than 1/3 the length of the latter. The mandible has a very short and straight anterior margin, and ascends posteriorly in an almost oblique line. No 'leptolepid' notch is visible. There are probably five infraorbitals, but only Io3, Io4 and Io5 are visible, making the postero-ventral margin of the orbit: Io3, contacting the anterior margin of the preopercular bone, is the largest element, while Io4 and Io5 are small quadrangular elements just in front of the suborbital. An elongate element, lying above the distal tip of the maxilla of the complete specimen (Fig. 7b) and in the space between left nasal and the rostral in the isolated skull of GMPKU-P-3181 (Fig. 7c) is interpreted as antorbital owing to its position and relationships with surrounding bones.

The ventral region of the preopercle appears smaller than in *M. nimaiguensis*.

The dorsal fin (Fig. 8a) and anal fin (Fig. 8b) are placed at the level of 22nd and 21nd scale rows, respectively. The left pelvic fin is visible and shows a large leaf-like well ossified pelvic axillary process as in all other pholidophorids[1] (Fig. 9).

Pterygial formula: $\dfrac{D22}{P9A21C35}T39.$

Taxonomic comparisons

The close affinity of the new genus with other Pholidophoridae genera is evident considering some of the most important synapomorphies, such as the nasals patterns, the trend in skull roof fusion, the presence of pelvic axillary process (following Arratia 2013), the characteristic longitudinal ridges of ganoine on jaw bones, the posterior region of Io3 extending below the suborbital bone and reaching the anterior margin of

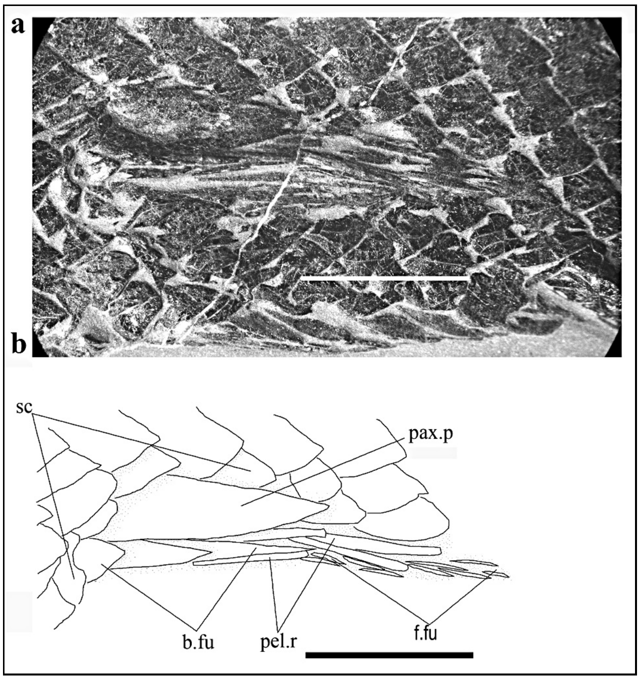

Fig. 9 - *Malingichthys wanfenglinensis* gen et sp. nov. a) Photograph, and b) drawing of pelvic axillary process and fulcra in lateral view (the holotype specimen GMPKU-P-3181). Scale bars equal 2 mm.

preopercle, and a well-developed, protruding lateral bony ridge extending along the dentary and separating dental and splenial regions. Additionally, supraneural bones are described for the first time in Pholidophoriformes: their very light structure could explain why usually they are not preserved/seen in the specimens of the other genera.

As already pointed out, the nasals pattern is one of the key features in distinguishing pholidophorid taxa (Zambelli 1990; Arratia 2013). Based on this character, most pholidophorid genera are ruled out from the comparison having nasals totally separated by the anterior tip of the frontal(s), but *Eopholidophorus*, *Pholidoctenus* and *Pholidophoretes*. In *Malingichthys*, as in the three above cited genera, the nasals are medially joined for most of their length, the anterior tip of the fused frontals being far from the rostral bone (Zambelli 1990; Arratia 2013). It must also be pointed out that this is the same pattern shown by *Prohalecites* (Tintori 1990), Late Ladinian in age as *Malingichthys* and previously considered as sister to Teleostei (Arratia 2013).

Pholidoctenus differs from *Malingichthys* as it shows important serrated posterior margin of several dermal bones and most scales, while in *Malingichthys* only extrascapulars have denticulated posterior edge and the scales are pectinated in their posterior margin. Differences are also in the shape of the preopercle and in the pattern of fusion of the dermal skull roof, almost totally fused in a single plate in *Pholidoctenus*. The first supramaxilla is much larger in *Pholidoctenus* than in *Malingichthys*.

Pholidophoretes and *Eopholidophorus* can be separated from *Malingichthys* mostly by the shape of the preopercle and by the rate of fusion of the frontal, parietal and dermopterotic, which appear almost totally fused in the former genera while they are still partly separated in *Malingichthys*. They are also larger (70-82 mm in SL) than the average *Malingichthys* specimens (55-70 mm). *Eopholidophorus* has the first supramaxilla larger than *Malingichthys*, while in *Pholidophoretes* this element is as elusive as in *Malingichthys* itself.

Leaving the different age (Late Ladinian vs. Early Carnian/Norian) and the geographical distribution (Eastern Tethys vs. Western Tethys) apart, the erection of the new genus *Malingichthys* is well supported by the anatomical differences mentioned above and by its autapomorphies.

Implications to a late Middle Triassic faunal turnover

The new finds in the Late Ladinian Xingyi Fauna suggest the origin of Pholidophoriformes to be two million years before the previous estimate and support an early diversification of pholidophorid teleosts, especially given that at least two species were already present in the Xingyi Fauna. The age of the new taxa corresponds to that of *Prohalecites porroi*, coming from the Kalkschieferzone (Meride Limestone) of the Monte San Giorgio area (Italy and Switzerland) and from the Perledo-Varenna Formation in the Grigna Mountains (Lecco, Italy) (Tintori 1990; Tintori et al. 2010). *Prohalecites* has been previously proposed as the oldest teleosteomorph sister to the Teleostei (Arratia 2000, 2013), or more primitive to other teleosteomorphs, like aspidorhynchiforms and pachycormiforms (Arratia & Tintori 1999).

Pholidophoridae was a clade traditionally considered typical of the Triassic Late Fish Fauna (TLFF) (Arratia 2013; Tintori et al. 2014) and restricted to the western Tethys, being most genera recorded from the Norian (Late Triassic) of Austria and Italy, where they were dominant, reaching in some cases the 70% of the collected specimens (Tintori et al. 2010). The Early Carnian genera, represented by *Knerichthys* from Raibl/Cave del Predil (Friuli, Italy) and *Pholidophoretes* from Lunz (Austria), seem to be rare, with relevant fish assemblages being still dominated by subholosteans such as Peltopleuriformes and Pholidopleuriformes (Griffith 1977; Tintori & Sassi 1992; Dalla Vecchia 2008), in particular for the Raibl Fauna (Friuli, Italy) which possibly covers most of the Julian (Early Carnian) with different sub-assemblages (A. T. pers. obs.).

Thus, the description of the oldest stem teleost from the Xingyi Fauna points to the Late Ladinian as one of the key events in the Mesozoic actinopterygians evolution. This turning point also corresponds to other bioevents, such as the disappearance of most of the miniature fossil fishes (less than 40 mm in SL) that had been common during most of the Middle Triassic. The Xingyi Fauna preserves the last blooming of small species, such as *Habroichthys orientalis* (Lin et al. 2011) with SL of up to 30 mm, and other unnamed peltopleurids with a SL not more than 40 mm. Small to very small fishes are easily overlooked if efforts for systematic excavations are lacking.

In the case of the Xingyi Fauna, *Habroichthys orientalis*, was known only from a few specimens (Su 1959; Lin et al. 2011) until our bed-by-bed excavation brought to the light hundreds of specimens from only a few square meters of a single bed (W-35). The newly revealed numerical dominance of small fishes in the Xingyi Fauna allows revising the previous interpretation of the structure of the vertebrate assemblage therein. The presence of very small fishes, with SL around 30-40 mm, namely *Habroichthys, Peltopleurus, Peripeltopleurus, Altisolepis, Placopleurus, Prohalecites, Marcopoloichthys*, is typical of the Triassic Middle Fish Fauna (TMFF) (Tintori et al. 2014) elsewhere in the world (Lombardo 1999; Lin et al. 2011; Tintori et al. 2014). In contrast, only a few species with SL being shorter than 30-40 mm are recorded from the subsequent Carnian and Norian fish assemblages of China and Alps (Tintori et al. 2014; Tintori et al. 2010), which became gradually dominated by pholidophorids. In the Norian, pholidophorids are the commonest small taxa but they are slightly larger, ranging from 50 to 100 mm (Tintori et al. 2010). Such a dramatic change in average body size in the fish faunas between the Ladinian and the Carnian has still to be understood, as doubtful remains its relevance to the recognition of the first appearance of pholidophorid teleosts.

Anyway, the appearance of stem teleosts probably coincided with a large-scale turnover in marine vertebrate assemblage (Tintori et al. 2014; Jiang et al. 2014).

Conclusions

The oldest fossil records of Teleostomorpha are all reported from the Late Ladinian (Middle Triassic ca. 238-239 Ma) of the Tethys. Of these teleostomorphs, *Malingichthys* is the only representative of Teleostei (sensu Arratia 2013). The paleontological record suggests that there was a rapid diversification of Triassic teleostomorph fishes, such as *Prohalecites* (Tintori 1990; Stockar et al. 2012; Tintori et al. 2014) at least in the Late Ladinian, giving also rise to stem-Teleostei. The new Pholidohoridae genus suggests that the South China Block was the area in which many novelties arose also in the Late Ladinian (Tintori et al 2012). This geographic pattern was already established since the end of the Early Triassic, when a diversified marine vertebrate fauna appeared in the area, while only sparse finds are known elsewhere (Sun et al. 2013; Motani et al. 2014; Tintori et al. 2014). The longitudinal migrations across Tethys possibly proceeded fast because both flying fishes and pholidophorids were then present in the western Tethys at least at the very base of the Carnian (Tintori & Sassi 1992; Dalla Vecchia 2008; Arratia 2013).

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