A new species of Saurichthys from the Middle Triassic (Anisian) of southwestern China (Postprint)

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Abstract

The saurichthyiform fishes were effective predators and hence the significant consumers in the aquatic ecosystems during the Early Mesozoic. They showed a notable diversification in the Anisian (Middle Triassic) Lagerst 鋞 ten of southwestern China. In this contribution, we report a new species of Saurichthys from the Anisian of Yunnan, China, that displays some peculiar modifications of the axial skeleton and the longate body of the group. This new species, Saurichthys spinosa is a small-sized saurichthyid fish characterized by a very narrow interorbital region of the skull roof, an anteriorly expansive and ventrally arched cleithrum, proportionally large abdominal vertebrae lacking neural spines and alternately bearing laterally-stretching paraneural plates, few fin rays in the median fins, and two paralleling rows of needle-like flank scales with strong thorns. This fish has slimmed down the body by reducing the depth of the head and the epaxial part of the trunk. The elongate paraneural plates inserted in the horizontal septum and the rigid interlocking of the flank scales render the fish a very stiff body, which is compatible with the functional consequence of the obvious decrease of the body (vertebral) segments. This discovery reveals the variability of the axial skeleton and the hydrodynamic properties of the saurichthyiform fishes. These factors, together with the innovations in the locomotion and feeding habit, might have intrinsically effected the evolutionary burst of the eastern Tethyan saurichthyiform fishes during the Anisian, a marked signature of the rapid radiation stage of the biotic recovery after the end-Permian extinction.

Full Text

Preamble

A new species of *Saurichthys* from the Middle Triassic (Anisian) of southwestern China

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Abstract

The saurichthyiform fishes were effective predators and significant consumers in aquatic ecosystems during the Early Mesozoic. They showed notable diversification in the Anisian (Middle Triassic) Lagerstätten of southwestern China. Here we report a new species of *Saurichthys* from the Anisian of Yunnan, China, that displays peculiar modifications of the axial skeleton and elongate body characteristic of the group.

This new species, *Saurichthys spinosa*, is a small-sized saurichthyid fish characterized by a very narrow interorbital region of the skull roof, an anteriorly expansive and ventrally arched cleithrum, proportionally large abdominal vertebrae lacking neural spines and alternately bearing laterally-stretching paraneural plates, few fin rays in the median fins, and two parallel rows of needle-like flank scales with strong thorns. The fish has slimmed its body by reducing the depth of the head and the epaxial part of the trunk. The elongate paraneural plates inserted in the horizontal septum and the rigid interlocking of the flank scales render the fish a very stiff body, which is compatible with the functional consequence of the obvious decrease in body (vertebral) segments.

This discovery reveals the variability of the axial skeleton and hydrodynamic properties of saurichthyiform fishes. These factors, together with innovations in locomotion and feeding habits, might have intrinsically effected the evolutionary burst of eastern Tethyan saurichthyiform fishes during the Anisian, a marked signature of the rapid radiation stage of biotic recovery after the end-Permian extinction.

Keywords: Luoping, Yunnan; Middle Triassic; *Saurichthys*; axial skeleton; body shape

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Following the devastating end-Permian mass extinction, the Triassic marine ecosystem underwent rapid recovery and eventual re-establishment by the Middle Triassic as a stable and complex system, a process that rebuilt high diversity of marine fishes [**?**, **?**, **?**]. The saurichthyiform fishes, characterized by a pointed head and long body with posteriorly set median fins, are one of the most iconic fish lineages during this period [**?**, **?**, **?**]. Soon after the mass extinction, they radiated globally, invading both marine and freshwater ecosystems, and became particularly speciose during the Triassic [?, ?, ?]. As specialized predators, they were important components of these aquatic ecosystems and retained the role of high-level consumers in the marine realm until their extinction in the Middle Jurassic [?, ?, ?].

Recent discoveries of saurichthyiform fishes from the Anisian Lagerstätten in southwestern China have vastly improved understanding of these fishes [?, ?, ?, ?, ?]. To date, up to seven morphologically and ecologically distinct species have emerged in a rather short interval (late Anisian). They show notable disparity in body size [?, ?, ?, ?], fin shape [?], and feeding apparatus [?], suggesting innovations in locomotory patterns and dietary preferences of saurichthyiform fishes. Beyond these superficial changes, they also exhibit variations in the bones inside the body, namely the axial skeleton, regarding the structure of the haemal elements [?]. The saurichthyiform axial skeleton, unique in the duplication of vertebral elements, serves as the most important structural unit supporting body elongation in this group [?], and its morphological changes therefore should have affected the functional properties of these fishes [?, ?].

According to current knowledge, the axial skeleton varies within this group in the degree of development of dorsal and ventral extensions of the vertebrae, the neural spines and haemal spines, or the prezygapophyses of the neural arches (summarized in [?, ?]). Notably, these variations are confined to the vertical septum of the body, with no signal of vertebral change in other aspects even in species that show some tendency toward widening the body [?]. Here we report a new species of *Saurichthys* from the Anisian Luoping biota of Yunnan that shows additional growth of the axial skeleton in the horizontal dimension as compensation for the loss of neural spines in the dorsal vertical septum, representing a new vertebral model for this group.

With a characteristic elongate body plan, saurichthyiform fishes are considered typical 'pike-like predators' that might have employed fast-start or ambush predation [?]. For this predation pattern, the stiffness of the axial skeleton (body) and body contour (e.g., fineness ratio, defined as the ratio of total body length to maximum body depth) are key functional properties influencing hunting efficiency [?, ?]. In generalized saurichthyiforms, stiffness can be achieved either in the exoskeleton by interlocking scutes along the dorsal and ventral midlines of the body [?, ?, ?, ?, ?] or occasionally in the endoskeleton (vertebral bones) by extraordinarily long processes directed both anteriorly and posteriorly from the neural arches [?, ?]. The fineness ratio is a good indicator of flow disturbance, pressure distribution, and drag coefficient during predation—crucial factors influencing hunting outcomes in saurichthyiform fishes [?]. This ratio is variable within the group but barely exceeds 18 and is mostly below 15; for example, it is 12 in *Saurichthys curionii*, the model used in hydrodynamic analyses [?]. The new species of *Saurichthys* has a very slim body with a fineness ratio of up to 20. Based on a detailed description of this new species, we highlight the peculiar modifications of the axial skeleton, the arrangement of the scale covering, and the changes in body shape and their contributions to stiffness and slimness.

This contribution demonstrates the variability of these functional properties in saurichthyiform fishes, which might represent one aspect underlying the evolutionary success of these fishes during the Anisian when the marine ecosystem was fully recovered.

1 Materials and Methods

The studied materials belong to the Institute of Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP) and the Geological Museum of Peking University (GMPKU) and include 15 well-preserved specimens. They are from the middle unit (strata of Luoping biota) of the Upper Member of the Middle Triassic Guanling Formation exposed near Dawazi Village, Luoping County, Yunnan Province, China, and co-occur with several other saurichthyid species [**?**, **?**] (Fig. 1 [Figure 1: see original paper]). Specimens were prepared using sharp needles. Line drawings were based on photos, aided by constant examination of specimens under a Nikon SMZ1500 binocular microscope. Neural arch numbers and maximum recorded length were collected from published scientific literature or personal observations. Sampled species are those known from complete materials. Scatter plots were drawn using Excel 2013 and Adobe Photoshop CS6. The goodness of fit (R2) and hypothesis test results were obtained using SPSS 21.0.

2 Systematic Paleontology

Saurichthyiformes Aldinger, 1937 (sensu Berg, 1940)
Saurichthyidae Owen, 1860 (sensu Stensiö, 1925)
Saurichthys Agassiz, 1834

Saurichthys spinosa sp. nov. (Figs. 2–6)

Diagnosis: A small-sized *Saurichthys* species characterized by a dorsoventrally compressed head with shallow mandibles; mandibular sensory canals opening via few longitudinal pits; very narrow interorbital region of cranial roof; heavily sculptured dermal skull roof with sensory canals marked by distinct ridges; cleithrum with an expanded anteroventral process, an accessory lateral process, and an arched ventral margin; axial skeleton comprising fewer vertebrae [ca. 54 (i.e., 108 neural arches, compared to 150–220 known in most other saurichthyids)]; neural arches lacking neural spines throughout vertebral column and alternately bearing a transversal paraneural plate in abdominal region; scale cover including two needle-like flank (mid-lateral and ventrolateral) scale rows on either side; pectoral fin deep-based; median fins round in distal margin and comprising few and sparsely-set fin rays; median fin rays un-jointed and un-branched; some axonosts supporting fin rays of median fins in a one-to-one relationship.

Holotype: IVPP V 23062 (Fig. 2A [Figure 2: see original paper]), a complete skeleton.

Other referred specimens: IVPP V 23063, 22832; GMPKU-P-1533–1545.

Locality: Dawazi Village, Luoping County, Yunnan Province, China (Fig. 1).

Horizon: Middle part of the Upper Member of the Guanling Formation at the type locality, within the conodont *Nicoraella kockeli* Zone, Pelsonian substage of Anisian, Middle Triassic [**?**].

Etymology: *spinosa*, referring to the peculiar spinous scale covering of the fish.

3 Description

General morphology: *Saurichthys spinosa* sp. nov. is a small-sized saurichthyid fish (Fig. 2) with an acuminate snout and elongate body covered with six longitudinal rows of spinous scales. It bears round, posteriorly arranged dorsal and anal fins and a slightly forked symmetrical caudal fin. Standard body length (SBL) ranges from 65 to 97 mm, and skull length occupies ca. 28%-29% of SBL.

Neurocranium: The neurocranium, partially exposed in the orbit, is well ossified and delimits the posterior wall of the orbit (Figs. 3B, 4B). One or two openings are observed, possibly related to cranial nerves or vessels.

Dermal skull roof: The skull roof is greatly constricted in the middle part of the frontals by the dorsal rims of the large orbits, making the interorbital part of the cranial table very narrow (Figs. 2A, 3, 4). On the inner side, this part is slightly hunched along the midline without longitudinal ridges (Figs. 3B, 4B). Posteriorly, the skull roof is notably broadened.

The parietals are represented by a heart-shaped region immediately behind the frontals, with no medial sutures clearly distinguishable. The paired dermopterotics meet along the midline, each having two embayments in the hind margin—the lateral one accommodating the extrascapular (Figs. 3A, 4A) and the median one likely for attachment of soft tissues. The extrascapulars are cordiform, each bearing a groove in the posterolateral part marking the temporal commissure of the sensory canals. The dermal cranial roof is heavily sculptured by irregular ridges and pits, except that the extrascapulars bear small tubercles on their surfaces (Figs. 3C, 4C), and the anterior portions of the frontals bear a series of thorns along the median suture.

The snout is long and acuminate (Figs. 2–4). The elongate rostro-premaxilla, fused with its antimere at the dorsal edge, tapers anteriorly to the tip and meets posteriorly with the maxilla below the anterior rim of the orbit. The triangular nasalo-antorbital wedges anteriorly between the frontal and rostro-premaxilla and posteriorly forms the anterior rim of the orbit. It bears two external nares on the outer surface, with the anterior one much larger than the posterior. The supraorbital sensory canal passes between the nares and downward meets the sensory canals from the rostro-premaxilla and infraorbitals in a tri-radiate structure on the nasalo-antorbital (Fig. 4B [Figure 4: see original paper]). The lachrymal is small and oval, bearing parts of the infraorbital canal. The rostro-premaxilla is covered with a few vertical stout ridges in the posterior part and is smooth anteriorly. The nasalo-antorbital is ornamented with coarse tubercles and a few vertical strong ridges.

Cheek region: The maxilla is slender in the suborbital part and greatly expanded in the postorbital region. The preopercle is boomerang-like with the posterior edge slightly inclined posteriorly, making an acute angle in the posterodorsal corner (Fig. 4A, B) rather than a right or obtuse one seen in other known *Saurichthys* species and saurichthyiforms [?, ?, ?, ?, ?, ?, ?, ?, ?, ?].

The maxilla is mainly ornamented with stout vertical ridges and some vermiculate rugae in the postorbital region, whereas the preopercle is much more weakly ornamented. No circumorbital bones are observed in any available specimens, and their absence may not be preservational bias.

Lower jaw: The mandible is shallow, with maximal depth slightly less than half the depth of the cheek region (measuring the height of the postorbital region of the maxilla plus the preopercle) (Figs. 3B, 4B). This differs from the mandible that is usually strong in the vast majority of saurichthyiform fishes, with maximal depth approximately equal to cheek depth [?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?], but is similar to three European Anisian species: *Saurichthys minimahleri* from Germany, *S. daubreei* from France, and *S. dianneae* from the Netherlands [?, ?]. The mandible comprises a dentary, angular, and supraangular on the lateral side and a prearticular, articular, and at least two coronoids and partially the ventral flange of the angular on the median side. Of these bones, the articular, dentary, supraangular, and prearticular form the adductor fossa (Fig. 5A [Figure 5: see original paper], B); however, it cannot be determined whether the coronoids also participate in that fossa.

The dentary occupies most of the lateral side of the mandible (Figs. 3B, 4B, 5A). It lacks ornamentation in the posteriormost and anterior third portions and displays a few stout vertical ridges in the middle portion. Along the oral edge of the dentary, large conical teeth are interspersed with smaller ones. The angular is roughly triangular and projects at its posteroventral corner, making a concave posterior edge of the lower jaw (Fig. 5A, B). It strongly flares inward along its ventral margin, producing a broad ventromedial flange toward the intermandibular region (Fig. 5B). This flange reaches maximal width at the level of the middle portion of the mandible, where it almost equals the maximal depth of the mandible (Fig. 5A, B). The supraangular is slender and smooth. The surface of the angular bears coarse, closely-set tubercles.

In medial view, the prearticular makes up most of the inner side of the mandible. It lacks teeth in the posterior portion and bears numerous irregular depressions in the middle part (Fig. 5B). The coronoids are located along the dorsal edge of the prearticular (Fig. 5B). Based on available materials, there are at least two coronoids, both bearing numerous tiny teeth much smaller than those on the dentary. Three foramina are present in the posteroventral corner of the mandible. One lies on the suture between the angular and prearticular, and two are on the angular, probably associated with branches of cranial nerves V and

VII (Fig. 5B).

Opercular apparatus: The opercle is roughly quadrate, slightly longer than deep (depth/length ratio ca. 0.93), with a slightly convex posterior edge [Figs. 3B, 4B, 5C (anterior edge incomplete)]. Its external surface is decorated with 18-20 stout vertical ridges and some irregular pits. Neither subopercle nor branchiostegal rays are discernible.

Sensory canals: The supraorbital and infraorbital sensory canals are arranged in a pattern similar to other saurichthyiforms [**?**, **?**, **?**, **?**, **?**, **?**, **?**, **?**]. However, these sensory canals in the new species are distinct in having prominent ridges marking their courses with large but relatively few openings (4–5 for the supraorbital canal and 6–7 for the postorbital canal) on the skull roof (Fig. 4A, C). In some specimens, paired pit lines are observed on the skull roof (Fig. 4A) comparable to the median branches of the infraorbital canals on the skull table in some Anisian *Saurichthys* species from Europe [**?**, **?**]. The preopercular canal has several openings along the posterior edge of the preopercle.

The mandibular canal opens outward via a few short slot-like structures in the ventral flange of the angular (Figs. 4B, 5B), showing a condition different from other saurichthyiforms, in which a continuous series of pores extends throughout the lower jaw [**?**, **?**, **?**, **?**, **?**, **?**, **?**, **?**].

Axial skeleton: The axial skeleton consists of paired neural and haemal elements attached to the persisting notochord. There are ca. 108 (i.e., 54 vertebrae) neural arches anterior to the caudal fin, representing far fewer vertebral elements than in the majority of known saurichthyiforms [**?**, **?**, **?**, **?**, **?**, **?**, **?**, **?**, **?**] but approximating that in two coeval species from central Europe [**?**, **?**]. The neural arches are relatively large, each roughly corresponding to one flank scale. The semi-neural arch meets its antimere along the midline (Fig. 5F, G). The prezygapophyses and postzygapophyses are very weakly developed. The neural arches lack neural spines throughout the vertebral column and bear a laterally extended plate at the base of every other abdominal arch (Figs. 3B, 4B, 5F, G, H, 6C). We name these plates 'paraneural plates' following Arratia's suggestions (personal communication, 2014). These plates are much longer than wide and gradually decrease in length posteriorly. The maximal length of these plates exceeds three times the width (in lateromedial dimension) of the neural arch, with the longest plate being at least three times the width of the associated neural arch. As the degree of ossification decreases distally, the possibility cannot be ruled out that these plates might have been longer in living forms than those preserved in fossils. In medial view, a foramen is present in each plate-bearing neural arch.

The haemal elements are not clearly discernible except for those in the anterior caudal region. They display a one-to-one relationship to the neural arches and possess distinct haemal spines (Figs. 6A).

Unpaired fins: The dorsal fin is rounded at the distal margin (Figs. 2, 6A). It comprises 22 sparsely arranged fin rays that are neither segmented nor bifurcated. Two radials (axonosts) can be observed; the first supports four rays and the second supports three rays.

The anal fin is slightly more posteriorly located than the dorsal fin (Figs. 2, 6A). It has 22 fin rays with outline and arrangement similar to those of the dorsal fin. Six anterior radials (axonosts) are observed; the first supports four fin rays, the second three, the third two, and the remaining three radials each hold a single fin ray. Posterior radials cannot be distinguished due to poor preservation.

The caudal fin is symmetrical with the body axis passing between the epi- and hypochordal lobes (Figs. 2, 6A). It has a relatively low aspect ratio with both lobes being shallow and distally rounded. The caudal fork is not deep. The caudal fin rays are rigid and sparsely arranged, neither segmented nor bifurcated. Eighteen and nineteen fin rays are counted in the epichordal and hypochordal lobes, respectively, with the 11th ray being the longest in both lobes. The endoskeletal support of the caudal fin cannot be observed in current materials. No fringing fulcra are developed on the leading edges of any median fins.

Appendicular skeleton and paired fins: The dermal pectoral girdle consists of a supracleithrum, cleithrum, and clavicle (Figs. 3A, B, 4A, B, 5C–E). No independent posttemporal is observed.

The supracleithrum (Figs. 4A, B, 5C) is roughly rectangular with a humped posterodorsal margin. The dorsal portion is smooth and the ventrolateral portion is decorated with small serrated protuberances, indicating the facet covered by the opercle. Two pores of the lateral line are observed in the middle and posterolateral parts of the supracleithrum.

The cleithrum is generally triradiate (Figs. 3B, 4B, 5C–E), consisting of dorsal, posteroventral, and anteroventral processes. The dorsal process increases in size dorsally until articulating with the supracleithrum, the posteroventral process tapers distally, and the anteroventral process expands ventrally and articulates with the clavicle with a notched anterior margin (Fig. 5C–E). The anteroventral and posteroventral processes converge ventrally, forming an arcuate ventral margin of the cleithrum. Besides these three principal processes, an accessory process emerges from the junction of the dorsal and posteroventral processes, bearing two or three spines at its tip (Fig. 5C, E). On the inner side of the cleithrum, a stout keel commences from the center of the bone and runs upward along the anterior edge of the dorsal process. The ventral margin of the cleithrum is arched and thickened. Ornamentation on the external surface consists of stout ridges radiating from the ossification center and some vermiculate ridges in the expanded portion of the anteroventral process. On the opercular facet enclosed by the anteroventral and dorsal processes are serrated ridges, similar to those on the comparable part of the supracleithrum.

The exact shape of the clavicle cannot be determined. However, in GMPKU-P-1533, the clavicle is partially exposed and shows serrated structures similar to those on comparable areas in other dermal pectoral girdle bones (Fig. 5C, E).

Of the endoskeletal girdle, the scapulocoracoid is well preserved in GMPKU-P-1533 (Fig. 5C). It is roughly rectangular, higher than wide, and anteriorly contacts the dorsal process of the cleithrum. Two fenestrae are present in the scapulocoracoid; the anterior one is large and lies immediately posterior to the cleithrum, and the posterior one is smaller and posterodorsal to the anterior fenestra (Fig. 5C). The radials of the pectoral fins are not preserved. The pectoral fin consists of 12–13 unjointed fin rays and is deep-based, suggesting nearly vertical insertion (Fig. 5C). No fringing fulcra are developed.

The pelvic fin is small and fan-like, comprising ca. 10 unjointed and unbranched fin rays (Figs. 2, 6B). The pelvic girdle is not detectable. No fringing fulcra are present on the leading edge.

Squamation: The new species bears six longitudinal scale rows on the trunk (a mid-dorsal, a mid-ventral, and paired mid-lateral and ventrolateral scale rows), plus numerous scattered tiny spinous scales in the dorsal aspect of the body (Figs. 2, 5H, 6). The most notable features of the scale covering are the well-developed spines on the scales and the needle- or rib-like flank scales (the mid-lateral and ventrolateral rows) (Figs. 2D, 5H, 6C–G).

The mid-dorsal scale row runs from the skull to the caudal fin, interrupted by the dorsal fin. There are 41 or 42 predorsal scales that are lanceolate and gradually increase in size posteriorly. Each mid-dorsal scale consists of a V-shaped depressed anterior portion overlapped by the preceding scale and a posterior exposed portion carrying a longitudinal row of thorns (Figs. 5H, 6C–G). The scales in the caudal peduncle are similar to the predorsal ones in shape and structure, slightly increasing in size posteriorly toward the caudal fin. In total, 11 mid-dorsal scales are counted in the caudal peduncle.

The mid-ventral scale row begins some distance behind the skull (Fig. 2B, D, 5H) and branches at the level of the pelvic fins to form the anal loop (Fig. 6B). There are ca. 34 pre-pelvic scales. The scale immediately in front of the anal loop is enlarged posteriorly to contact that loop (Fig. 6B). The loop is composed of five scales of different shape and size on each branch. The first is a small triangular scale tapering posteriorly to superimpose upon the succeeding scale. The second is broad anteriorly but narrows posteriorly to articulate with the next scale. The third is the largest and ladle-like with a depressed anterior part and gently laterally-bent body. Immediately next are two much smaller loop scales converging posteriorly toward the mid-ventral scale row anterior to the anal fin. Five lanciform mid-ventral scales are seen between the anal loop and anal fin, bearing strong spines. The mid-ventral scales in the caudal peduncle mirror the morphology of the corresponding mid-dorsal scales (Fig. 6A). Notably, the spines on the abdominal mid-ventral scales are much more weakly developed (Fig. 2C) than those on the mid-dorsal scales in this region.

The mid-lateral scale row extends continuously throughout the trunk to the end of the body (Figs. 2, 5H, 6A, C–F). Just anterior to the caudal fin, the mid-lateral scales are triangular. More anteriorly, they increase rapidly in size and extend and taper both dorsally and ventrally, possessing a needle- or rib-like appearance, especially in the abdominal region. When approaching the skull, they decrease in size again until attaching to the supracleithrum. These scales all bear strong, posteriorly directed spines in their central part, located in a row on the scale midline. Scales in the mid-abdominal region carry more spines (usually three per scale) than scales elsewhere in the row. On the inner side, each abdominal scale bears an anteriorly tapering projection that underlies and extends to the anterior margin of the preceding scale, a structure also seen in abdominal ventrolateral scales (Fig. 6H, I). This connecting pattern between neighboring flank scales is not seen in any other known saurichthyiform fishes [?] and references therein, even those bearing similarly needle-like mid-lateral scales [?, ?, ?, ?, ?, ?]. No openings for the lateral line canal can be detected on the mid-lateral scales.

The ventrolateral scale row begins behind the pectoral fin and is interrupted at the level of the pelvic fins and anal loop (Figs. 2, 5H, 6A–E, H, I). These scales are generally similar in size but mirror the shape of the corresponding mid-lateral scales in the abdominal region and caudal peduncle. However, they are drastically enlarged in the length between the pelvic and anal fins, such that one ventrolateral scale roughly spans two mid-lateral scales (Figs. 2, 6A, B, D). In medial view, all neighboring abdominal ventrolateral scales (except the anteriormost one) show similar articulation to that of the mid-lateral scales described above (Figs. 6H, I). Most abdominal scales have one or two posteriorly directed spines (occasionally three) on the central portion. The ventrolateral and mid-lateral scales are arranged in an interdigital pattern in the abdominal region, producing a unique flank scale covering never seen in most known saurichthyiform fishes to date [?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?], including some *Saurichthys* species with similar mid-lateral scales [?, ?, ?, ?]. Interestingly, a similar arrangement of flank scales is seen in two *Saurichthys* species from the Anisian of Germany and France [?], although the ventrolateral row is continuous in those species.

Besides the continuous scale rows, numerous tiny spinous scales are confined to the region between the mid-dorsal and mid-lateral scale rows (Figs. 5H, 6C). Each scale has a round base from which a spine emerges. This type of spinous scale is not seen in the ventral aspect of the body.

4 Discussion

Comparison: Many saurichthyid fishes have been discovered from the Anisian of southwestern China (i.e., Panxian fauna in Guizhou and Luoping biota in Yunnan) [?, ?, ?, ?, ?], and their excellent preservation warrants detailed comparison with the new species. *Saurichthys dawaziensis* is clearly distinguished from *S. spinosa* sp. nov. by having four rows of scales including small, round mid-lateral scales and well-developed neural spines in the abdominal neural arches (Fig. 7A [Figure 7: see original paper]). *S. yangjuanensis* is much larger than the new species and has totally different flank scale morphology, extensive segmentations of the lepidotrichia of the median fins, and an axial skeleton with well-developed neural spines [?]. *S. yunnanensis* resembles the new species in having rib-like mid-lateral scales but is distinct in having a much deeper lower jaw, higher opercle, and normally triangular ventrolateral scales in the abdominal region. Additionally, *S. yunnanensis* has many more neural arches (at least 50 more than in the new species) and much larger body size [?].

The *Sinosaurichthys* species differ from the new species in having an unconstricted interorbital region on the skull roof, boot-like cleithrum, round mid-dorsal scales, much deeper opercles, and triangular mid-lateral and roughly quadrate ventrolateral scales [?]. They also differ from *S. spinosa* in having many more neural arches surmounted with long neural spines and lacking paraneural plates in the abdominal section of the axial skeleton [?]. Additionally, two *Sinosaurichthys* species show peculiar elongation of the fins, which is not seen in the new species [?]. *Yelangichthys macrocephalus* shows more notable differences in the very broad interorbital part of the skull table, different arrangement of the parietal bones, deep lower jaw, and other differences in opercular shape and cleithral structure, as well as small screwdriver-like teeth [?].

Extensive constriction of the interorbital region in the skull roof is also recorded in some Anisian European species, e.g., *Saurichthys daubreei*, *S. hoffmanni*, *S. minimahleri*, and *S. dianneae* [?, ?]. They share with the new species similar numbers of neural arches, lack of well-developed neural spines in the abdominal neural arches (Fig. 7B), and rib-like mid-lateral scales. However, *S. daubreei* has a deeper opercle with depth ratio of 0.7 (vs. 0.9 in the new species) and continuous ventrolateral scales spanning the pelvic fins and anal loop [?], contrasting with the interruption of this scale row in *S. spinosa*.

The materials of *S. hoffmanni* are very incomplete, inhibiting detailed comparison, but the acute embayment in the rear of the skull and numerous oblique striae on the lower jaw clearly distinguish it from the new species. *S. minimahleri* differs from the new species in having a clearly quadripartite parietal complex, continuous ventrolateral scales above the pelvic fins and anal loop, a deeper opercle, and lacking paraneural plates in the abdominal neural arches [?]. Meanwhile, *S. dianneae* diverges from *S. spinosa* in its tubercular ornamentation on the skull roof, cleithrum with smaller dorsal and anterior processes, and absence of rib-like ventrolateral scales and paraneural plates [?].

Needle-like mid-lateral scales also occur in *Saurichthys costasquamosus*, *S. paucitrichus*, and *S. breviabdominalis* (i.e., species of the subgenus *Costasaurichthys* proposed by Tintori, 2013, also see [?]). However, the axial skeleton structure in *S. spinosa* shows little resemblance to that of the *Costasaurichthys* species group, which have well-developed neural spines, many more neural arches, and lack paraneural plates. *Saurichthys striolatus* resembles the new species in lacking neural spines but differs in lacking paraneural plates and in scale morphology. Moreover, *S. striolatus* has many more neural arches [?] than the new taxon.

The modification of the body: a slim and stiffened body and possible functional implications: The new species has a typical saurichthyiform body shape, with relative head length falling within the range of most saurichthyiform fishes known from complete specimens. However, it modifies this basic profile by reducing body depth in both dorsal and ventral parts. The abdominal change can be reflected in skull depth change, as the latter roughly equals maximal body depth in saurichthyiform fishes. A much shallower lower jaw in the new species than in other saurichthyiforms leads to reduction of the hypaxial depth of the trunk (Fig. 8A1, B1). Dorsally, the relevant feature is associated with backbone variation. The vast majority of other saurichthyiform fishes usually bear well-developed neural spines in the abdominal vertebrae (Figs. 7A, 8A2); in sharp contrast, the new species completely lacks this part (Figs. 7C, 8B2), a specialization shared with few coeval species from the Middle Triassic of Europe [**?**] (Fig. 7B). The loss of dorsal extensions (neural spines) of the axial skeleton and consequent close proximity of the vertebral column to the dorsal ridge (mid-dorsal scales) (Fig. 6F) means the axial column was embedded very close to the body surface and the epaxial part of the body was mostly squeezed out (Fig. 8B2). These modifications produce a very slim body with a fineness ratio of ca. 20, much higher than that in other contemporaries in China [*Saurichthys dawaziensis*, 17; *Sa. yunnanensis*, 12.7; *Sa. yangjuanensis*, ca. 15; *Sinosaurichthys longipectoralis*, 16; *Si. longimedialis*, average 16; *Si. minuta*, average 13; *Sinosaurichthys* sp., average 13 (IVPP V 23547 and V 23548)] and other saurichthyids worldwide [**?**]. A body with such a high fineness ratio may experience less drag and cause less flow disturbance during swimming, providing significant advantages for predation [**?**]. To utilize these advantages, the fish must maintain a steady body to minimize undulation during the crucial attack phase [**?**]. For the slim new *Saurichthys*, one solution is to increase body stiffness.

The vertebral counts (neural arches) of the new species are among the minimal records in known saurichthyiforms (see [**?**, **?**]) except for a few coeval *Saurichthys* species from Europe [**?**, **?**], indicating the new fish has many fewer body segments than the vast majority of saurichthyiform fishes (see [**?**, **?**]), approximating only half that of its contemporary *Sinosaurichthys longipectoralis* from the adjacent and coeval Panxian fauna in Guizhou Province [**?**]. This is reminiscent of Lindsey' s (1975) 'Pleomerism,' a phenomenon of vertebral number being positively correlated with maximal body length in fishes, as the new species is among the smallest members of saurichthyiform fishes [**?**]. Indeed, the scatterplot diagram shows correlation between body length and vertebral number within this group (Fig. 9). Interestingly, if the sampling list excludes the *Sinosaurichthys* species, the correlation between these two parameters becomes more significant (Fig. 9). However, there are exceptions, such as the Late Triassic species *Saurichthys striolatus* with 180-190 neural arches in a body of ca. 10-18 cm long, though its exceptionally large skull/body length ratio (40%-45%, vs. less than 30% in the new species) implies the measured specimens [**?**] may represent juvenile individuals according to the ontogenetic trajectory of the skull in saurichthyiform fishes [?, ?].

Functionally, the quantitative reduction of vertebrae makes sense for the new fish. The notable decrease in the number of body (vertebral) segments in a given body plan consequently reduces lateral flexibility of the fish body [?]. This is consistent with the functional consequences of specializations of the axial skeleton and flank scales. Judging from the general arrangement of myotomes and septa in fishes [?], the wide, horizontally-set paraneural plates (Fig. 7C) must be inserted in and tightly fixed by the horizontal septum (Fig. 8B2). In this way, these plates would minimize lateral displacement of the backbone and thereby stiffen the axial skeleton and eventually the fish body, probably as epineural tendons do in living fishes [?]. Additionally, the articulation pattern and parallel arrangement of the needle-like flank scales contribute to body stiffness. The peculiar interlock of successive flank scales (e.g., mid-lateral scale row) (Fig. 6H, I) limits lateral undulation of the body, an effect further strengthened by its duplication in another parallel flank scale row (ventrolateral row) (Fig. 2). Given these peculiar modifications, some unique herein, the new fish therefore might have a stiffer body than its saurichthyiform relatives known to date, naturally having greater potential to optimize predation by minimizing additional drag and flow disturbance to avoid detection by prey [?].

Fig. 9: Relation of mean neural arch number to maximum body length in saurichthyid fishes known from complete materials. The plot is presented in logarithmic axes. Each point represents a *Saurichthys* or *Sinosaurichthys* species.

The saurichthyiform fishes were abundant and diverse, both morphologically and taxonomically, in the Middle Triassic faunas of southwestern China. *Saurichthys spinosa* sp. nov. is the ninth species of this group in this region during the late Anisian of the early Middle Triassic [?, ?, ?, ?, ?], with undescribed materials and ongoing field explorations promising more findings ahead. It highlights the evolutionary history of marine fishes during this crucial stage of biotic recovery, as no other contemporary fish group known to date has diversified to such magnitude [?, ?, ?, ?, ?, ?]. The new species expands the spectrum of body size of this group in the eastern Tethys and suggests considerable disparity in axial skeleton, scale covering, and relevant functional properties of the body. This reflects the extraordinary plasticity of saurichthyiform fishes, which may represent the intrinsic mechanism underlying their evolutionary burst during the radiation stage of the marine ecosystem after the end-Permian mass extinction [?, ?].

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