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A small-sized dinocephalosaurid archosauromorph from the Middle Triassic of Yunnan, southwestern China

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Abstract Among numerous marine reptiles discovered in the Triassic eastern Tethys, today's Southern China, *Dinocephalosaurus* is a bizarre animal comparable to European *Tanystropheus* in developing a prominently long neck. These two taxa are respectively assigned to Dinocephalosauridae and Tanystropheidae, and the two families and other basal members collectively form an early-diverging clade of Archosauromorpha. Here we report a new archosauromorph specimen, IVPP V18579, excavated from the lower Middle Triassic (Anisian), from Luoping, Yunnan in southwestern China. Compared with all the hitherto known dinocephalosaurids and tanystropheids, this skeletally mature individual is exclusively similar to *Dinocephalosaurus* in a number of characteristics, particularly with the long posterodorsal process of the premaxilla extending posteriorly beyond the level of the external nares, the concave posterior margin of the anteroposteriorly broad quadrate, and the strongly expanded distal end of the chevron in most of the caudal vertebrae. However, this reptile is much smaller than *Dinocephalosaurus* and different from *Dinocephalosaurus* and the other dinocephalosaurid, *Pectodens*, in many aspects, such as an anteriorly tapering long rostrum, the dentition composed of short conical teeth with less heterodonty, relatively but obviously tall neural spines of the axis and the anterior cervical vertebrae. Our phylogenetic analysis suggests that the new archosauromorph is a dinocephalosaurid, and then we erect *Austronaga minuta* gen. et sp. nov. based on this specimen. Detailed comparisons in osteological anatomy and the discussion about its potential aquatic adaptation of this new taxon are also provided.

Key words Luoping, Yunnan; East Tethys; Triassic; marine reptile; Archosauromorpha; Dinocephalosauridae; osteological anatomy

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1 Introduction

The Middle Triassic of southern China has yielded remarkable marine vertebrate assemblages that are drastically changing our understanding of the biotas of the Tethys Sea and its shorelines (e.g., Li, 1999; Li et al., 2006, 2011, 2016; Motani et al., 2015; Jiang et al., 2016; Wang et al., 2022). A group of Triassic non-archosauriform archosauromorphs take a prominent place among these discoveries. They were traditionally termed "Protorosauria" or "protorosaurs" but are now considered as a paraphyletic group (e.g., Ezcurra, 2016; Pritchard and Nesbitt, 2017; Spiekman et al., 2021; Wang et al., 2023).

One taxon belonging to this group of reptiles, *Dinocephalosaurus orientalis*, is one of the most intriguing reptiles discovered in recent years from the Triassic of southern China (Li, 2003; Li et al., 2004; Rieppel et al., 2008; Liu et al., 2017). Its greatly elongated neck recalls a similar condition as seen in another aquatic archosauromorph, *Tanystropheus*. Both taxa possess a neck that is more than twice as long as the trunk. *Tanystropheus* was first established on the basis of isolated neck vertebrae from the German Muschelkalk (Meyer, 1847-1855), and later described in detail based on the discovery of complete skeletons from the Middle Triassic of the Monte San Giorgio region of Alpine Europe (Bassani, 1886; Peyer, 1930; Nosotti, 2007). Furthermore, *Tanystropheus* has been intensively investigated and its anatomical features have been documented during the last few years (Spiekman and Scheyer, 2019; Spiekman et al., 2020a, b). Although the cervical vertebrae of *Dinocephalosaurus* are elongate and bear low and elongate neural generally resembling those of *Tanystropheus*, part of the excessive elongation of the neck in *Dinocephalosaurus* can also be attributed to a significant increase in the number (31 or 32) of neck vertebrae (Spiekman et al., in review). Significantly, both *Dinocephalosaurus* and *Tanystropheus* possess slender and elongate cervical ribs that were oriented parallel to the long axis of the neck and extending across multiple intervertebral joints so that collectively they formed a stiffening bundle of rib shafts. However, in many more respects, *Dinocephalosaurus* is unlike other long-necked archosauromorphs, as it suggested by solid rather than hollow limb elements that are indicated by collapses on the shafts, carpal and tarsal elements reduced to simple sub-circular bones, a straight fifth metatarsal, paddle-like manus and pes that recall the nothosaurian condition and a solid puboischiadic plate lacking any trace of a thyroid fenestra (Li et al., 2004; Rieppel et al., 2008). Recent studies (Spiekman et al., 2021; Wang et al., 2023; Spiekman et al., in review) reveal that *Tanystropheus* and *Dinocephalosaurus* are members of basal archosauromorphs, non-crocopodan archosauromorphs, but belonging to separate families, Tanystropheidae and Dinocephalosauridae, respectively. Additional taxa from the Triassic of southern China considered as non-crocopodan archosauromorphs include *Macrocnemus fuyuanensis* (Li et al., 2007; Jiang et al., 2011; Scheyer et al., 2020), *Fuyuansaurus acutirostris* (Fraser et al., 2013), *Pectodens zhenyuensis* (Li et al., 2017a), *Gracilicollum latens* (Wang et al., 2023), and an embryonic specimen with undetermined affiliation (Li et al., 2017b).

In this study, we report on a new non-crocopodan archosauromorph from Yunnan Province, southwestern China. This new taxon represented by a small-sized but skeletally mature specimen, IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences) V18579 shares many features with *Dinocephalosaurus* and together with the latter are distinguishable from other long-necked archosauromorphs. However, this new taxon also exhibits many anatomical features different from *Dinocephalosaurus*, and therefore a new genus and species are suggested for it.

2 Systematic paleontology

Diapsida Osborn, 1903

Archosauromorpha Huene, 1946 *sensu* Dilkes, 1998

Dinocephalosauridae Spiekman et al., 2021

***Austronaga minuta* gen. et sp. nov.**

https://zoobank.org/References/a1f2091c-254a-4fa0-bfdb-6f92b28b5df2

Etymology *Austronaga*, from the Latin "auster" or "austral" meaning south or southern referring to the South China Block where this taxon occurred, combining with "naga", an Asian mythological figure that is snake-like and associated with water; *minuta* meaning small refers to the relatively small body size of this animal compared with most of its Triassic marine archosauromorph relatives.

Holotype IVPP V18579, a nearly complete skull with articulated anterior cervical vertebrae and most of the caudal vertebrae that are associated and jointly preserved on the same block.

Type locality Waina Village, Luoping County, Yunnan Province, China.

Type horizon Member II of Guanling Formation, middle Anisian (Pelsonian), Middle Triassic.

Diagnosis A small-sized dinocephalosaurid with a unique combination of anatomical features: quadrate broad and plate-like in lateral view with concave posterior margin; ax-shaped tall neural spine of axis with the ratio between it and axial posterior articular surface of about 1.5; neural spines of anterior vertebrae prominent with convex dorsal margin and no anterodorsal or posterodorsal projections; chevron bones of mid caudal region distinctively hatchet-shaped, with prominent distal expansion and a notch at the mid-point of its ventral margin.

3 Description

The specimen, IVPP V18579, includes an almost complete, albeit greatly compressed, skull, the anterior part of the neck in articulation with the skull, and most of the tail of approximately 60 caudal vertebrae (Fig. 1). These elements occur on a single block with a crack through the proximal region of the tail and a calcite vein crossing the posterior tip of the tail. There is a second block with additional remains representing the same individual under

further preparation and examination.

Skull The skull is mostly exposed in right lateral view but is laterally compressed (Fig. 2). As a result, it is difficult to unequivocally distinguish bone sutures from cracks on the bone surfaces. It is a long-snouted form with elongate external nares and is measured as 47.5 mm from the anterior tip of the rostrum to the occiput, which indicates this animal to be relatively small (Table 1) compared to many other tanystropheid and dinocephalosaurid archosauromorphs. Much of the dorsal roof of the skull, including the frontals, is not preserved although there are impressions of where these bones were positioned (Fig. 2). In addition, it seems that much of the parietals, the postfrontals, the postorbitals, and anterior parts of the squamosal and the dorsal part of the jugal are broken or lost. Some parts of the palate can be observed through the large orbit, though the detailed palatal structure is difficult to interpret.

Fig. 1 Holotype of *Austronaga minuta* (IVPP V18579) discovered from Luoping, Yunnan, China, with the skull, anterior cervical vertebrae, and most of the caudal vertebrae preserved on a block

Premaxilla The premaxillae are low, elongate elements that are essentially complete although their extreme anterior tips might be missing. The left premaxilla is observed in dorsal view, while the right one is fully exposed in lateral view. The posteromedial processes of both premaxillae are very elongate, extending posteriorly beyond the level of the external nares and almost reaching the frontals in life. The posterodorsal processes share a midline suture with their counterpart along their entire length (Fig. 2). On the right side, the posterodorsal process contributes to most of the dorsal margin of the external naris, while its posteroventral process forms the anterior margin of the external naris, and shortly passes below the external naris to limitedly meet the maxilla.

Nasal The nasals are small, paired elements that are somewhat elongate and similar in size to the external nares. On the right side, the anterior part of the nasal clearly forms the posterodorsal margin of the external naris. Due to the disarticulation of the left nasal, the left and right nasals are partly separated. The nasal laterally sutures to both the prefrontal and the maxilla.

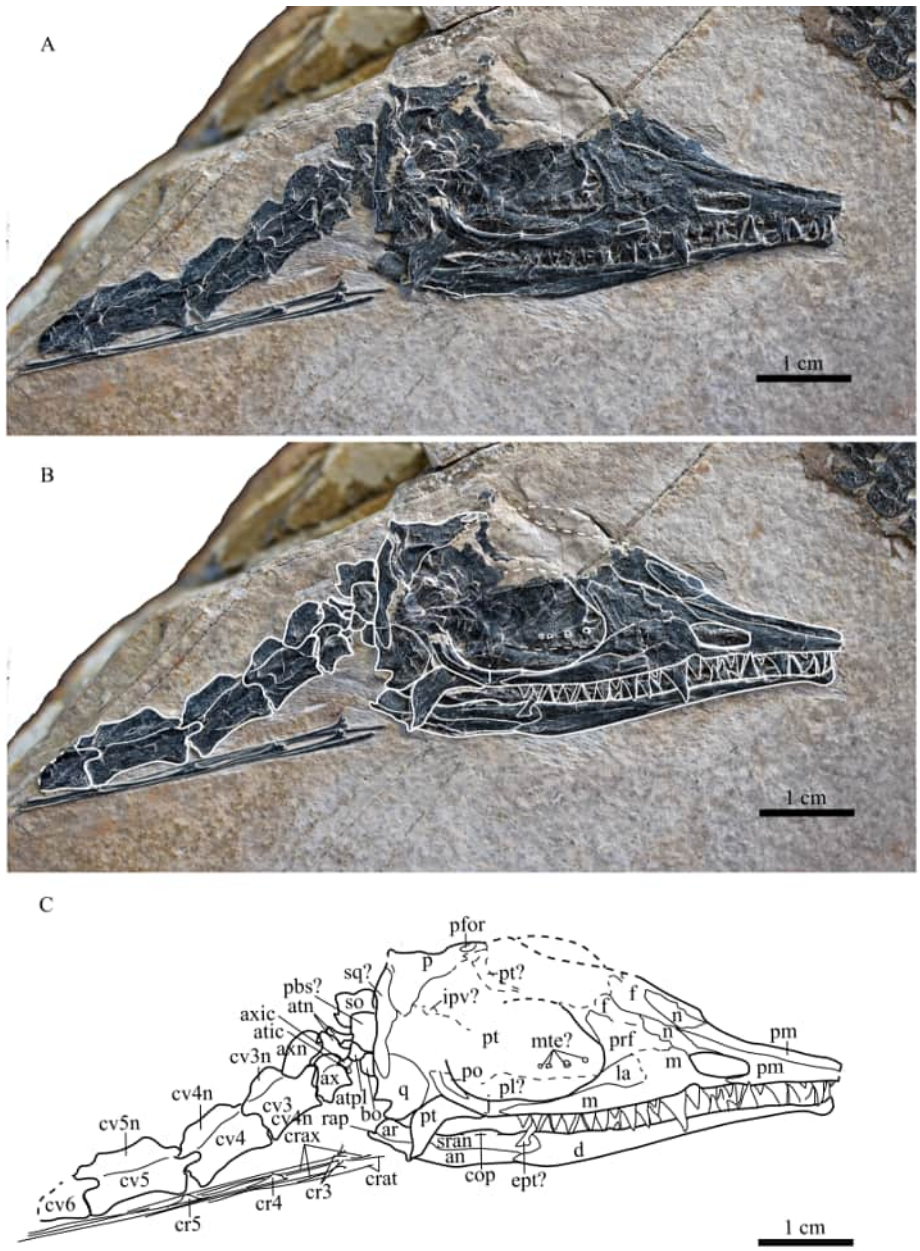

Fig. 2 Skull and anterior cervical vertebrae (A) with interpretative line drawings (B, C) of the holotype of *Austronaga minuta* (IVPP V18579) from the Middle Triassic in Luoping, Yunnan, China
Abbreviations: an. angular; ar. articular; atic. atlas intercentrum; atpl. atlas pleurocentrum; atn. atlas neural arch; ax. axis (pleurocentrum); axic. axis intercentrum; axn. axis neural spine; bo. basioccipital; cop. coronoid process; cr(3–5). (third to fifth) cervical rib; crat. cervical rib of atlas; crax. cervical rib of axis; cv(3–6). (third to sixth) cervical vertebrae (centra); cv(3–5)n. (third to fifth) cervical vertebral neural arches; d. dentary; ept. ectopterygoid; f. frontal; ipv. interpterygoid vacuity; j. jugal; la. lacrimal; m. maxilla; mte. maxillary teeth; n. nasal; p. parietal; pbs. parabasisphenoid; pfor. parietal foramen; pl. palatine; pm. premaxilla; po. postorbital; prf. prefrontal; pt. pterygoid; q. quadrate; rap. retroarticular process; so. supraoccipital; sq. squamosal; sran. surangular

Maxilla The right maxilla is well exposed. Its ascending process is rather crushed, and it is difficult to unequivocally determine the natural margins, and, in particular, its sutures with the lacrimal and prefrontal. Nevertheless, the ascending process seems to have been moderately developed and it meets the nasal in a broad contact just behind the external naris. The anterior process of the maxilla is dorsoventrally very low and contributes to the posterior rim and posterior half of the ventral rim of the external naris. The posterior process of the maxilla reaches slightly posterior to the anteroposterior midpoint of the orbit, and it forms a posterodorsal articulation with the jugal.

Lacrimal The lacrimal seems to have taken the form of an elongate triangular element (Fig. 2), contributing to the anteroventral corner of the orbit. Its elongate posteroventral process is thin in lateral view and tapers posteriorly. However, in this region teeth from the left maxilla have been forced through the side of the skull further complicating the interpretation of the sutures of the lacrimal with the maxilla and prefrontal. There is no foramen or fossa present on the lacrimal.

Prefrontal The prefrontal is a prominent triangular bone with a thickened posterior portion forming the anterior border of the orbit. The prefrontal medially contacts the nasal and the frontal, and laterally abuts the maxilla and the lacrimal, although the sutures are poorly defined.

Frontal Only the anterior portions of the frontals remain, but an impression of the posterior part of the frontals remains in place. It seems that the frontal is longer than wide, forming the dorsal skull roof between the orbits. The frontal likely possesses an anterolateral process extending to the anterodorsal corner of the orbit. At least in their anterior parts, the frontals are not fused with each other.

Parietal At least the posterior portions of both parietals are preserved, and the left one displays a characteristic curved margin of the supratemporal fossa, clearly demarcated by a curved, longitudinal shelf, which extends into the upper temporal fenestra in a manner similar to that seen in *Tanystropheus*. The dorsal surface of the parietal is possibly very lightly pitted. Although the anterior part of the bone is fragmented and mostly missing, a smooth, apparently finished edge of the bone may represent the posterior margin of a parietal foramen.

Jugal The jugal is crescent-shaped and clearly lacks any posterior process, which represents a typical feature of dinocephalosaurids (Spiekman et al., 2021). It has been

Table 1 Measurements of the holotype of *Austronaga minuta* (IVPP V18579) from the Middle Triassic in Luoping, Yunnan, China (mm)

Item	Length	Item	Length (centrum)	Height at midpoint
Skull	47.5	Atlas	–	–
Snout	24.1	Axis	3.1*	6.4
Orbit approximately length	15.9	Cervical V3	6.1	5.6
Temporal region	7.5	Cervical V4	9.0	5.1
Mandible	46.6	Cervical V5	10.4	5.0

* Axis centrum measured.

somewhat displaced posteriorly and ventrally, perhaps thereby giving the impression that the orbit was larger than its actual size. Anteriorly the jugal passes behind and along the posterior ramus of the maxilla and thereby forms the entire ventral margin of the orbit.

Postorbital The ventral tip of the postorbital is preserved in articulation with the anterior side of the jugal, but the rest of the element is missing.

Quadrate The quadrate is laterally exposed as a broad, squat, yet somewhat plate-like element that is still in articulation with the mandible. It has a broad semicircular anterior margin and a prominent notch on the posteroventral margin.

Squamosal Details of the rest of the temporal region are difficult to determine due to crushing and the absence of a significant part of the surface part. Nevertheless, the posterior edge of the squamosal is preserved. This preserved part of the squamosal is long and separates the parietal from the quadrate. Because of the poor preservation of the squamosal, the parietal, the postorbital, and other elements surrounding the supratemporal fenestra, the configuration of the temporal structure cannot be fully determined.

Palate A distinct portion of the crushed palate is visible in dorsal view through the orbit. Although the left pterygoid is only largely represented by an impression, a significant portion of the right pterygoid is still preserved, including its medial margin, which would have formed an extensive midline suture with its counterpart. This is indicative of a short interpterygoid vacuity. The broad right pterygoid extends backward but has been displaced under the jugal, and the large posterior flange that articulated with the quadrate lies across the mandible (Fig. 2). A small fragment of bone with an expanded distal end protrudes from the gap between the upper and the lower jaws, and this may represent part of the right ectopterygoid.

Neurocranium Elements of the braincase are rather crushed and difficult to interpret, but there appear to be fragments of the parabasisphenoid, supraoccipital, and basioccipital preserved (Fig. 2). The tentative parabasisphenoid is a thickened element, while other fragments of the occiput are relatively flattened. The supraoccipital is almost completely exposed. It is a bilaterally symmetrical bone, with a slightly concave dorsal edge, roughly straight lateral margins, and a weak midline suture.

Mandible The lower jaw is occluded with the skull, which consequently limits the view of the anatomical details of the mandible. The elements of the mandible, particularly the dentary, is strongly ornamented with longitudinal striations. Anteriorly, the ventral edge of the right dentary is slightly expanded, giving the symphysis a bulbous appearance. The dentary extends posteriorly to a level slightly anterior to the posterior ramus of the maxilla or approximately to the anteroposterior midpoint of the orbit. There is a low but distinct coronoid process behind the alveolar portion, but it is unclear whether this process is formed by a separate coronoid bone. The surangular, angular, and articular can be recognized. The surangular and angular are unsculptured in lateral view and form a margin that is straight to slightly curved. Posterior to the mandibular fossa, the articular forms a short, slightly upturned retroarticular process.

Dentition An almost complete dentition is preserved on the right side of the skull, and all teeth exhibit smooth enamel surfaces devoid of striations. The right premaxilla preserves six teeth *in situ*, but the complete premaxillary tooth count was likely around eight (Fig. 2). These teeth vary in size along the length of the element, but all generally have the same acutely conical shape. A markedly enlarged tooth on the right premaxilla, probably the third, is slightly recurved. There is another particularly prominent tooth, probably corresponding to the fifth, which is the largest of the preserved premaxillary teeth. The right maxilla bears 14 teeth, of which the fourth is a caniniform tooth as the largest and most prominent one in the entire dentition. These maxillary teeth are conical, straighter, mesiodistally wider, and less varied in size compared with those on the premaxilla. The tooth-bearing portion of the maxilla extends posteriorly to the mid-point of the orbit. Part of the lateral edge of the right pterygoid seems to possess a single row of teeth. However, these teeth certainly belong to the left dentary, and they are deflected due to the compression of the skull and run underneath the palate (Fig. 2). There is no unequivocal evidence for palatal dentition. It is difficult to determine the dentary tooth count. We estimate that the dentary may have more than 20 teeth, which is consistent with the dentition on the premaxilla and the maxilla. Three or two largest teeth of the dentary are positioned just behind the symphysis, although they appear to be smaller than those of the upper jaw.

Cervical vertebrae The preserved cervical series of the vertebral column is in articulation with the skull, although only the anterior half of the sixth cervical vertebra is preserved (Figs. 1, 2). The neural arch of the atlas is aligned with the occipital region. The atlas is broken and represented by a relatively short centrum and partial neural arch overlapping onto the axis. The neural arch of the axis exhibits an ax-shaped dorsal spine, which is taller than the centrum. The centrum of the axis is short and half the length of the third cervical centrum (Fig. 2; Table 1). The third to fifth cervical vertebrae are complete and well exposed in right lateral view. Their neural spines are elongate and low, so that they are longer than tall. They are trapeziform in shape in lateral view (Fig. 2), lacking both anterior and posterior projections of their dorsal portions, in contrast to *Tanystropheus* spp. (Spiekman and Scheyer, 2019). The dorsal margin of the neural spine is slightly concave in lateral view, with increasing degrees of concavity from the third to the fifth cervical vertebrae. There is a tendency for an increase in the length of the centrum from the anterior cervical vertebrae to the posterior ones in this preserved series, as well as the lengths of their neural spines and centra (Fig. 2). On these anterior cervical vertebrae, both diapophysis and parapophysis have a small and elongate facet. The parapophysis is situated at the very anteroventral extremity of the vertebral centrum, and the diapophysis is positioned immediately above it as a slightly lateroventrally projecting bony pedicel. The prezygapophyses are well-developed and broadly overlap the postzygapophyses of the preceding vertebra.

Cervical ribs The first pair of cervical ribs possibly articulated on the centrum of the atlas in life but displaced here, and they have expanded and stout proximal ends that are essentially single headed, and these ribs taper posteriorly and seem to extend across three

intervertebral joints. Alongside the first pair of cervical ribs are two exceptionally slender elements, and they have no obvious rib head and presumably attach to the axis centrum (Fig. 2) with the reference of some archosaurs (Cong et al., 1998). Each of the ribs associated with the third cervical vertebra has a very characteristic "three-headed" appearance (Fig. 2). The "three-headed" rib comprises a very short but separate capitulum and tuberculum plus a short free bony spur that is ventrally positioned. On the fourth and fifth cervical rib pairs, the free process shifts further incrementally anteriorly from the capitulum and tuberculum.

Caudal vertebrae A total of 65 articulated caudal vertebrae are preserved on the same block as the skull (Fig. 1). One or two additional elements may be missing because the last of the 65 vertebrae does not taper off posteriorly as in other reptiles such as the extant *Alligator sinensis* (Cong et al., 1998:fig. 77C) or a Triassic eosauropterygian, *Brevicaudosaurus jiyangshanensis* (Shang et al., 2020:fig. 6D) where the last caudal centrum becomes pointed posteriorly. The caudal centrum is essentially rectangular with a weak central constriction. A clear suture separates the neural arch and centrum. On the most anterior caudal vertebrae, the neural spines are well developed and plate-like with a distinctly convex dorsal margin in lateral view. From the mid-region of the tail, the neural spines gradually decrease in size and become

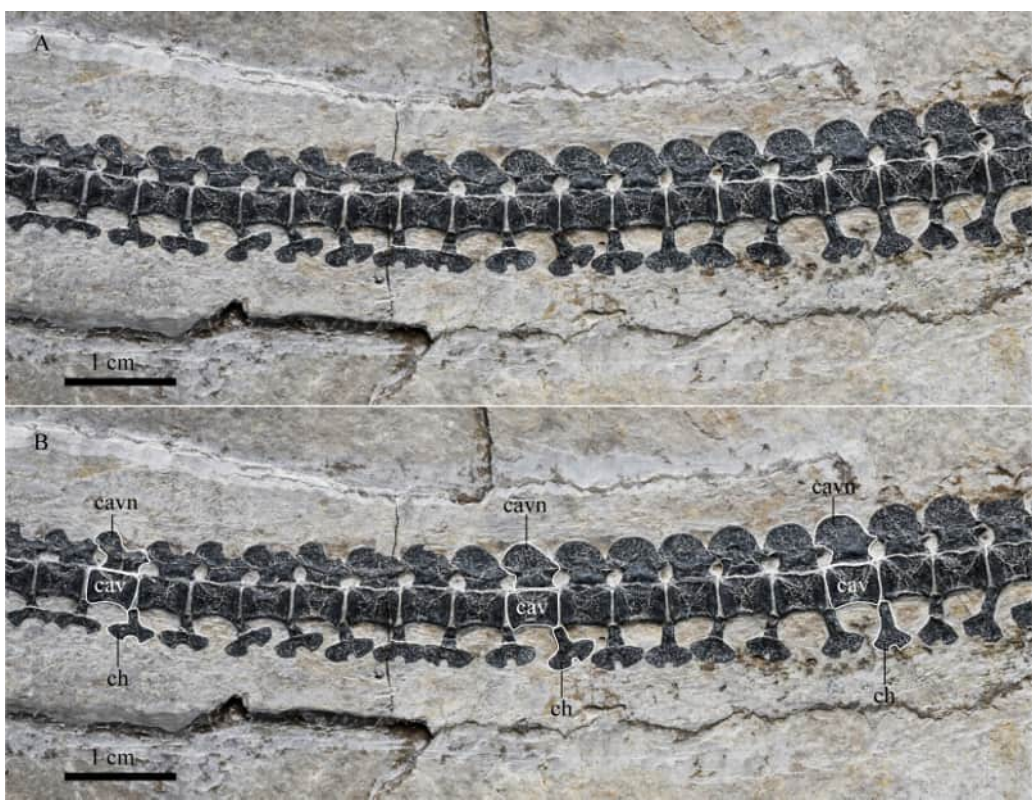

Fig. 3 Middle region of the tail (A) with interpretative line drawings (B) of representative caudal vertebrae in the holotype of *Austronaga minuta* (IVPP V18579) from the Middle Triassic in Luoping, Yunnan, China
Abbreviations: cav. caudal vertebra (centrum); cavn. caudal vertebral neural arch; ch. chevron

posteriorly inclined in a way that results in a saddle shape (Fig. 3). The neural spine finally disappears on the posterior-most caudal vertebrae (Fig. 1). The pre- and postzygapophyses are prominently developed throughout the caudal series.

Chevrons The chevrons (or haemal arches with haemal spines) on the preserved anterior caudal vertebrae are essentially strap-like elements in lateral view, although they do expand slightly towards their distal tips. The first two vertebrae and their associated chevrons that are preserved to the right of the crack as seen in Fig. 1 are too fragmented to permit further description. However, a fragment of the chevron from the preceding vertebra indicates that from this point onwards they start to transversely expand distally in lateral view. The next two vertebrae have chevrons with rather rounded distal ends, followed by one with a distinct notch that divides the distal lamina of the bone into anterior and posterior parts. Moving progressively backward, the haemal arches take the form of a very distinct hatchet shape or "ginkgo leaf" shape (Figs. 1, 3). This notch becomes incrementally wider in the posterior caudal region, resulting in a T-shape of the chevrons. Anterior to this point the chevrons are deflected posteriorly, but at the point where they become notched, they are oriented ventrally, perpendicular to the intervertebral joints (Fig. 3). The notch becomes more marked and the anterior and posterior subdivisions more extensive so that in some places the posterior process of one chevron is in contact with the anterior process of the succeeding chevron (Fig. 3). These chevrons continue posteriorly and gradually become smaller, persisting almost to the end of the tail. They disappear either at the fourth or the fifth vertebra counted backwards.

4 Phylogenetic analysis

To investigate the phylogenetic position of this new specimen, we employed the data matrix of Wang et al. (2023), which was modified from the data matrix of Spiekman et al. (2021) and includes almost a comprehensive sample of known non-crocopodan archosauromorphs. Based on IVPP V18579, the new operational taxonomic unit, *Austronaga minuta*, was scored and added to the data matrix (see Appendix). The data was analyzed using TNT 1.5 (Goloboff and Catalano, 2016). The analysis follows the same methodology as in Wang et al. (2023), setting *Petrolacosaurus kansensis* as the outgroup and excluding the operational taxonomic units (OTUs) *Czatkowiella harae*, *Tanystropheus* "*conspicuus*", "*Tanystropheus antiquus*", GMPKU (Geological Museum of Peking University) P 1527, and AMNH (American Museum of Natural History) FARB 7206 from the analysis as a priori. Furthermore, characters 1, 2, 4, 5, 7, 9, 13, 35, 43, 62, 73, 77, 78, 83, 84, 88, 89, 110, 114, 118, 128, 136, 140, 144, 153, 158, 159, 162, 178, 185, 187, 194, 195, 200, 205, 209, 219, 220, 224, 230, 232, 242, 248, 251, 258, 259, 264, 267, 276, 292, 294, 297, 298, 299, and 305 were treated as ordered, and a traditional search was used, employing 1000 replications of Wagner trees and TBR branch swapping holding 10 trees per replicate. The calculation of the support values and the application of the iter PCR protocol (Pol and Escapa, 2009) to identify unstable OTUs also follows the methodology of Wang et al. (2023). We recovered 594 most parsimonious trees of 1147 steps, and the consistency index

(CI) is 0.386 and the retention index (RI) is 0.538 (Fig. 4). Incorporating *Austronaga minuta*

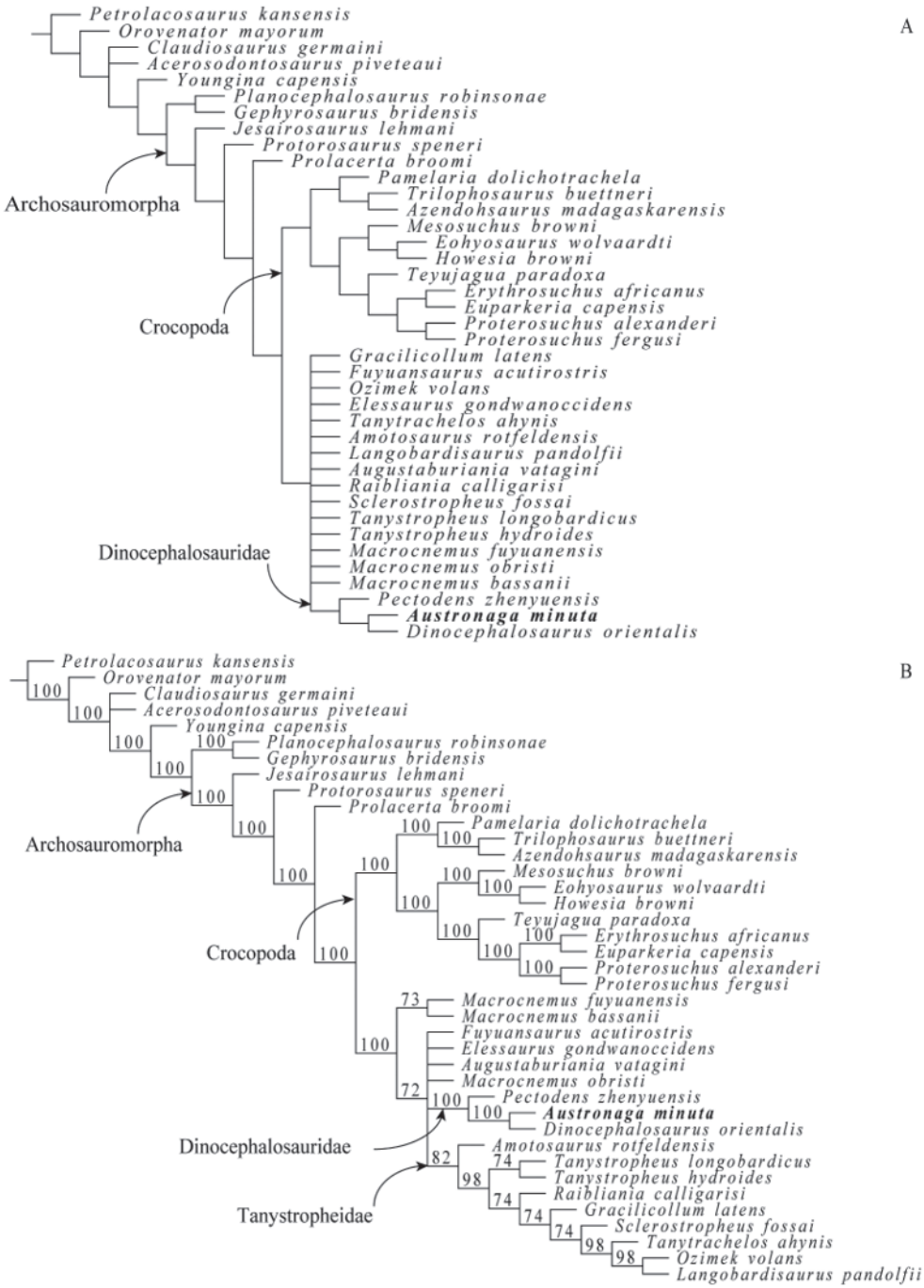

Fig. 4 Phylogenetic results showing the position of *Austronaga minuta* in Dinocephalosauridae and other relationships within Archosauromorpha

A. strict consensus tree; B. majority-rule reduced consensus trees

(nodes with bootstrap proportion > 50% remained with values labeled above)

in the dataset and analysis, the relationships among these non-crocopodan archosauromorphs become even less resolved compared to the topology of the previous studies (Spiekman et al., 2021; Wang et al., 2023). The strict consensus tree (Fig. 4A) confirms the monophyly of these long-necked early diverging archosauromorphs as the sister group to the Crocopoda, although the internal phylogenetic relationships are largely unresolved within the former. The majority rule consensus (Fig. 4B) recognizes two monophyletic families, Dinocephalosauridae and Tanystropheidae, with the latter including *Amotosaurus*, *Tanystropheus*, *Gracilicollum*, *Tanytrachelos*, and *Langobardisaurus* as in Wang et al. (2023).

Despite the low resolution of the phylogeny in most of the long-necked archosauromorphs, *Pectodens*, *Austronaga*, and *Dinocephalosaurus* form a clade representing the family Dinocephalosauridae, as previously identified (Spiekman et al., 2021, Wang et al., 2023), which is in contrast with the topology in de Oliveira (2020). These three taxa form successive clades in all the most parsimonious trees (Fig. 4). Hence, we can confidently refer *Austronaga* to Dinocephalosauridae. Additionally and significantly, in the reduced strict consensus tree, two species of *Macrocnemus*, *M. fuyuanensis* and *M. bassanii*, are recovered outside of Tanystropheidae, and instead, they form an early diverging lineage that forms the sister group of the clade including tanystropheids, dinocephalosaurids, and several of the other non-crocopodan archosauromorphs such as *Fuyuansaurus* (Fig. 4B).

5 Discussion

5.1 Maturity of IVPP V18579

Despite the relatively small body size of this individual compared to *Tanystropheus hydroides* and *Dinocephalosaurus orientalis*, it is comparable in size with many other tanystropheids including *Tanystropheus longobardicus*, *Tanytrachelos ahynis*, and *Macrocnemus bassani*. The extent of ossification in the skull and preserved cervical vertebrae indicates that IVPP V18579 represents a mature specimen (Griffin et al., 2021). The cranium and mandible are well ossified with all preserved elements apparently tightly sutured (Fig. 2). The dentition seems highly developed with a few enlarged fangs. The neural arches and the respective vertebral centra of the preserved cervical vertebrae are fully fused in V18579 (Figs. 1, 2), while the neurocentral sutures in the caudal series are present. Normally in reptiles, the closure of this kind of suture follows a posterior-to-anterior sequence with the occurrence earlier in caudal vertebrae and later in the cervical region (Griffin et al., 2021). The fusion between the cervical neural arch and the corresponding centrum suggests at least a late ontogenetic stage of this individual if it is not a full adult, and the unfused status in the caudal vertebra can be interpreted as skeletal paedomorphosis attributed to the secondarily aquatic adaptation in the tail (Rieppel, 1989b). Despite the caudal neurocentral sutures, the caudal

neural spines and the chevrons are well-developed by showing remarkable distal expansions, which indicate that its tail should be skeletally mature (Figs. 1, 2, 3). The erection of the new taxon, *Austronaga minuta* gen. et sp. nov., is therefore based on a mature specimen. Even if V18579 is a subadult, the diagnostic characters provided in this study are still reliable and seem hardly variable in further growth.

5.2 Comparisons with related non-crocopodan archosauromorphs

Our phylogenetic study confidently assigned this taxon to a non-crocopodan archosauromorph clade including Dinocephalosauridae and Tanystropheidae and some of the other basal archosauromorphs (Fig. 4). Therefore, here we discuss the anatomical similarities and differences between *Austronaga* and other members of Dinocephalosauridae and Tanystropheidae.

At first glance, the skull looks rather different in proportions to that of *Dinocephalosaurus*. Overall, the orbits are relatively large, and the temporal region is perhaps shorter than those of *Dinocephalosaurus*, but these differences can be easily attributable to allometric changes related to the large size discrepancy between the two taxa, as well as a certain degree of distortion in the temporal region in IVPP V18579. The constricted and tapering rostrum is distinct from those of *Dinocephalosaurus* (Li, 2003; Li et al., 2004; Rieppel et al., 2008) and *Tanystropheus hydroides* (Spiekman et al., 2020a, b). As in *Pectodens zhenyuensis* (Li et al., 2017a), *Macrocnemus fuyuanensis* (Jiang et al., 2011; Jaquier et al., 2017), *Fuyuansaurus acutirostris* (Fraser et al., 2013), and *Tanystropheus longobardicus* (Nosotti, 2007; Spiekman et al., 2020a), and likely in *Langobardisaurus* (Renesto, 1994) and *Gracilicollum* (Wang et al., 2023), the snout is narrow and tapers anteriorly in *Austronaga*. In fact, the portion of the snout anterior to the external naris is even narrower than in the abovementioned taxa, with a possible exception of *Fuyuansaurus* (Fraser et al., 2013).

Austronaga possesses several autapomorphic features, whilst also preserving traits that are diagnostic to Dinocephalosauridae, thus allowing this new specimen to be confidently assigned to a new taxon within this group (Fig. 2). The posterodorsal process of the premaxilla is very elongate, extending posteriorly beyond the level of the external nares. This corresponds closely to the condition seen in *Dinocephalosaurus orientalis* (Spiekman et al., in review). Although the exact posterior extent is unknown, the posterodorsal process of the premaxilla also clearly extends far posteriorly in the other known dinocephalosaurid taxon, *Pectodens* (Li et al., 2017a). Similarly, *Austronaga* also shares the absence of a posterior process of the jugal with both *Dinocephalosaurus* and *Pectodens*. Unlike *Dinocephalosaurus* (Li, 2003; Li et al., 2004; Spiekman et al., in review), *Tanystropheus hydroides* (Spiekman et al., 2020a, b), and *Macrocnemus fuyuanensis* (Jiang et al., 2011, there is no evidence in *Austronaga* for a narial gutter extending from the external naris onto the surface of each nasal. The quadrate in *Austronaga* has a strongly concave posterior margin resembling that

of *Dinocephalosaurus* and differing from the species of *Macrocnemus* and *Tanystropheus* (Spiekman et al., 2020a, b), but the quadrate here is distinctively large and plate-like in lateral view while it is anteroposteriorly much narrower in *Dinocephalosaurus* (Rieppel et al., 1998; Spiekman et al., in review). The posterodorsal end of the quadrate is hooked in *Tanystropheus* species, but such a hook is absent in *Austronaga* and other non-crocopodan archosauromorphs (Spiekman et al., 2021). The distinctly wide dorsal surface of the pterygoid as preserved in *Austronaga* is similar to a condition in both *Dinocephalosaurus* (Rieppel et al., 2008; Spiekman et al., in review) and *Tanystropheus hydroides* (Spiekman et al., 2020b). The bulbous mandibular symphysis due to the ventrally expanded anterior tip of the dentary recalls the condition in *Dinocephalosaurus* (Spiekman et al., in review) and *Tanystropheus* spp. (Spiekman et al., 2020a, b). The retroarticular process is present and upturned but poorly developed in *Austronaga*, and this morphology is more comparable to those in *Pectodens* (Li et al., 2017a) and *Dinocephalosaurus* (Rieppel, 1998; Spiekman et al., in review) rather than the more projecting one in the species of *Macrocnemus*, *Tanystropheus*, *Fuyuansaurus*, and *Gracilicollum* (Spiekman et al., 2021; Wang et al., 2023).

The dentition is distinguishable in *Austronaga* from those in other related non-crocopodan archosauromorphs (Fig. 2), especially the nearly contemporaneous Triassic taxa from southwestern China. The posterior extent of the maxillary dentition is subequal to that of the dentary dentition in *Austronaga* and *Dinocephalosaurus*, when the former is posteriorly further beyond the latter in *Macrocnemus* and *Tanystropheus* spp. (Spiekman et al., 2021, in review). There are no striations on the crown of any tooth in *Austronaga*, even on the enlarged ones, which represents a marked distinction of *Austronaga* from the other known semi-aquatic to aquatic non-crocopodan archosauromorphs *Tanystropheus*, *Dinocephalosaurus*, and *Gracilicollum* (Wang et al., 2023). The degree of heterodonty seen in *Austronaga*, with several fangs, resembles the condition seen in *Gracilicollum* (Wang et al., 2023). It is considerably less heterodont than the marginal dentition of *Dinocephalosaurus* and *Tanystropheus hydroides*, which possess larger fangs (Spiekman et al., 2020b, in review), whereas it is also clearly distinct from the homodont dentitions of *Macrocnemus*, *Pectodens*, *Amotosaurus* and *Fuyuansaurus* (Fraser and Rieppel, 2006; Fraser et al., 2013; Li et al., 2017; Miedema et al., 2020). *Austronaga* also lacks the remarkable tricuspid marginal teeth seen in *Tanystropheus longobardicus* and *Langobardisaurus* (Renesto and Dalla Vecchia, 2000; Nosotti, 2007).

Of the postcranium, only the cervical and caudal vertebrae can be compared between *Austronaga* and other non-crocopodan archosauromorphs. In general, the cervical neural spines, at least on the axis to the fifth cervical vertebrae, are much more prominent than those in *Tanystropheus*, *Dinocephalosaurus*, *Pectodens*, and *Fuyuansaurus* (Spiekman et al., 2021). In this respect, they are perhaps more reminiscent of the cervical vertebrae of *Macrocnemus* or even *Protorosaurus* (Gottmann-Quesada and Sander, 2009). Nevertheless,

the dorsal margins of the fourth and the fifth cervical neural spines are concave rather than straight, which represents a morphology that is only present in *Dinocephalosaurus* among known early archosauromorphs, and even rare in reptiles generally (Romer, 1956). There is no anterior or posterior distal expansion on the neural spines here in *Austronaga* unlike those in *Macrocnemus*, *Tanystropheus*, and *Gracilicollum* (Wang et al., 2023), and in this aspect, the shape of cervical neural spines in *Austronaga* again resembles that of *Dinocephalosaurus* (Spiekman et al., in review). The "three-headed" rib is remarkable and recalls the condition observed in *Tanystropheus* (Nosotti, 2007:fig. 55), but the morphology of the ribs accompanying the atlas-axis complex is poorly known among non-crocopodan archosauromorphs. On the tail, the prominent neural spine with a convex dorsal margin and the distally expanded chevron seen in *Austronaga* (Figs. 1, 3) is otherwise only known for *Dinocephalosaurus* (Spiekman et al., in review), but not present either in *Macrocnemus* and *Tanystropheus* spp., or in *Pectodens* (Spiekman et al., 2021). Notably, in contrast to the T-shaped chevrons in *Dinocephalosaurus* (Spiekman et al., in review), the chevrons of the middle region of the caudal series in *Austronaga* have generally convex ventral margin with a mid-point notch (Fig. 3). Conclusively, the morphologic configuration of the cervical neural arches and the chevrons is unique and thus diagnostic for *Austronaga*.

5.3 Potential aquatic habits of *Austronaga*

An aquatic lifestyle is inferred for *Dinocephalosaurus* based on a wide range of morphological traits. Most notably, extensive paedomorphosis is present within the limbs (Li et al., 2004; Rieppel et al., 2008), for example through the spatia separating the zeugopodial bony elements, the rudimentary condyles on the distal ends of the long bones, and the round contours of the carpals and tarsals. These aquatic features are considerably more prominent compared to the limbs of *Tanystropheus* (Nosotti, 2007; Rieppel et al., 2008). Whether the species of *Tanystropheus* are aquatic or not has been being controversial (Nosotti, 2007; Renesto and Saller, 2018), but the latest research on the cranium provides strong indicators for an at least semi-aquatic mode of life, based on their piscivorous dentition, dorsally placed external nares, and dorsoventrally flattened and lateromedially widened snout (Spiekman et al., 2020a, b). In contrast to *Dinocephalosaurus* and *Tanystropheus*, the slender limbs and the distally further developed long bones in *Pectodens* and *Macrocnemus* suggest better musculature supports for these two genera, and terrestrial habits for them are readily accepted (Rieppel, 1989a; Li et al., 2017a).

A dinocephalosaurid status of *Austronaga* is suggested by our phylogenetic analysis (Fig. 4). Specifically, *Austronaga* is the sister taxon of *Dinocephalosaurus* within the dinocephalosaurid clade. The dentition of *Austronaga* (Fig. 2) is less specialized than that of *Tanystropheus* and *Dinocephalosaurus*, yet it possesses some enlarged teeth as in these taxa, which corresponds to a likely diet of small aquatic animals like fishes and cephalopods.

Other potential indicators for aquatic locomotion come from the tail of *Austronaga*. Elaborate structures on caudal neural spines and chevrons (Fig. 3) are only observed in *Austronaga* and *Dinocephalosaurus* among these non-crocopodan archosauromorphs. These structures on the tail are not essential for aquatic propulsion considering their absence in other aquatic reptiles and even in several aquatic lineages. Nevertheless, a similar morphology is convergently present in many aquatic reptiles. For example, plate-like caudal neural spines are developed in the basal ichthyosaurs, *Sclerocormus* (Jiang et al., 2016) and *Chaohusaurus* (Huang et al., 2019). T-shaped chevrons are found in the enigmatic sauropterygiform *Atopodentatus* (Cheng et al., 2014; Wang et al., 2022), and in the primitive placodonts *Paraplacodus* and *Placodus* (Rieppel, 2000; Jiang et al., 2008). Therefore, we consider the morphology of the caudal vertebrae in *Austronaga* to correspond to an aquatic or at least semi-aquatic animal.

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云南中三叠世一恐头龙科小型主龙型类

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摘要：现在的中国南方地区在三叠纪时期曾位于特提斯洋东部。在该区域产出的众多海生爬行动物中，恐头龙(*Dinocephalosaurus*)的形态特化，颈部极度增长，可与时代略晚的长颈龙(*Tanystropheus*)相比拟。这两种爬行动物分别归属于恐头龙科(Dinocephalosauridae)和长颈龙科(Tanystropheidae), 而这两个科的成员加之另外一些基干物种代表了主龙型类(Archosauromorpha)中一系列早期分异出的支系。报道一件产自云南罗平地区中三叠世安尼期地层的主龙型类成年个体新标本IVPP V18579, 与目前已知的早期主龙型类成员相比，该标本显示出与恐头龙属一致但区别于其他属种的特征，主要包括前颌骨发育有超过外鼻孔后缘的较长后背侧突，方骨前后向较宽大且具有后边缘的凹缺，大部分尾椎上的人字骨带有远端前后向的延展。然而，新标本体型明显小于恐头龙，且显示出与恐头龙属和梳齿

龙属(另一恐头龙科成员)不同的鉴别特征，例如吻部窄长、牙齿短锥状且异齿性弱、枢椎和前部颈椎的神经棘显著更高等。基于最新的用于早期主龙型类系统发育分析的特征矩阵，系统发育分析结果确定V18579代表一个新的恐头龙科成员，在恐头龙科中与恐头龙属互为姊妹群关系。于是基于V18579建立了一新属新种：玲珑南蛇龙(*Austronaga minuta*), 同时对其进行了详细的解剖学特征描述，并讨论了它可能具有的水生适应性。

关键词：云南罗平，东特提斯，三叠纪，海生爬行动物，主龙型类，恐头龙科，骨骼学解剖

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Appendix Scores of character states for the holotype of *Austronaga minuta*

char. 1–50	11?30?1111	??[0/1]0000???	?0?0000-01	11002?0000	???0?00001
char. 51–100	???00?????	??????0?1?	?0?1??0???	?????????1	0?????-??1
char. 101–150	-------?1?	??????????	??????????	??????????	???000?1?0
char. 151–200	?01?10?11?	01100001[0/4]0	00010?1220	21??210211	1?00????2[1/2]
char. 201–250	??????????	??????????	?03???????	??????????	??????????