New saurichthyid actinopterygian fishes from the Anisian (Middle Triassic) of southwestern China

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A new genus *Sinosaurichthys* of the Saurichthyidae with three new species, *S. longipectoralis*, *S. longimedialis*, and *S. minuta*, are described and compared with *Saurichthys*. The new genus is represented by more than a hundred almost complete skeletons, collected from the strata corresponding to the Upper Member of the Guanling Formation (Pelsonian, Anisian, Middle Triassic) of two localities: Yangjuan of Panxian County, Guizhou Province, and Dawazi of Luoping, Yunnan Province, China. *Sinosaurichthys* differs from *Saurichthys* in having an unusual dermal pectoral girdle, high insertion of pectoral fin, relatively dorsally positioned axial skeleton in the abdominal region, and in the absence of branchiostegal rays. These differences are supposed to reflect the different life styles between the two genera. *Sinosaurichthys*, like the extant needlefish, probably has a better ability for cruising in surface water than *Saurichthys*. In addition, these species of *Sinosaurichthys* are compared, and their morphological differences also probably reflect individual adaptations for different habitats at the two localities.

Key words: Actinopterygii, Saurichthyidae, *Sinosaurichthys*, Anisian, Triassic, Guizhou, Yunnan, China.

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Introduction

The Saurichthyidae (Saurichthyiformes) is a group of specialized Mesozoic actinopterygian fishes, characterized by a long and slender body and rostrum, posteriorly located dorsal and anal fins, abbreviated diphycercal caudal fin and generally reduced squamation with several longitudinal rows of scales. They were originally interpreted to be ambush predators with a life style similar to that of the pike *Esox* or garpike *Lepisosteus* (Tintori 1990; Rieppel 1992). The fossil record of this family showed great morphological variations and a world-wide distribution (Beltan and Tintori 1980; Rieppel 1985; Thies 1985; Gozzi 2004; Mutter et al. 2008; Kogan et al. 2009; Wu et al. 2009). A handful of genera (*Saurichthys* Agassiz, 1834; *Ichthyorhynchus* Bellotti, 1857; *Belonorhynchus* Bronn, 1858; *Giffonus* Costa, 1862; *Acidorhynchus* Stensiö, 1925; *Brevisaurichthys* Beltan, 1972; *Systolichthys* Beltan, 1972; and *Eosaurichthys* Liu and Wei, 1988) were proposed previously, but some of them (e.g., *Ichthyorhynchus*, *Belonorhynchus*, *Giffonus*, *Brevisaurichthys*, *Systolichthys*) were considered to be synonyms of *Saurichthys*

(Stensiö 1925; Cartanyà 1999). Except the Late Permian *Eosaurichthys* from southeastern China (Liu and Wei 1988) and the Early Jurassic *Acidorhynchus* from Europe and North America (Stensiö 1925; Gardiner 1960; Neuman and Wilson 1985; Thies 1985), all other taxa of this group are restricted to the Triassic and so far ascribed only to the genus *Saurichthys* (sensu Stensiö 1925). More than 30 species were named under *Saurichthys* based not only on isolated teeth or fragmentary bones (see Rieppel 1985 and references therein; Mutter et al. 2008; Kogan et al. 2009; Wu et al. 2009; Zhang et al. 2010). However, the lack of distinguishable generic features among these species, except those shared by all saurichthyids (such as the elongate, slender jaws, conical teeth, and the so-called abbreviated diphycercal caudal fin), leaves great challenges to a taxonomic revision of this group.

In recent years, abundant fossil fishes have been recovered from the Middle Triassic in western Guizhou and eastern Yunnan (Fig. 1), including diverse actinopterygians and a few sarcopterygians (Tintori et al. 2008; Sun et al. 2009). Among these actinopterygians, the saurichthyids are abundant both in quantity and diversity, but only two species of
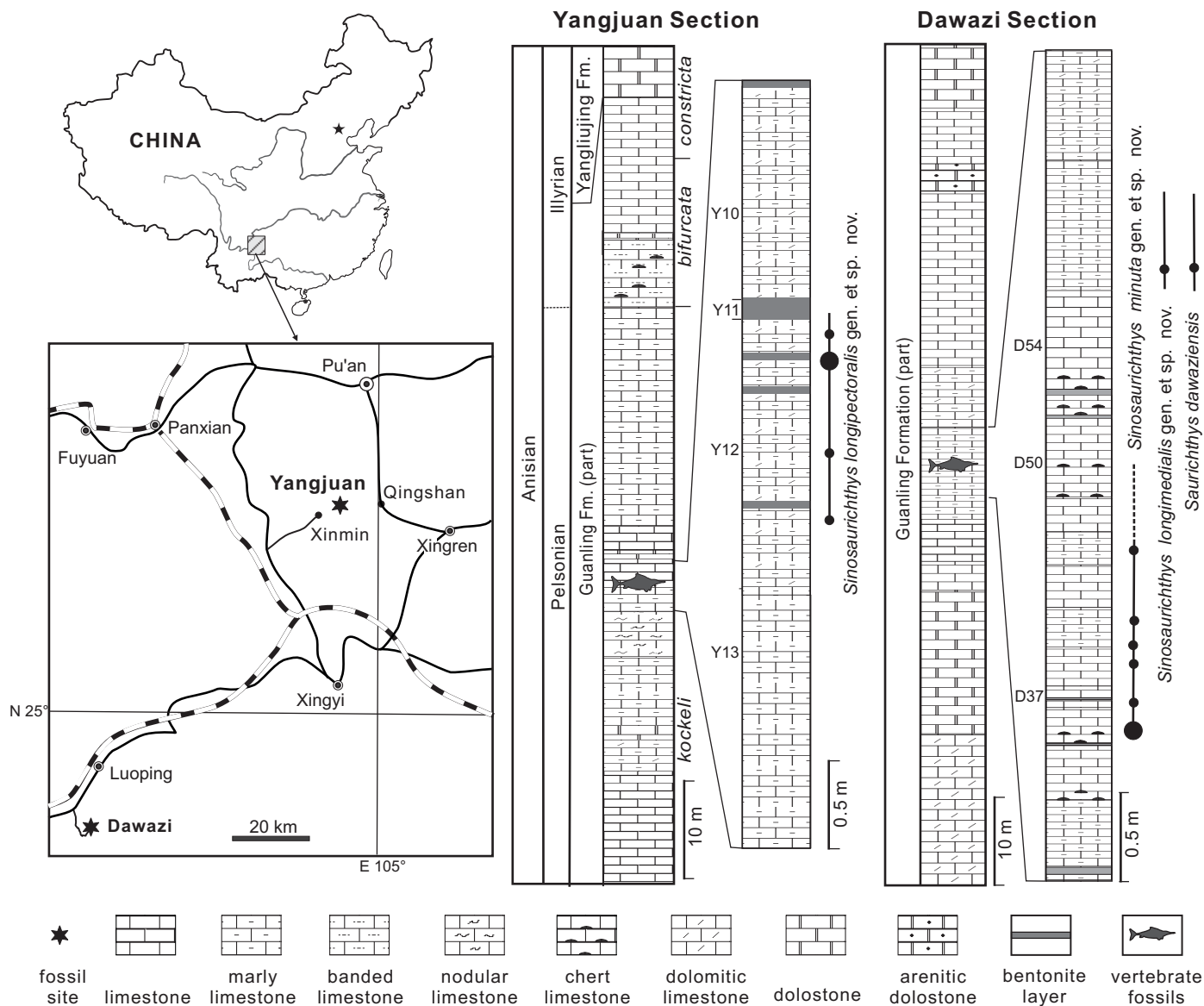
Fig. 1. Locality map and lithological columns of two sections in Guizhou and Yunnan Provinces, China.

Saurichthys have been described recently (Wu et al. 2009; Zhang et al. 2010). Here, we name and describe three other new species of the Saurichthyidae assigned to a new genus, *Sinosaurichthys*, from the two localities mentioned above. The morphological differences between the new genus and *Saurichthys* and their life styles are specially discussed.

Institutional abreviations.—GMPKU, Geological Museum of Peking University, Beijing, China.

Geological setting

The three new saurichthyid species described here come from two localities: one from Yangjuan of Panxian County, Guizhou Province and the other two from Dawazi of Luoping County, Yunnan Province (Fig. 1).

In the Yangjuan area of Panxian, *Sinosaurichthys longipectoralis* gen. et sp. nov. was recovered from a 3-meter thick vertebrate-rich layer in the upper part of the Guanling Formation, associated with abundant, well preserved marine reptiles and other fossil fishes (Sun et al. 2008). This species is one of the quantitatively dominant vertebrates in that locality. Conodont analysis revealed that the fossiliferous layer is within the *Nicoraella kockeli* Zone, suggesting an early middle Anisian age (Sun et al. 2006).

In the Dawazi area of Luoping, the studied materials were collected from a more than 10-meter thick vertebrate-rich layer near the top of the Third Member of the Gejiu Formation (a local lithostratigraphic unit applied in Yunnan Province, spanning from the upper Lower Triassic to upper Middle Triassic, and its Third Member corresponding to the Guanling Formation used in adjacent Guizhou Province), associated with abundant other fossil fishes. *Sinosaurichthys*

minuta was recovered from the lower part while *S. longimedialis* occured in the upper part of the fossiliferous layer, about 3 to 5 meters above the former. The conodont *Nicoraella kockeli* was also recovered in samples collected from the fossiliferous layer, suggesting the same age for this fauna as that from Yangjuan of Panxian.

Material and methods

This study is based on more than 150 specimens. Most of them were well-preserved and mechanically prepared with sharp needles under a stereomicroscope. The line drawings were done based on photos, assisted with observation of the specimens under a Nikon SMZ1500 binocular microscope. All specimens are deposited in the GMPKU.

The terminology of bones used in this paper follows Stensiö (1925), Rieppel (1985), and Gardiner and Schaeffer (1989). The method of measurement is shown in Fig. 2.
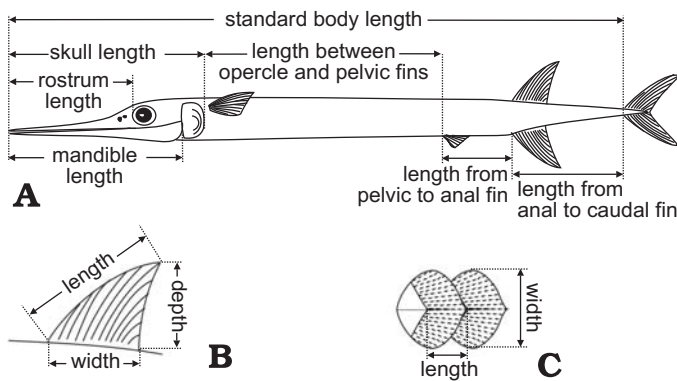

Fig. 2. Illustration showing measurement conventions. **A**. Body in lateral view. **B**. Median fin in lateral view. **C**. Mid-dorsal scales in dorsal view.

Systematic paleontology

Actinopterygii Woodward, 1891

Saurichthyiformes Aldinger, 1937

Saurichthyidae Stensiö, 1925

Genus *Sinosaurichthys* nov.

Type species: *Sinosaurichthys longipectoralis* sp. nov.; see below.

Etymology: From Greek *sino*, China; *saurichthys*, the only genus of saurichthyids from the Triassic heretofore.

Diagnosis.—Pectoral fin inserting high on flank, at or above midline of body; cleithrum boot-shaped with high rectangular posterior blade, slender anterodorsal stem and short horizontal anteroventral arm; presence of large posttemporal-supracleithrum; parasphenoid with highly elevated posterior stem; axial skeleton arranged high in abdominal region of body; absence of branchiostegals; anal fin situated closer to pelvic fin than to caudal fin; cordate mid-dorsal scales much wider than midventral ones; and extremely elongated first paired scale in anal loop, expanding anteriorly and tapering posteriorly.

Species included.—*Sinosaurichthys longipectoralis* sp. nov., *S. longimedialis* sp. nov., and *S. minuta* sp. nov.

Stratigraphic and geographic range.—Anisian, Middle Triassic, Guizhou and Yunnan, China.

Sinosaurichthys longipectoralis sp. nov.

Figs. 3–9.

Etymology: From Latin *longus* and *pectoralis*, referring to its exceptionally elongated pectoral fins.

Type material: Holotype GMPKU-P1233, a laterally compressed skull with part of the postcranial skeleton. Paratypes: GMPKU-P1214, a postcranial skeleton with complete caudal region; and GMPKU-P1215, a laterally compressed skull.

Type locality: Yangjuan Village, Xinmin, Panxian County, Guizhou Province, China.

Type horizon: The vertebrate fossiliferous horizon in the Upper Member of the Guanling Formation (Pelsonian of Anisian, Middle Triassic) (Sun et al. 2006).

Referred specimens.—GMPKU-P1089, 1097, 1099, 1126, 1141, 1183, 1211, 1223, 1225, 1227, 1234, 1247, 1253, 1361, 1362, 1366.

Diagnosis.—Type species of *Sinosaurichthys*, pectoral fin sickle-shaped and extremely long, reaching about or more than mandible length; cleithrum bearing anteriorly inclined dorsal stem and rather deep posterior blade with depth/length ratio about 1.8; posttemporal-supracleithra meeting at midline; pelvic fin relatively long; axial skeleton consisting of no less than 210 neural arches between opercle and caudal fin (compared with 157–172 in *S. longimedialis* and 154–156 in *S. minuta* described below), including ca. 180 anterior ones with neural spines; at least 90 mid-dorsal scales anterior to dorsal fin. Fin formula: P 24–25, V 23–24, D/A ~55/~50, C 36–38/36–38.

Description

General appearance.—As a shared feature of the Saurichthyidae, *Sinosaurichthys longipectoralis* has a long rostrum and an elongated, slender body. The standard length of the largest specimen is over 560 mm. The skull length is 27% of the standard body length. The rostrum makes up 73–76% of the mandible length (Figs. 3A–C, 4; Table 1). It is similar to other members of the same genus described below in having the pectoral fins located near to the posterodorsal corner of the opercle, in contrast to *Saurichthys* that have pectoral fins much lower located as commonly in other actinopterygians. The pelvic fins are closer to the caudal fin than to the opercle. The dorsal and anal fins are opposite to each other and are much closer to the pelvic fins than to the caudal fin.

Endocranium.—The endocranium is poorly ossified and only the posterodorsal part of the orbitotemporal region was preserved in some of laterally compressed specimens to carry two foramina (Fig. 4A), probably related to the oculomotor nerve (III).

Snout.—The snout is composed of the paired rostro-premaxillae and nasalo-antorbitals, with a length up to 61–65% of the skull length (Fig. 4). The rostro-premaxilla is elon-
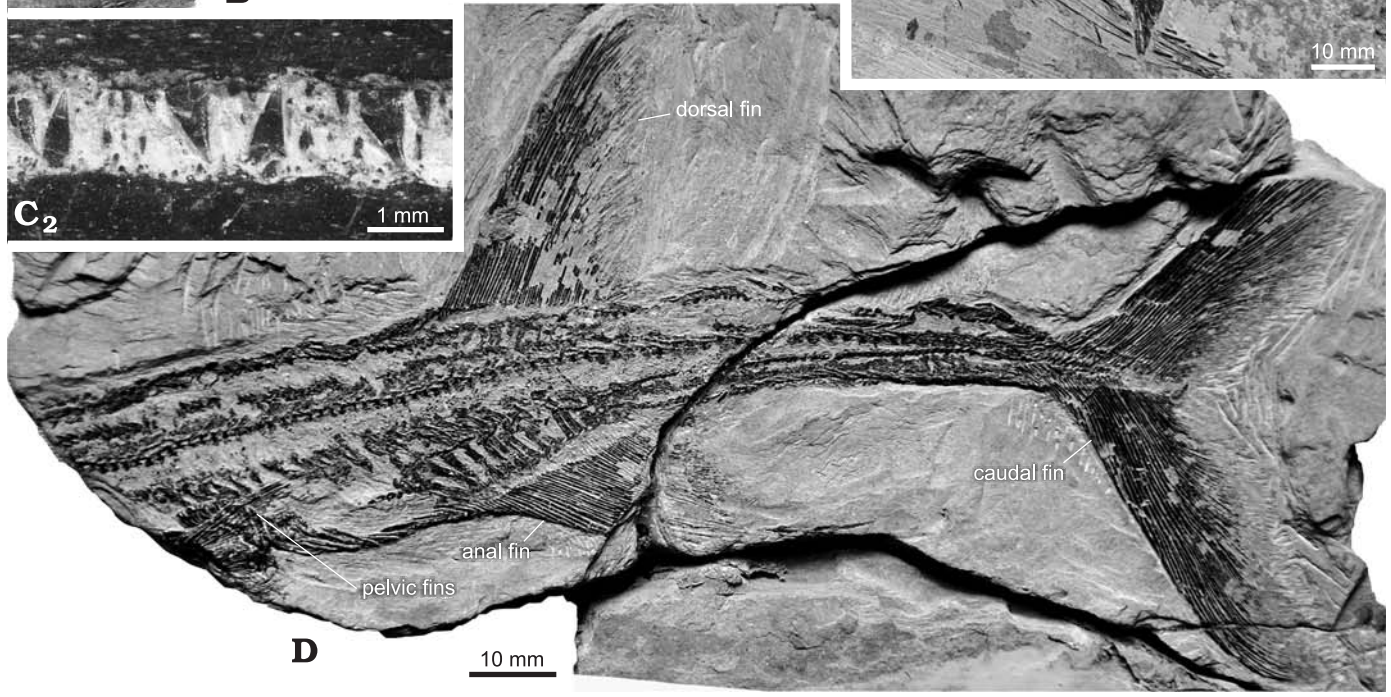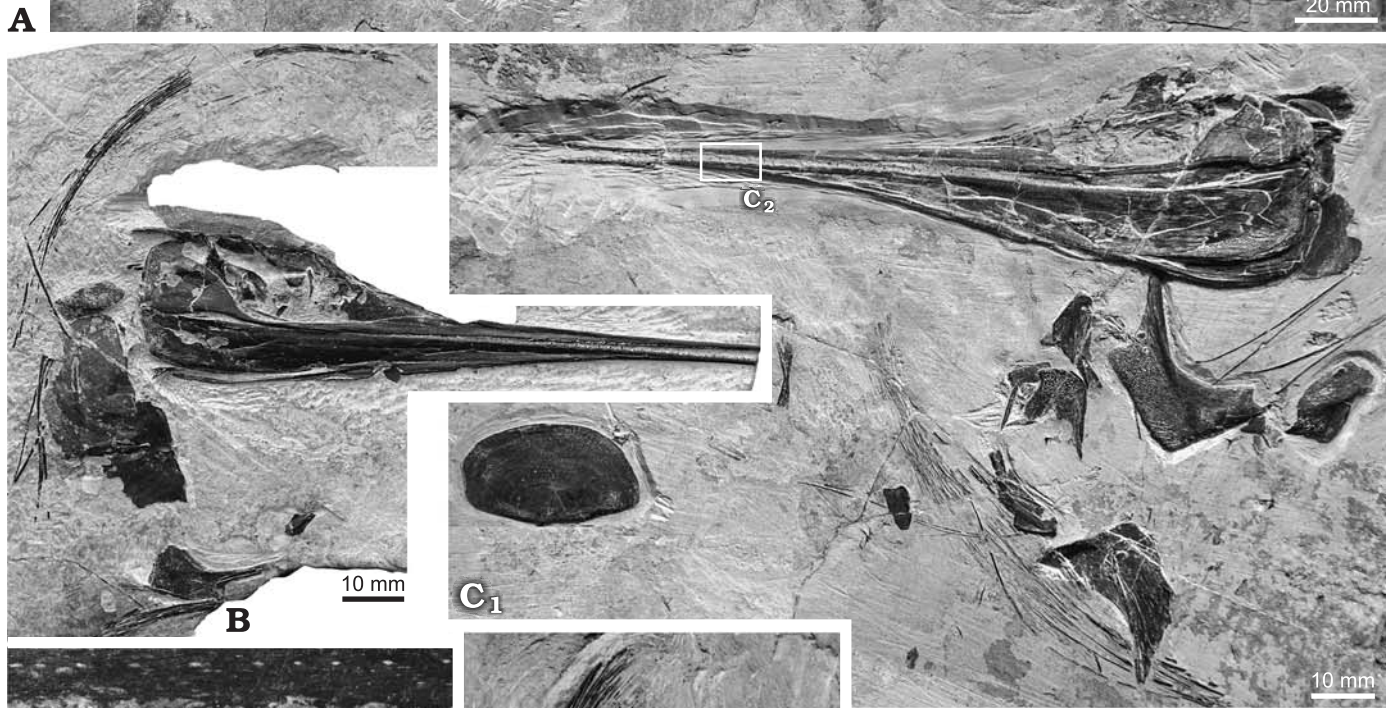
A 20 mm

B 10 mm

C₁ 10 mm

C₂ 1 mm

dorsal fin

caudal fin

anal fin

pelvic fins

D 10 mm

Table 1. Measurements (in mm) of three new species of *Sinosaurichthys* gen. nov. See Fig. 2 for measurement conventions.

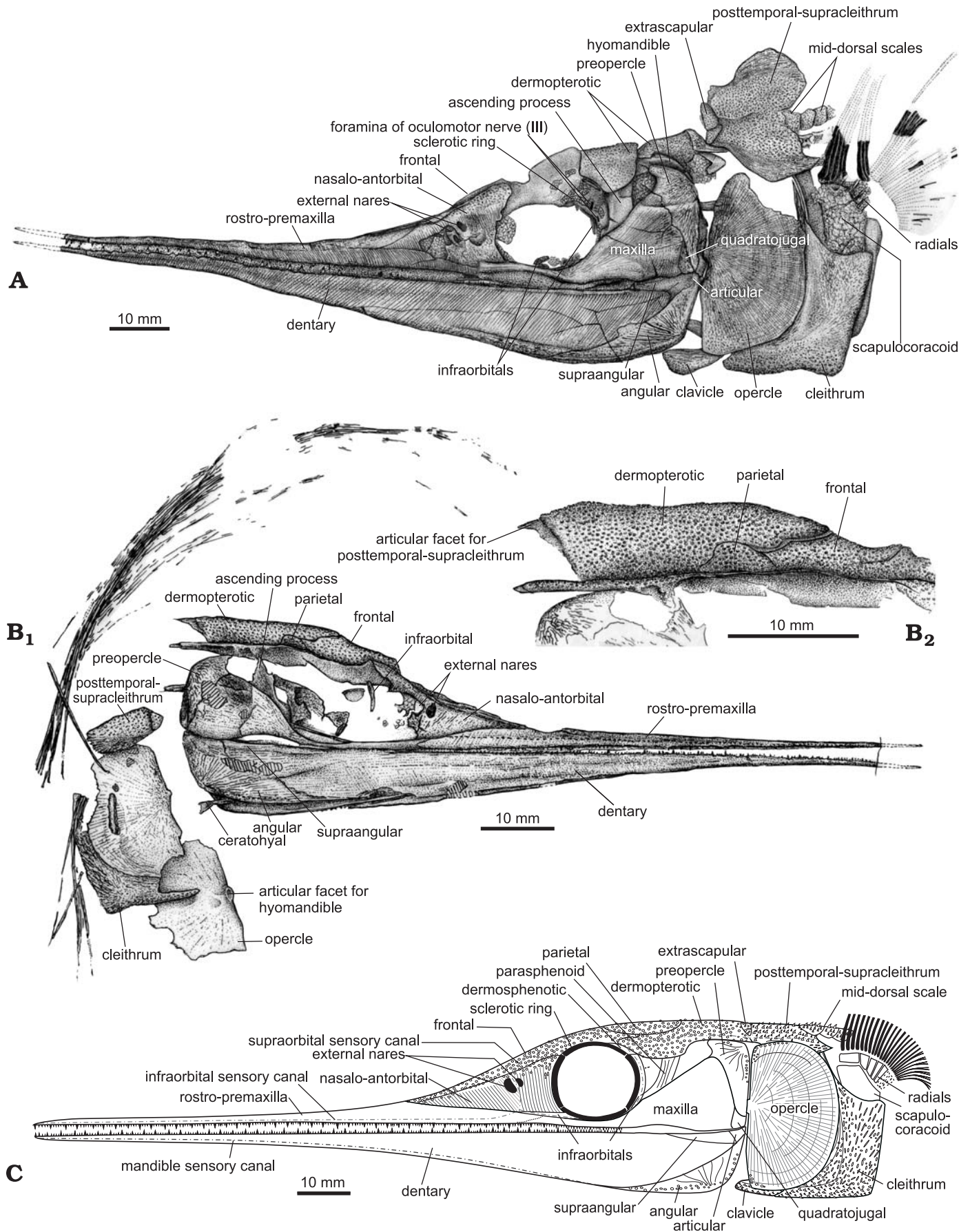| Species	Specimen	Standard body length	Skull length			Postcranial length			
			total	rostrum	mandible	total	opercle-pelvic fin	pelvic-anal fin	anal-caudal fin
Sinosaurichthys longipecotoralis	1097	>562	~150	–	~130	>412	>270	57	85
	1099	495	135	87	~117	360	230	40	90
	1122	–	–	–	–	–	~210	~40	–
	1126	–	–	–	–	–	–	~50	~95
	1214	–	–	–	–	–	–	~35	~77
	1215	–	~125	~79	~110	–	–	–	–
	1233	–	~131	~80	~115	–	–	–	–
	1234	–	138	88	120	–	~235	–	–
Sinosaurichthys longimedialis	1367	–	98	53	82	–	–	–	–
	1543	453	103	58	87	350	230	30	90
	1586	~381	~81	~46	~70	300	–	–	80
	1927	316	96	58	84	220	137	25	58
	1939	~400	~88	~47	~76	312	–	–	~80
	1945	–	~80	~51	72	–	–	20	50
	1949	387	102	65	91	285	188	31	66
	1954	~287	~82	54	75	~205	~135	20	~50
	1958	–	–	–	–	–	–	32	100
	1960	~386	~101	~63	~83	285	175	30	80
Sinosaurichthys minuta	1370	199	65	39.5	56	134	83	15	36
	1372	182	59	37	52	114	70	12	32
	1382	139	49	30	43	90	55	10	25
	1390	150	54	34	47	96	55	13	28
	1928	>183	~63	40	55	>120	>75	11	34
	1929	~208	70	43	61	~138	~85	15	38
	1931	191	65	40	57	126	79	11	36
	1933	107.5	40	25	36	67.5	43	8.5	16
	1938	151	50	30	43.5	101	63	12	26
	1948	169.5	56.5	35	50	113	68	12	33
	1955	125	45	27.5	40	82	52	8	22

gated and triangular, tapering anteriorly and carrying the ethmoid commissure at its anterior tip. The rostro-premaxilla meets its opposite pair medially and contacts with the frontals and nasalo-antorbitals posterodorsally, and the maxilla posteriorly, with a series of conical teeth along its oral margin (Figs. 4, 5). The rostro-premaxilla is ornamented with parallel striations, dipping posteroventrally, and a few tubercles near its dorsal edge. The nasalo-antiorbital is triangular, in contact with the frontal dorsally and the rostro-premaxilla ventrally, and forms the anterior rim of the orbit. Two subovate external nares are present on this bone, arranged in the same way as in other saurichthyids, and the anterior one is distinctly larger than the posterior. The supra-orbital sensory canal enters the nasalo-antorbital from the frontal and passes between the two nares to join the infra-orbital sensory canal at the ventral portion of this bone. The

nasalo-antorbital is ornamented with posteroventrally inclined striations and patch of tubercles near the dorsal edge.

Dermal skull roof.—The skull roof consists of paired frontals, parietals, dermopterotics and extrascapulars (Figs. 4, 5A, C). The frontals are elongated and triangular, tapering anteriorly and forming the main part of the anterior portion of the skull roof above the orbit. Posteriorly, the frontals are in contact with the parietals and dermopterotics. The parietals are subcircular and relatively large in proportion to the skull width, with a width about 60% of the skull width (Fig. 5A, C). The dermopterotics compose the major part of the posterior portion of the skull roof. The posterior end of the dermopterotic is located at the level of the anterior margin of the opercle. As a characteristic feature of this family, the dermopterotics meet at the mid-line of the skull roof posterior to the parietals with a distinct notch at the anterolateral margin of the bone on each side (Figs. 5A, C, 6A) which was interpreted to accommodate the opening of the spiracle canal in *Saurichthys* (Stensiö 1925). The dermopterotic has a posterolaterally protruding process as the articular facet for the extrascapular and post-temporal-supracleithrum. The part of the dermopterotic anterior to the notch is laterally bent downward to form a triangular

Fig. 3. Photographs of saurichthyid fish *Sinosaurichthys longipectoralis* gen. et sp. nov. from Middle Triassic of Yangjuan Section, Panxian, Guizhou, China. **A**. Holotype GMPKU-P1233. **B**. Paratype GMPKU-P1215. **C**. GMPKU-P1253 (C₁), teeth in squared region (C₂). **D**. Paratype GMPKU-P1214. Anterior facing left in A, C, D and right in B.

lateral lobe to cover part of the cheek region between the orbit and the preopercle. The extrascapulars are small and subovate (Figs. 3A, 4A, 5C). The external surface of the skull roof is ornamented with dense tubercles.

Cheek and opercular series.—The orbit is subcircular to ellipse shaped. Similar to *Saurichthys curionii* (Rieppel 1985), no supraorbital bones are developed and the frontal directly forms the dorsal margin of the orbit (Figs. 4, 5A, C). The dermosphenotic is a small slender bone, forming the posterodorsal margin of the orbit. The infraorbital sensory canal extends upward in the posterior half of this bone to enter the dermopterotic. The infraorbitals are poorly preserved and only a few fragments can be identified along the posterior and ventral margins of the orbit in the holotype (Fig. 4A). The sclerotic ring is partly exposed along the edge of the orbit in several specimens. The ring probably has four ossification centers because three elements are exposed in GMPKU-P1183 which occupies almost 3/4 of the orbital circumference (Fig. 6A).

The postorbital region is rather short, with a length evidently less than the skull depth, differing from that in most known species of *Saurichthys* (Stensiö 1925; Rieppel 1985) in which the length of the postorbital region is generally greater than or equal to the skull depth. The maxilla and preopercle are the main dermal elements of the cheek region. The maxilla is composed of a long and slender anterior orbital portion that contacts the rostro-premaxilla anteriorly and a highly expanded postorbital portion that contacts with the preopercle. The oral margin of the maxilla is slightly concave behind the orbit. The preopercle is deep and almost vertical, with a distinct concave anterior margin. The dorsal portion is expanded and ventral portion is narrowed, showing a primitive condition as commonly in other lower actinopterygians (Fig. 4A, C). The quadratojugal is relatively small, in contact with the maxilla anteriorly and the preopercle dorsally (Fig. 4A), showing more or less a plesiomorphic condition as in other lower actinopterygians (e.g. *Mimia*, *Moythomasia*, *Pteronisculus*, and *Birgeria*) (Nielsen 1942, 1949; Lehman 1952; Gardiner 1984). This bone is greatly deduced or lost in neopterygians such as *Amia* (Grande and Bemis 1998).

As a shared feature of the Saurichthyidae, *Sinosaurichthys longipectoralis* has a single large, semicircular opercle and lacks an independent subopercle (Figs. 3A–C$_1$, 4A, B$_1$, C). The opercle reaches 85–88% of the skull depth in height, with a depth/width ratio varying from 1.55 to 1.97 (average 1.76; Table 2). A small process is developed in its straight anterior margin at the level slightly higher than the joint of the upper and lower jaws. Externally the opercle shows radiating and concentric striations with some tubercles near its dorsal and ventral edges. The medial side of the opercle is smooth except for a distinct circular recess posterior to the process

mentioned above. Neither gular plates nor branchiostegal rays are developed. In *Saurichthys*, the gular plates are absent but there is generally one pair of branchiostegal rays.

Mandible.—The elongated lower jaw is as long as the upper jaw. Its maximum depth is less than half of the skull depth. The symphyseal region occupies about two fifth of the mandible length. There is little difference in the arrangement of the dermal elements in lateral side of the mandible from that of most species of *Saurichthys* (Fig. 4A, B$_1$, C). The dentary is the largest ossification and covers almost the whole lateral side of the mandible. It is ornamented with anteroventrally inclined fine striations and a few tubercles along the ventral edge. The angular is triangular, occupying the posteroventral portion of the mandible and sutures with the dentary anterodorsally (Fig. 4A, B$_1$, C). In the lateral side, the angular extends to the level anterior to the posterior rim of the orbit, whereas ventrally the bone bends up dorsomedially to wrap the mandible along its ventral edge and continues forward beyond the anterior rim of the orbit. The angular is ornamented with coarse ridges that radiate from its posteroventral corner, and some tubercles along its posterior and ventral edges. The supraangular is a small slender element, located at the posterodorsal corner of the mandible anterior to the articular.

In the lingual side of the mandible a long bone with many small teeth can be seen in specimen GMPKU-P1141, covering almost the whole length of the mandible (Fig. 5B). It should be the fused prearticular and coronoids (= mixcoronoid of Stensiö 1925). It is roughly acute triangular, high in the posterior part and tapering anteriorly, with a straight dorsal edge. The posterior part of this bone contacts the angular posteroventrally (Fig. 5B). In the joint region with the upper jaw, there are two transverse depressions related to the articulation with the quadrate; therefore this region should be the ossification of the articular, similar with the situation in some other known saurichthyids (Stensiö 1925; Beltan 1968; Rieppel 1985). The adductor fossa is elongated and deep, enclosed laterally by the dentary and supraangular, medially by the prearticular-coronoid, and posteriorly by the articular (Fig. 5B, E).

Palate.—The palate includes a pair of long and slender vomers (Fig. 6C, E), and a median parasphenoid. Although the parasphenoid is incompletely preserved in all specimens, its general morphology and structure can still be restored (Fig. 6D). As in the Lower Triassic *Saurichthys* from Spitsbergen and Madagascar (Stensiö 1925; Beltan 1968), the parasphenoid consists of a long anterior stem that has extended between the paired vomers, a pair of large ascending processes that have dorsolaterally extended to cover considerable portion of the otic and orbitotemporal regions of the neurocranium, and a posterior stem that has extended posteriorly over the occipital region. It shows the following features that differ from that of *Saurichthys* described by Stensiö (1925): (1) the posterior stem is highly elevated above the mid-point of the skull depth with a high plate-like ventral crista (Fig. 6A, B, D) while in *Saurichthys* it is only slightly elevated with a low ridge-like ventral crista. The elevation of the pos-

Fig. 4. Line drawings of saurichthyid fish *Sinosaurichthys longipectoralis* gen. et sp. nov. from Middle Triassic of Yangjuan Section, Panxian, Guizhou, China. **A**. Skull, holotype GMPKU-P1233. **B**. Paratype GMPKU-P1215; skull (B$_1$) and skull roof (B$_2$). **C**. Tentative restoration of skull in left lateral view. Anterior facing left in A, C and right in B.

Table 2. Measurement (in mm) of opercle and paired fins of *Sinosaurichthys* gen. nov.

Species	Specimen	Skull depth/ mandible length	Opercle			Length of paired fins	
			depth	width	depth/width	pectoral fin	pelvic fin
Sinosaurichthys longipectoralis	1097	–/~130	36	20	1.80	197	60
	1099	–/~117	28.5	16.5	1.73	~150	>23
	1122	–	28	16	1.75	>110	33
	1126	–	–	–	–	>115	>23
	1211	22/–	22	13	1.69	>130	25
	1214	–	–	–	–	–	>30
	1215	22/~110	22	12	1.83	>100	–
	1223	–	–	–	–	–	>40
	1227	35/–	31	20	1.55	–	–
	1233	28/~115	28	17	1.65	150	–
	1247	25/	21.5	11	1.95	>90	–
	1253	28/–	28	15	1.87	–	–
	1362	–	–	–	–	>65	24
Sinosaurichthys longimedialis	1927	24/84	19	12	1.58	22	11
	1935	18/–	13	7.5	1.73	–	–
	1949	25/91	20	11	1.82	~23	19
	1954	20/75	15	9	1.67	20	8
	1367	27/82	23	14	1.64	31	–
	1543	28/87	24	15.5	1.55	28	~15
	1958	–	–	–	–	–	18
Sinosaurichthys minuta	1372	14/52	10.5	6.5	1.62	>9	6
	1928	–/55	11	7	1.57	–	6
	1931	14/57	11	7	1.57	12	6
	1932	12/50	9	5	1.80	10	5
	1938	13/44	10	7	1.43	8	–
	1955	11/40	8	4.5	178	12	4

terior stem of the parasphenoid in *Sinosaurichthys* is apparrently related to the elevation of the axial skeleton in the abdominal region and is unique; (2) the tooth plate or patch in the ventral (oral) face of the parasphenoid extends posteriorly on the ventral crista posterior to the ascending process while that in *Saurichthys* is relatively short, and only restricted anterior to the ascending process; (3) the anterior stem is very long, about three times of the length of the posterior one (Fig. 6C–E) while in the Lower Triassic *Saurichthys* the anterior stem is almost as long as the posterior one. But in some later representatives of *Saurichthys* the anterior stem may be longer than the posterior one because this feature is evidently related to the shortening of the postorbital region in the saurichthyids; (4) the efferent pseudobranchial arteries penetrate the parasphenoid through a pair of small ear-like processes anterior to the ascending process (Fig. 6A, B, D). This paired ear-like process, more or less, resembles to the dermal basipterygoid process in some low actinopterygians in morphology and position but it leaves no trace for articulating with the palatoquadrate. Maybe it represents an incipient or highly reduced basipterygoid process. A similar condition is present or probably present in some of the Middle Triassic *Saurichthys*, such as *Saurichthys dawaziensis* (Wu et al. 2009) and *S. curionii* (Rieppel 1985) but proballly absent in the Early Triassic *Saurichthys* (Stensiö 1925); (5) the fo-

ramina of the common carotid arteries are situated in the lateral wall of the ascending process with openings directed more or less lateroventrally (Fig. 6A, B, D). In *Saurichthys ornatus* the same foramina (originally interpreted as for the external carotid arteries by Stensiö (1925), and later assumed to have transmitted the common carotid arteries by Patterson (1975) are in the underside of the parasphenoid beneath the posterior margin of the ascending process (Stensiö 1925) and in *S. curionii* they are even anterior to the ascending process (Rieppel 1985).

Hyoid arches.—The hyomandible is almost vertical, having a slightly broad, blade-like dorsal portion and a narrow, slender posteroventral portion (Figs. 5B, 6A, B, F_1), slightly different from the hockey stick-like one in *Saurichthys hamiltoni* (Stensiö 1925) and *S. costasquamosus* (Rieppel 1985). The blade-like dorsal portion has a distinct posteroventrally directed ridge running through its medial surface and the posteroventral portion seems to contact with the palatoquadrate at a point slightly high above the mandibular articulation. No opercular process is present in the hyomandible. The symplectic is absent as in *Saurichthys* and other lower actinoptergyians. The ceratohyal can be seen in GMPKU-P1215 and 1253, being of a typical hour glass shape, narrow rod-like in the middle and expanded plate-like at the two ends (Figs. $4B_1$, $6F_2$).
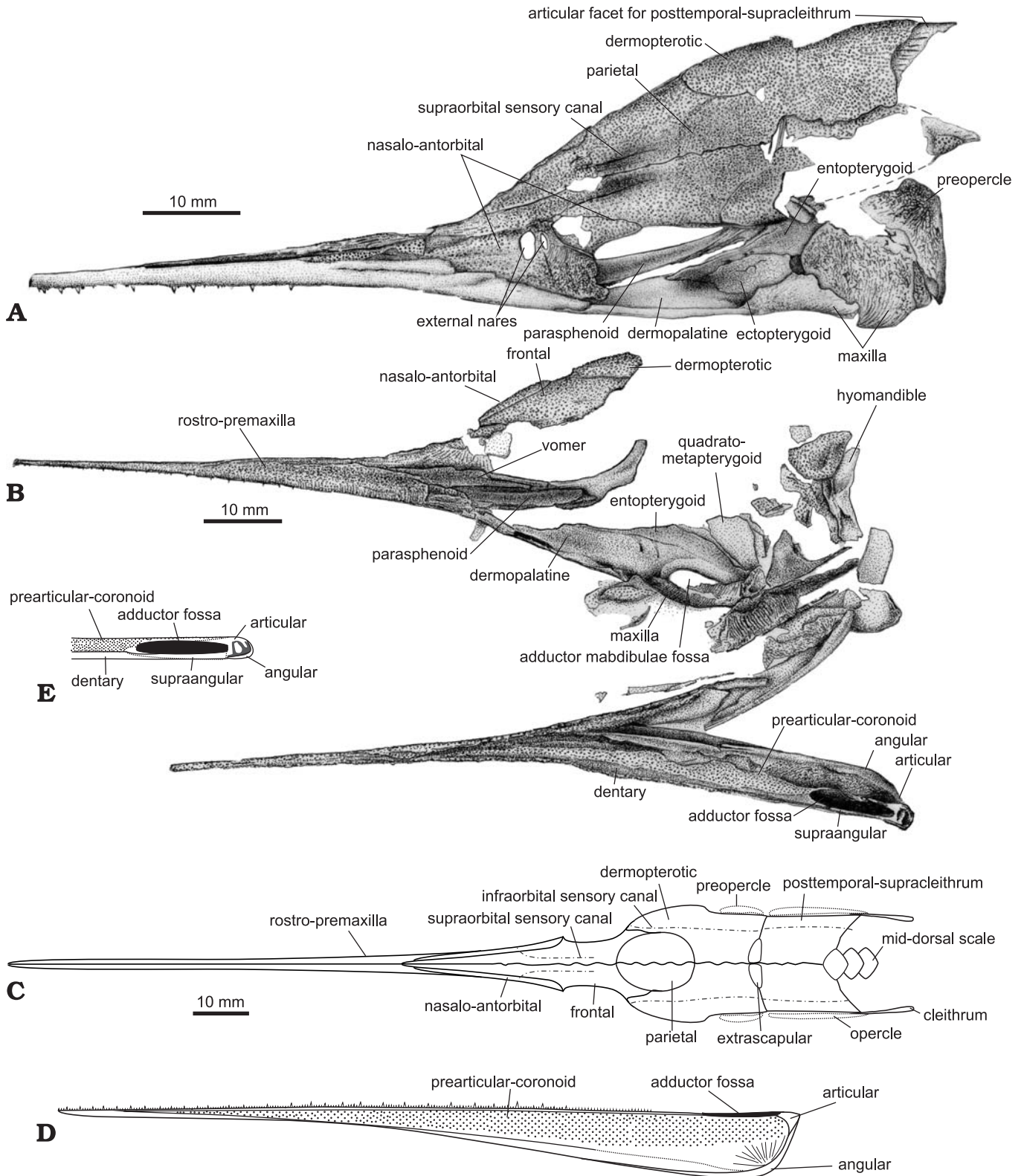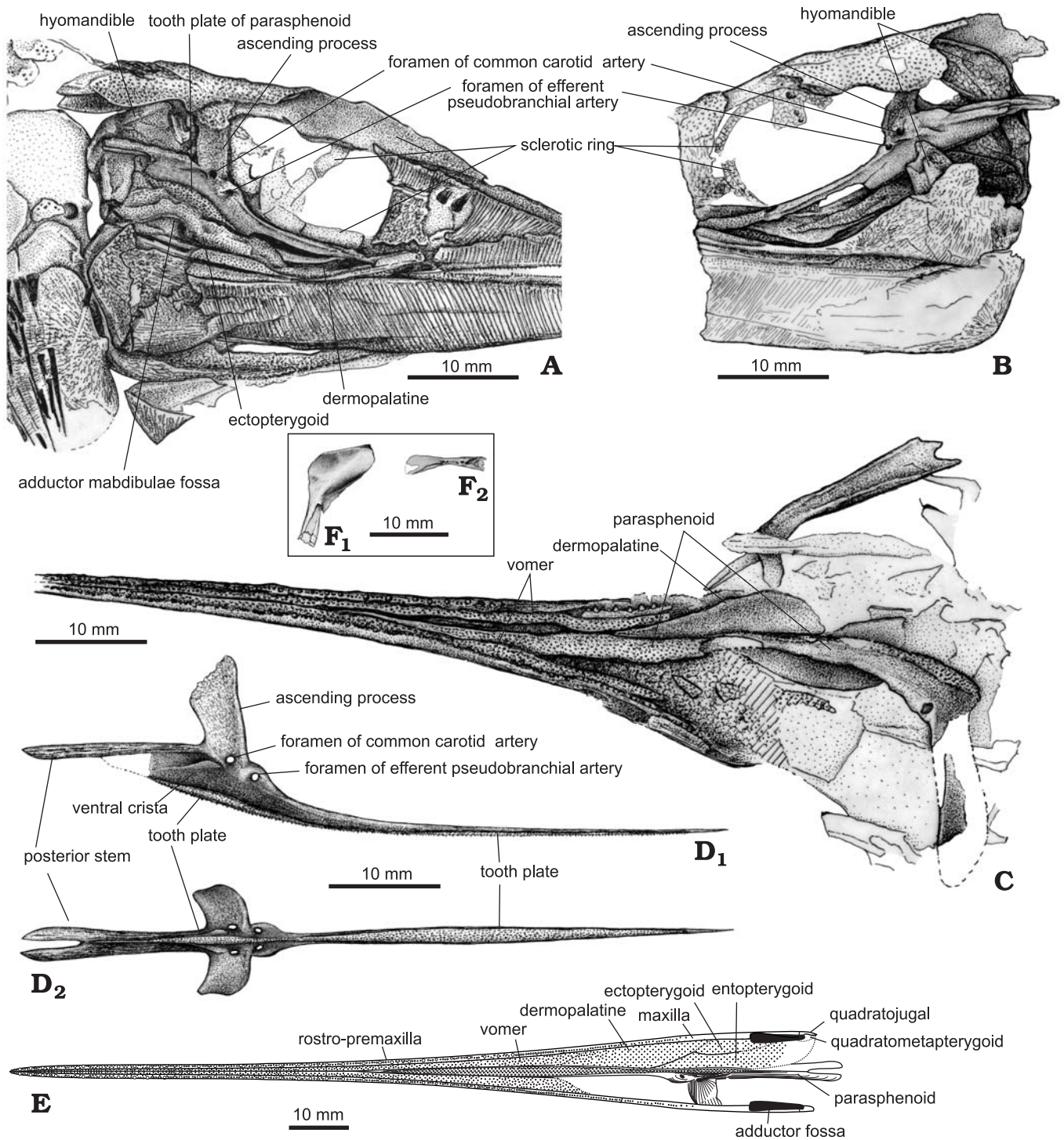
Fig. 5. Line drawings of saurichthyid fish *Sinosaurichthys longipectoralis* gen. et sp. nov. from Middle Triassic of Yangjuan Section, Panxian, Guizhou, China. **A**. GMPKU-P1225. **B**. GMPKU-P1141. **C**. Tentative restoration of skull in dorsal view. **D**. Lower jaw in medial view. **E**. Posterior part of lower jaw in dorsal view; anterior facing left.

Palatoquadrate complex and related dermal bones.—Only the qudratometapterygoid portion of the palatoquadrate is ossified and can be observed in two specimens. The posteroventral part of the quadratometapterygoid portion is well ossified, rather thick and condense, to articulate with the lower jaw (Fig. 3C$_1$), and the dorsal part of this portion occurs as thin perichondral

Fig. 6. Line drawings of saurichthyid fish *Sinosaurichthys longipectoralis* gen. et sp. nov. from Middle Triassic of Yangjuan Section, Panxian, Guizhou, China. **A**. Posterior part of the skull GMPKU-P1183. **B**. Skull GMPKU-P1361. **C**. Skull GMPKU-P1099. **D**. Restoration of parasphenoid in lateral (D₁) and ventral (D₂) views. **E**. Tentative restoration of upper jaw in ventral view, size referred from GMPKU-P1233. **F**. Isolated left hyomandible in medial view (F₁) and ceratohyal (F₂) from GMPKU-P1253. Anterior facing right in A, D, F and left in B, C, E.

lining (Fig. 5B). Three dermal bones contacting the palato-quadrate ventromedially, i.e., the dermopalatine, ectopterygoid and entopterygoid can be distinguished (Figs. 5A, B, 6A, C). The dermopalatine is roughly obtuse triangular to trapezoid in outline, in contact with the vomer anteriorly, with the parasphenoid medially and with the maxilla laterally. Posterior to the dermopalatine, the ectopterygoid contacts the ventromedial edge of the maxilla ventrally. Medially, it is in contact with the entopterygoid and posteriorly forms the anterior margin of the adductor fossa of the upper jaw. The entopterygoid is roughly triangular and tapers forward along the dorsal edges of the dermopalatine and ectopterygoid.
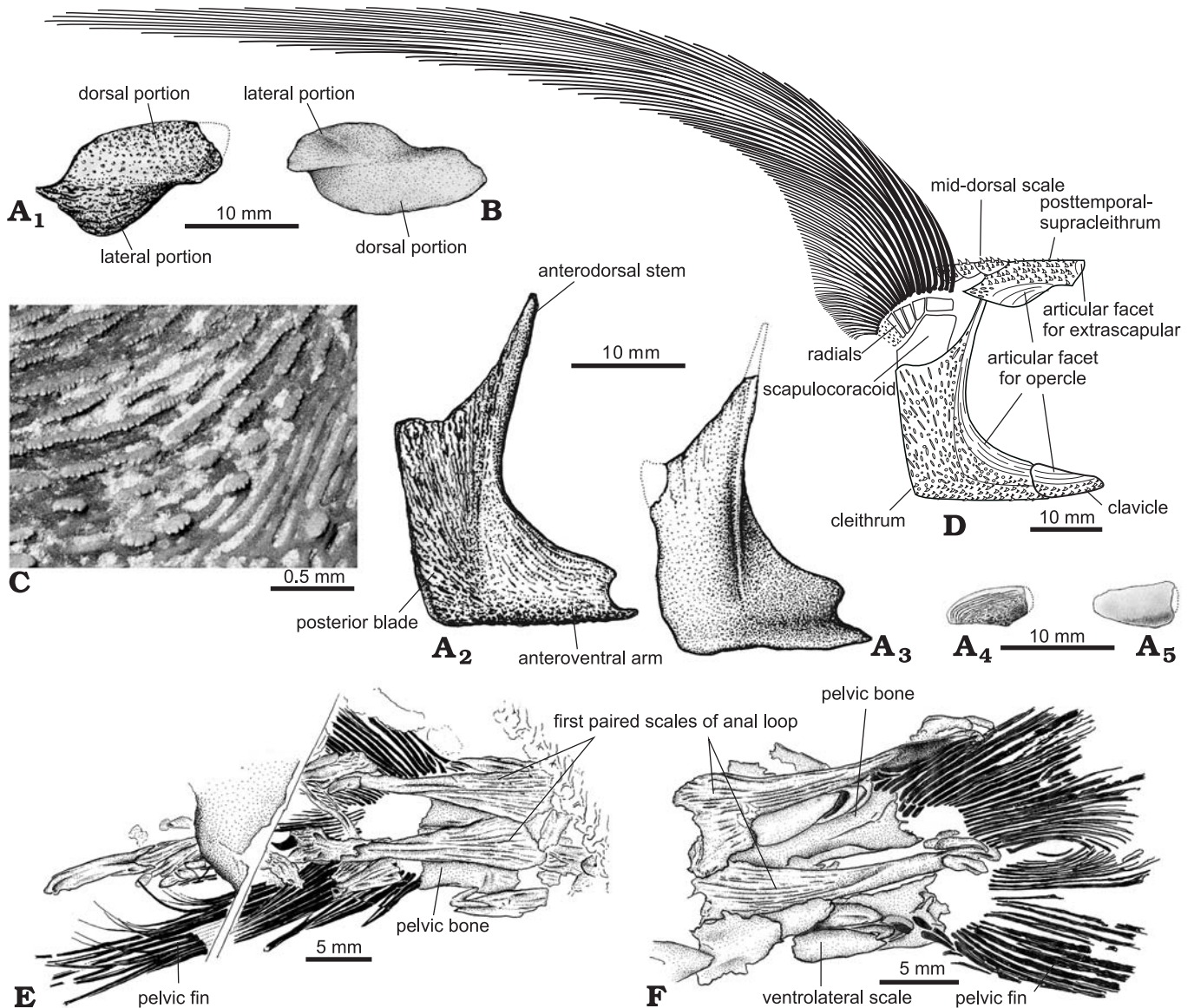
Fig. 7. Saurichthyid fish *Sinosaurichthys longipectoralis* gen. et sp. nov. from Middle Triassic of Yangjuan Section, Panxian, Guizhou, China. **A**. Line drawings of right posttemporal-supracleithrum form GMPKU-P1253 in dorsal view (A_1), right and left cleithrum in lateral (A_2), and medial (A_3) views, and left and right clavicles in lateral (A_4) and medial (A_5) views. **B**. Line drawing of right posttemporal-supracleithrum from GMPKU-P1126 in ventral view. **C**. Photograph of the micro-ornamentation in the articular facet of the cleithrum for the opercle from GMPKU-P1361. **D**. Reconstructed left pectoral girdle and pectoral fin, mainly based on GMPKU-P1233 (holotype). **E**, **F**. Pelvic girdle and pelvic fins in GMPKU-P1362 (E) and GMPKU-P1211 (**F**). Anterior facing left in A_4, A_5, C, F and right in A_1–A_3, B, D, E.

Dentition.—There is a single row of large teeth on the oral margin of the upper and lower jaws, arranged in the same pattern as in *Saurichthys curionii* (Rieppel 1985), with small ones in between and around (Fig. $3C_2$). The oral surfaces of the vomer, parasphenoid, dermopalatine, ectopterygoid, entopterygoid, and prearticular-coronoid are covered by small teeth. The large teeth are relatively smaller than those in *Saurichthys*. In adult specimens the diameter of the large teeth is 0.25–0.6 mm at the base and its depth 0.45–0.86 mm, with the depth/width ratio ranging from 1.7–2.1. All teeth are conical, with a semitransparent enamel acrodin cap that is slightly over one-third of the tooth depth. Numerous faint vertical striations exist in the basal part of the teeth.

The depressions for receiving the tips of the large teeth of the upper jaw can be seen in the anterior part of the lower jaw lateral to the tooth row. These "incissivlücken" are also known in some other saurichthyids, such as *Saurichthys krambergeri* (Griffith 1962), *Saurichthys dawaziensis* (Wu et al. 2009), and an undetermined species of *Saurichthys* from the Eotrias of South Africa (Griffith 1978), and in the Early Jurassic saurichthyid genus *Acidorhynchus* (Gardiner 1960; Thies 1985).

Paired fins and girdles.—The pectoral fins and girdles are preserved almost in the original articulated state in the holotype (Figs. 3A, 4A), showing a condition that the pectoral fins are much more dorsally inserted than those in *Saurich-*

thys. Although most of the fin rays were weathered away, their impressions remain on the matrix. The bases of the fin rays are arranged in an arc that slightly curves down backward dorsal to the radials. The fins are sickle-shaped, as long as or longer than the mandible length. The longest pectoral fins are recorded in GMPKU-P1097, reaching 257 mm long, about 1.84 times of the mandible length. In *Saurichthys* the pectoral fins are generally fan-shaped, with a length generally no more than 1/6 of the mandible length. No segmentation is observed in the fin rays. The anterior four to five fin rays are unbranched and the remainder branch distally five times maximally and twice minimally. The 7th fin ray is the longest.

The dermal elements of the pectoral girdle are well preserved (Figs. 3A–C_1, 4, 7A, B). The posttemporal (= suprascapular sensu Stensiö 1925; Lehman 1952; Rieppel 1980) and supracleithrum are fused into a large bone (here tentatively named as posttemporal-supracleithrum) consisting of a rectangular, horizontal dorsal portion (= posttemporal) and a triangular, vertical ventrolateral portion (= supracleithrum) posterior to the dermopterotic and extrascapular and dorsal to the opercle. The dorsal portion of the bone meets its fellow of the opposite side at the midline and the ventrolateral portion of this bone is partially overlapped by the opercle ventroanteriorly and contacts the cleithrum posteriorly. The pores of the infraorbital sensory canal can be seen distributed along the border of the two portions of this bone to extend anteriorly into the dermopterotic and runs posteriorly into the body. The exposed surface of this composite bone is ornamented with tubercles and the area overlapped by the opercle has longitudinal ridges with serrations pointing upwards. The postcleithrum is absent. The cleithrum is boot-shaped and consists of a deep rectangular posterior blade, a long, slender and curved dorsal stem, and a short horizontal anteroventral arm (Figs. 3A, 4A, C, $7A_2$, A_3, D), different from the typical triradiate one in other saurichthyids. The bone is concave anteriorly and borders the posterior margin of the opercle. The anterodorsal tip of the dorsal stem articulates with the posttemporal-supracleithrum. The depth of the posterior blade of the bone is more than half of the skull depth with a depth/length ratio of about 1.8. The horizontal anteroventral arm is low, with its anterior edge concave to fit the posterior margin of the clavicle. A prominent keel in the medial surface runs from the radiation center of the bone upward to the tip of dorsal stem. The clavicle is suboval to subtriangular (Figs. 3A, 4A, $7A_4$, A_5), with its expanded posterior end articulating with the cleithrum, ventral to the opercle (Fig. 7D). The exposed surfaces of the cleithrum and clavicle are decorated with spiny tubercles while the areas overlapped by the opercle are ornamented by similar ridges to those on posttemporal-supracleithrum with serrations pointing away from the opercle (Fig. 7C).

The endoskeletal pectoral girdle is best preserved in the holotype, including the scapulocoracoid and the radials. The scapulocoracoid is a deep plate-like structure emerging behind the dorsal stem of the cleithrum. It bears at least seven radials along its dorsal margin. Except the anteriormost and largest one, the rest decrease gradually in size posteriorly. These radials support approximately 25 fin rays distally (Figs. 3A, 4A, 7D).

The pelvic fins are situated closer to the caudal fin than to the pectoral ones, with its distance to the caudal fin slightly more than one-third of the distance between the opercle and the caudal fin. Compared to *Saurichthys* and other species of *Sinosaurichthys*, the pelvic fins are quite long, more than the skull depth (Table 2). In *Saurichthys* and other two species of the new genus, the pelvic fins are generally less than or as long as half of the skull depth. Each pelvic fin consists of 23–24 unsegmented, distally branched fin rays that articulate with the posterior edge of the pelvic bone (Fig. 7E, F). The pelvic bone is subrectangular. No radials are preserved.

Unpaired fins.—The unpaired fins are relatively well preserved in three specimens. The dorsal and anal fins are triangle-shaped and situated opposite to each other, slightly posterior to the pelvic fins (Fig. 3D). The depth/width ratio of the dorsal and anal fin is over 1.7, showing a higher aspect ratio (defined as depth^2/area) than that in *Saurichthys* and the other two species of *Sinosaurichthys*. The estimated fin rays of the dorsal and anal fin in GMPKU-P1214 are no less than 55 and 50, respectively. The anterior 12 fin rays are stout and unbranched, whereas the following ones are distally branched once or twice. The 12th fin ray is the longest. Generally, a maximum of three to four segments are counted in the longest fin ray of both the dorsal and anal fins, but six segments are recorded in the anal fin in GMPKU-P1223. Both the dorsal and anal fins are supported by the radials consisting of slender proximal axonosts and small distal baseosts. There are 16 axonosts on each fin. The axonosts are posterodorsally and anterodorsally directed in the dorsal and anal fin, respectively, and tend to decrease in depth posteriorly. The small and rectangular baseosts are poorly ossified, lying distal to the axonosts.

The caudal fin is deeply forked and symmetrical, with 36–38 fin rays in each lobe directly supported by the axial endoskeleton and with an angle between the leading edges of the two lobes varying from 84° to 100°. There are at least six segments in the epichordal lobe and five segments in the hypochordal lobe of the caudal fin with maximal three times of distal bifurcation in GMPKU-P1089. The depth of the caudal fin is about 2.8 times of the maximal body depth in GMPKU-P1214.

The basal and fringing fulcra are present in all median fins. Six to seven basal fulcra can be seen in the anal fin in GMPKUM-P1214 and P-1122. Two to three basal fulcra exist on each lobe of the caudal fin. The fringing fulcra occur as small spine-like elements lying on the surface of margin leading rays distally, distinctly shorter than the basal fulcra and overlapping one by one. This condition probably can be assigned to the pattern B as proposed by Arratia (2008: 229).

Axial skeleton.—The axial skeleton consists of the neural and haemal arches applied to the persisting notochord. In GMPKU-P1099, approximately 140 and 70–72 neural
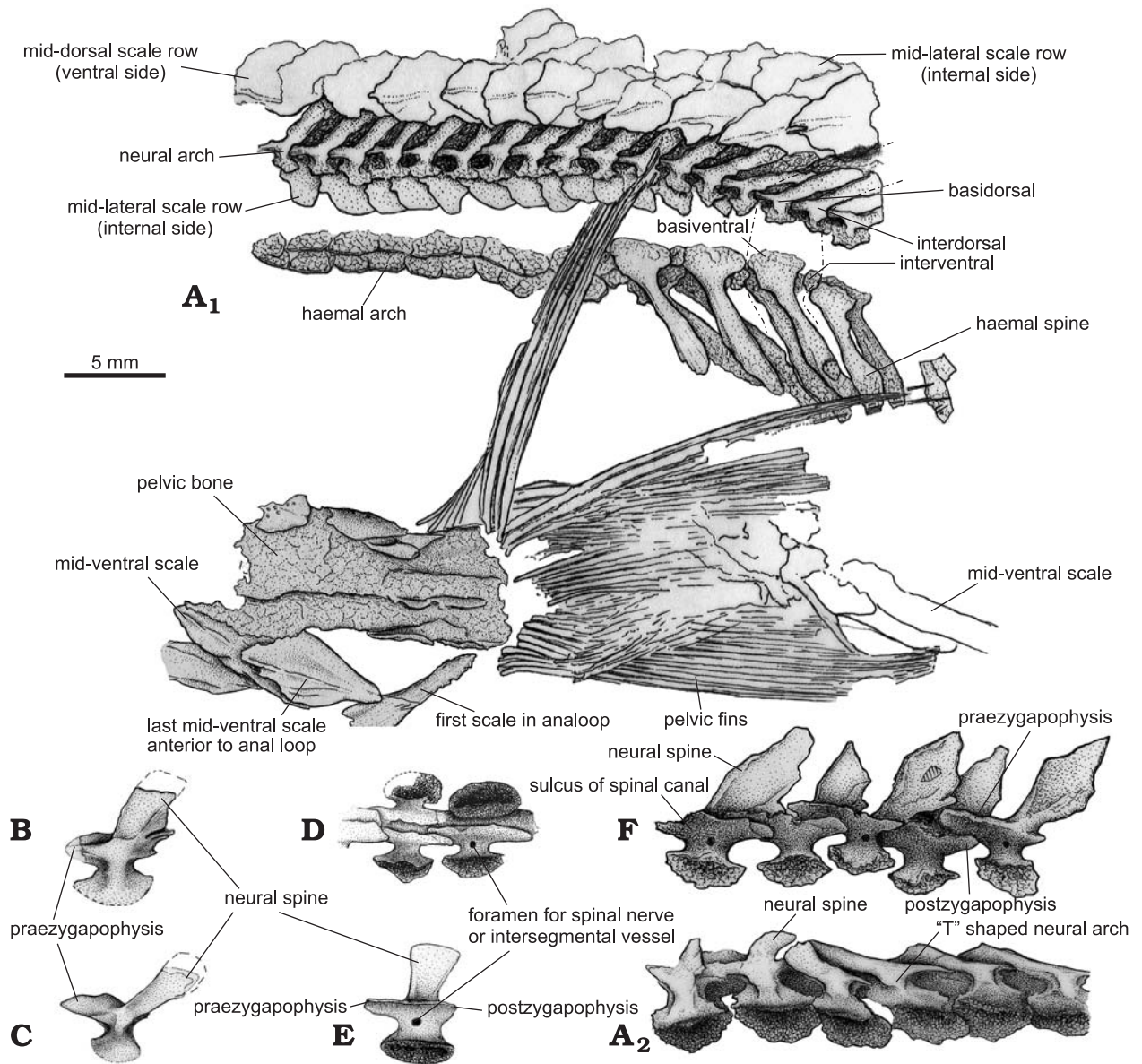
Fig. 8. Line drawings of saurichthyid fish *Sinosaurichthys longipectoralis* gen. et sp. nov. from Middle Triassic of Yangjuan Section, Panxian, Guizhou, China. **A**. Axial skeleton in posterior abdominal region (A_1) and neural arches (left) in anterior caudal region (A_2) from GMPKU-P1126. **B**. Isolated neural arch (left) immediately behind skull of GMPKU-P1233 (holotype) in lateral view. **C**. Isolated neural arch (left) in mid-abdominal region of GMPKU-P1211 in lateral view. **D**. Paired neural arches in middle part of caudal peduncle of GMPKU-P1089 in ventral view. **E**. Restoration of right neural arch bearing foramen in medial view. **F**. Neural arches (right) closely behind skull of GMPKU-P1366 in medial view. Anterior facing left.

arches exist in front of the pelvic fins and between the pelvic and caudal fin, respectively. In GMPKU-P1234, 140–150 neural arches are estimated in front of the pelvic fins. Thus, the total number of the neural arches in the trunk is no less than 210 and this figure does not include the ones hidden by the opercle and those (approximately 14–18) supporting the fin rays of the epichordal lobe of the caudal fin. The neural arches are paired structures. In their medial face there is a sulcus parallel to the longitudinal axis of the notochord (Fig. 8D–F). The sulcus, together with its counterpart in the neural arch of the opposite side, is supposed to form the canal for the spinal cord. A small foramen, probably related to the spinal nerve or intersegmental vessel, can

be observed in the sulcus of every other neural arch all through the axial skeleton in some specimens (Fig. 8D–F), suggesting that one neural arch corresponds to only half sclerotome or one dorsal arcualian element (basidorsal or interdorsal). Each neural arch carries a prae- and a post-zygapophysis along its dorsal edge. When in articulation, each praezygapophysis overlaps the postzygapophysis of its preceding neural arch (Fig. 8A_1, F). Each neural arch is expanded at its ventral base (Fig. 8A_2–F) with an acetabula-like concavity, presumed to house the cartilaginous part of the dorsal arcualia elements which rest on the dorso-lateral aspect of the notochord. The elongated paired neural spines are developed distally to all the neural arches ante-
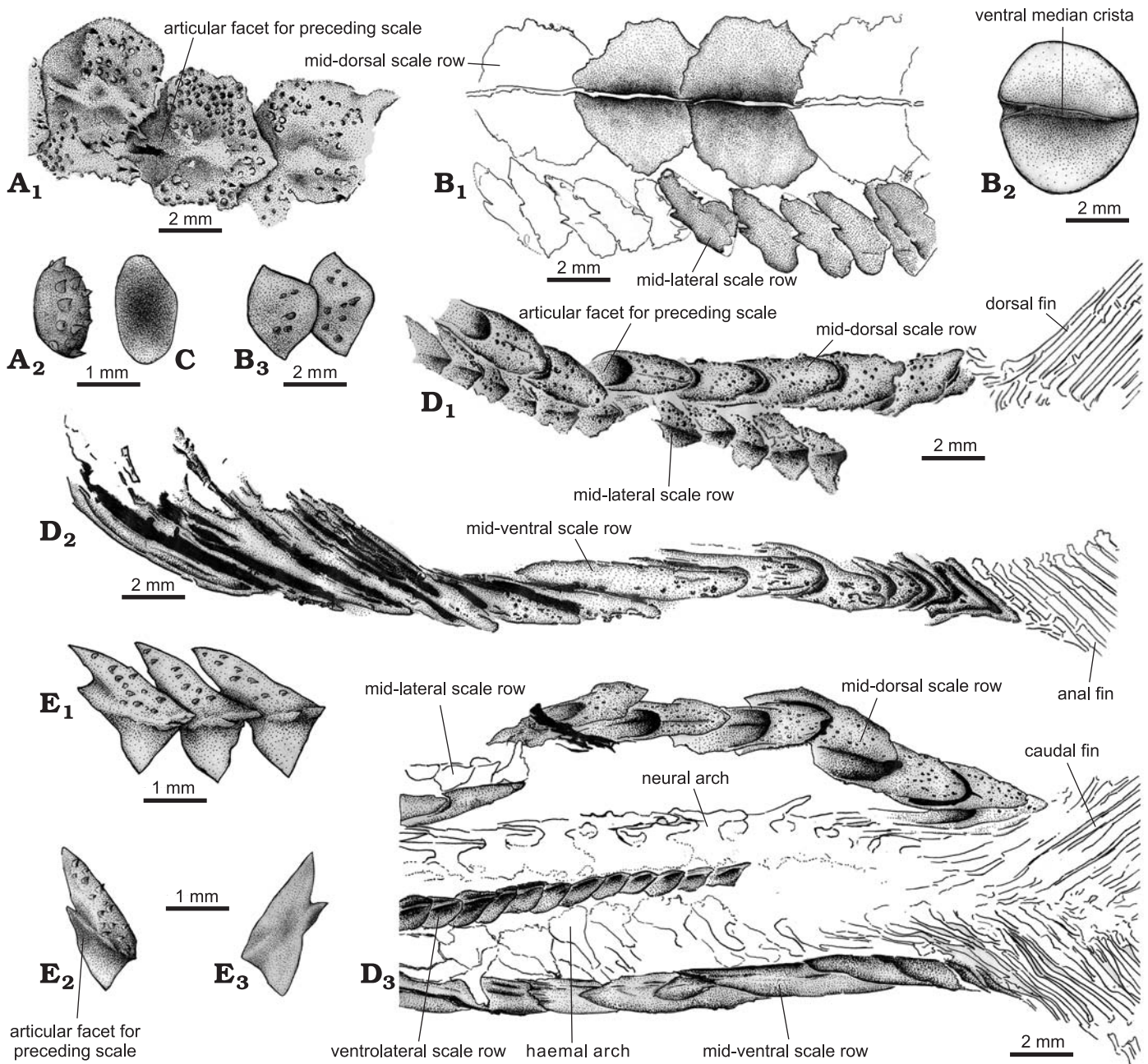
Fig. 9. Line drawings of saurichthyid fish *Sinosaurichthys longipectoralis* gen. et sp. nov. from Middle Triassic of Yangjuan Section, Panxian, Guizhou, China. **A**. Mid-dorsal scales slightly behind skull of in dorsal view (A_1) and an isolated mid-ventral scales behind skull in external view (A_2) from GMPKU-P1233 (holotype). **B**. Mid-dorsal and mid-lateral scales in anterior part of trunk in ventral (internal) view (B_1), a single mid-dorsal scale behind skull in ventral view (B_2), and ventrolateral scales in lateral view (B_3) from GMPKU-P1126. **C**. An isolated mid-ventral scales behind skull in internal view from GMPKU-P1366. **D**. Mid-dorsal and mid-lateral scale rows anterior to dorsal fin (D_1) and mid-ventral scales anterior to anal fin (D_2), and squamation in caudal peduncle region (D_3) from GMPKU-P1214. **E**. Mid-lateral scales in lateral view (E_1), mid-lateral scales in anterior part of trunk in medial (E_2), and lateral (E_3) views from GMPKU-P1211. Anterior facing left in A–D, E_1, E_2 and right in E_3.

rior to the caudal peduncle and the following 28 neural arches anterior to the caudal fin do not carry neural spines, and thus look "T" shaped in lateral view (Fig. $8A_2$). When approaching the caudal fin, the neural arches support the fin rays of the epichordal lobe of the caudal fin.

The haemal arches are paired and lie along the ventro-lateral aspects of the notochord, opposite to the neural arches (Fig. $8A_1$). The haemal arches occur as poorly ossified small

suboval plates in the abdominal region and consist of two kinds of alternatively arranged bony plates in the caudal region. One of them is well ossified and considerably large, almost corresponding to two neural arches in length and bearing a distinct haemal spine, and the other is poorly ossified and very small, without a haemal spine. These two kinds of haemal arches should represent the separate basi- and inter-ventral arcualia elements (Fig. $8A_1$). Nearly twenty haemal

arches with distinct haemal spines can be counted between the pelvic and anal fin in GMPKU-P1214.

Based on the size relationship of haemal and neural arches in *Saurichthys ornatus*, Stensiö (1925) supposed that the basidorsal and interdorsal elements are equally developed and possess the same shape in *Saurichthys*, but this viewpoint was not widely accepted. The presence of the foramen of the intersegmental vessels in the haemal arches of *Saurichthys madagascariensis* (Lehman 1952), and one haemal arch corresponding to one neural arch in *Saurichthys curionii* (Rieppel 1985) had led to the idea that the neural arches of the saurichthyids represent only the basidorsals (Arratia et al. 2001). However, the alternative distribution of the foramen in the neural arch in *Sinosaurichthys longipectoralis* and in *Saurichthys dawaziensis* (Wu et al. 2009) provides evidence to support Stensiö's (1925) hypothesis and strongly suggests that the neural arches in saurichthyids, at least in some species of *Saurichthys* and *Sinosaurichthys* are alternate basidorsal and interdorsal. In other lower actinopterygians, the ossification of basidorsal is always larger than the interdorsal and neural spines are usually only developed in the basidorsals. Consequently, the basidorsal and interdorsal equally-developed should be considered as a possible synapomorphy of the saurichthyids.

Squamation.—Similar to the Middle Triassic *Saurichthys* from Monte San Giorgio (Rieppel 1985, 1992) but different from the species of *Saurichthys* of other areas of the world, *Sinosaurichthys* bears six longitudinal rows of scales, including one mid-dorsal, one mid-ventral, two mid-lateral and two ventrolateral rows. In the GMPKU-P1126, in addition to the six rows, numerous small bony plates are scattered between the scale rows.

The mid-dorsal scale row runs through the body length and only interrupted by the dorsal fin. Because of the incomplete preservation, in specimen GMPKU-P1099, 81 mid-dorsal scales can be counted only between the skull and the level slightly posterior to the pelvic fins. In the other two specimens, 16–17 mid-dorsal scales can be counted in the area between the pelvic and dorsal fins. Thus, the total number of the mid-dorsal scales anterior to the dorsal fin is no less than 90 and this number does not include those of the basal fulcra of the dorsal fin. The exposed part of the mid-dorsal scales are cordate, generally wider than long but tend to be narrower toward the dorsal fin with the width/length ratio varying from about 2–2.1 to 0.7–0.75 from the skull to the dorsal fin (Fig. $9A_1$, B_1, B_2, D_1). The posterior exposed part of each scale overlaps about the anterior one-third of the succeeding scale and bears a plate-like ventral median crista (Fig. 9B). The surface of each scale is ornamented with 12 to 20 longitudinal rows of posteriorly directed spine-like tubercles. The exposed parts of the scales just behind the dorsal fin are relatively thick, longer than wide, with blunt spearhead shaped end. These scales tend to increase in size posteriorly. In the anterior part of each scale there is a concaved facet to accept the posterior part of the preceding scale (Fig. $9A_1$, D_1, D_3).

Different from the Middle Triassic *Saurichthys* from Monte San Giorgio (Rieppel 1985) the mid-ventral scale row of *Sinosaurichthys longipectoralis* begins to develop just behind the skull. This scale row consists of loosely articulated small suboval plates (Fig. $9A_2$, C) in anterior one-third part between the skull and pelvic fins. The following scales increase in length posteriorly and become lanceolate toward the pelvic fins. Slightly anterior to the pelvic fins, the mid-ventral scale row is branched to form the anal loop. Five pairs of the scales are, at least, involved in the anal loop but the accurate number is not clear due to the preservation. The last scale anterior to the anal loop is elongated, with its posterior part expanded into a rhombic plate to overlap on the first paired scale in the anal loop, which is also very large, as long as four to five times of each of the subsequent anal loop scales, expanding anteriorly and tapering posteriorly with some longitudinal fine grooves on its surface and a hook-like spine in the posterior end (Fig. 7E, F). This paired large scale was incorrectly considered by Wu et al. (2008) as a "clasper-like" gonopodium. The mid-ventral scales in the caudal region are lanceolate and similar to the mid-dorsal ones of the same region (Fig. $9D_3$).

The mid-lateral scale row runs through to the end of the body. The scales are roughly triangular to rhombic in outline, differentiated into a narrow dorsal half that is ornamented with some posteriorly directed spine-like tubercles and a wider, smooth ventral half (Fig. 9E). The dorsal half is evidently higher and more acute than the ventral half in the scales anterior to the dorsal fin and tends to decrease in height posteriorly and becomes as deep as the ventral half posterior to the dorsal fin. Generally, the length of two mid-lateral scales equals that of one mid-dorsal scale. No lateral line openings are observed in the scales.

The ventrolateral scale row commences a short distance anterior to the pelvic fins and are interrupted by the pelvic fins. The scales are suboval to rhombic (Fig. $9B_3$) and smaller than the mid-lateral scales.

Sinosaurichthys longimedialis sp. nov.
Figs. 10–16.

Etymology: From Latin *longus* and *medialis*, referring to its exceptionally elongated median fins.

Type material: Holotype GMPKU-P1927, a laterally compressed, almost complete skeleton. Paratypes: GMPKU-P1543, P1936, 1949, 1954.

Type locality: Dawazi, Luoping, Yunnan Province, China.

Type horizon: Upper part of the fossiliferous strata near the top of the Third Member of the Gejiu Formation (Pelsonian of Anisian, Middle Triassic).

Referred specimens.—GMPKU-P1367, 1380, 1388, 1586, 1769, 1935, 1936, 1939, and 1958. Most of them are complete skeletons.

Diagnosis.—Medium-sized *Sinosaurichthys* (standard body length ranging from 270–470 mm) with unusually elongated median fins with relatively few segments of fin rays; less number of neural arches between opercle and caudal fin (approxi-
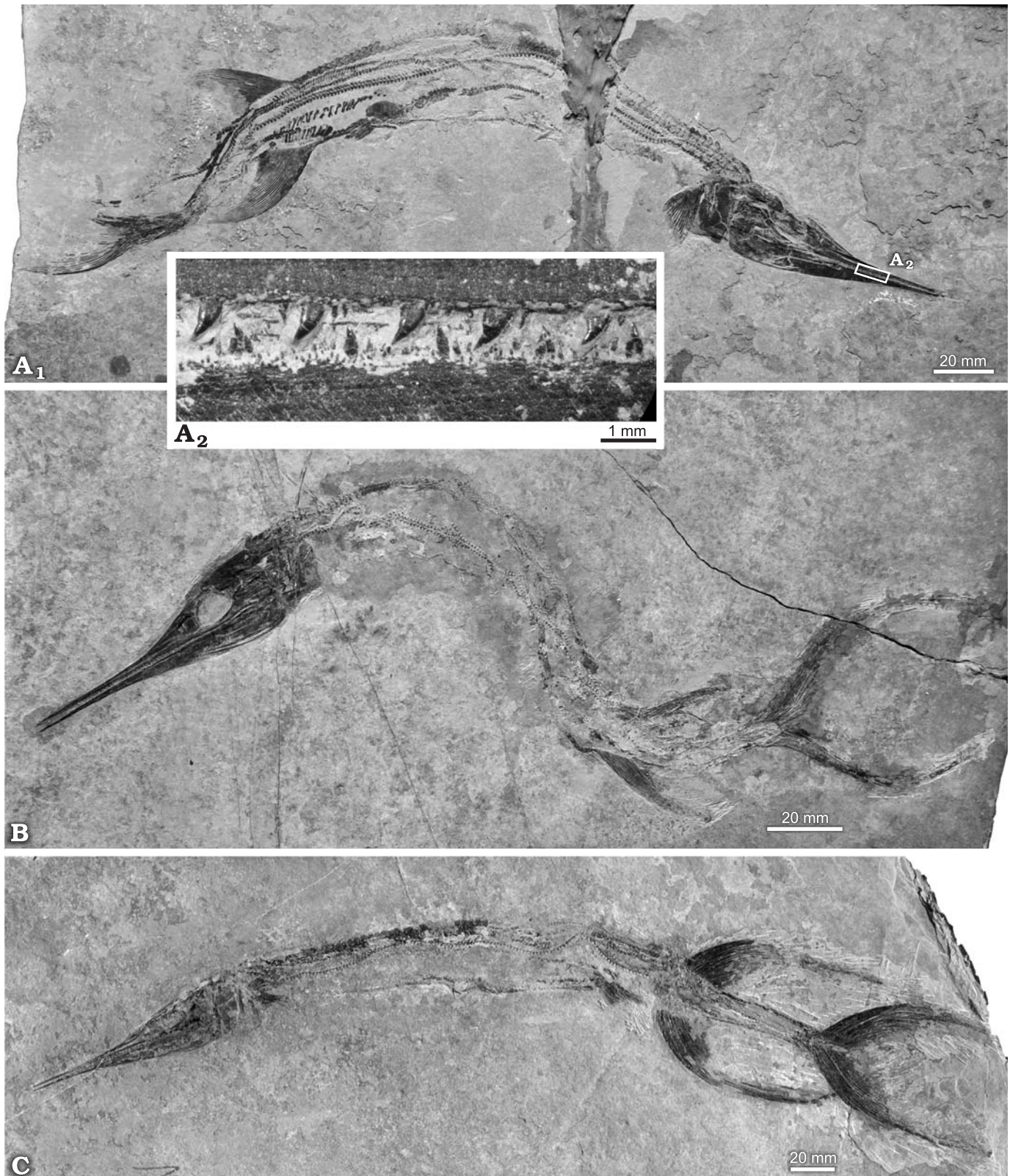
Fig. 10. Photographs of saurichthyid fish *Sinosaurichthys longimedialis* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. **A**. Holotype GMPKU-P1927 (A$_1$), teeth in squared region (A$_2$). **B**. GMPKU-P1954. **C**. GMPKU-P1949. Anterior facing right in A and left in B, C.

mately 157–172), less number of anterior ones with neural spines (130–146); and less number of mid-dorsal scales in front of dorsal fin (69–86) than in type species; 14–15 distinct

haemal spines in caudal region; pectoral fin triangular shaped with length about 1/3 of mandible length (shared with *S. minuta* described below); posttemporal-supracleithrum from
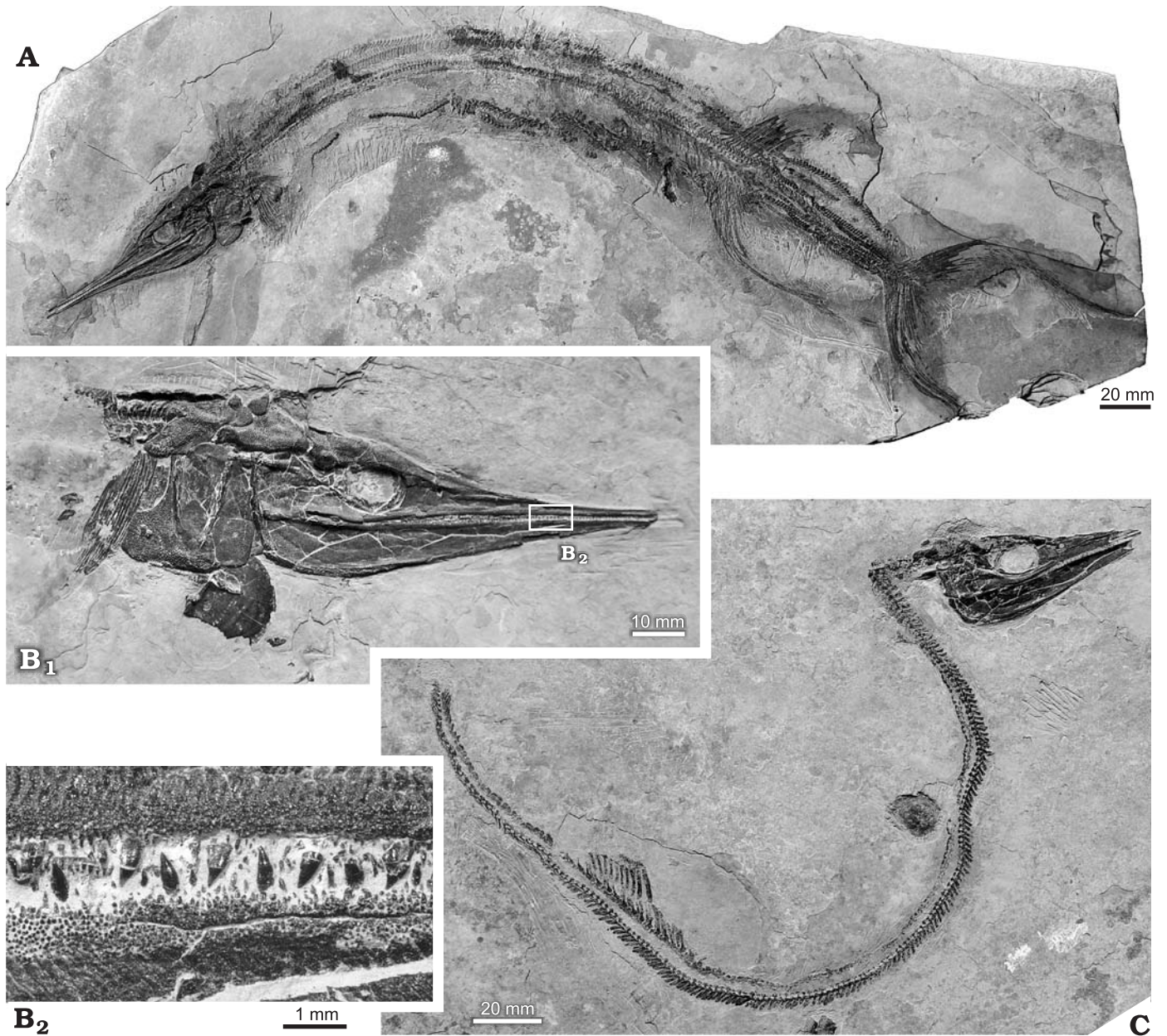
Fig. 11. Photographs of saurichthyid fish *Sinosaurichthys longimedialis* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. **A**. Paratype GMPKU-P1543. **B**. GMPKU-P1367 (B₁), teeth in squared region (B₂). **C**. GMPKU-P1939. Anterior facing left in A and right in B, C.

either side separated from each other by anterior mid-dorsal scales (shared with *S. minuta* described below); cleithrum plate (depth/length ratio ca. 1.2–1.25) much lower than in type species (approximately 1.8), but close to that in *S. minuta* (approximately 1). Fin formula: P 18–19, V 18–20, D/A 44–49/>40–48, C 37–39/37–39.

Description

General appearance.—The body of *Sinosaurichthys longimedialis* is long and slender (Fig. 14), with a standard body length in adult varying from 270–470 mm. The skull occupies about 22–30% of the standard body length. It is worthy to note that the specimens attributed to this species can be divided into two distinct morphological types that one is characterized with relatively long rostrum (60–66% of the skull length or more than 70% of the mandible length) and fewer neural arches between the opercle and the caudal fin (approximately 157–158 with the anterior 131–131 bearing distinct neural spines) and mid-dorsal scales in front of the dorsal fin (approximately 70) (Fig. 10); and the other is featured by relatively short rostrum (less than 57% of skull length or 66% of the mandible length) and more neural arches between the opercle and the caudal fin (approximately 167–172 with the anterior 141–146 bearing distinct neural spines) and mid-dorsal scales in front of the dorsal fin (>80) (Fig. 11A). These differences probably reflect
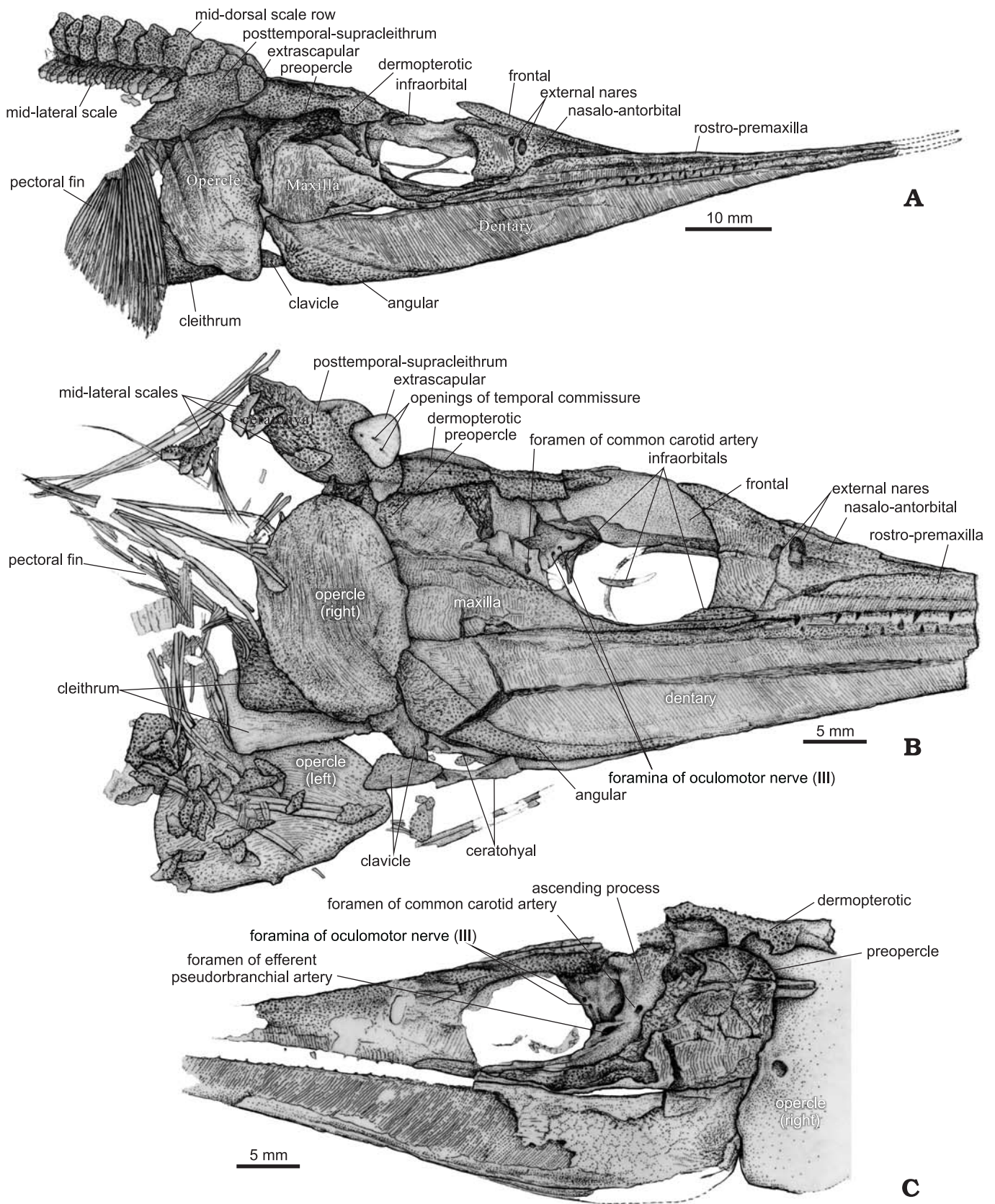
Fig. 12. Line drawings of skulls of *Sinosaurichthys longimedialis* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. **A**. Holotype GMPKU-P1927. **B**. GMPKU-P1388. **C**. GMPKU-P1769. Anterior facing right in A, B and left in C.
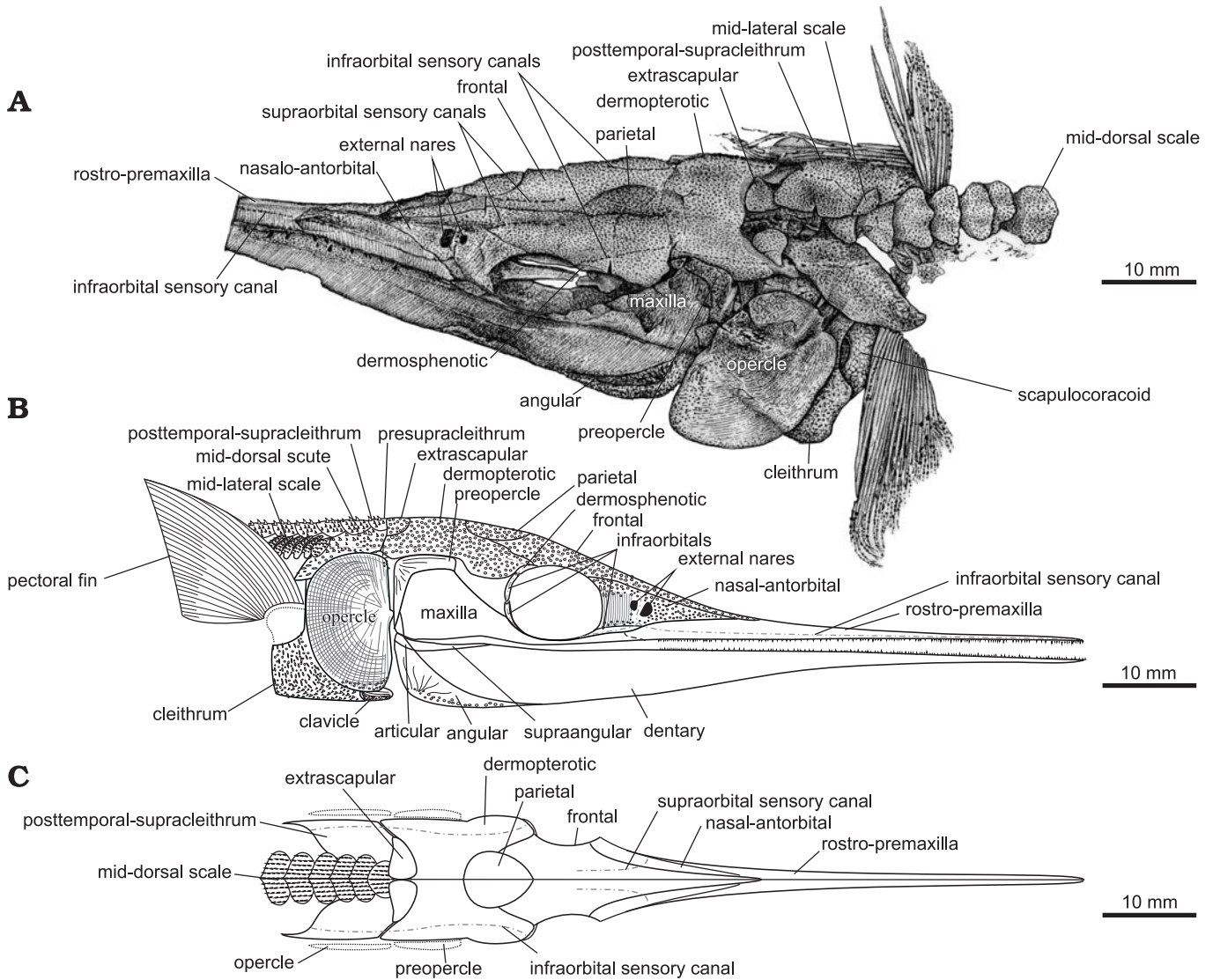
Fig. 13. Line drawings of skull of saurichthyid fish *Sinosaurichthys longimedialis* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. Paratype GMPKU-P1380. **A**. General view. **B**, **C**. Tentative restoration of skull in lateral (B) and dorsal (C) views; size referred from GMPKU-1954. Anterior facing left in A and right in B, C.

sexual dimorphism. We tentatively attribute the former as male and the latter as female based on the specimen abundance between the two morphotypes (approximately 5–6: 1) and the existence of possible breeding tubercles in the pectoral fins in a specimen (GMPKU-P1380, presumed as male; Fig. 13A). The pectoral fin inserts high on the flank, but somewhat lower than in the type species, lying close behind the upper portion of the opercle. The pelvic fins are placed nearer to the caudal fin than to the opercle. The dorsal and anal fins are symmetrically arranged, much closer to the pelvic fins than to the caudal fin (Figs. 10, 11; Table 2). The median fins are considerably elongated, generally longer than the mandible length.

Endocranium.—Similar to the type species, only part of the orbitotemporal region can be seen (Fig. 12C) and nothing can be added besides the foramina possibly related to the oculomotor nerve.

Snout.—The snout of the presumed female is shorter in proportion to skull length (Fig. 14) than that of the presumed male (Figs. 12A, 13B). The nasalo-antorbital probably has more portions involved in the skull roof. The dermal bones of the snout are, on the whole, arranged in the same pattern as in the type species (Figs. 12–14). The only difference from the type species is that the anterior part of the nasalo-antorbital is mainly decorated with tubercles rather than striations.

Dermal skull roof.—The skull roof may be rather wide in proportion to the skull depth judged from the width of the mid-dorsal scales immediately behind the skull, possibly the widest among the species of *Sinosaurichthys*. The general shape and arrangement of the dermal bones in the skull roof are similar to that in the type species. The extrascapular is rounded triangular and it is so large that it almost separates the posttemporal-supracleithrum from the dermopterotic, and directly overlaps on the first mid-dorsal scale posteromedially
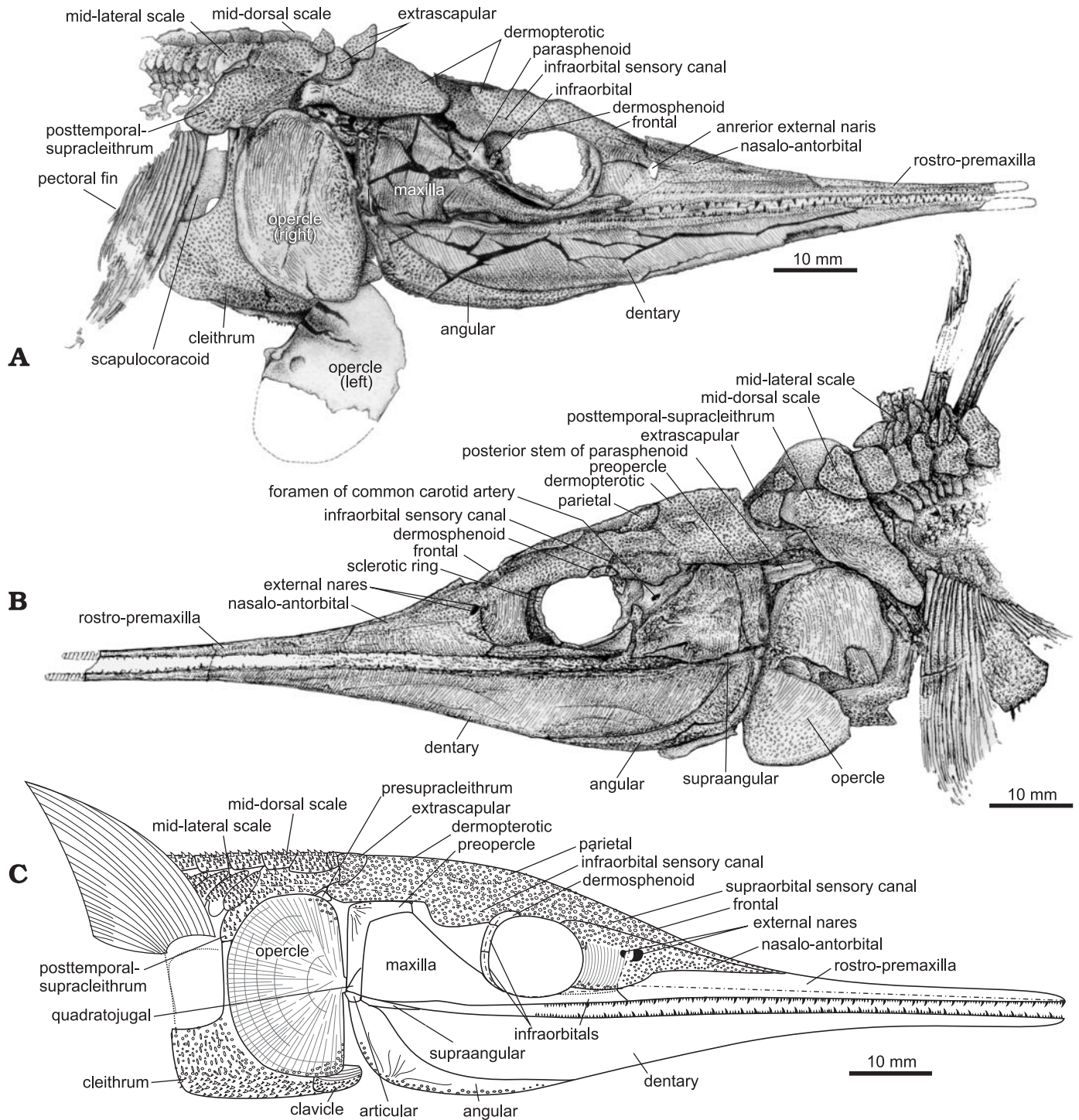
Fig. 14. Line drawings of saurichthyid fish *Sinosaurichthys longimedialis* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. **A**. Skull of GMPKU-P1367. **B**. Skull, paratype GMPKU-P1543. **C**. Tentative restoration of skull in left lateral view. Anterior facing right in A and left in B, C.

(Fig. 13A, C). Three openings of the temporal commissure of the sensory canal can be seen in the ventral surface of the extrascapular in GMPKU-P1945 (Fig. 12B).

Cheek and opercular series.—The orbit is elliptical to circular, slightly smaller than that of the type species in proportion to the skull depth, confined by the nasalo-antorbital anteriorly and by the frontal dorsally. The dermosphenotic is small

and crescent shaped, occupying the posterodorsal corner of the orbit between the frontal and dermopterotic. The infraorbitals consist of three elements: the anteriormost one (lacrimal) is lanceolate, forming the anteroventral rim of the orbit ventral to the nasalo-antorbital; the other two compose the posterior rim of the orbit (Figs. 13B, 14C).

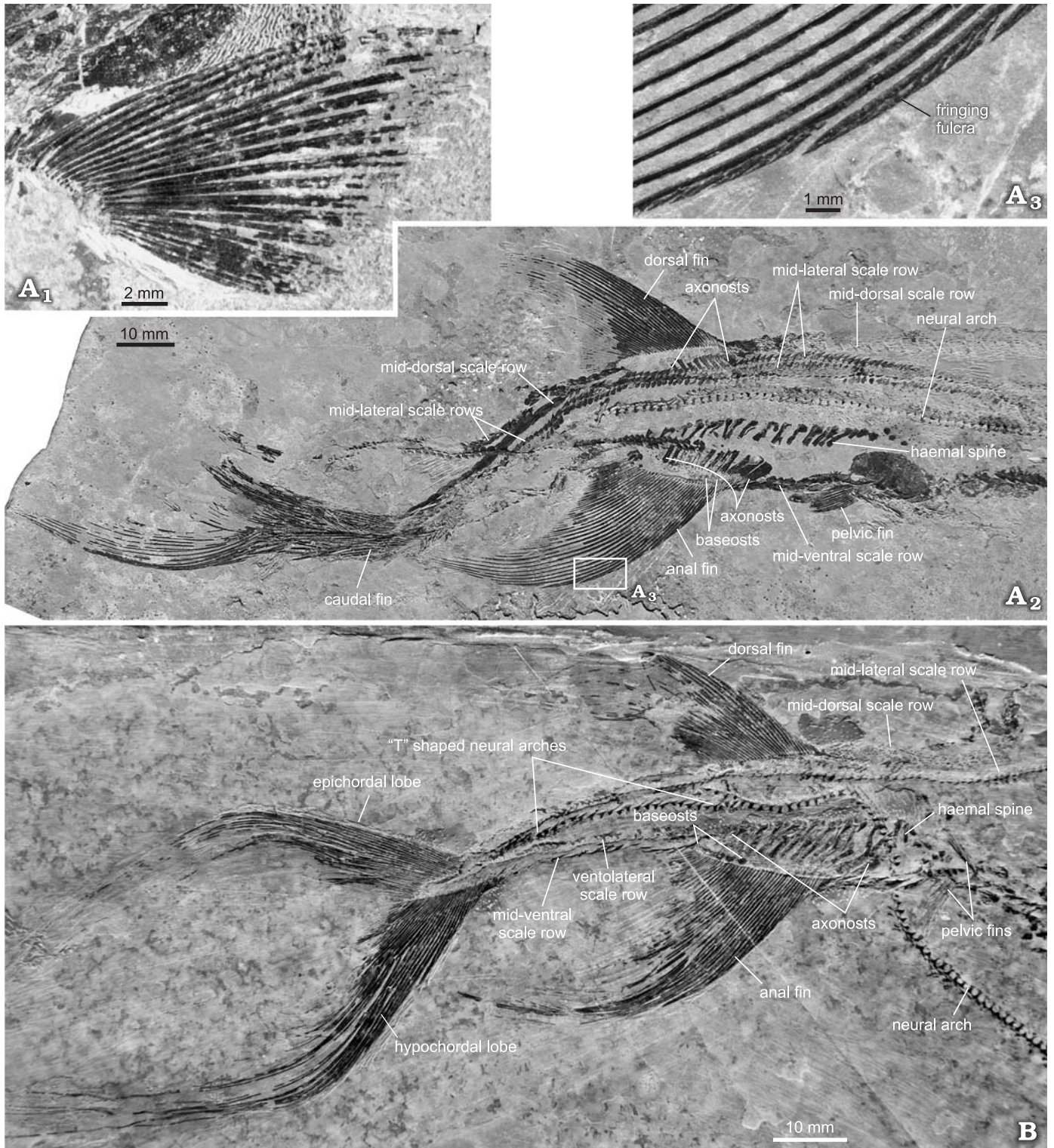The postorbital lobe of the maxilla is rather high with a

Fig. 15. Photographs of saurichthyid fish *Sinosaurichthys longimedialis* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. **A**. Holotype GMPKU-P1927. Left pectoral fin (A₁). Skeleton of posterior abdominal and caudal regions (A₂). Magnification of squared region (A₃) to show fringing fulcra in anal fin. **B**. Skeleton of posterior abdominal and caudal regions of GMPKU-P1388. Anterior facing left inA₁ and right in A₂, A₃, B.

truncated rather than a convex dorsal margin that is almost fully covered by the dorsal portion of the preopercle (Figs. 12–14), different from that in the type species, but similar to that in *S. minuta* described below.

Similar to the type species, the opercular series consists of a single large semicircular opercle (Figs. 12–14), with the depth/width ratio varying from 1.55 to 1.82 (average 1.67) (Table 2). The gular and branchiostegal rays are absent.

Table 3. Measurements (in mm) of unpaired fins of two species of *Sinosaurichthys* from Dawazi Section, Luoping, Yunnan, China.

Species	Specimen	Mandible length	Dorsal/anal fin					Caudal fin (epichordal/hypochordal)		
			maximal length	basal fulcra	fin rays	segmentation	radials	maximal length	fin rays	segmentation
Sinosaurichthys longimedialis	1927	84	37/47	3/5	~44/>40	3/3	10/13	–/69	–	–/5
	1945	72	>45/59	3/5	44/48	3/3	–/12	>65/105	39/38	4/6
	1949	91	91/124	–/–	~41/~47	2/2	–	>80/94	38/35	3/4
	1954	75	39/>46	3/–	~44/–	3/2–3	–	66/79	~38/37	4/5
	1543	87	>70/>110	4/5	~49/–	2/2	15/16	>110/>110	38/38	4/3
	1958	–	~132/128	–/–	~43/–	3/3	11/9	>75/>50	–/–	–/–
Sinosaurichthys minuta	1370	55	20/18	4/4	~42/42	4/4	–	23/24	~38/36	4/5
	1372	52	~15/16	4/4	~40/40	3/4	–/12	~20/21	37/37	>3//>3
	1382	43	9/12	–/–	~33/34	2/2	–/7	14/>14	35/35	1/2
	1928	56	–/19	–/–	–	–	–	19/23	37/33	5/5
	1955	40	10/11	~3/~3	~40/~42	2/2	–/10	15/16	36/37	3/3

Mandible.—The shape and arrangement of dermal bones in the lateral side of the mandible is almost the same as in the type species (Figs. 12–14). However, the ventral margin in the specimens of the presumed female seems to be more convex than in these of the presumed males (Fig. 14).

Palate.—No information about the vomers is available due to the preservation. The parasphenoid is only partially exposed in the current materials. The parasphenoid passes across the orbit in a similar way as in the type species with paired large ascending processes posterior to the orbit and the foramina of both the efferent pseudobranchial and the common carotid arteries penetrating the parasphenoid in the same positions as in the type species (Fig. 12C). The posterior stem of the parasphenoid also extends posteriorly under the occipital region, beyond the anterior margin of the opercle with a distinct notch in the posterior tip (Fig. 12C).

Hyoid arches.—Only the ceratohyal is preserved (Fig. 12B). In GMPKU-P1388, it has a shape similar to that in the type species.

Dentition.—Teeth along the labial edge of both jaws are arranged in the same way as in the type species, one row of large teeth intercalated with several small ones (Figs. 10A$_2$, 11B$_2$). The apical tip of most large teeth bends posteriorly, differing from that in the type species.

Paired fins and girdles.—The pectoral fin is of typical triangular shape consisting of 19 unsegmented fin rays in the holotype (Figs. 10A$_1$, 12A, 15A$_1$). The 6th is the longest. The length of the pectoral fin varies from less than to more than the skull depth (Table 2). The fin rays begin to branch dis-
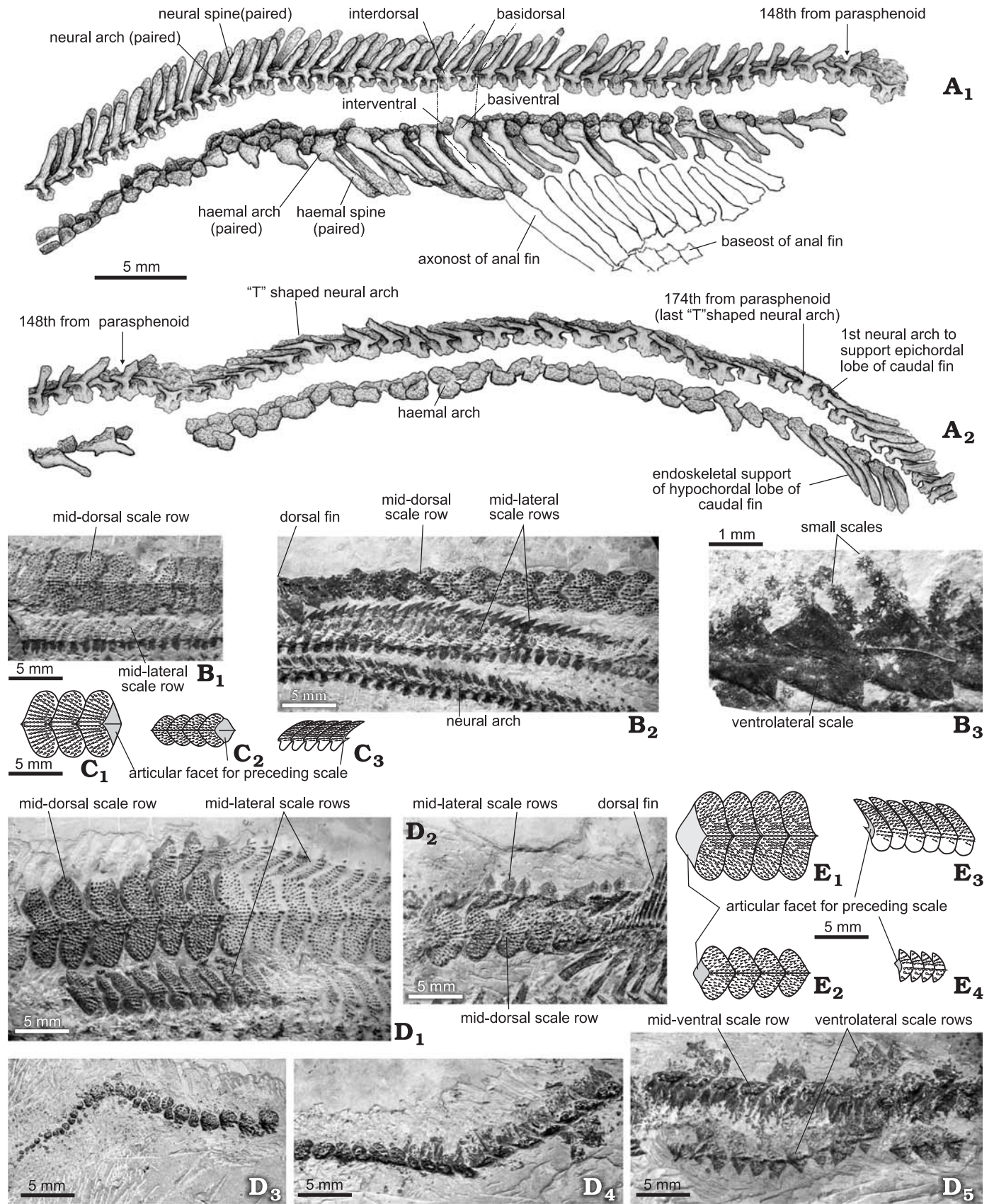
tally from the 10th one. In GMPKU-P1380, many small tubercles are present on the surface of the distal part in the pectoral fin rays (Fig. 13A), a feature probably related to breeding (nuptial) behavior of adult male individuals.

Little information of radials can be added whereas the scapulocoracoid can be partially seen in some specimens with a large foramen in the anterodorsal part behind the dorsal stem of the cleithrum (Figs. 13A, 14A).

The dermal pectoral girdle is well preserved in most of the specimens. The posttemporal-supracleithrum, as in the type species, consists of a dorsal and a ventrolateral portion (Figs. 13A, 14A, B), but the dorsal portion of this bone is separated from its opposite pair by the mid-dorsal scales and the ventrolateral portion is deeper (Figs. 13A, 14A, B). Anteriorly, this bone bears a subcircular articular facet for the extrascapular and posteriorly an articular facet for the mid-lateral scale between its two portions. Although the cleithrum is also boot-shaped, the rectangular posterior blade of this bone is less deep (approximately 1/3 of the skull depth) than in the type species and the dorsal stem is vertically oriented rather than anterodorsally inclined (Fig. 14A). The clavicle is subovate to round triangular, and articulates posteriorly to the cleithrum (Figs. 12B, 13B, 14C). In addition, a small triangular shaped bone can be observed in some specimens attached to the lateral side of the posterior process of the dermopterotic and anterior to the posttemporal-supracleithrum, with ornamentation similar to that on areas of other dermal bones of the pectoral girdle covered by the opercle, possibly suggesting a presupracleithrum.

The pelvic fin is relatively small and triangle-shaped, consisting of 18–22 unsegmented but distally branched fin

Fig. 16. Saurichthyid fish *Sinosaurichthys longimedialis* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. **A**. Line drawings of anterior (A$_1$) and posterior (A$_2$) parts of axial skeleton from the posterior part of abdominal region to caudal fin of GMPKU-P1939. **B**. Photographs of squamation of the holotype GMPKU-P1927. Mid-dorsal and mid-lateral scale rows in anterior (B$_1$) and posterior (B$_2$) parts of the abdominal region; ventrolateral scales and small scales in posteroventral (B^3) abdominal region. **C**. Idealized mid-dorsal scale row slightly posterior to skull (C$_1$) and anterior to dorsal fin (C$_2$), and right mid-lateral scale row slightly posterior to skull (C$_3$); restoration mainly based on the holotype GMPKU-P1927. **D**. Photographs of squamation on GMPKU-P1543. Mid-dorsal and mid-lateral scale rows slightly posterior to skull (D$_1$) and in front of dorsal fin (D$_2$); mid-ventral scale →

row in anterior (D$_3$) and middle parts of abdominal region (D$_4$); mid-ventral and ventrolateral scale rows anterior to pelvic fins (D$_5$). **E.** Idealized mid-dorsal scale row (dorsal view) near skull (E$_1$) and in front of dorsal fin (E$_2$), left mid-lateral scale row in abdominal region in lateral view (E$_3$), and left ventrolateral scale row in posteroventral abdominal region (E$_4$). Restoration mainly based on holotype GMPKU-P1543. Anterior facing right in B, C and left in A, D–I.

rays. No information about the pelvic bone is available in the current materials.

Unpaired fins.—The dorsal and anal fins are arranged in the same way as in the type species. The dorsal fin consists of about 44–49 and the anal fin of 47–48 fin rays, which are segmented proximally two to three times. In the holotype (GMPKU-P1927) the anterior 17 fin rays of the dorsal fin are unbranched and the rest are branched once distally, with the 14–16th fin rays longest. Both the dorsal and anal fins show considerable elongation to different extents that make the fins quite flexible in their distal part. The length of the fins varies from about half of to even more than the mandible length in different specimens (Figs. 10, 11, 15A₂, B; Table 3). The elongation of the median fins is unique to this species. In some large specimens, a total of 15 and 16 elongated axonosts can be seen in the dorsal and anal fins, respectively. In other smaller specimens only parts of them are ossified.

The caudal fin is deeply forked, and its lobes are extremely elongated, longer than the mandible length (Figs. 10, 11, 15A₂, B). Each lobe consists of 37–39 fin rays, with three to four and three to six segments in the epi- and hypochordal lobes, respectively, and bifurcate once to twice distally.

The basal and fringe fulcra are developed in all median fins. There are 3–4 and 5 basal fulcra in the dorsal and anal fin, respectively, and 2–3 in each lobe of the caudal fin. The fringing fulcra are distally developed on the surface of the margin leading fin rays of the median fins, consisting of small spin-like plates overlapping one by one (Fig. 15A₃).

Axial skeleton.—The neural and haemal arches are similar to those in the type species in structure and morphology (Fig. 16A). The total number of the neural arches in front of the caudal fin is about 157–158 in the presumed male individuals and about 167–172 in the presumed female ones, both are less than that in the type species. The neural spines are developed in the anterior 131–132 and 141–146 ones in the two presumed sexual morphotypes, respectively. In the caudal fin region, the neural arches continue to the tip of the fin to support the fin rays of the epichordal lobe.

The haemal arches between the pelvic and anal fin are similar to those of the type species, consisting of two kinds of alternatively arranged bony plates, one with a distinct haemal spine and the other without. They represent the basi- and inter-ventral arcualia elements, respectively (Fig. 16A). However, the ossifications of the interventrals are much larger in proportion to those of the basidorsals than in the type species. There are 14–15 distinct haemal spines in the caudal region.

Squamation.—Similar to the type species of the genus, *Sinosaurichthys longimedialis* also bears six longitudinal rows of scales.

The mid-dorsal scale row runs through the body length, only interrupted by the dorsal fin, generally consisting of 67–70 scales in the presumed male and 86 in the presumed female individuals. The mid-dorsal scales are also cordate in shape, with the width/length ratio of the exposed portion reaching about 2–2.9 near the skull and decreasing gradually toward the dorsal fin to about 1–1.33 (Fig. 16B, C₁, C₂, D₁, D₂, E₁, E₂). The exposed portion of the scales is fully covered with posteriorly-directed spines (Fig. 16B₁, D).

Similar to the type species, the mid-ventral scale row begins just behind the skull. The anterior scales are small, subovate, and tend to be larger posteriorly (Fig. 16D₃–D₅). A distinct feature of the mid-ventral scales of *S. longimedialis* is that each scale has a remarkable root that looks like a spiny structure (Fig. 16D₄, D₅). The scale row divides into two rows slightly anterior to the pelvic fins to form the anal loop. As in the type species, the last scale anterior to the anal loop is enlarged and elongated with a rhombic posterior portion and the first paired scales of the anal loop is also elongated, expanding anteriorly and tapering posteriorly. The exact number of scales forming the anal loop is not clear due to the preservation.

The mid-lateral scales have similar shape with those of the type species and the external surface of the dorsal part is ornamented by posteriorly directed spines (Fig. 16C₃, D₁, E₃).

The ventrolateral scale row begins to develop from the level some distance anterior to the pelvic fins, generally as small rounded triangular or rhombic scales. Their external surfaces are decorated by one to three rows of posteriorly curved spines. The last two to three scales anterior to the pelvic fins tend to be enlarged, and heart-shaped as the basal fulcra. Posterior to the pelvic fin the scale row continues to the caudal fin.

In addition to the scale rows mentioned above, many less ossified small scales, each less than 0.5 mm wide, are scattered between the scale rows (Fig. 16B₃), similar to the condition in all other saurichthyids described in the current paper.

Sinosaurichthys minuta sp. nov.

Figs. 17–20.

Etymology: From Latin *minutus*, small, referring to the small size of the new species.

Type material: Holotype GMPKU-P1955, a laterally compressed, complete skeleton. Paratypes: GMPKU-P1928, 1369, 1370 and 1372.

Type locality: Dawazi, Luoping, Yunnan Province, China.

Type horizon: Lower part of the fossiliferous strata near the top of the Third Member of the Gejiu Formation (Pelsonian of Anisian, Middle Triassic).

Referred specimens.—GMPKU-P1382, 1390, 1929, 1931, 1932, 1933, 1936, 1938, and 1948. Most of them are complete skeletons.

Diagnosis.—Small-sized *Sinosaurichthys* with standard body length of adults no more than 210 mm; low triangular-shaped dorsal and anal fins with relatively numerous segments in fin rays; fewer neural arches between opercle and caudal fin (154–156) and those bearing neural spines (126–127), fewer distinct haemal spines in caudal region (10–11), and fewer mid-dorsal scales in front of dorsal fin (62–63) than those in the other species of *Sinosaurichthys*; cleithrum plate lowest (depth/length ratio approximately1) among three species of *Sinosaurichthys*. Fin formula: P 14–16, V 18–20, D/A 40–42/40–42, C 34–38/34–37.
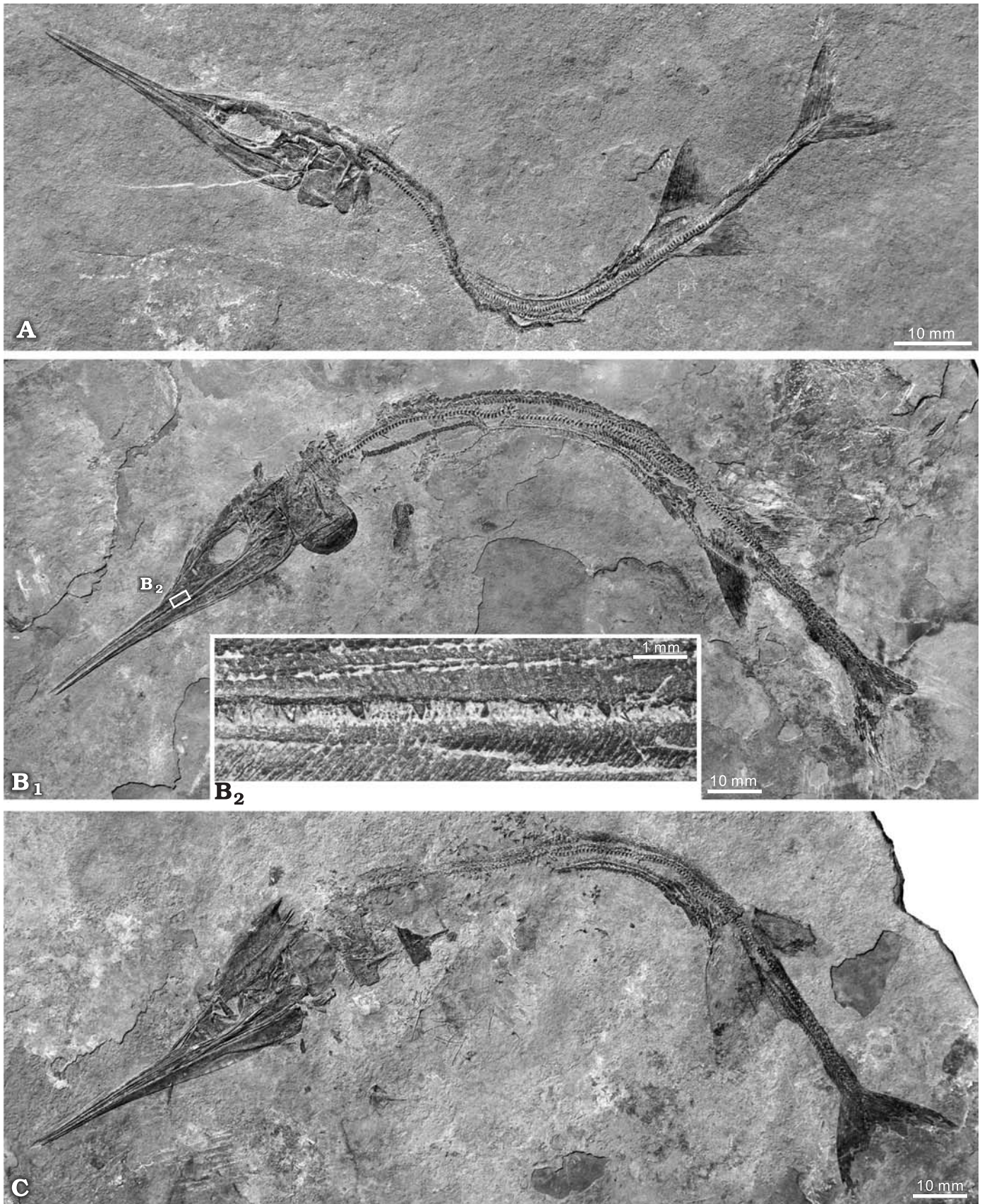
Fig. 17. Photographs of saurichthyid fish *Sinosaurichthys minuta* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. **A**. Holotype GMPKU-P1955. **B**. Paratype GMPKU-1372 (B₁), teeth in squared region (B₂). **C**. Paratype GMPKU-P1928. Anterior facing left.
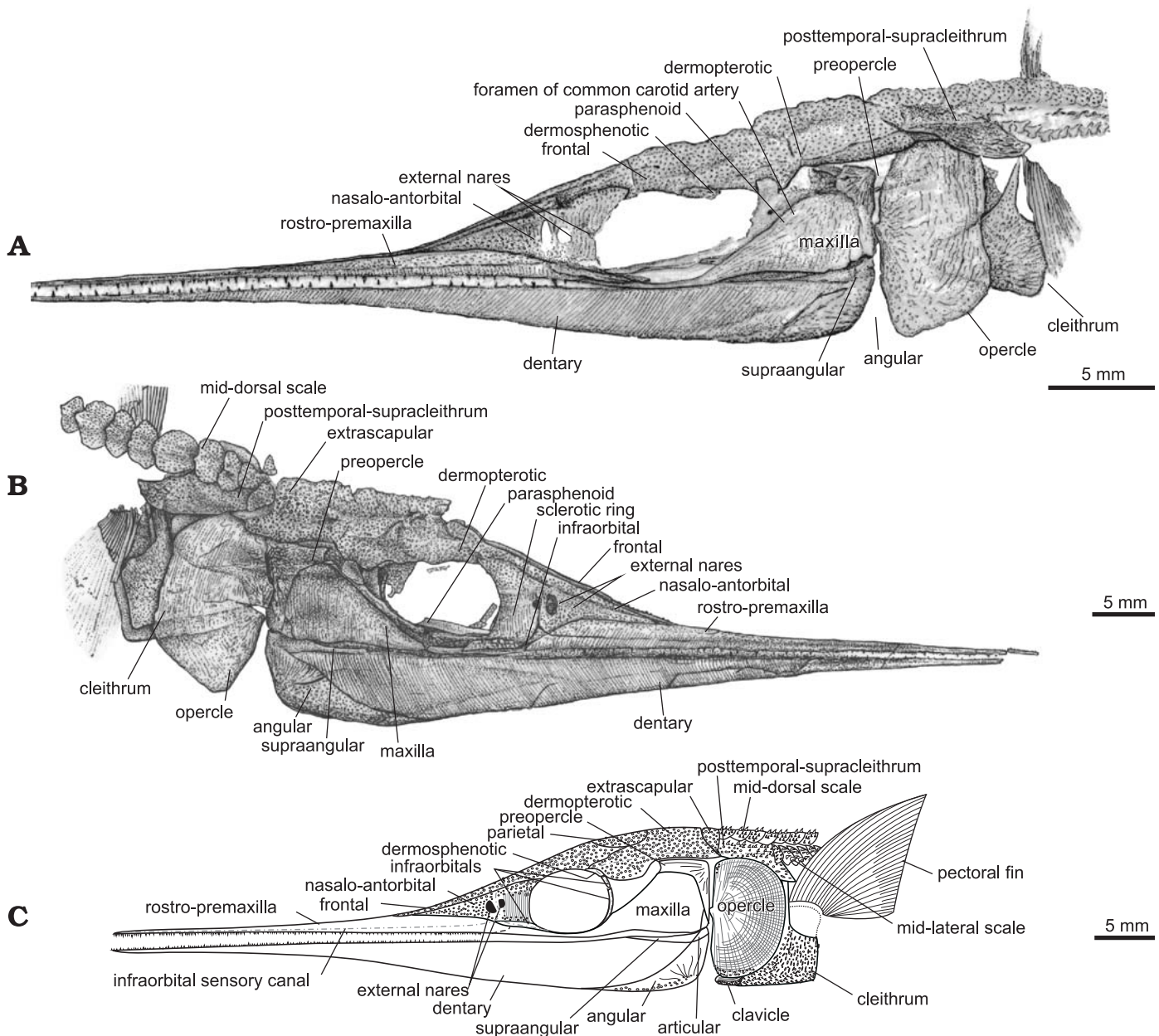
Fig. 18. Line drawings of saurichthyid fish *Sinosaurichthys minuta* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. **A**. Skull of the holotype GMPKU-P1955. **B**. Skull of the paratype GMPKU-P1370. **C**. Tentative restoration of skull in left lateral view (size referred from GMPKU-P1369). Anterior facing left in A, C and right in B.

Description

General appearance.—The body is long and slender (Fig. 17A, B₁, C), with a standard body length varying between 100–210 mm. The skull length is about 33–37% of the standard body length and the rostrum makes up about 60–63.5% of the skull length and about 68.7–72.7% of the mandible length (Table 1). The pectoral fins lie above the midline of the body, close behind the opercle. The pelvic fins are placed nearer to the caudal fin than to the opercle. The dorsal and anal fins are symmetrically arranged, much closer to the pelvic fins than to the caudal fin (Table 2).

Snout.—The rostrum is also rather long and slender and the dermal bones are almost arranged in the same pattern with the other two species of *Sinosaurichthys* (Figs. 17A, B₁, C, 18, 19A₁, B₁). The only difference from the type species is the anterior part of the nasalo-antorbital is mainly decorated with tubercles rather than striation.

Dermal skull roof.—The composition of the dermal skull roof of *S. minuta* is almost the same as that of *S. longimedialis*, wider in proportion to skull depth than that of *S. longipectoralis* (Fig. 19A₁, B₁). The paired extrascapular is also relatively large in proportion to the skull roof width, and is of a
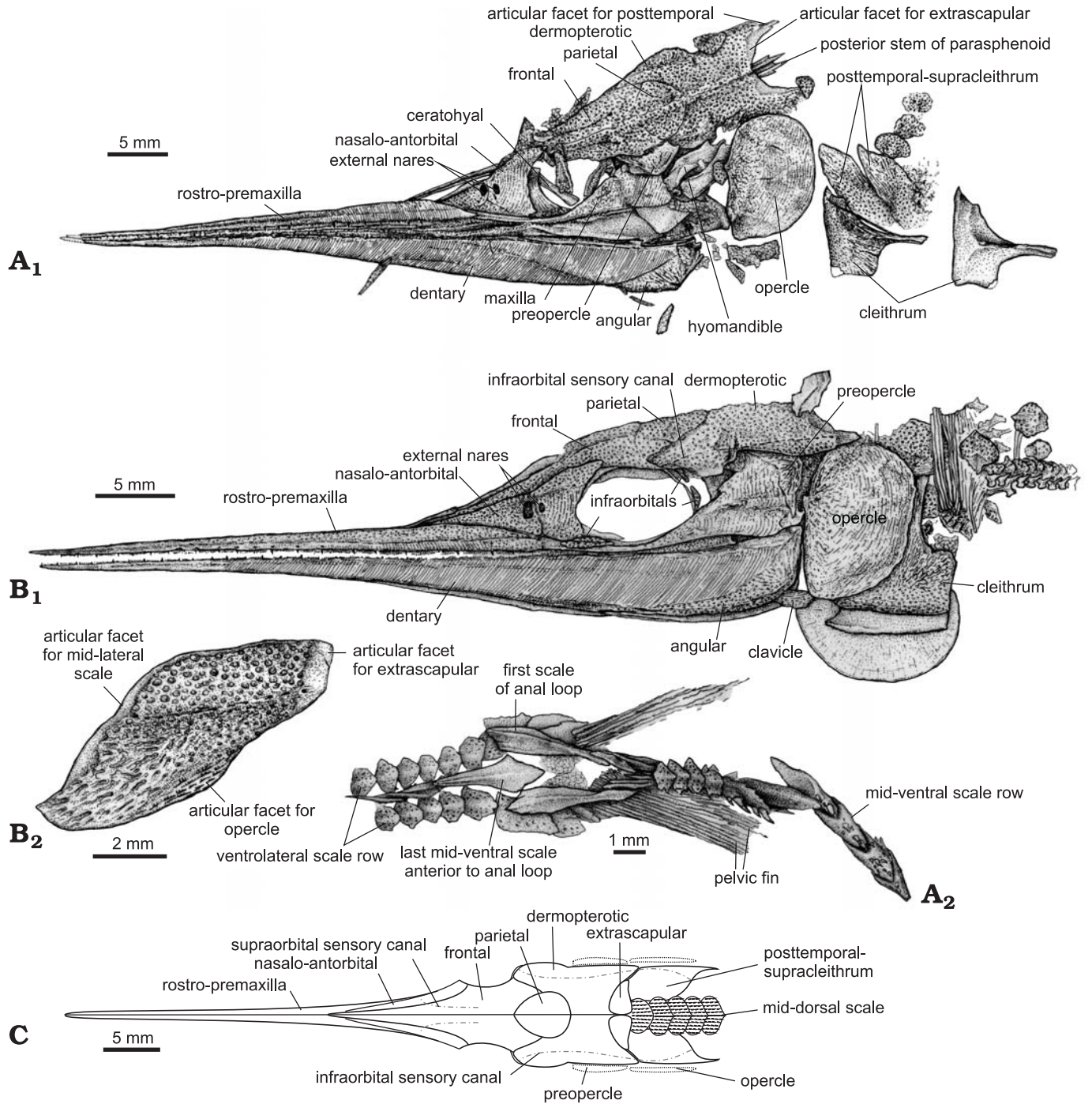
Fig. 19. Line drawings of saurichthyid fish *Sinosaurichthys minuta* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. A. Skull of the paratype GMPKU-P1372 (A_1) and the scales around pelvic fins (A_2). B. Skull of the paratype GMPKU-P1369 in left lateral view (B_1) and its right posttemporal-supracleithrum (B_2). C. Tentative restoration of skull in dorsal view (size referred from GMPKU-P1369). Anterior facing right in B_2 and left in A, B_1, C.

rounded triangular shape, almost completely separates the posttemporal-supracleithrum from the dermopterotic, and in direct contact with the first mid-dorsal scale posteromedially (Figs. 18B, C, 19C).

Cheek and opercular series.—The orbit and the dermal cheek bones are highly consistent with those in *S. longimedialis* in shape and arrangement (Figs. 17–19B_1) and

nothing can be added besides the infraorbitals, which clearly consist of three elements: the anteriormost one (lacrimal) is lanceolate, forming the anteroventral rim of the orbit ventral to the nasalo-antorbital; the other two compose the posterior rim of the orbit (Figs. 18C, 19B_1).

The opercular apparatus consists of a single large semi-circular opercle with the depth/width ratio varing from 1.43 to 1.8 (average 1.64) (Table 2). The surface of the opercle is

ornamented mainly with fine and dense concentric lines and tubercles. As in the other two species of *Sinosaurichthys*, the gular and branchiostegal rays are absent.

Mandible.—The shape and pattern of dermal bones in the lateral side of the mandible is almost the same with that of the two species described above (Fig. 18).

Palate.—Because of the preservation only part of the parasphenoid can partially been seen, similar to the situation in *S. longimedialis*. This includes the long anterior stem across the ventral part of the orbit, a posteriorly forked posterior stem between the dermopterotic and opercle, and a large paired ascending process posterior to the orbit (Figs. 18A, B, $19A_1$), but suggestive for the same morphology and construction to that in the type species of the genus.

Hyoid arches.—The hyomandible is more or less hockeystick shaped (Fig. $19A_1$), with a horizontally extended dorsal portion and a posteroventrally inclined ventral portion, slightly different from that in the type species in shape.

Dentition.—The teeth along the labial edge of both jaws are arranged in the same way and shape as in the other species of *Sinosaurichthys* (Fig. $17B_2$). The large teeth are quite small and some of them curved posteriorly, similar to those in *S. longimedialis* (Fig. $17B_2$).

Paired fins and girdles.—The pectoral fin is roughly triangle-shaped, consisting of 14–16 unsegmented fin rays. The length of the pectoral fin varies from slightly less than to more than the skull depth (Table 2), much shorter than that of the type species of the genus.

No radials or endoskeletal elements of the pectoral girdle can be discerned, but the dermal pectoral girdle is well preserved in most of the specimens and its elements are consistent with those in *S. longimedialis* in shape and configuration (Figs. 18, $19A_1$, B_1, B_2).

The pelvic fins are relatively small and triangular in shape (Fig. 20C), each consisting of about 18–20 unsegmented fin rays. Little information about the pelvic bone is available in the current materials.

Unpaired fins.—The dorsal and anal fins are arranged in the same way as in the other species of *Sinosaurichthys*. They are triangular-shaped, much lower than those in the two species described above, with the depth almost equal to width (Fig. $20A_2$). The dorsal fin consists of about 41–50 and the anal fin of 42–48 fin rays, with a maximal segmentation of three to four times in the dorsal and four times in the anal fin.

Only the anterior radials of the dorsal and anal fins are ossified, eight and seven to ten radials can be distinguished in the dorsal and anal fin respectively.

The caudal fin is deeply forked, generally with 35–38 fin rays in each lobe (Figs. 17A, B_1, C, $20A_1$, Table 2). The fin rays are generally segmented three to four times proximally, occasionally five times, and branched distally once or twice.

In the holotype, two basal fulcra are seen at the origin of the dorsal fin and three of the anal fin. The fringing fulcra, as in *S. longimedialis*, are present in all unpaired fins, consisting of small spine-like elements overlapping one by one in the distal part of the leading edge of the marginal fin rays.

Axial skeleton.—The axial skeleton consists of the neural and haemal arches similar in structure to those in the other species of *Sinosaurichthys*. The neural arches between the opercle and caudal fin number about 154–156 and the anterior 126–127 ones bear distinct neural spines, slightly fewer than that in *S. longimedialis*. In the caudal fin region, there are about 13–14 neural arches supporting the fin rays of the epichordal lobe of the caudal fin. Distinct haemal spines are developed in the initial 10 to 11 haemal arches in the caudal region, the fewest among the three species of the genus.

Squamation.—Similar to the two species described above, *Sinosaurichthys minuta* also bears six longitudinal scale rows.

There are 62–63 mid-dorsal scales in front of the dorsal fin. These scales are also cordate in the posterior exposed portion (Fig. 20B, E_1, E_2), wider than those in the type species and narrower than in *S. longimedialis*, with the width/length ratio about 2.1–2.3 near the skull and 1–1.5 near the dorsal fin, and are decorated with spine-like tubercles (Fig. 20B).

The mid-ventral scale row divides into two rows slightly anterior to the pelvic fins to form the anal loop and each branch consists of four scales (Figs. $19A_2$, $20A_2$, C). As in the type species, the last scale anterior to the anal loop is enlarged and elongated with a rhombic posterior portion and the first of paired scales of the anal loop is also elongated, expanding anteriorly and tapering posteriorly. In the caudal peduncle, the mid-ventral scales are similar with the mid-dorsal ones in both shape and ornamentation, bearing some strong posteriorly pointed tubercles (Fig. 20D).

The mid-lateral scales have a similar shape to that of type species and the dorsal part of the external surface is decorated with a few posteriorly-directed spines (Fig. $20E_3$).

The ventrolateral scale row commences a short distance posterior to the skull and generally consists of small semicircular to rhombic scales, decorated with a few posteriorly pointed tubercles, and the scales are evidently enlarged near the origin of the pelvic fins (Fig. $19A_2$). Posterior to the pelvic fins, the scale row continues backwards to the caudal fin (Fig. $20A_1$).

Remarks.—*S. minuta* is very similar to *S. longimedialis* in the general morphology. The lack of substantial differences between the two species, except for the body size and the shape of the unpaired fins, makes it easy to regard *S. minuta* as the juvenile of *S. longimedialis*. However, the degree of the segmentation in the unpaired fins between the two species does not support the juvenile-adult relationship because the number of the segments of the fin rays usually increases accompanying with the growth of fin rays during ontogeny. It would be contradictory that the segmentation of the fin rays is fewer in adults than in juveniles. The number of rays in the pectoral fin and ossified haemal spines in the caudal region is also different between the two species. Thus, here we treat *S. minuta* as a separate species from *S. longimedialis*. Additionally, the two species occur in different stratigraphic levels. Field excavation
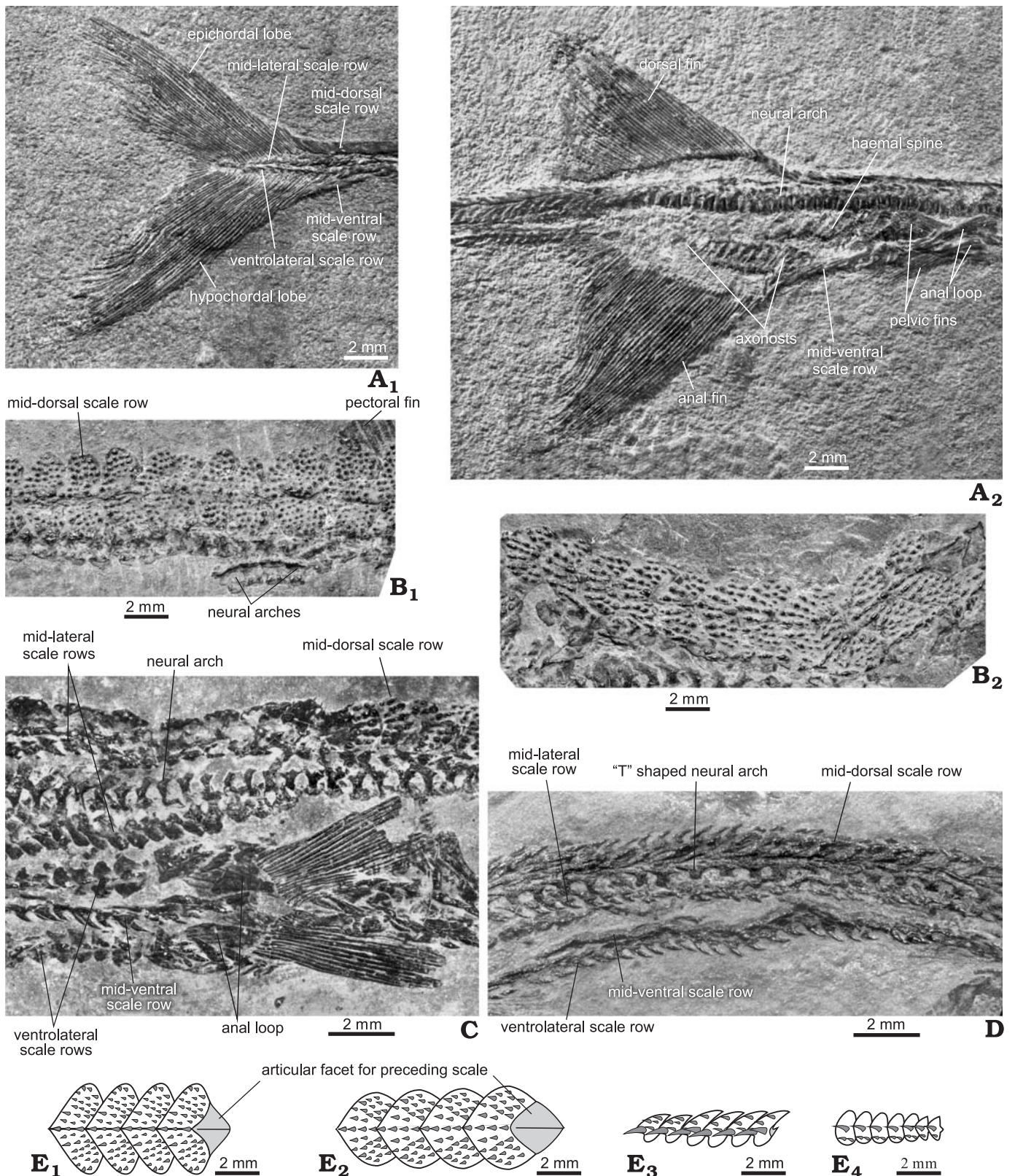
Fig. 20. Saurichthyid fish *Sinosaurichthys minuta* gen. et sp. nov. from Middle Triassic of Dawazi Section, Luoping, Yunnan, China. Photographs (**A–D**) and line drawings (**E**). **A**. Caudal fin (A$_1$) and dorsal and anal fins (A$_2$) of the holotype GMPKU-P1955. **B**. Mid-dorsal scale row just behind skull in dorsal view (B$_1$), mid-dorsal scale row in posterior abdominal region (B$_2$) (14th to 24th scales counted anteriorly from dorsal fin) of GMPKU-P1369. **C**. Skeleton around pelvic fins of the paratype GMPKU-P1372. **D**. Skeleton around middle part of caudal peduncle of the paratype GMPKU-P1928. **E**. Idealized line drawings of dorsal scale row (dorsal view) near skull (E$_1$) and around posterior abdominal region (E$_2$), right mid-lateral scale row of abdominal region in lateral view (E$_3$), and right ventrolateral scale row anterior to pelvic fins (E$_4$). Anterior facing left in C, D and right in A, B, E.

reveals that *S. longimedialis* is restricted to the upper part of the fossiliferous strata, about 3–5 m above the level containing *S. minuta* in the Dawazi Section.

Comparison of the new genus with *Saurichthys*

As the type species of *Saurichthys*, *S. apicalis*, was established on the basis of a broken snout and isolated teeth (Agassiz 1834), the type material of the genus shows no clear diagnostic features except the elongated, slender jaws and conical penetrating teeth, which caused a big confusion in the subsequent studies. Stensiö (1925) and Rieppel (1985) tried to clarify the diagnosis of *Saurichthys* based on their comprehensive work on the relatively well-preserved materials. However, the dozens of species attributed to the genus, mostly described based on rather poor and fragmentary materials or even isolated teeth and showing great morphologic variation, made it very difficult to get clear and appropriate diagnostic features for the genus. Under this situation, only some species erected on the basis of relatively well-preserved materials are chosen as representatives of *Saurichthys* for comparison with the current new genus.

Sinosaurichthys is very similar to *Saurichthys* in the general morphology. However, *Sinosaurichthys* differs clearly from *Saurichthys* in having peculiar pectoral girdles, dorsally inserted pectoral fins, highly elevated posterior stem of the parasphenoid, and relatively dorsally positioned axial skeleton in the abdominal region of the body, as well as different configuration in squamation.

The pectoral girdle of the new genus connects with the skull through a large dermal element (here termed as posttemporal-supracleithrum). In *Saurichthys* the pectoral girdle may connect with the skull through two elements (independent posttemporal and supracleithrum), such as in *Saurichthys ornatus* and *Saurichthys madagascariensis* (Stensiö 1925; Rieppel 1980), or through a small supracleithrum sensu Rieppel (1985). The cleithrum of the pectoral girdle of *Sinosaurichthys* also differs from that of *Saurichthys* in shape. The posterior blade of this bone in *Sinosaurichthys* is expanded to a rectangular plate, much deeper than the anterior arm, making the cleithrum look like a boot in lateral view. The cleithrum in *Saurichthys* is generally triradiate or inverted "T" shaped with a low, round posterior blade that is generally as deep as or even lower than the anterior arm of this bone (see Stensiö 1925; Lehman et al. 1959; Griffith 1962, 1977; Rieppel 1985, 1992; Mutter et al. 2008; Wu et al. 2009). Only one specimen (GMUH VP992) attributed to *Saurichthys* cf. *ornatus* Stensiö, 1925, was mentioned to have L-shaped cleithrum (Mutter et al. 2008: 118) but without further detailed information. The pectoral girdle in *Sinosaurichthys* shows more or less similar trend of specialization to that in the hatchetfish (Gasteropelecidae) of South America, the only extant fishes able to actively flap their ex-

tended pectoral fins in the air to obtain thrust (Rayner 1986) and whose posttemporal and supracleithrum are fused into a single large bone with the pectoral girdle extremely expanded (Brousseau 1976; Weitzman and Palmer 2003). The fusion of the posttemporal and supracleithrum in the hatchet fish is considered as a peculiar osteological feature related to specialization of their pectoral girdle and fins for jumping and flying behavior (Wiest 1995). Although it is hard to say that *Sinosaurichthys* had obtained similar jumping and flying ability, it is undoubted that the similarity in the modification of the pectoral girdle in *Sinosaurichthys* and the hatchetfish reflects a functional convergence to enhance the pectoral girdle supporting stronger pectoral musculatures.

Although the pectoral fins in both *Sinosaurichthys* and *Saurichthys* are inserted between the dorsal stem and posterior blade of their cleithrum, the different shape and depth of the cleithrum makes the insertion of the pectoral fins above the midpoint of the body depth in *Sinosaurichthys* and distinctly below that in *Saurichthys*. The pectoral fins are also different in shape between the two genera. It is triangular to sickle shaped and relatively long in *Sinosaurichthys* and is small fan shaped in the Middle–Late Triassic *Saurichthys* from Europe (Griffith 1959, 1962, 1977; Rieppel 1985). The posterior stem of the parasphenoid in *Sinosaurichthys* is elevated much high above the mid-point of the skull depth and correspondingly the axial skeleton in the abdominal region is also situated in the level above the mid-point of the body depth.

The information about the parasphenoid was recorded only in a few species of *Saurichthys*, e.g., *S. ornatus*, *S. hamiltoni*, and *S. wimani* from Spitsbergen (Stensiö 1925), *S. madagascarensis* from Madagascar (Beltan 1968), *S. obrutchevi* and *S. proximus* from Central Asia (Minich 1981) and *S. curionii* from Monte San Giorgio (Rieppel 1985). All of them show that the posterior stem of the parasphenoid is just slightly elevated and the ventral crista is rather low and their vertebral column is therefore situated close to the mid-point of the body depth. The differences in the dermal pectoral girdle, the insertion of the pectoral fins and the position of the axial skeleton in the abdominal region between the two genera are apparently related to their difference in locomotion behavior and ecological adaptation (see discussion below).

As for the squamation, the different configuration of the mid-dorsal and mid-ventral scales of *Sinosaurichthys* also makes it distinguishable from *Saurichthys*. In the species of *Sinosaurichthys*, the mid-dorsal scales anterior to the dorsal fin are so broad that they are much wider than narrow mid-ventral scales. This unique feature is different from the majority of *Saurichthys* with the narrow, lanceolate mid-dorsal and mid-ventral scales and few species with mid-ventral scales as broad as the wide mid-dorsal ones in the abdominal region, such as *S. madagarscariensis*, *S. gigas*, and *S. dayi* (Woodward 1890; Piveteau 1945; Rieppel 1980; Mutter et al. 2008). This feature makes sense for it suggests that *Sinosaurichthys* probably has a bodly form of an inverted drop in the transverse section, i.e., the dorsal ridge comparatively

broad and ventral edge narrow, which consequently means a relatively dorsally positioned center of gravity, mechanically correlated with the elevation of its axial skeleton and the high insertion of the pectoral fin.

Other important features distinguishing *Sinosaurichthys* from *Saurichthys* are related to the branchiostegal rays and position of the pelvic and unpaired fins. In all known saurichthyids, the branchiostegal rays are highly reduced. Among the relatively well-known species of *Saurichthys* the branchiostegal rays are generally reduced to one pair (Stensiö 1925; Rieppel 1985), though two pairs occur in a species of *Saurichthys* under description from the Panxian fauna (Wu 2009) and possibly three pairs in *Saurichthys madagascariensis* (Lehman 1952). However, among the over one hundred specimens of *Sinosaurichthys* we checked, none shows any trace of branchiostegal rays.

Among *Saurichthys*, the position of the pelvic and unpaired fins in the trunk is recorded in quite a few species, e.g., *S. gigas* from Australia (Woodward 1890), *S. krambegeri* and *S. calcaratus* from Austria (Griffith 1962; 1977), *S. curionii*, *S. macrocephalus*, and *S. costasquamosus* from Monte San Giorgio (Rieppel 1985), *S. dayi* and *S. toxolepis* from Canada (Mutter et al. 2008), and *a. dawaziensis* from South China (Wu et al. 2009). Although the pelvic fins in certain species, such as *S. gigas*, *S. dayi*, and *S. costasquamosus*, are positioned in similar place as in *Sinosaurichthys*, i.e., behind the mid-point of the distance between the opercle and caudal fin, the anal fin of them is exclusively situated in place closer to the pelvic than to the caudal fin. The available information indicates that the positions of the anal fin in species of *Saurichthys* are generally closer to the caudal than to the pelvic fins or near the mid-point between the pelvic and caudal fins.

Thus *Sinosaurichthys* is easily distinguished from all known species of *Saurichthys* based on the features discussed above.

Ecology and functional morphology

As noted above, one of the most distinguishable morphological features between *Sinosaurichthys* gen. nov. and *Saurichthys* is the position and shape of their pectoral fins, which are long, triangular to sickle shaped and dorsally inserted in *Sinosaurichthys* and small, fan shaped and ventrolaterally positioned in *Saurichthys*. The pectoral fins of fish are primarily responsible for controlling body stability, turning and braking while swimming, especially for the forms using body/caudal fin propulsion. The morphologic similarity to the extant needlefish suggests that the locomotion mode of these saurichthyids should resemble that of the belonids, representing anguilliform (Liao 2002) to carangiform body/caudal fin propulsion type (sensu Lindsey 1978). For fishes with pectoral fins situated low on the body, Breder (1926) supposed that the reaction of the braking force to the center of body mass will exert a substantial pitching or "somersaulting" movement due to lack of a vertically oriented lift component in the braking force because the center of pressure of the pectoral fin lies below the center of the body mass. For fishes whose pectoral fins extend higher up on the body, Harris (1938) suggested that the braking force is comprised of both a horizontal and vertical component so that the reaction force vector intersects the center of body mass, eliminating the destabilizing pitching moment. Modern experimental study also reveals that high positioned pectoral fins can generate higher forces for turning and direct braking forces closer to the center of the body mass and will tend to have a greater ability to control body rotation during braking (Drucker and Lauder 2002), which may be of advantage for fish to maintain the body balance and agility in sustained swimming. Among extant actinopterygians, some rapid and persistent swimmers, such as the scombrids, belonids, and exocoetids, have relatively long and high inserted pectoral fins. *Saurichthys* had originally been considered as a kind of pelagic predator, like the extant needlefish (Stensiö 1925; Beltan and Janvier 1978). This conclusion is supported by the presumed absence of an opercular process on the hyomandible suggesting a rather weakly developed operclular pump (Stensiö 1925; Rieppel 1992). However, the relatively small and lower positioned pectoral fins seem to exclude *Saurichthys* from the category of the persistent and rapid swimmers that can chase their prey long distances. It is likely that *Saurichthys* is an ambush or *Esox*-like predator (Rieppel 1985, 1992; Tintori 1990), using its fast-start capability to waylay rather than pursue its prey. On the other hand, although *Sinosaurichthys* also possessed a typical "acceleration specialist" morphology like *Saurichthys* and the extant pike (Family Esocidae), the distinct resemblance in the body shape and fin arrangement to the needlefish (Fig. 21) suggests that *Sinosaurichthys* was a typical belonid-like predator and probably had similar locomotion behavior and ecological habits as the needlefish. Most of the needlefish are swift surface-cruising predators, primarily inhabiting marine environments and feeding largely on small fishes which they catch sideways in their long jaws. Some were reported to have a similar migratory pattern as the mackerels (Muus and Nielsen 1999). Thus, we believe that *Sinosaurichthys* represents a lineage of saurichthyids derived from *Saurichthys* to adapt to a surface-cruising life style similar to the extant needlefish, and the dorsally positioned pectoral fins might suggest the acquisition of sustained swimming ability in this genus. Field excavation at the two fossil sites revealed that the specimens of *Sinosaurichthys* discovered are much more abundant than those of *Saurichthys* and always clustered together in certain mass death layers. This tends to support the interpretation that *Sinosaurichthys* is a surface-cruising swimmer and *Saurichthys* is an ambush predator, because the cruising swimmers generally swim in schools contrary to the solitary ambush predators, and thus have more individuals than the latter in a living community. The taphonomic records of the mass death events can more or less reflect the difference of the relative individual abundance of each taxon in a natural local community.
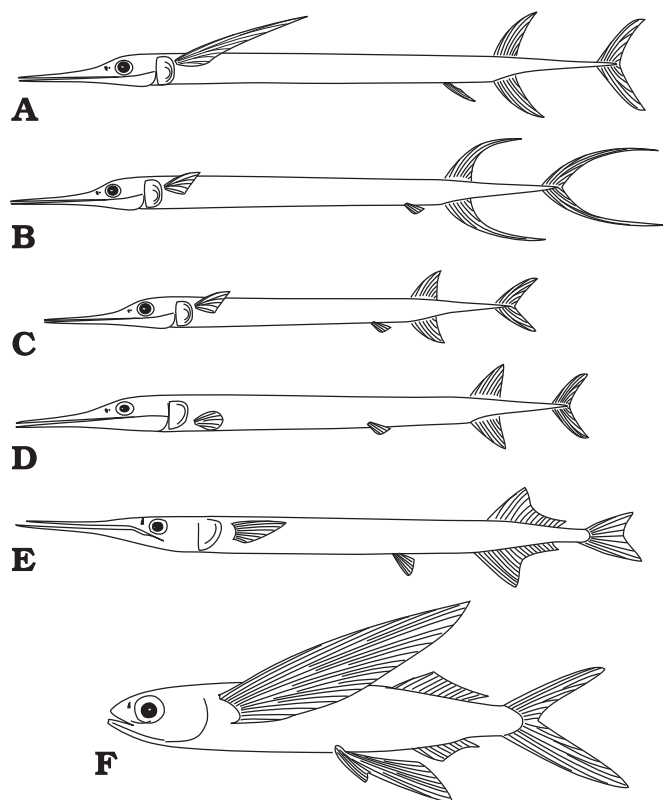
Fig. 21. Morphological comparison of saurichthyids with extant needlefish and flying fish. **A**. *Sinosaurichthys longipectoralis*. **B**. *Sinosaurichthys longimedialis*. **C**. *Sinosaurichthys minuta*. **D**. *Saurichthys dawaziensis* from Middle Triassic of Dawazi Section, Luoping, Yunnan, China (based on Wu et al. 2009). **E**. Atlantic needlefish *Strongylura marina* (Family Belonidae). **F**. Bluntnose flyingfish *Prognichthys gibbifrons* (Family Exocoetidae). E and F redrawn from images at http://www.fishbase.org/images/species that were originally from Cervigón et al. (1992).

It is interesting to note that three species of *Sinosaurichthys* from the two fossil sites show different trends in the development of their fins. In the type species of the genus, *Sinosaurichthys longipectoralis* from Panxian of Guizhou, the paired fins are extremely elongated, whereas in the two species from Luoping of Yunnan, one (*S. minuta*) keeps normal sized fins, the other (*S. longimedialis*) has extremely elongated median fins. This difference in fin morphology likely reflects a further differentiation in locomotion behavior and habits.

For *Sinosaurichthys longipectoralis*, the configuration of its paired fin is more or less similar to that of the extant flying fish (Family Exocoetidae) (Fig. 21), a close relative of the needlefish. Exocoetids are known as having the capability of leaping out of the water and gliding for long distances above the water surface to escape from predators (Gibbs 1978; Kutschera 2005), in which both pectoral and sometimes pelvic fins are evidently extended to act as "wings" when gliding (Kutschera 2005). However, the distal part of the fin rays of the pectoral fins in *S. longipectoralis* seems too fine to support flying fish-like gliding. Possibly, this species possessed only simple leaping ability like some extant needle-

fishes (Collette 1977; Helfman et al. 1997). However, this species has high aspect ratio median fins. The aspect ratio (defined as depth^2/area) of its caudal fin is about 4–5, higher than that of other saurichthyids (Fig. 21) and within the lower range of typical thunniform swimmers like recent mackerel or tunas (aspect ratio 4.5 to 7.2; Sambilay 1990), which renders this species one of the fast swimming fishes during that time. A high aspect ratio is thought to be characteristic of pelagic marine fishes that have enhanced cruising speed, enabling them to travel for long distance in search for food and breeding locality (Webb 1994). Thus, we believe that the elongation of the paired fins in *S. longipectoralis* probably represents a trend of adaptation to enhance the rapid swimming performance and, possibly, for a low-efficiency gliding ability. Field observation and excavation revealed that no benthonic organism was associated with this species except thin-shelled bivalves. The presence of other actinopterygian fishes and ichthyopterygian reptile *Mixosaurus panxianensis* (Jiang et al. 2006) suggests a relatively open offshore rather than a near-shore coastal habitat. The enhancement of rapid swimming performance is no doubt advantageous for the species to search for food and escape from larger predators (such as *Birgeria* and *Mixosaurus*) in an open pelagic environment. In addition to using the long pectoral fins to keep the body in balance and enhance swimming ability (even gliding), it is also possible that the species uses the pectoral fins to drive its prey, like recent sailfish using the sail-like dorsal fin to hunt (Holland 2008).

For *S. longimedialis* from the Luoping of Yunnan, the elongation of the median fins is obviously a disadvantage for rapid swimming, as compared to *S. longipectoralis*. Although no solid answer can be put forward for why this species has such elongated median fins, a possible reason is that it lived in a more structurally complicated, near-coastal habitat, in which persistent rapid swimming performance may not be as important as in an open pelagic environment. This interpretation is supported by the taphonomic evidence that many benthonic invertebrates, such as shrimps, echinoderms, gastropods, and even freshwater-related isopods, were associated with this species in the upper part of the fossiliferous strata in the Dawazi Section.

Conclusions

Sinosaurichthys is a new genus of the Saurichthyidae differing from *Saurichthys* in having a peculiar pectoral girdle and high-inserted pectoral fin, and some other related features. These differences reflect the variation in the locomotion mode and ecological adaptation of saurichthyids. The new genus represents a lineage closely related with *Saurichthys* but adapted to achieve improved sustained swimming for cruising in surface water, like the extant needlefishes. The different fin morphology between the species of the new genus might suggest a further differentiation in locomotion behavior and ecologic habitats.

Acknowledgements

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