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A NEW BASAL NEOPTERYGIAN FROM THE MIDDLE TRIASSIC OF LUOPING COUNTY (SOUTH CHINA)

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Abstract. A new taxon belonging to Neopterygians is described, based on very nicely preserved specimens from the rich vertebrate levels recently discovered in Luoping County, Yunnan Province, South China. This new assemblage dates to Pelsonian (Anisian, Middle Triassic), about the same age of the Panxian Fauna from the nearby Guizhou Province. The Luoping Fauna, yielding this new taxon, is turning out to be one of the most important fish faunas of the whole Middle Triassic and the oldest evidence of the fish radiation of this time span. This new genus of basal neopterygian shows unique derived characters, especially for the almost naked body, with a single row of urodermals covering the body lobe in the tail and a row of very small and thin scales bearing the lateral line canal along the flank. Also in the axial skeleton the new taxon shows peculiar characters such as the neural spines perfectly aligned to each paired neural arches and abdominal ribs well developed. Concerning skull bones, no suborbitals have been detected.

Riassunto. Viene descritto un nuovo taxon appartenente ai Neopterygii basali rinvenuto in un livello fossilifero a vertebrati della Provincia dello Yunnan (Cina Meridionale), recentemente scoperto. Il giacimento fossilifero è situato nei pressi del villaggio di Dawazi, Luoping County, ed ha un'età pelsonica (Anisico medio, Triassico Medio) venendo a costituire al momento la principale e più antica fauna a pesci del Triassico Medio stesso. Il nuovo genere e nuova specie presenta caratteri peculiari in quanto privo di copertura di scaglie ganoidi, ad eccezione di un fila di urodermali che ricoprono il lobo assiale dorsale della coda e di piccole scaglie prive di ganoina lungo la linea laterale. L'endoscheletro assiale presenta pure una struttura peculiare nei rapporti tra gli archi neurali pari e le spine neurali mediane: questi elementi, presenti fino al termine della pinna dorsale, si presentano infatti perfettamente allineati. Questo nuovo taxon dimostra come la radiazione medio-triassica sia stata da un lato molto importante e dall'altro più antica rispetto a quanto finora supposto sulla base delle faune della Tetide occidentale e del Monte San Giorgio in particolare.

Introduction

The recent discovery of a new vertebrate assemblage in the Upper Member of the Guanling Formation (Pelsonian, Middle Anisian, Middle Triassic), exposed around the Dawazi village (Luoping County, Yunnan Province, South China), proved to be one of the most important finds in the last decades for marine fishes of that age (Fig. 1). The preliminary field investigation suggests that it could yield more than 25 taxa of Actinopterygians and Crossopterygians, most of them represented by very well-preserved specimens. Among others, *Saurichthys* is known with at least 8 species (Wu et al. 2009) and it is found also in mass mortality surfaces, while *Sangiorgioichthys* (*Archaeosemionotus* in Sun et al. 2009), seems to be by far the most common fish, found in very crowded mass mortality surfaces too (López-Arbarello, submitted; Sun et al. 2009). The vertebrate level is subdivided in a lower part (LVH, Lower Vertebrate Horizon, 2 m thick), and in an upper part (UVH, Upper Vertebrate Horizon, 10 m thick): the lithology is quite different throughout the UVH and the much thinner LVH, meaning that paleoenvironment varied during the depositional interval. Very preliminary field works during the summer 2008 pointed to the presence of *Sangiorgioichthys* and *Placopleurus* in all the beds of the LVH, while other taxa have been recorded only in one or few beds. The fossil assemblages are made also of marine reptiles, different arthropod groups (isopods, decapods, horse-shoe crabs, mysidiaceans, etc.), molluscs (mainly gastropods, concentrated in a

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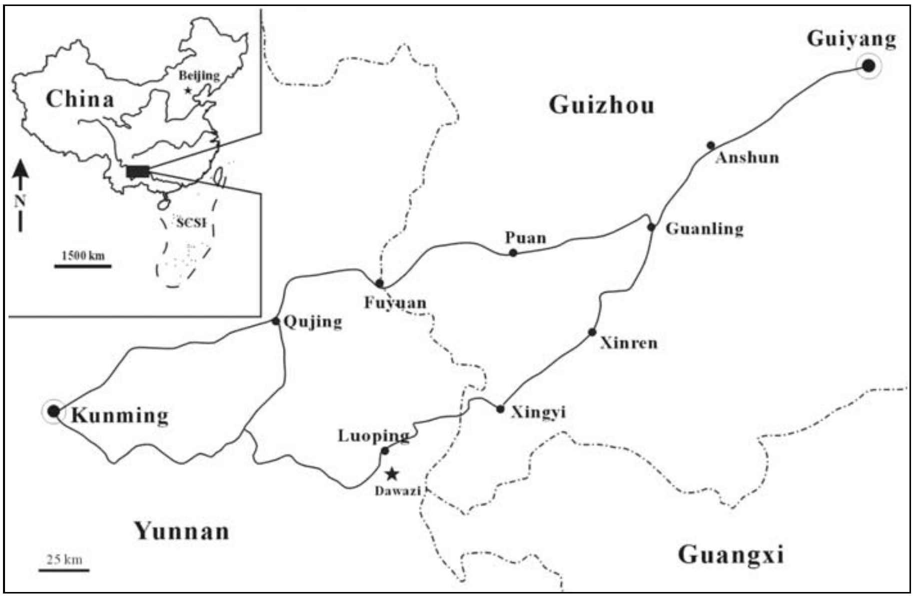

Fig. 1 - Geographic localization of the village of Dawazi (Yunnan Province, South China), where the new middle Anisian fossiliferous level crops out.

few beds) and terrestrial plants. A few beds in the LVH are also rich in large bioturbations. Although we know that many fish specimens are from the UVH, no detailed work by the PKU team has been done so far in this part.

Following the traditional Chinese way of naming the fossil fauna from the nearby major locality, this vertebrate fauna was considered as ‘the Luoping Fauna’ (Tintori et al. 2008; Sun et al. 2009) of Pelsonian age (middle Anisian, Middle Triassic), based on the presence of the conodont *Nicoraella kockeli* from the fossil-bearing layers. This new fish-assemblage should be considered of about the same age of the Panxian Fauna (Motani et al. 2008; Jiang et al. 2009). However, it is clear that there are some interesting differences regarding the fish taxa yielded by the two faunas, even if we must keep in mind the very different preservation quality from the two sites, with the Panxian Fauna being quite poor in both number of specimens and quality of preservation. The Luoping Fauna seems to be much richer in taxa, such as for *Saurichthys* species (Wu et al. 2009) and other new taxa under study, while, on the other hand, *Colobodus,* common in Panxian (Sun et al. 2008) seems to be absent.

Among Luoping Fauna highly diverse fossil fishes, we describe herein a new taxon, an almost totally naked actinopterygian showing very peculiar features in its postcranial skeleton (Fig. 2). Middle Triassic fishes with a naked body are very rare, as both paleopterygians and basal neopterygians are usually totally covered by more or less heavy ganoid scales. However, *Saurichthys* and *Birgeria*, large or very large predators with a highly reduced scale covering, present in most Triassic sites all over the world, were among the most successful Triassic fishes. Scaleless basal neopterygians were on the other hand very small, such as *Prohalecites* (Tintori 1990) and *Marcopoloichthys* (Tintori et al. 2008) and so far only the latter genus shows a wide stratigraphical and geographical range. Then, the new taxon here described can be considered as the largest naked basal neopterygian so far known in the Triassic deposits. Lack of information regarding the postcranial skeleton for most of the paleopterygians and basal neopterygians makes the characters discovered in the vertebral column elements or in the fins endoskeleton not easy to be interpreted and compared as we do not know the actual inner anatomy of most taxa.

Institutional Abbreviations: GMPKU, Geological Museum of Peking University, Beijing, China.

Abbreviations: afr, anal fin radials; ang, angular; ant, antorbital; br, branchiostegal rays; cl, cleithrum; dcs, dorsal caudal scute; dfr, dorsal fin radials; dpt, dermopterotic; dsph, dermosphenotic; ect, ectopterygoid; end, endopterygoid; exsc, extrascapular; fr, frontal; gu, gular; ha, haemal arches; haI, first haemal arch; hs, haemal spines; hyI, first hypural; hym, hyomandibular; ifo, infraorbitals; iop, interoperculum; ldfr, last dorsal fin radial; llj, left lower jaw; llls, last lateral line scale; lls, lateral line scales; mx, maxilla; na, nasal; ns, neural spines; op, operculum; pa, parietal; pcl, postcleithrum; pmx, premaxilla; pna, paired neural arches; pop, preoperculum; psph, parasphenoid; pt, posttemporal; q, quadrate; qj, quadratojugal; r, ribs; rlj, right lower jaw; ro, rostral; scl, supracleithrum; smx, supramaxilla; sop, suboperculum; ud, urodermals.

Paleontological Descriptions

Class **Osteichthyes** Huxley, 1880

Subclass **Actinopterygii** Cope, 1887

Infraclass **Neopterygii** Regan, 1923
(sensu Patterson 1973)

Genus *Gymnoichthys* gen. n.

Type species: *Gymnoichthys inopinatus* sp. n., by monotipy.

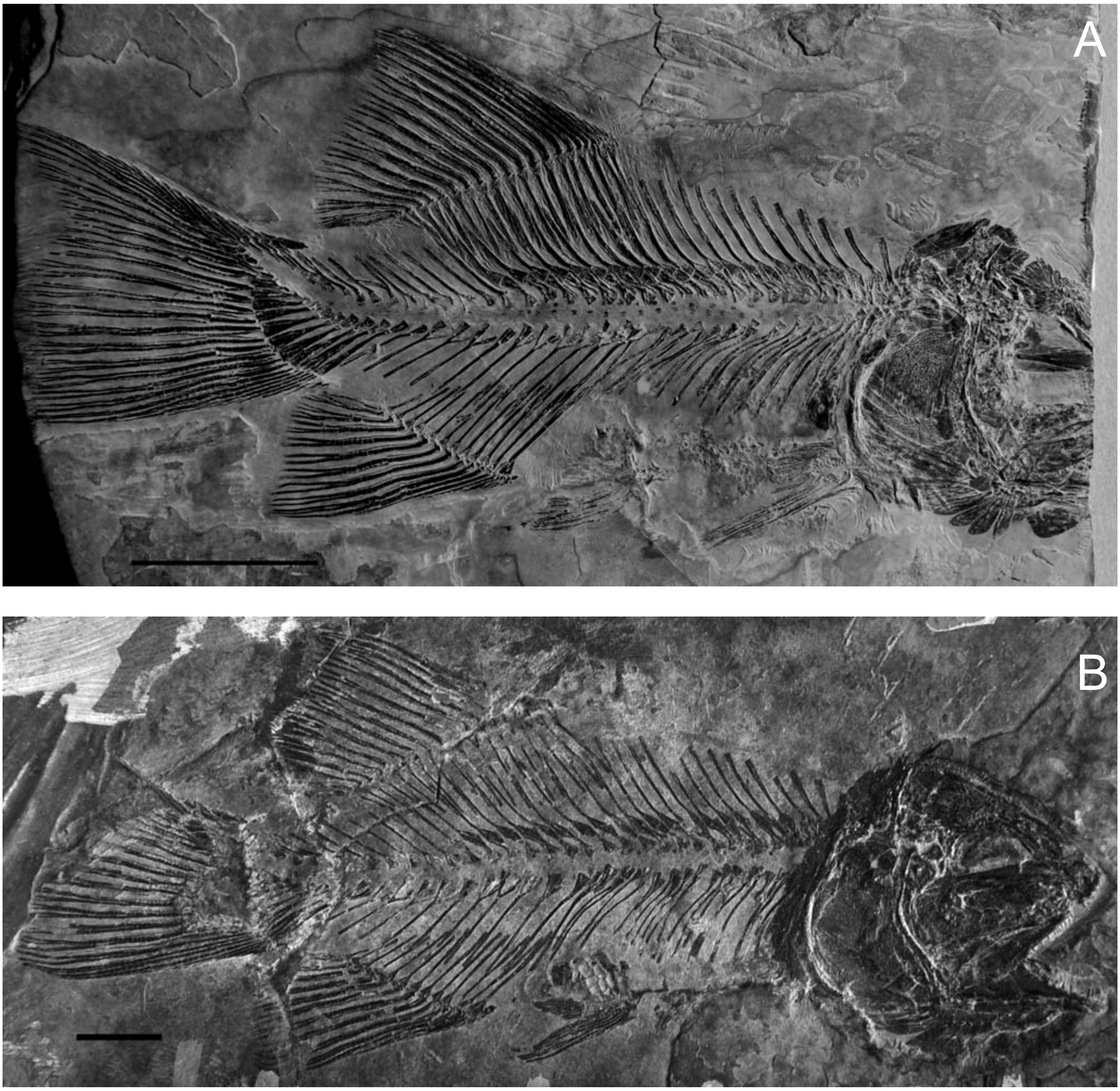

Fig. 2 - *Gymnoichthys inopinatus* gen. n. sp. n. A) The holotype, specimen GMPKU-P-1483, scale bar: 20 mm; B) specimen GMPKU-P-1687 (horizontally reversed); scale bar: 10 mm.

Etymology: From the old Greek "gymnos", naked, and "ichthys", fish.

Diagnosis: as for the type and so far only known species.

Gymnoichthys inopinatus gen. n. sp. n.

Figs 1-6; Pl. 1

Etymology: From Latin word *inopinatus*, unexpected, unrehearsed, as the new taxon is devoid of the ganoid scale-covering, unusual in that time for the neopterygian fishes.

Type locality: Near the village of Dawazi, Luoping County, Yunnan Province, South China).

Holotype: Specimen GMPKU-P-1483, an almost complete specimen lacking only the tip of the snout, probably from the UVH.

Paratypes: Specimens GMPKU-P-1484-1485-1686-1687-1688 (specimens only partly prepared).

Other material: Specimen GMPKU-P-1683-1689, unprepared specimens.

Age and stratigraphic distribution: From the Pelsonian conodont *Nicorella kockeli* zone (middle Anisian, Triassic); Vertebrate Level of the Upper Member of Guanling Formation, mainly from UVH.

Geographic distribution: So far know only around the village of Dawazi (Luoping County, Yunnan Province, Southern China).

Diagnosis: Medium size, almost naked basal neopterygians with a high fusiform body. Postero-ventral infraorbital much larger than the others; no suborbitals. Ventral surface of parasphenoid and median surface of palatal bones totally covered by small teeth. Skull dermal bones with a ridged external surface, but with scarce ganoine covering. Vertebral column with no ossified or calcified centra. Auto-

Fig. 3 - *Gymnoichthys inopinatus* gen. n. sp. n. A) Skull of the holotype GMPKU-P-1483; scale bar: 10 mm; B) snout of specimen GMPKU-P-1484; scale bar: 5 mm; C) skull of specimen GMPKU-P-1688; scale bar: 5 mm.

geneous neural spines showing an enlarged leaf-like proximal end articulated to the corresponding enlarged distal area of paired neural arches. Short neural arches fused to the neural spines beginning from the end of the dorsal fin. Ossified ribs present, followed by haemal arches with a median spine at level of the insertion of the anal fin. Squamation constituted only by very small scales, arranged in a discontinuous row along the lateral line and in a single urodermal row on the dorsal body lobe of the hemiheterocercal tail. Last radial in both dorsal and anal fins supporting the last two or three lepidotrichia. Median fins with very small scutes, several basal fulcra, very few and thin fringing fulcra. Size up to at least 105 mm (S.L.); about 44 vertebral segments comprising the ural ones. All fins large and made by rather elongate lepidotrichia. Pectoral and pelvic fins made respectively by 13 and 8 lepidotrichia, dorsal and anal fin by 19 and 14 lepidotrichia. Caudal fin with 10 dorsal caudal fulcra, 3 dorsal unbranched, 17 segmented and branched, 3 ventral unbranched (at least two of them bearing few tiny fringing fulcra), 2-3 ventral caudal fulcra and 1-2 ventral scute. Dorsal body lobe with a single row of 12-13 urodermals. Cleithrum and postcleithrum ornamented by very low ridges with a dendritic pattern posteriorly directed.

Description. The description is mainly based on the holotype and on paratypes: although the skull is well preserved in all these specimens (Fig. 3), most of the information are yielded by the holotype and GMPKU-P-1484-1688. The size of the specimens varies from about 70 to 110 mm in s.l. (90 to 135 mm in total length). The body is quite short, in the adult stage, the maximum depth of the body (measured at the origin of the dorsal fin) varying from about 20% (GMPKU-P-1485, s.l. of 71 mm) to 30% (GMPKU-P-1484, s.l. of 80 mm) and to 36% (the holotype, s.l. of 105 mm) of the s.l. itself.

Skull (Figs 3-4). The snout is not preserved in the holotype while in the specimen GMPKU-P-1688 is well visible, even if the delicacy of the bones and their crushing makes difficult to detect the relative positions of elements or some of their details. The elements making the snout region consist of narrow tube-like bones bearing sensory canal: a wide median area lacks dermal bone covering. The antorbitals are L-shaped, with dorsal and medial regions of nearly equal length. They probably contacted the first infraorbital with the vertical posterior region and the rostral and ventral part of the nasals with the horizontal one. The nasals are slender and elongated dorso-ventrally: pores of the sensory canal are not detectable. The rostral is also tube-like, a rather short curved element included between the antorbitals. The frontals are broad, made by an almost rectangular anterior region, with a lateral constriction corresponding to the dorsal orbital margin, and a more expanded posterior one. The anterior margin shows two lateral short projections and a wide median tip, while the posterior border, contacting the parietals, is rounded and strongly irregular, with a well developed prong at about the middle of its depth. The interfrontal suture is only slightly wavy. The supratemporal sensory canal entered

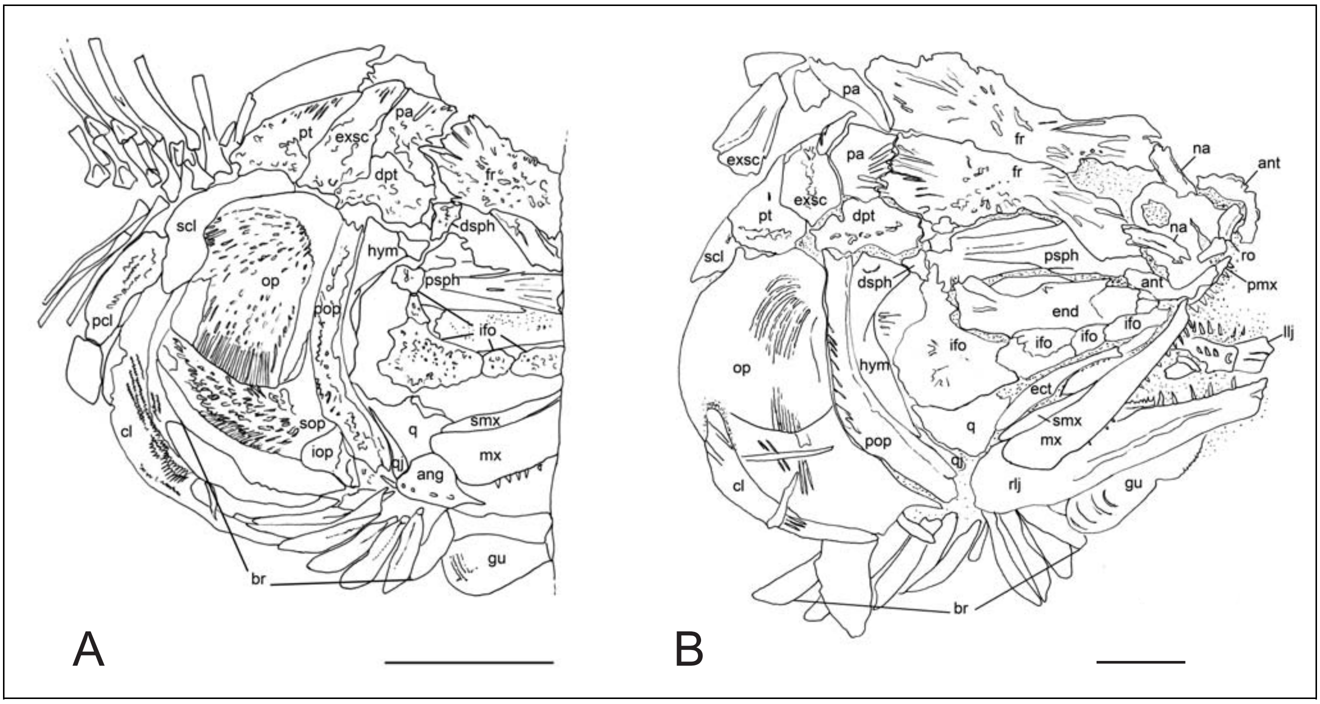

Fig. 4 - *Gymnoichthys inopinatus* gen. n. sp. n. A) Camera lucida drawing of the holotype head, specimen GMPKU-P-1483; scale bar: 10 mm; B) camera lucida drawing of the skull of specimen GMPKU-P-1688; scale bar: 5 mm.

the frontal in the antero-lateral corner of the element, in correspondence to the short lateral projection, and ran along the lateral border, at the level of the orbit. In the posterior region of the frontal the sensory canal moves towards the median region, but its precise course is not detectable, owing to the irregular surface of the bone; in this region, at about 2/3 of its length, the frontals show ridges and numerous openings radiating from the median part of the bone. The sensory canal enters the parietal in correspondence to the posterior projection.

The parietals are small and rectangular, elongated dorso-ventrally; the sutures between the two elements and with extrascapulars are wavy, while the contact with frontals and dermopterotics is very irregular. The sensory canal coming from the frontal ran on the lateral region of the bone and stopped before the posterior margin of the element; the single pores are not detectable. Also in the parietals, crests of ganoine tend to be arranged in the same radiating pattern as they are in frontals. Dermopterotics are rectangular, longer than deep, with an irregular outline. Each element is surrounded by extrascapular, parietal, frontal and dermosphenotic; ventrally, contacts are not clear, but they probably reached the dorsal end of preopercular. Sensory canal ran along the ventral border of the bone, but the irregular surface disguises the real course of the pores. Two deep triangular extrascapulars are enclosed between posttemporal posteriorly and parietal and dermopterotic anteriorly and they probably met medially. The anterior border is slightly thickened and smooth while the rest of the surface of the bones shows the irregular ornamentation seen on the other dermal elements of the skull.

The anteriormost elements of the infraorbital series are not well detectable. Ventral to the orbit at least two bones are recognizable: the anterior one is elongate antero-posteriorly and slender, the following small and irregular in shape. At the postero-ventral corner of the orbit a large sub-trapezoidal element is placed, followed dorsally by the last one/two elements of the series, small and squarish. Still, the arrangement of the pores of the infraorbital sensory canal is not detectable, being the series made of thin bones, irregularly ornamented. A small dermosphenotic, with an irregular outline, is placed in front of the dermopterotic, and contacts it along its posterior border. The antorbitals are well detectable in specimen GMPKU-P-1688; these are two L-shaped tube-like bones, with a vertical posterior branch probably contacting the first infraorbital and the horizontal region, lying over premaxilla, reaching the rostral bone. No suborbital and supraorbital bones have been detected in the available prepared specimens: as all the other bones seem to be in anatomical connection, it is probable that those elements were not present. The preoperculum is narrow and crescentic, with a ventral region only slightly wider than the dorsal one. The anterior border of the element is thickened and smooth, in correspondence to the passage of the preopercular sensory canal. The remaining part of the bone is ornamented with short anastomosed ridges of ganoine.

The opercular region is broad and kidney-shaped, with operculum about three times deeper than suboperculum. The operculum is subrectangular, with a depth equaling one and a half times its width. The rounded dorsal border is narrower than the ventral one, contacting the suboperculum with a ligthly concave suture. The suboperculum is much longer than deep, with a ratio of about 3:1. Dorsal and ventral margins are curved and there is a well-developed antero-dorsal process abutting the antero-ventral margin of the operculum. The interoperculum is small and triangular. The ornamentation of opercular region is made by short, anastomosed ridges of ganoine except for the antero-dorsal margins, showing a smooth surface; ridges are dorso-ventrally arranged on the operculum, and antero-posteriorly on the suboperculum.

The maxilla is elongate and narrow, ending with a short articular process bending upward. The general shape is subtriangular and the posterior edge is gently wavy. The straight oral margin bears spaced conical teeth with short acrodin cups all along its length, but the very posterior region. The supramaxilla is narrow and long, covering about 2/3 of the dorsal margin of maxilla. The whole shape of premaxilla is not detectable, being partly covered by antorbitals; it is well visible its oral margin, bearing up to six robust teeth, stronger than those borne by maxilla. The lower jaw consists at least of strong angular and dentary. The oral margin is straight in the anterior region of the element and it bears conical teeth, larger than those of maxilla. The depth of lower jaw increases significantly at about 1/3 of its length proceeding posteriorly, with teeth becoming smaller. The coronoid process seems to be quite large, even if its actual size is unknown: the articulating facet is rather low on the posterior margin. The dorsal border of lower jaw, both in its anterior and poterior region, is thick and smooth; the ventral margin is characterized by thin ganoine ridges underlining the path of the sensory canal, detectable by large openings all along the length of the bone.

The quadratojugal is a rather long element: its proximal region is very powerful and abuts the head of the quadrate, but it is not possible to verify the condition of jaw joint. The hyomandibular is always well exposed: this fact supports the lack of the suborbitals. The ventral region is almost vertical and it is narrower than the dorsal region. This latter is gently tilted forwards and it is almost flat apart from the thickened edges. No other anatomical details are visible.

About ten branchiostegal rays are counted: the anteriormost elements are leaf-like, with a low medial keel and a well developed articular process. The posterior edge of each bone covers the anterior of the previous ray. Proceeding posteriorly the elements lenghten, with the last one becoming as long as the ventral margin of subopercular. At the level of the fifth ray there is the reverse of the direction of the covering with the anterior edge of each ray abutting the posterior margin of the following one. The surface of the branchiostegal rays is smooth.

A large oval median gular is present and it expands almost to the symphysis of the lower jaw.

The palatal bones are almost totally covered by teeth that seem to be arranged in rows. The largest teeth are present in the anterior region: even if it is impossible to detect the single bones, it is possible that this patch of large teeth was borne by palatine/vomer bones. A very large parasphenoid covers the median region of the mouth roof: it is made of a large rectangular region, lying in front of the processes: here the ventral surface is flat, while the dorsal surface is more complex showing an elevated anterior region, narrowing backward to the base of the processes. Low lateral wings contributed to maintain the rectangular outline in dorso-ventral view. The ascending process is not very long and is not possible to surely detect any foramen in the central region. The posterior region is quite elongate, possibly about one half of the anterior one (specimen GMPKU-P-1684). Its ventral surface is totally covered by teeth as it is well visible on paratype GMPKU-P-1686: the largest teeth are located on the anterior region of the element.

The posttemporals are large and triangular with a rounded posterior margin, and they probably met in the midline. These elements have the external surface ornamented by short crests of ganoine dorso-ventrally aligned. The sensory canal ran on the ventral region of the elements and its course is underlined by the presence of a series of pores irregularly arranged. The large supracleithrum contacting the posttemporal ventrally, and partly covered by the operculum, is elongated dorso-ventrally and shows a rounded posterior border. Its surface is smooth. The well-developed cleithrum is crescent shaped; its surface is characterized by low ganoine ridges showing a thinly denticulate posterior edges, arranged in longitudinal rows. This complex digitate/dendritic pattern of ornamentation is present on the antero-ventral region of the element and also on the single postcleithral scale, a rectangular element placed immediately behind the supracleithrum.

Vertebral column. Apart from the first vertebral segments, hidden by the pectoral girdle, and the last ones, covered by the urodermals, all the vertebral column is well exposed (Figs 2, 5, 6; Pl. 1).

All along the column there are no traces of centra or chordacentra. The anterior abdominal region shows the most peculiar characters, especially dorsally to the notochord (Fig. 5). Here, there is a sequence of 23 paired neural arches (14 of them in front of the dorsal

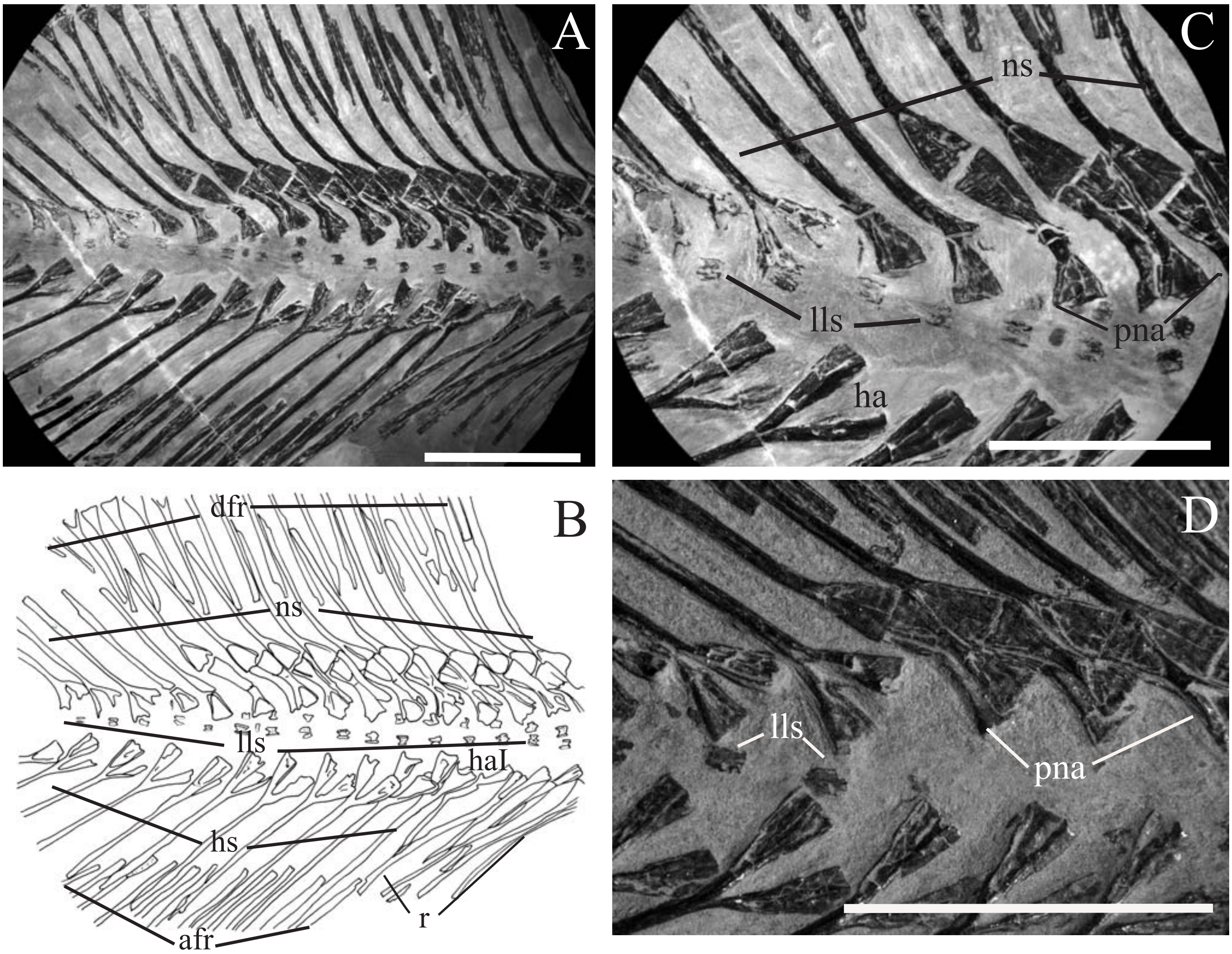

Fig. 5 - *Gymnoichthys inopinatus* gen. n. sp. n., A-C, specimen GMPKU-P-1483, the holotype. A) Median region of the body, scale bar: 10 mm; B) camera lucida drawing of the median region of the body, scale bar: 10 mm; C) detail showing the transition between paired neural arches sutured to the median neural spine and single neural element (arch fused with the spine), scale bar: 5 mm. Note that the first two fused elements are in lateral view, so that the right side of the arch is flattened and broken at the top; the following ones are in front view; D) specimen GMPKU-P-1485, same as in C, but the first fused element in front view, scale bar: 5 mm.

fin), each showing an enlarged distal part perfectly lined, but not fused, with the proximal ends of the corresponding neural spines. Actually, there is always an indented suture between these elements and this is also visible for both side of the pair when they are not perfectly overlapped (Fig. 5C). Thus, we can confidently affirm that there are independent paired neural arches throughout the anterior region.

The long neural spines are peculiarly shaped, with remarkably expanded leaf-like proximal ends; they increase their length up to the beginning of the dorsal fin, then decrease very gently till the first fused neural spine just at the end of the fin. In both the holotype and specimen GMPKU-P-1687, a single pair of neural arch bears two neural spines. From the end of the dorsal fin, the neural elements are made of short arch (about half the length of the anterior ones) and elongate median spine: the shift from one region to the other is very sharp, no transitional element being present (Fig. 5C-D). Possibly 21 neural segments made the caudal region, the first 6 till with sutured neural spine. The dorsal elements seem to loose the one to one relationship to the haemal ones already in tre preural region (specimens GMPKU-P-1485). When well visible (specimens GMPKU-P-1483 (holotype) and -1485) the last four elements are differentiated, as the neural arches become possibly paired and sutured to the neural spine (epural *Auct.*), in one (specimens GMPKU-P-1485) or two (holotype) elements then disappearing in the very last three-two where only the long median spines remain. The first two modified neural elements can be considered as preural, corresponding to the last four preural haemal elements and the last two epurals make all the neural ural region being very elongate. The distal part of these last elements is covered by the dorsal scute and the lateral region of the basal fulcra.

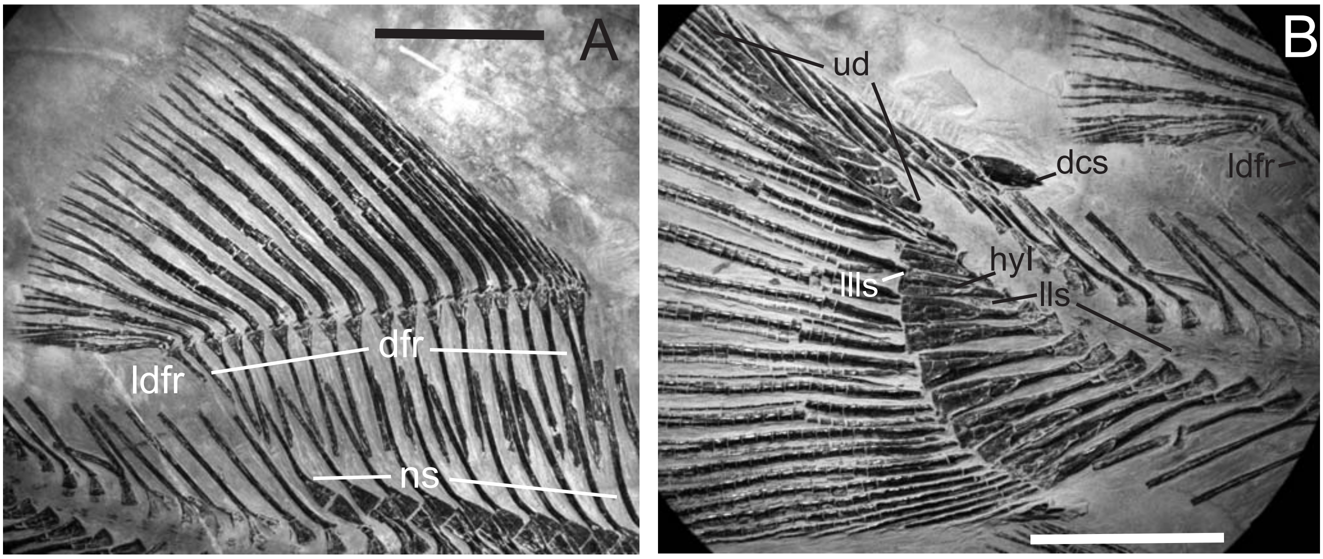

Fig. 6 - *Gymnoichthys inopinatus* gen. n. sp. n., specimen GMPKU-P-1483, the holotype. A) Dorsal fin, scale bar: 10 mm; B) caudal fin, scale bar: 10 mm.

Ventral to the notochord there are 16 elongate couple of ribs. Beginning from the single element just in front of the first radial of the anal fin, there are 20 arches yielding median haemal spines, 8 of which are enlarged to give support to the ventral lepidotrichia of the caudal fin. At least 6-7 hypurals follow these modified preural haemal arches. The last scale of the lateral line lies at the postero-dorsal corner of the first hypural in the holotype. However it is very difficult to state if the lateral line is dorsal or ventral to the first hypural itself even if in GMPKU-P-1485 the last visible scale is just in front of the proximal tip of the first hypural.

Scale covering (Figs 2, 5, 6). This fish can be considered naked apart from 12-13 urodermals on the dorsal body lobe, arranged in a single row. Furthermore, a series of very small, thin lateral line scales is present: these scales are isolated from each other and do not form a continuous line.

Fins. All the fins are made of quite elongate lepidotrichia: they are always well spaced and stout as branching took place only distally.

The lepidotrichia of the pectoral fins are elongated, reaching about 20% of the S.L. Each fin is made of 2 basal fulcra and 13 lepidotrichia; the longest ray is the fourth, the anteriormost three being short and unbranched. The proximal segment of each lepidotrichium is very long and the following segments are always longer than wide. All the longer lepidotrichia branched only once. The pelvic fins are somewhat smaller, and they are made of four basal fulcra and eight lepidotrichia: only the first is unbranched, while the others branch only once. The length of the longest ray is about 16% of the S.L. The pelvic plates are made of an elongate anterior (proximal) region and a large fan-shaped posterior (distal) one.

The dorsal fin (Figs 2, 6A) is very large and stout and probably its insertion was at the level of the maximum height of the body. Concerning the structure, there are two very small scutes plus five basal fulcra articulating to the first radial; they are followed by two quite short rudimentary rays, which articulate with the second radial, each one bearing one very thin fringing fulcrum. The following two long unbranched and 15 branched lepidotrichia articulate with one radial each, except the last two, articulating together with the last radial; moreover, these last shorter rays lie parallel to the dorsal edge of the caudal peduncle. Each lepidotrichium is made of long and quite broad proximal elements, gradually decreasing in length towards the posterior part of the fin, and of squarish distal ones; their number ranges from about 15 to 5, proceeding towards the posterior part of the fin. Thin, elongate ridges of ganoine are present on the posterior half of all the most proximal segments. The first bifurcation takes place in the fifth ray and occurs at about 2/3 of the length of the lepidotrichium. Each ray branches twice. In the holotype there are 19 radials, made of single elements. In specimen GMPKU-P-1687 there are only 14 branched lepidotrichia and, thus, 18 radials.

The anal fin is roughly trapezoidal, showing an almost vertical posterior edge which reached the base of the caudal fin with the last two rays, lying almost parallel to the ventral margin of the caudal peduncle. The pattern of the anal fin is very similar to that of the dorsal one, being only somewhat smaller. One very small scute, four basal fulcra and one short rudimentary ray articulate with the first radial; the following second short rudimentary, one long unbranched and 8 segmented and branched rays, articulate with one radial each. As happens in the dorsal fin, the last radial supports the two last, shortest lepidotrichia. The number of bifurcations and the ratio between unbranched and branched part of the rays is the same as in the dorsal fin. There are 12 radials in the holotype and 13 in GMPKU-P-1687, where there is one more branched lepidotrichium too.

The caudal fin (Fig. 2, 6B) is of abbreviated heterocercal type, the dorsal body lobe being quite elongate but narrow: a single row of urodermal, made of 12-13 elements, is present.

The dorsal margin of the fin is lined by a series of 10 dorsal caudal (basal) fulcra. A few, thin, fringing fulcra are present only on the first of the three dorsal segmented and unbranched lepidotrichia. These are followed by 17 segmented and branched rays which branch twice, except for the first dorsal and the last ventral one, which branch only once. The ventral edge of the fin is made of three segmented but unbranched rays, followed by three ventral caudal fulcra and two smaller scutes. A couple of fringing fulcra are borne by each of the ventralmost rays. The endoskeleton is made of eight enlarged haemal spines plus 6-7 hypurals while dorsally only a few elements (three preural and two ural) support the dorsal scute and fulcra: all bone appear to be stout, making a stiff support to the fin itself.

Comparison and discussion. The Triassic basal Neopterygians are assuming more and more interest as descriptions of new taxa from the marine rocks of the Tethys proceed, especially from the new sites recently discovered in Southern China. Neopterygian radiation in the early Middle Triassic is therefore revealing so important to dim the primacy of the Norian (Late Triassic, about 20 Ma after) one, that has been considered so far the first major neopterygian radiation (Tintori 1998). *Gymnoichthys inopinatus* gen. n. sp. n. is one of these new taxa that contribute to change our point of view about this significant evolutionary moment in the history of Actinopterygians.

One of the most peculiar characters of *Gymnoichthys* gen. n. consists in its almost naked body, devoid of ganoid scales, usually covering the body of almost all the non-teleost neopterygians. The complete ossification of the skeleton, both cranial and postcranial, excludes this character to be due to ontogeny. Furthermore, the comparison between the smallest (GMPKU-P-1485, S.L.= 71 mm) and the largest (the holotype, S.L.= 105 mm) specimens, reveals no differences in the scales, both in distribution and size, or in the length and branching pattern of lepidotrichia, meaning that the 71 mm long fish was already an adult, showing the definitive pattern of the scale covering. The character can be therefore interpreted as paedomorphic, with the scales addition stopped just after their placement on body lobe and lateral line. It is worth to remember that all Triassic actinopterygians, with heterocercal or abbreviate heterocercal tail and reduced scale covering, show well ossified scales at least along the dorsal body lobe: e.g. in *Prohalecites,* where urodermals appeared very early in the ontogeny (Tintori 1990a), in *Marcopoloichthys* showing only one or two very small urodermals (Tintori et al. 2008), or in *Birgeria*, where the scales-field extends from the last part of the lateral line sensory canal throughout the axial body lobe (Romano & Brinkmann 2009; AT pers. obs.).

Among basal fossil neopterygians only few genera show a naked body, being *Prohalecites* (Tintori 1990a; Arratia & Tintori 1999) and *Marcopoloichthys* (Tintori et al. 2008) the best known.

Nevertheless, the unusual morphology of the elements of the vertebral column of *Gymnoichthys* gen. n. (Fig. 5; Pl. 1E) is clearly different from that of the other taxa. However, many other differences besides the vertebral column pattern can be detected between the new genus and these other two.

Concerning *Prohalecites,* the presence in this genus of large contiguous nasals, narrow infraorbitals, suborbitals and tube-like preopecular bone, prevents a strict comparison with the skull of the new genus. The postcranial skeleton also is totally different, as *Prohalecites* has calcified chordacentra and shows diplospondily in the caudal region (Pl. 1A); moreover there are not the 'leaf-like' structures formed by the ends of the neural arches and the supraneurals visible in *Gymnoichthys* gen. n. (Fig. 5, Pl. 1E). The urodermals are arranged in a main row but usually there are one or two more scales placed dorsally to it (Tintori 1990a; Arratia & Tintori 1999). The neural ural region is also totally different as in *Prohalecites* paired neural arches are present throughout this region (Arratia & Tintori 1999), while in *Gymnoichthys* gen. n. there is only a reduced number of median elements (epurals).

Marcopoloichthys, present with a single species in the same unit of *Gymnoichthys* gen. n., shows a different skull and jaw pattern (L-shaped preoperculum, elongate premaxilla, modified lower jaw), as well as different caudal fin, with a very reduced body lobe covered by only one or two small urodermals. The postcranial skeleton in *Marcopoloichthys* (Pl. 1B) shows also derived characters in the median fin endoskeleton (with modified first and last radials) and diplospondily in the caudal region of the vertebral column but it lacks the peculiar morphology and structure of neural arches and neural spines shown by *Gymnoichthys*.

Marcopoloichthys and *Prohalecites* share several characters in the vertebral column, with the anterior median autogenous elements (supraneurals) lying in front of the paired neural arches before the insertion of the dorsal fin, surmounted by other more distal bones

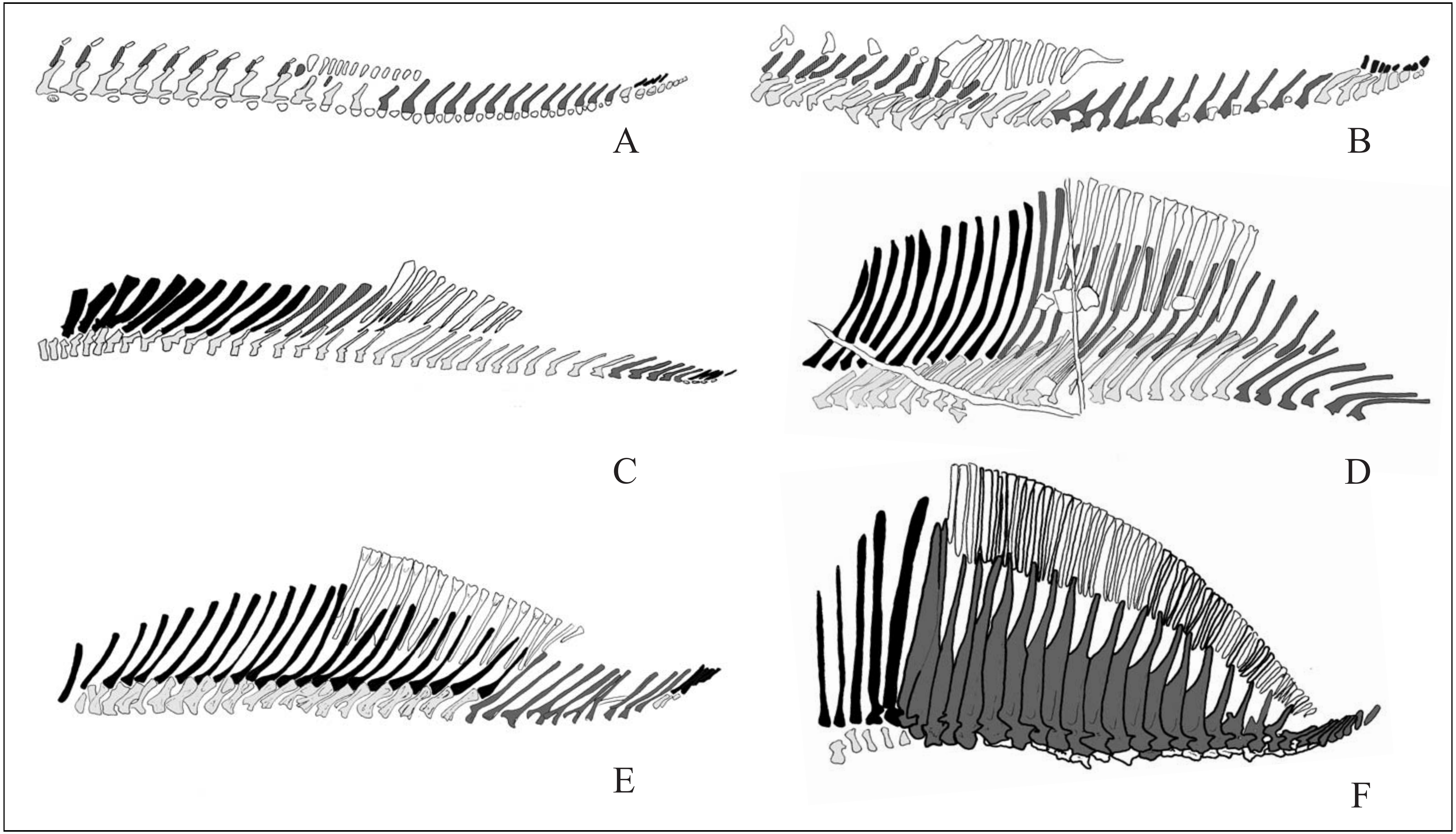

PLATE 1

Neural region of vertebral column of different neopterygians taxa.
A) *Prohalecites porroi* (modified from Tintori 1990); B) *Marcopoloichthys ani* (Tintori et al. 2008); C) *Semionotus* ind. (modified from Olsen & McCune 1991); D) *Paralepidotus ornatus* (modified from Tintori 1996); E) *Gymnoichthys inopinatus* gen. n. sp. n., specimen GMPKU-P-1483, the holotype; F) *Turbomesodon praeclarus* (modified from Poyato-Ariza F. & Wenz S. 2004).
White= paired neural arches; gray= neural spines fused to the neural arches; black= median neural spines aligned with neural arches; cross-hatching area= median neural spines lying in front of neural arches.
Drawings not to scale.

(supradorsals). At the base of the dorsal fin there are only the elongated paired neural arches, without any median element. After the dorsal fin, the distal ends of the paired neural arches seem to fuse together, giving rise to the median neural spine, as the total length of paired arches vs arches + median spine is absolutely comparable.

Though basal neopterygians are usually totally covered by ganoid scales, some specimens of selected Triassic/Jurassic species show the postcranial endoskeleton, allowing a detailed restoration: Olsen & McCune (1991) described the vertebral column of the Early Jurassic *Semionotus elegans* group (1991) and Tintori (1996) that of Late Triassic *Paralepidotus ornatus*, both genera belonging to Semionotidae. Also Bartram (1977), even if only through X-rays, described the endoskeleton of the macrosemiid *Propterus elegans*. This latter genus is characterized by a dorsal fin occupying most of the dorsal edge, being esternally subdivided in two lobes but with a rather undifferentiated endoskeleton. Following Bartram (1977, pag 176, fig. 22), *Propterus* has only six supraneurals, four in front of the dorsal fin and two intercalated to the first radials: all of them are well separated from the short paired neural arches. All the other vertebral segments are dorsally represented by elongated paired elements.

In *Semionotus* (Olsen and McCune 1991) there is a similar pattern, even if the dorsal fin is much shorter and consequently its insertion is much posterior. Autogenous median elements, called supraneural by these Authors, are present: at least the 10-11 anteriormost elements are aligned with the paired arches (possibly like in *Propterus*), while the posterior ones lay just in front of them, as usual for supraneurals. The median bone series ends at the beginning of the dorsal fin. The neural arches keep their paired nature also throughout most of the preural region and only the last three to five elements show a median neural spine (Pl. 1C).

In *Paralepidotus* the median neural elements of the vertebral column show the same pattern as in *Semionotus elegans* group, at least until the beginning of the dorsal fin: they are in fact aligned with the neural arches, then lay in front of them just before the insertion of the dorsal fin. However, *Paralepidotus* is different since the neural arches extend into median spines beginning from the posterior part of the elongate dorsal fin, with supraneurals still present (Pl. 1 D). Thus, *Paralepidotus ornatus* shows in few segments supraneurals together with a median neural spine fused to the arch, while most of the remaining preural region has just median neural spines. It must be pointed out that *Paralepidotus* seems to be the only case in which supraneurals are present at the base of the dorsal fin for almost its entire length; in all other genera they disappear just after the beginning of the fin.

In *Gymnoichthys* gen. n. the median bones are always lined with the arches, then suddenly they fused together, slightly changing their morphology. Neopterygians showing a similar pattern are the pycnodonts, here represented by *Turbomesodon* (Poyato-Ariza & Wenz 2004) who shows only the first five independent neural spines, while the remaining are fused to the correspondent arches (Pl. 1F).

It is worth remembering that also some subholosteans have median neural spines in the caudal region: for instance, the gliding fish *Thoracopterus* (Tintori & Sassi 1992) has a very specialized caudal region, possibly related to its peculiar way of life. The fused neural elements appear at the end of the dorsal fin and the spines become very large to support the strong muscles related to the 'flight', as happens in modern flying fishes (Tintori & Sassi 1992). In the abdominal region of *Thoracopterus*, the anterior median bones, called supraneurals, lie anterior to the paired arches.

Regarding the basal actinopterygians, we have very different patterns. For instance, *Saurichthys* has usually reduced scale covering but along the vertebral column there are only paired elements, that can be more or less complicated (Tintori 1990b; Wu et al. 2009) but always without any median bone. The coeval and highly specialized predator *Birgeria,* on the contrary, shows a series of thin supraneurals reaching the insertion of the dorsal fin while the caudal region has only the paired elements, with diplospondily (Stensiö 1921).

Nielsen (1942) describing the endoskeleton in the abdominal region of *Glaucolepis* from the Early Triassic of Greenland, showed a series of supraneurals apparently aligned with the corresponding paired arches (basidorsals in Nielsen 1942), although well separated from each others. Supraneurals disappear at the level of the insertion of the dorsal fin and all the posterior neural elements are paired (Nielsen 1942, p. 218).

It is now clear that in both non-neopterygians actinopterygians and non-teleostean neopterygians there are different kinds of autogenous neural median elements: the supraneurals (in *Prohalecites* and *Marcopoloichthys* as well as in many non-teleostean actinopterygians) and the ones we have called 'neural spines' that are always close to, and aligned with, the distal ends of the paired neural arches. These elements can be free (*Semionotus elegans* group, *Paralepidotus ornatus*, *Turbomesodon*) or sutured with the arches (*Gymnoichthys* gen. n.). Supraneurals abut the distal anterior end of the arches and in neopterygians they are usually present until the insertion of the dorsal fin, thus more or less in the abdominal region. However, in the reported semionotids both structures are present together, with neural spines related to a few anterior segments, followed by more or less numerous supraneurals. In the caudal region of neopterygians there are differences also after supraneurals disappear: in *Semionotus* neural arches remained mainly paired while in *Paralepidotus* there are mainly median elements.

Thus, the vertebral column structure can be well considered as autopomorphic to *Gymnoichthys* gen n., together with the single row of urodermals and reduced number of epaxial with no paired arches in the ural region.

Regarding the dermal skull pattern, lack of suborbitals can be considered a derived character among the basal neopterygians as well as the snout bone reduced almost to tub-like elements leaving a large uncovered area in the ethmoidal region. This latter character recall the snout pattern of advanced semionotids (López-Arbarello & Codorniú 2007; Olsen & McCune 1991) even if presence of a large gular and lack of suborbitals prevent to consider *Gymnoichthys* a close relative to semionotids.

While this combination of characters, some of them never found in other taxa, makes necessary the erection of a new genus and species, *Gymnoichthys inopinatus*, nevertheless the scarcity of data about the Middle Triassic basal neopterygians suggests to put it in the Neopterygii *incertae sedis*.

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REFERENCES

Arratia G. & Tintori A. (1999) - The caudal skeleton of the Triassic neopterygian *Prohalecites*. In: G. Arratia & H.-P. Schultze (Eds) - Mesozoic fishes 2 - Systematics and the fossil record: 121-142, Verlag Dr. Pfeil, München.

Bartram A.W.H. (1977) - The Macrosemiidae, a Mesozoic Family of holostean fishes. *Bull. Br. Mus. nat. Hist. (Geol)*, 29(2): 17-234.

Jiang D.-Y., Motani R., Hao W.-C., Rieppel O., Sun Y.-L., Tintori A., Sun Z.-Y. & Schmitz L. (2009) - Biodiversity and Sequence of the Middle Triassic Panxian marine Reptile Fauna, Guizhou Province, China. *Acta Geol. Sin.*, 83: 451-459.

López-Arbarello A., Sun Z.-Y., Sferco E., Tintori A., Xu G.-H., Sun Y.-L., Wu F.-X. & Jiang D.-Y. (Submitted) - New species of *Sangiorgioichthys* Tintori and Lombardo, 2007 (Neopterygii, Semionotiformes) from the Anisian of Luoping (Yunnan Province, South China). PLoS ONE.

Motani R., Jiang D.-Y., Tintori A., Sun Y.-L., Hao W.-C., Boyd A., Hinic-Frlog S., Schmitz L., Shin J.-Y. and Sun Z.-Y. (2008) - Horizons and assemblages of Middle Triassic Marine reptiles from Panxian, Guizhou, China. *J. Vert. Paleontol.*, 28(3): 900-903.

Nielsen E. (1942) - Studies on Triassic Fishes I: *Glaucolepis* and *Boreosomus*. *Medd. Grønl.*, 138: 1-394.

Olsen P. E. & McCune A. R. (1991) - Morphology of the *Semionotus elegans* Species Group from the Early Jurassic part of the Newark Supergroup of Eastern North America with comments on the Family Semionotidae (Neopterygii). *J. Vert. Paleontol.*, 11(3): 269-292.

Poyato-Ariza F. & Wenz S. (2004) - The new pycnodontid fish *Turbomesodon*, and a revision of *Macromesodon* based on new material from the Lower Cretaceous of Las Hoyas, Cuenca, Spain. In: Arratia G. & Tintori A. (Eds) - Mesozoic Fishes 3 - Systematics, Palaeoenvironments and Biodiversity: 341-378, Verlag Dr. Pfeil, München.

Romano C. & Brinkmann W. (2009) - Reappraisal of the lower actinopterygian *Birgeria stensioei* Aldinger, 1931 (Osteichthyes; Birgeriidae) from the Middle Triassic of Monte San Giorgio (Switzerland) and Besano (Italy). *N. Jb. Geol. Paläont. Abh.*, 252(1): 17-31.

Stensiö E. (1921) - Triassic Fishes from Spitzbergen. 307 pp., A. Holzhausen Ed., Wien.

Sun Z.-Y., Tintori A., Lombardo C., Jiang D.-Y., Hao W.-C., Sun Y.-L, Wu F.-X. & Rusconi M. (2008) - A new species of the genus *Colobodus* Agassiz, 1844 (Osteichthyes, Actinopterygii) from the Pelsonian (Anisian, Middle Triassic) of Guizhou (South China). *Riv. It. Paleont. Strat.*, 114(3): 363-376.

Sun Z.-Y., Tintori A., Jiang D.-Y., Lombardo C., Rusconi M., Hao W.-C. & Sun Y.-L. (2009) - A new Perleidiform (Actinopterygii, Osteichthyes) from the Middle Anisian (Middle Triassic) of Yunnan, South China. *Acta Geol. Sinica*, 83: 460-470.

Tintori A. (1990a) - The actinopterygian fish *Prohalecites* from the Triassic of Northern Italy. *Palaeontology*, 33(1): 155-174.

Tintori A. (1990b) - The vertebral column of the Triassic fish *Saurichthys* (Actinopterygii) and its stratigraphical significance. *Riv. It. Paleont. Strat.*, 96(1): 93-102.

Tintori A. (1996) - *Paralepidotus ornatus* (Agassiz, 1833-43): a semionotid from the Norian (Late Triassic) of Europe. In: Arratia G. & Viohl G. (Eds) - Mesozoic fishes - Systematics and Paleoecology: 167-179, Verlag Dr. Pfeil, München.

Tintori A. (1998) - Fish biodiversity in the marine Norian (Late Triassic) of Northern Italy: the first Neopterygian radiation. In: Bianco P.G. (Ed.) - Proceedings of CEI9 "Fish biodiversity", 1997, Trieste. *Ital. J. Zool.*, 65 (Suppl.): 193-198.

Tintori A. & Sassi D. (1992) - *Thoracopterus* Bronn (Osteichthys: Actinopterygii): a gliding fish from the Triassic of Europe. *J. Vert. Paleont.*, 12(3): 265-283.

Tintori A., Sun Z.-Y., Lombardo C., Jiang D.-Y, Sun Y.-L., Rusconi M. & Hao W.-C. (2008) -New specialized basal neopterygians (Actinopterygii) from Triassic of the Tethys realm. *Geologia Insubrica,* 10/2 (2007): 13-20.

Wu F.-X., Sun Y.-L., Hao W.-C., Jiang D.-Y., Xu G., Sun Z.-Y. & Tintori A. (2009) - New species of *Saurichthys* (Actinopterygii: Saurichthydae) from Middle Triassic (Anisian) of Yunnan Province, China. *Acta Geol. Sin.,* 83: 440-450.