Nothosaurus luopingensis n. sp. (Sauropterygia) from the Anisian, Middle Triassic of Luoping, Yunnan Province, China Postprint

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Date: 2022-06-07T00:00:00+00:00

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Nothosaurus luopingensis n. sp. from Member II of the Guanling Formation (Anisian, Middle Triassic) of Luoping, Yunnan, China is described based on a specimen comprising the skull and most of the postcranial skeleton. The specimen is assigned to Nothosaurus of Eosauropterygia as suggested by a series of skull characters, such as the maxillary tooth row extending posteriorly beyond the level of the anterior margin of the upper temporal fenestra, the longitudinal diameter of the upper temporal fenestra is more than twice as long as that of the orbit, and the presence of maxillary fangs. Compared with Lariosaurus, the following morphological features of the pectoral girdle and the limbs also support the assignment of the specimen to Nothosaurus, i.e., the clavicles with expanded anterolateral corners, the characteristically curved humerus with a straight preaxial angle and a postaxial concavity, the distinct deltopectoral crest on the proximal part of the humerus, no hyperphalangy in the manus, and the absence of pachyostosis in the vertebrae and ribs. On the other hand, the specimen possesses some postcranial features that were previously considered to occur mainly in Lariosaurus, such as there being more than three ossifications in the carpus, having four sacral ribs, and an interclavicle without any trace of a posterior stem. These postcranial characters may no longer be used as the diagnostic features of Lariosaurus. N. luopingensis is distinguished from other Nothosaurus species by a unique combination of derived characters, including that the jugal enters the orbit, the nasals are separated, the posterior end of the frontal is bifurcate, pedal digits V and IV are long and subequal in length, and the ungula phalanx is stout. Our phylogenetic analysis reconfirms the monophyly of Nothosaurus and suggest that N. luopingensis is the sister group of N. yangjuanensis within the genus.

Full Text

Preamble

A New Species of Nothosaurus (Sauropterygia) from the Anisian, Middle Triassic of Luoping, Yunnan Province, China

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Abstract

Nothosaurus luopingensis n. sp. from Member II of the Guanling Formation (Anisian, Middle Triassic) of Luoping, Yunnan, China is described based on a specimen comprising the skull and most of the postcranial skeleton. The specimen is assigned to *Nothosaurus* of Eosauropterygia as suggested by a series of skull characters, such as the maxillary tooth row extending posteriorly beyond the level of the anterior margin of the upper temporal fenestra, the longitudinal diameter of the upper temporal fenestra being more than twice as long as that of the orbit, and the presence of maxillary fangs. Compared with *Lariosaurus*, the following morphological features of the pectoral girdle and the limbs also support the assignment of the specimen to *Nothosaurus*: the clavicles with expanded anterolateral corners, the characteristically curved humerus with a straight preaxial angle and a postaxial concavity, the distinct deltopectoral crest on the proximal part of the humerus, absence of hyperphalangy in the manus, and lack of pachyostosis in the vertebrae and ribs. On the other hand, the specimen possesses some postcranial features that were previously considered to occur mainly in *Lariosaurus*, such as more than three ossifications in the carpus, four sacral ribs, and an interclavicle without any trace of a posterior stem. These postcranial characters may no longer be used as diagnostic features of *Lariosaurus*. *N. luopingensis* is distinguished from other *Nothosaurus* species by a unique combination of derived characters, including the jugal entering the orbit, the nasals being separated, the posterior end of the frontal being bifurcate, pedal digits V and IV being long and subequal in length, and the ungual phalanx being stout.

Our phylogenetic analysis reconfirms the monophyly of *Nothosaurus* and suggests that *N. luopingensis* is the sister group of *N. yangjuanensis* within the genus.

Key words: *Nothosaurus*, eosauropterygian; Luoping, Yunnan, China; Anisian, Middle Triassic

Citation: Shang Q H, Li C, Wang W in press. *Nothosaurus luopingensis* n. sp. (Sauropterygia) from the Anisian, Middle Triassic of Luoping, Yunnan Province,

China. *Vertebrata PalAsiatica*.

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1 Introduction

Nothosaurus (Eosauropterygia, Diapsida), a secondarily aquatic genus of reptiles, was widespread in both the western and eastern Tethyan faunal provinces during the Middle to early Late Triassic (Rieppel, 2000; Li and Rieppel, 2004; Shang, 2006; Jiang et al., 2006a; Liu et al. 2014). Although *Nothosaurus* was well documented in previous studies (Rieppel and Wild, 1994; Rieppel, 2000, 2001), the monophyly of this genus has remained highly debated in recent years, partly due to new fossils recently discovered from both the western and eastern Tethyan faunal provinces. Klein et al. (2015) hypothesized the genus as a monophyletic clade, then including *N. giganteus* Münster, 1834; *N. mirabilis* Münster, 1834; *N. marchicus* Koken, 1893; *N. juvenilis* Edinger, 1921; *N. edingerae* Schultze, 1970; *N. tchernovi* Haas, 1980; *N. haasi* Rieppel et al., 1997; *N. jagisteus* Rieppel, 2001; *N. youngi* Li and Rieppel, 2004; *N. rostellatus* Shang, 2006; *N. yangjuanensis* Jiang et al., 2006; *N. winkelhorsti* Klein and Albers, 2009; and *N. zhangi* Liu et al., 2014. Later, Klein et al. (2016) questioned the status of *N. juvenilis*, *N. youngi*, and *N. winkelhorsti*. After these restudies, Lin et al. (2017) demonstrated that *Nothosaurus* is not monophyletic and reassigned *N. juvenilis*, *N. youngi*, and *N. winkelhorsti* to the genus *Lariosaurus*. Hinz et al. (2019) described a new species of *Nothosaurus*, *N. cristatus*, from the Lower Keuper of Vellberg-Eschenau, southern Germany, and emphasized the presence of a monophyletic clade formed by some European species, but the monophyly of the genera *Nothosaurus* and *Lariosaurus* remains uncertain.

To date, four *Nothosaurus* species have been reported in China. Among them, three species are from the Anisian and only *Nothosaurus youngi* (now *Lariosaurus youngi*) is from the Ladinian. Among the three Anisian species, *N. rostellatus* and *N. yangjuanensis* are members of the Panxian Fauna in Guizhou, and *N. zhangi* is a member of the Luoping Fauna in Yunnan.

The Luoping Fauna exhibits a highly diversified eosauropterygian assemblage (Liu et al., 2011, 2014; Shang et al., 2011, 2015; Cheng et al., 2016). In addition to *Nothosaurus zhangi*, four genera and species of eosauropterygians have been described, including *Dianopachysaurus* (Liu et al., 2011), *Diandongosaurus* (Shang et al., 2011), *Dianmeisaurus* (Shang et al., 2015), and *Dawazisaurus* (Cheng et al., 2016), all of which are relatively small-sized (adult body length $<$ 50 cm). The eosauropterygian remains with medium or large body size are rare in the Luoping deposits, except for *N. zhangi*, which is a gigantic apex predator with an estimated body length of more than 500 cm (Liu et al., 2014). The holotype, which is the only known individual of *N. zhangi*, is merely represented by a lower jaw and few postcranial bones.

Here, a new eosauropterygian skeleton from the Luoping Fauna is described. It is a nothosaur with a medium-sized body (defined as a body size of more than 50 cm but less than 150 cm in length), but it is relatively small within *Nothosaurus*. Although the specimen is not very complete, the well-preserved skull and articulated postcranial skeleton provide considerable anatomical information on *Nothosaurus*, which is significant especially when complete specimens are comparatively rare.

The discovery of the new nothosaur increases our knowledge regarding the diversification of nothosaurs in their early history and provides a chance to test the phylogenetic hypotheses obtained by previous studies for nothosaurids. It also improves our understanding of the secondarily aquatic adaptations of *Nothosaurus* in general.

2 Material and Methods

The studied specimen was collected from a Middle Triassic outcrop near Waina Village of Luoping County, Yunnan Province, China. It comes from a highly fossiliferous, thinly bedded, dark-colored micritic limestone with a layer thickness of ~5 m. This deposit is considered to be chronologically close to the nearby 16 m thick succession of richly fossiliferous beds of the Shimenkan section at Da' aozi (or Dawazi) Village and of Anisian Middle Triassic age (Benton et al., 2014). As in the Shimenkan section, the bioturbated, pale-colored micritic limestone is present in the basal and top members of the fossiliferous beds. It is referred to the middle part of Member II of the Guanling Formation. The Luoping Fauna in the Luoping area was assigned to the *Nicoraella kockeli* zone based on the associated conodonts (Zhang et al., 2009).

The skeleton consists of a complete skull with the mandible tightly occluded and most of the postcranial skeleton (Fig. 1 [Figure 1: see original paper] A). The skull is prepared in dorsal view, and thus the mandible, dental formula, and details of the palate remain largely concealed. The incomplete postcranium comprises an articulated vertebral column in ventral view, which lost some elements of the abdominal region and most of the caudal section of the column. The pectoral girdles are preserved with some elements of the left side missing. The pelvic girdle is fractured, and some of the girdle elements are poorly preserved. Only the right forelimb is preserved. Two hind limbs are dislocated, but the elements of them are still articulated. The right hind limb is complete and exposed in dorsal view, while the left hind limb lost some phalanges and is preserved in ventral view. The specimen represents an adult individual based on the fused frontal and parietal and the well-ossified carpals and tarsals.

The skeletal elements have been measured with a slide caliper (accuracy 0.5 mm). The phylogenetic character data matrix was analyzed using PAUP* version 4.0b10 (Swofford, 2002) and PAUP* version 4.0a169 (Swofford, 2021), with all characters being equally weighted and unordered.

3 Systematic Paleontology

Sauropterygia Owen, 1860
Eosauropterygia Rieppel, 1994
Nothosauridae Baur, 1889
Nothosaurus Münster, 1834

Type species: Nothosaurus mirabilis Münster, 1834

Diagnosis: Small to large nothosaurs with maxillary tooth row extending well beyond level of anterior margin of upper temporal fenestra; paired maxillary fangs followed by a palisade of densely set, distinctly smaller, conical teeth, longitudinal diameter of the upper temporal fenestra between two and four times the longitudinal diameter of the orbit (Rieppel and Wild, 1996; Rieppel, 2000). Characteristically curved humerus with straight preaxial angle and postaxial concavity; distinct deltopectoral crest and latissimus dorsi insertion on the proximal humerus head; phalangeal formula in the manus: 2-3-4-5-3 (Romer, 1976; Rieppel et al., 1999; Rieppel, 2000; Bickelmann and Sander, 2008).

Nothosaurus luopingensis n. sp.
Figs. 1-3

Etymology: Named after Luoping County, where the specimen was excavated.

Holotype: IVPP V 24895, a complete skull with most of the postcranial skeleton.

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

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

Diagnosis: A small to medium-sized species of *Nothosaurus* (the condylobasal skull length = 13 cm); rostrum short and rounded; five fangs in each premaxilla, the fifth slightly smaller than the preceding fangs; five small maxillary teeth anterior to the maxillary fangs; posterior (nasal) processes of premaxillae contact frontal at the level of posterior margin of external naris; jugal broadly entering the posteroventral margin of orbit; frontal bifurcates posteriorly; supratemporal fenestra 2.1-2.2 times the length of the orbit; four sacral vertebrae; five carpal ossifications; pedal digit V long and subequal to IV; ungual phalanx of pes expanded.

4 Description

IVPP V 24895 is relatively small compared to other species of *Nothosaurus* (Rieppel, 2000): the condylobasal skull is 13 cm long and the presacral length is ~80 cm (Fig. 2A [Figure 2: see original paper]).

4.1 Cranium

Overall Morphology (Fig. 1B). The rostrum is short and broad with a weak constriction lying in front of the external nares. The postorbital region is longer than the preorbital region. The skull is broadest at the level of the anterior margin of the upper temporal fenestra. The external nares are round, the orbits are oval, and the upper temporal openings are elongated kidney-shaped.

The upper temporal fenestra is about twice the length of the orbit (LT/LO ap. 2.1-2.2). The pineal foramen is posteriorly placed on the distinctly constricted parietal table, but it is relatively more anterior in position compared with that of other nothosaurs. The distance from the tip of the snout to the posterior margin of the parietal skull table is 12 cm; the length of the skull from the tip of the snout to the posterior margin of the mandibular condyle of the quadrate is 14.5 cm. Its surface is sculptured with tiny, scattered pits.

Skull. The premaxilla forms the rostrum (here meaning the part anterior to the naris). Its dorsal process extends backward between the external nares to meet the frontal and forms the medial margin of the external naris. More posteriorly, the tapering posterior process of the premaxilla is intercalated between the nasal and the anteromedial process of the frontal and ends at the level of the posterior margin of the external naris.

The nasal is a roughly triangular element. It is separated from one another by the nasal processes of the premaxillae and anteromedial process of the frontal. Its short anteromedial process forms the posteromedial margin of the external naris. Posteriorly, the nasal tapers and is embraced by the anterolateral and the anteromedial processes of the frontal. The posterior margin of the nasal contacts the frontal near the level of the anterior margin of the orbit. The nasal is excluded from the prefrontal by a narrow anterolateral process of the frontal.

The frontal is a large, elongated, and unpaired (fused) element. It has a long and slender anteromedial process that extends between the nasals and then inserts between the tapered posterior tips of the premaxilla. Its short anterolateral process contacts the nasal medially and the ascending (medial) process of the maxilla laterally. A deep cleft in the posteromedial part of the fused frontals and some impression of the ridges and grooves along the posterior margin of the frontal prevent proper identification of the frontal-parietal suture. Most likely, here the frontal bifurcates posteriorly and forms two posterolateral processes, which differs from the known species of *Nothosaurus*. The long and tapering posterolateral process of the frontal meets the parietal in an interdigitating suture at a level behind the anterior margin of the upper temporal fenestra.

The prefrontal is a small element located at the anteromedial corner of the orbit and does not contact the nasal. The prefrontal and postfrontal remain widely separated at the dorsal margin of the orbit.

The postfrontal is an irregular element. It forms the posteromedial margin of the orbit. It contacts the postorbital laterally and the frontal medially. There is a distinct constriction at the mid part of its lateral margin. Posteriorly, it enters the anteromedial margin of the upper temporal fenestra and contacts the parietal at a level behind the anterior margin of the upper temporal fenestra.

The anterior process of the maxilla extends along the lateral margin of the external naris. The ascending (medial) process of the maxilla defines the posterolateral margin of the external naris and the anterior margin of the orbit and meets the nasal as well as the lateral process of the frontal. More posteriorly, the maxilla extends to a level just behind the anterior margin of the upper temporal fenestra without protruding into the open cheek.

The jugal is a slender bone. Anteriorly, it forms the posterolateral margin of the orbit. Posteriorly, it tapers gradually, inserts between the maxilla and the postorbital, and ends at a level very near the posterior end of the maxilla. Behind the posterior tip of the jugal, a contact between the postorbital and the maxilla is obscured.

The postorbital shows a narrow entry into the posterior margin of the orbit at the posterolateral corner of the orbit, and a broad entry along the anterior margin of the upper temporal fenestra. Dorsally, it contacts the postfrontal medially and the parietal posteromedially within the upper temporal fenestra. Ventrally, it sutures with the jugal. More posteriorly, the postorbital tapers to become a slender process forming the lateral margin of the upper temporal fenestra and sutures with the anterior process of the squamosal as it extends backwards slightly beyond the level of the midpoint of the longitudinal diameter of the upper temporal fenestra.

The parietal is unpaired and broad anteriorly. Anteromedially, it meets the frontal by an interdigitating suture with a sharp median process projecting into the frontal. Anterolaterally, it contacts the postfrontal and the postorbital respectively. It gradually narrows posteriorly. The parietal skull table is strongly constricted to form a sagittal crest. The pineal foramen is situated at a spot near the posterior third of the length of the parietal. The posterolateral processes of the parietal enclose an angle of approximately 110°. It meets the squamosal in an oblique suture.

As in most eosauropterygians, the squamosal is a triradiate element. Its anterior ramus extends forward to contact the postorbital, and its medial ramus is sutured to the parietal at the posteromedial margin of the upper temporal fenestra. This medial ramus forms the posterolateral margin of the upper temporal opening and meets the paraoccipital process of the opisthotic as well as the supraoccipital bone. Posterolateral to the upper temporal fenestra, the squamosal is drawn out into an elongate lateral ramus, which caps the cephalic condyle of the quadrate.

The quadrate trends in a somewhat lateral direction, which results in the lateral displacement of the mandibular joint. The joint surface is laterally broadened, and the facet is subdivided by a longitudinal groove. The cranio-quadrate passage is floored by the quadrate ramus of the pterygoid and roofed over by the squamosal. The lateral ramus of the parietal and the anterior medial ramus of the squamosal rise above the occiput to form a distinct occipital crest which separates the occipital surface from the dorsal surface of the skull.

The occiput is closed and plate-like, and it shows the typical morphology of the braincase of *Nothosaurus* as described by Rieppel (1994). The supraoccipital is a broad, irregular element exposed in a horizontal position. It carries a weak medial crest. A small post-temporal fenestra is situated at the posterolateral margin of the supraoccipital, which is bordered by the exoccipital ventrally. The foramen magnum is still recognizable, although compressed. The exoccipital rests on the dorsolateral aspect of the occipital condyle. Laterally, the exoccipital meets the opisthotic in a distinct suture. The jugular foramen is not exposed. The suture between the opisthotic and the squamosal is not well defined. Further details of the occiput are obscured by the severe compression of the skull.

The palatine and the pterygoid are only partially exposed inside the orbits and the upper temporal fenestrae. Their exact shapes and relationships with other palatal elements are unknown. The pterygoid seems to form a weakly developed transverse process that, together with the ectopterygoid, forms a pterygoid-ectopterygoid transverse flange.

Mandible. Only the posterior portion of the mandible is exposed and available for description. The dentary is seen to extend backwards to a level well behind the anterior margin of the upper temporal fenestra. It contacts the surangular posterodorsally and the angular posterolaterally.

The elongate surangular forms the dorsal half of the posterior portion of the mandible. Ventral to the cheek region, the surangular carries a laterally protruding flange for the insertion of superficial jaw adductor muscle fibers as in *Nothosaurus* and *Lariosaurus* (Rieppel, 2000). Posteriorly, it forms the lateral wall of the articular fossa and abuts against the articular in the retroarticular process.

The articular is transversely broadened below the mandibular articulation. It forms most of the articular fossa and the distinct retroarticular process. The articular fossa is divided into two parts, with the medial part larger than the lateral one. The retroarticular is modestly elongated and bears a longitudinal trough on the dorsal surface.

Dentition. An exact tooth count on the maxillae and dentaries is impossible due to the tight occlusion of the skull with the mandible. However, the premaxillary teeth and some maxillary teeth could be observed in lateral view.

There are five premaxillary teeth, of which the anterior four are relatively large, fang-like, and procumbent, and the fifth is the smallest. The maxilla contains approximately 22 teeth, of which the anterior five teeth are small and similar in size. The sixth and possibly the seventh maxillary teeth are large, and the other posterior teeth (~15, estimated by exposed teeth and the covered areas) are small and subequal in size. The preserved small maxillary teeth are subconical and slightly recurved with fine striations on the crown surface.

4.2 Axial Skeleton

Vertebral column and ribs. The cervical section is completely preserved but suffered a strong twist before burial so that the anterior three cervical vertebrae are exposed in lateral view and all the others in ventral view, which contrasts with the dorsally exposed skull.

The neck is long, comprising 22 or 23 cervical vertebrae, which are identified on the basis of their position in front of the clavicular-interclavicular complex, as well as by the relative length and articulation characters of the associated ribs.

The atlas cannot be well defined due to the neck twist, but the axis is identified by the extremely large axial neural spine. The amphicoelous cervical centra are barrel-shaped. They are slightly constricted in the middle portion. A distinct longitudinal ridge is developed on the ventral surface of the cervical centrum. This ventral keel completely disappears posteriorly starting from the 20th cervical.

The cervical ribs gradually increase in length towards the pectoral girdle. The anterior ones are a little more than small bony stubs with relatively broad proximal articulation heads, a somewhat constricted middle part, and a distal part that is expanded into a short, anteriorly pointing process. The articular heads are not all visible, but it is supposed that the anterior cervical ribs are double-headed. Posteriorly, the cervical ribs still develop broad proximal articular heads, but with a distinct posteriorly directed shaft and a free-ending anterior process, which is more distinctly set off from the main body of the rib. From the 20th cervical, the cervical ribs become more elongated rapidly (Fig 2A). The 22nd cervical ribs are slender and slightly curved without forming a "shoulder." The shaft of the 22nd ribs tapers distally and points more laterally. The 23rd preserved ribs are partly covered by the clavicular-interclavicular complex. The 24th preserved rib is more elongated, with the "shoulder" distinctly curved, and the shaft pointing posteriorly. It also articulates on the transverse process of the neural arch, as is characteristic for the dorsal region. Therefore, there are 22 or 23 cervical vertebrae.

Because some vertebrae in the middle region of the dorsal section are lost and some in the posterior region are partially obscured by gastral ribs and the pelvic girdles, the precise number of dorsal vertebrae cannot be identified. Based on the number of the preserved dorsal vertebrae and the missing distance, it is speculated that there may have been at least 20 dorsal vertebrae.

The dorsal centra exhibit smooth ventral surfaces. They are barrel-shaped and slightly constricted in the middle part. The centra have no distinct differences among the dorsal, sacral, and the two preserved caudal vertebrae.

The dorsal ribs are not pachyostotic. They are single-headed and articulate on stout transverse processes which project laterally from the neural arches. They are distinctly bowed in the proximal region, with shallow longitudinal grooves developed on the proximal part of the ventral surface, and the shaft of the dorsal ribs is moderately expanded distally.

In the region of the pelvic girdle, six short, straight, and tightly juxtaposed ribs converge toward the dorsal process of the ilium (Fig. 2B). Four of them are identified as sacral ribs due to their widened distal ends. The other ribs with tapering distal ends toward the ilium are identified as the last dorsal rib and the anterior-most caudal rib respectively.

The first caudal rib is slightly longer than the last sacral rib, and the second caudal rib decreases in length. The anterior caudal ribs are bar-like, slightly taper distally, and terminate with a truncated end.

Gastralia. The gastral ribs cover the posterior 2/3 of the abdomen of the trunk and begin at about the 7th dorsal vertebra. They are composed of five segments, i.e., a medioventral one and two lateral ones on either side as in most eosauropterygians. The medioventral element is distinctly angulated and carries a short stubby anterior projection on the anterior dorsal region. Posteriorly, the distal end of the lateral element is less pointed.

4.3 Appendicular Skeleton

Pectoral girdle. The pectoral girdle (Fig. 2A) is well preserved in ventral view, though some elements on the left side are damaged. The pectoral girdle shows the typical morphotype of sauropterygians (Romer, 1976). It greatly resembles that of the type species *N. mirabilis* (Peyer, 1939: Textfig. 20; Rieppel, 2001: Fig. 8), except for some differences in the interclavicle.

The interclavicle is "crown hat"-shaped, with the lateral processes of both sides overlapping on the ventromedial surfaces of the clavicles. Its posterior margin is slightly concave and lacks any posterior protrusion.

The clavicles meet each other in front of the interclavicle in an interdigitating suture. Its medial bar is straight. The anterolateral corner of the clavicle is evidently expanded.

The scapula is of the typical nothosaurian type. It is composed of a ventrally expanded glenoidal portion and a slender posterodorsal process. It meets the coracoid in a relatively short suture. The scapular part of the glenoid fossa is well developed.

The coracoid is a broadened and waisted element with concave anterior and posterior margins, and its medial (symphyseal) margin is straight. The coracoid foramen is represented by a notch in the lateral (glenoidal) margin of the coracoid, and it should be enclosed by the scapula.

The pectoral girdles of both sides enclose a broad pectoral fenestra on the ventral surface.

The pelvic girdle. The elements of the pelvic girdle (Fig. 2B) are badly squashed in some places, but all of them can be unequivocally identified. It shows a typical sauropterygian type, having the broadened pubis and ischium and a tiny ilium with an extremely reduced dorsal blade.

The right ilium is exposed in medial view, and its ventrally expanded acetabular portion is separated by a neck from a dorsal blade which trends posterodorsally and forms a short stick. The acetabulum is represented by a concavity on the lateral surface of the ventral part of the ilium, which is observed in the left ilium.

The pubis is a plate-like, biconcave element. The outline of its convex medial (symphyseal) margin is not well-preserved. The margin of the pubis is thickened at the sutural contact with the ischium. The obturator foramen is slit-like and open.

The ischium is a relatively broad element with a flattened convex ventral margin. It is constricted just behind the acetabular facet, which results in the formation of a slender shaft.

Forelimb. The forelimb (Fig. 3A [Figure 3: see original paper]) is shorter and slightly stouter than the hindlimb.

The humerus is slightly curved, with a convex preaxial border, whereas the postaxial border is concave. The preaxial margin of the shaft in dorso-ventral view shows a straight angle, which is the same as the humeral morphotype II of *Nothosaurus* sp. (Bickelmann and Sander, 2008). The proximal end is broadly oval and slightly wider than the mid-shaft. The distal end is also slightly expanded. On the proximoventral surface, there is a low but clearly marked crest which served for the insertion of the deltoideus muscle. The entepicondylar foramen is present on the distoventral part of the humerus. The ectepicondylar groove is open and does not have an anterior notch.

The radius is medially concave and laterally straight, with slightly expanded proximal and distal ends. The proximal facet for the humerus is flat, and the distal articular facet is convex.

The ulna is approximately as long as the radius, but the former has a more broadened proximal head compared with that of the latter. The distal end of the ulna is slightly expanded as is the distal end of the radius.

There are five ossified carpals, i.e., the intermedium and ulnare forming the proximal row and distal carpals 2 to 4 of the distal row. The intermedium is the largest one and is kidney-shaped. It is slightly displaced and sits between the distal ends of the radius and ulna. Distally, it attaches to the ulnare and all the carpals of the distal row. The ulnare is rounded and much smaller than the intermedium. It tightly abuts the intermedium, distal carpal 4, and metacarpal V. Distal carpals 2 to 4 are also articulated with metacarpals II to IV respectively, and distal carpal 4 is the largest.

The metacarpals are rod-like with a constricted shaft. Metacarpal III is the longest and metacarpal I is the shortest but the most robust.

The phalangeal elements are cylindrical, slightly constricted at the mid shaft, and get shorter in length towards the penultimate phalanges. The ungual phalanges are markedly expanded in digits I and II, but not well ossified in digit IV and absent in digit V. The phalangeal formula of the manus is 2-3-4-5-3.

Hindlimbs. The femur (Fig. 3B) is a biconcave, rather straight, and slender element. Its proximal head is slightly expanded. The internal trochanter is reduced, and the intertrochanteric fossa is absent. The articulation for the tibia and fibula is confluent and does not project markedly beyond the shaft.

The tibia is a nearly straight element, distinctly wider than the fibula, and lacks a significant diaphyseal contraction.

The fibula shows a curved appearance, with an almost straight postaxial margin and a deeply concave preaxial margin.

The tarsus comprises three ossifications. The astragalus has an irregular outline. It articulates with the fibula proximally, the calcaneum medially, distal tarsal 3+4 medially and distally, and the tibia proximo-laterally and metatarsal I distolaterally. The calcaneum is roughly rounded. It articulates with the fibula proximally and the astragalus and distal tarsal 3+4 laterally. Distal tarsal 3+4 meets metatarsals III, IV and V distally.

Metatarsal I is short and broader than the others, with its proximal head markedly expanded as in the small-sized eosauropterygians *Diandongosaurus* (Shang et al., 2011) and *Dianmeisaurus* (Shang et al., 2017). Metatarsals III and IV are similar in length (~24 mm), and metatarsals II and V are comparable in length (~22 mm), though the latter is slightly shorter than the former.

The length of the pedal digits increases from I to IV, and digit V is long and subequal to digit IV (~35 mm). The phalangeal elements are cylindrical, slightly constricted at the mid shafts, and get shorter in length towards the penultimate phalanges. As in *Dianopachysaurus* (Liu et al., 2011), *Diandongosaurus* (Shang et al., 2011), *Dianmeisaurus* (Shang et al., 2015), and *Dawazisaurus* (Cheng et al., 2016), the ungual phalanges in the pes are remarkably expanded, with a size distinctly larger than the penultimate phalanx. The phalangeal formula of the pes is 2-3-4-5-5, also as in the case of *Dianmeisaurus* (Shang et al., 2017).

5 Phylogenetic Analysis

The present analysis is based on the data matrix of Hinz et al. (2019), which was modified from the data matrix of Liu et al. (2014) and Lin et al. (2017). Hinz et al. (2019) revised some incorrectly coded characters as well as identified two pairs of correlated characters, which are all accepted here. In addition, we revised two incorrectly coded characters (Appendix 1A). Two additional taxa were added to the revised data matrix of Hinz et al. (2019: Supplemental Data2): one is *N. luopingensis*, the other is *Lariosaurus sanxiaensis* (we recoded the characters based on Li and Liu, 2020 data matrix) (Appendix 1B). The new data matrix has 25 taxa and 72 characters.

The analysis leads to a single most parsimonious tree (Fig. 4A [Figure 4: see original paper]) with a tree length of 267. The result supports the monophyly of *Nothosaurus* but leaves *N. haasi* outside the genus. As for *N. luopingensis*, the analysis considers it as the sister species of *N. yangjuanensis*. However, there is no resolution within *Lariosaurus* and among *Germanosaurus*, *Nothosaurus*, *Lariosaurus* and *N. haasi*.

Of the included taxa, *L. sanxiaensis* is a poorly known species and only 17 characters (23.6%) can be coded. Furthermore, it might not belong to *Lariosaurus* based on the unusual shape of its coracoid. When *L. sanxiaensis* is excluded, the new analysis also yields a single most parsimonious tree (Fig. 4B) with a tree length of 230. This new result supports the monophyly of both *Nothosaurus* and *Lariosaurus*, but interrelationships among *Germanosaurus*, *Nothosaurus*, and *Lariosaurus* remain unresolved as in the first analysis.

We also attempted to exclude *L. sanxiaensis*, but include *Brevicaudosaurus* (Shang et al., 2020) in this analysis (Appendix 1B). The analysis leads to a single most parsimonious tree (Fig. 4C) with a tree length of 242. The result shows no change in the *Nothosaurus* clade, but the interrelationships within *Lariosaurus* remain unresolved, and *Brevicaudosaurus* shows a closer relationship with *Lariosaurus* than with *Nothosaurus*. *Germanosaurus* is the sister group of the Nothosauridae (*Nothosaurus*, *Lariosaurus*, *Brevicaudosaurus*) clade. As for the species of *Nothosaurus*, this analysis does not alter their interrelationships obtained by the first and second analyses and further suggests *N. haasi* as the basal-most clade within the genus. All three analyses confirm the reassignment of *N. juvenilis*, *N. yongi*, and *N. winkelhoursti* to *Lariosaurus* as suggested by Klein et al. (2016), Lin et al. (2017), and Hinz et al. (2019).

Based on the second analysis, the monophyly of *Nothosaurus* is supported by four unambiguous synapomorphies: character 2(2), the ratio of longitudinal diameter between the upper temporal fenestra and the orbit is 2.0 or more; character 17(1), the parietal extending anteriorly and not beyond the anterior margin of the upper temporal fenestra; character 18(2), the parietal skull table strongly constricted; and character 58(1), the prominent insertional crest of the humerus for latissimus dorsi muscle. The monophyly of *Lariosaurus* is supported by five unambiguous synapomorphies: character 1(1), the ratio of the condylobasal skull length to the longitudinal diameter of the upper temporal fenestra between 3.0 and 3.4; character 13(0), the nasals large; character 54(0), the anterolaterally expanded corners absent in the clavicles; character 65(2), five carpal ossifications; and character 66(1), the presence of hyperphalangy in manus.

The paraphyly of *Nothosaurus* considered by previous analyses such as Lin et al. (2017) and Hinz et al. (2019) might be related to insufficient sampling. The addition of the new taxon does not, however, increase the fit between the phylogenetic relationships and the stratigraphic records of the species of *Nothosaurus*. The relatively derived position of the *N. luopingensis-N. yangjuanensis* clade needs to be verified after new species or better materials are found in the future.

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6 Discussion

As suggested by the phylogenetic analysis of this study, IVPP V 24895 represents a new species of *Nothosaurus*. This is supported by some cranial features, including a long and flattened skull, rostrum anteriorly constricted, postorbital region long and the elongated upper temporal fenestrae more than twice as long as the orbits, frontals fused, posterior parietal skull table strongly constricted, supraoccipital horizontally exposed, and maxillary caniniform teeth present (Rieppel and Wild, 1996; Rieppel, 2000; Klein and Albers, 2009; Albers, 2011; Klein et al., 2016).

In the meantime, the skull of IVPP V 24895 displays a distinct combination of derived characters, such as no contact between the nasals, jugal broadly entering the posteroventral margin of the orbit, a temporal fenestra 2.1-2.2 times the length of the orbit, and the posterior end of the frontal forked (unique).

In most species of *Nothosaurus*, the nasals contact each other along the dorsal midline of the skull; only a few species show separated nasals, e.g., *N. edingerae* (Rieppel and Wild, 1994; Rieppel, 2000). This character is variable in *N. mirabilis* (Rieppel and Wild, 1996) in which the two nasals may contact or separate to variable degrees. The two nasals are contacted in all previous species of *Nothosaurus* and *Lariosaurus* known in China (Li et al., 2002; Li and Rieppel, 2004; Shang, 2006; Jiang et al., 2006a, b) except for *N. zhangi* whose skull is not preserved (Liu et al., 2014).

The jugal is excluded from the orbit in most nothosaurs, which is even considered as a diagnostic character of the Nothosauridae (Rieppel and Wild, 1996) or Nothosauria (Rieppel, 2000). However, there is an exception from an incomplete skull that is referred to *N. mirabilis* (Rieppel and Wild, 1996); and the fact that the jugal enters into the ventral margin of the orbit was regarded as a plesiomorphic character of *N. winterswijkensis* from the Lower Muschelkalk of Winterswijk by Albers and Rieppel (2003). Albers (2011) considered that *N. winterswijkensis* is a junior synonym of *N. marchicus*, therefore the jugal entering into the ventral margin of the orbit is variable in *N. marchicus*. The postorbital contacts the parietal in the new species, which is different from all of the previously known species of *Nothosaurus* and *Lariosaurus* from China (Li et al., 2002; Li and Rieppel, 2004; Jiang et al., 2006a, b; Shang, 2006), but the same as the species of *Nothosaurus* found in Europe (Rieppel, 2000).

In IVPP V 24895, the frontal-parietal suture is deeply interdigitated. The posterior end of the frontal is forked to form distinct posterolateral processes to receive the sharp posterior process of the parietal. This character has not been seen in the other species of *Nothosaurus* or even any of *Lariosaurus*, but it is present in many Chinese stem eosauropterygians such as *Qianxisaurus* (Cheng et al., 2012), *Diandongosaurus* (Shang et al., 2011), *Dawazisaurus* (Cheng et al., 2016), and *Dianmeisaurus* (Shang et al., 2015, 2017). However, in these species, the posterolateral processes of the frontal do not form such a complicated and interdigitated suture with the parietal as seen in IVPP V 24895.

On the other hand, the skull of IVPP V 24895 shows a suite of plesiomorphic characters for *Nothosaurus* (Rieppel, 2001; Albers and Rieppel, 2003), such as the relatively short, broad, and rounded rostrum; less proportion of the upper temporal fenestrae compared to the orbits; the relatively short posterior extension of the maxillary tooth-row; and the more anterior location of the pineal foramen. In all of these plesiomorphic characters plus the jugal entering into the ventral margin of the orbit and the skull shape and proportions, *N. luopingensis* closely resembles *N. winterswijkensis* (Albers, 2011: *N. marchicus*) from the Lower Muschelkalk of Winterswijk of the Netherlands. It differs from *N. winterswijkensis* (*N. marchicus*) only in the separated nasals, shorter posterior extension of the maxillary tooth-row, and the bifurcated posterior end of the frontal. These plesiomorphic characters, however, are not present in the Chinese *N. rostellatus* and *N. yangjuanensis* from the Panxian Fauna, probably because these two species may be slightly younger than the new species from the Luoping Fauna, though both are within the *Nicoraella kockeli* Zone of Anisian age (Benten et al., 2014).

The articulated postcranial skeleton of IVPP V 24895 provides more information on the interspecific variation of *Nothosaurus.* In contrast with the skull, the postcranial skeleton of IVPP V 24895 has more similarities with *Lariosaurus.* IVPP V 24895 has five carpals, four sacral ribs, 22-23 cervicals, and an interclavicle without any trace of the posterior stem. One of the diagnostic characters for *Nothosaurus* is no more than three ossifications in the carpus or tarsus of adults, while the diagnostic characters of *Lariosaurus* include four or more sacral ribs and the interclavicle of rhomboidal (triangular) shape without any trace of a posterior stem (Rieppel, 2000).

In fact, though the holotype of *N.* "*raabi*" (reassigned to *N. marchicus* by Rieppel and Wild, 1996) shows three ossifications in the carpus (Schröeder, 1914), four ossifications in the carpus have also been reported in "Paranothosaurus amsleri" (reassigned to *N. giganteus* by Rieppel and Wild, 1996) and *N. yangjuanensis* (Yin et al., 2014). Due to the paucity of information available from other species of *Nothosaurus*, it remains unclear whether the presence of five carpals really represents an autapomorphy of *N. luopingensis.* Most eosauropterygians had been considered to have preserved three carpal ossifications, and only lariosaurs show a distinct increase in the number of carpal ossifications (Rieppel, 1998; Rieppel, 2000). However, some stem eosauropterygians found in South

China lately show more carpal ossifications, such as at least four carpals in *Dianopachysaurus dingi* (Liu et al., 2011), six carpals in *Dawazisaurus brevis* (Cheng et al., 2016), and at least six carpals in *Panzhousaurus rotundirostris* (Jiang et al., 2019). These species were all found in early Middle Triassic strata, and the first two species were even found in the same horizon where the new species was recovered. It is likely that this larger amount of carpal ossifications may reflect the fact that these groups were less well adapted to an aquatic mode of life (Tschanz, 1989) than the taxa with fewer carpal ossifications.

Nothosaurus was described as having no posterior stem on the interclavicle by Koken (1893), and the same is true for "Paranothosaurus amsleri" (Peyer, 1939) and *N. yangjuanensis* (Yin et al., 2014). However, the holotype of *Nothosaurus jagisteus* from the upper Muschelkalk and a specimen of *Nothosaurus* cf. *N. mirabilis* were described as having such a posterior stem on the interclavicle (Rieppel, 2001: Fig.7, 8). Therefore, the genus could be considered with either a present or absent posterior stem on the interclavicle.

Furthermore, three functional sacral ribs were present in *Nothosaurus* "raabi" (Schröeder, 1914) and "Paranothosaurus amsleri" (Peyer, 1939). Four sacral ribs were reported in *N. yangjuanensis* (Yin et al., 2014). The number of sacral ribs varies from four to five pairs in *Lariosaurus* (Rieppel, 1998).

Therefore, according to the Chinese eosauropterygians, some postcranial features that were previously used to distinguish *Nothosaurus* from *Lariosaurus* are no longer applicable, such as the number of carpal ossifications in adults, the number of sacral ribs (Rieppel, 2000; Lin et al., 2017), and the interclavicle with or without a posterior stem (Rieppel, 2000).

On the other hand, the characteristics of the limbs, especially the humerus of *N. luopingensis*, possibly provide some clues to distinguish *Nothosaurus* from *Lariosaurus*. The characteristically curved humerus with the straight preaxial angle and the postaxial concavity and the distinct deltopectoral crest on the proximal humerus head (which corresponds to morphotype II of the humerus identified by Bickelmann and Sander in 2008) may be considered as diagnostic features of the *N. winterswijkensis*-*N. marchicus* clade. In contrast, the humerus is rather straight in *Lariosaurus calcagnii* (Peyer, 1931), slightly curved and flattened in *L. buzzii* (Tschanz, 1989), curved but bears a broadened preaxial border in *L. balsami* (Mazin, 1985), and short, curved, and has a smoothly curved anterior margin and an expanded distal end in *L. hongguoensis* (Jiang et al., 2006). However, whether these differences of the humerus represent taxonomic differences or sexual dimorphism needs to be further studied.

In addition to the interclavicle, the other bones of the shoulder girdle of *N. luopingensis*, such as the clavicle, scapula, and coracoid, are very similar to the corresponding bones of *Nothosaurus* cf. *N. mirabilis* (Rieppel, 2001), especially the expanded anterolateral corner of the clavicle and the relatively large coracoids.

The hind limbs of *N. luopingensis* show certain autapomorphies within

Nothosaurus, e.g., the long pedal digit V and the well-expanded ungual phalanx. The length of pedal digit V and the pedal terminal phalanges in *N. luopingensis* are different from those of other species of *Nothosaurus* in their general configuration. The markedly expanded ungual phalanx is not seen in any previously known species of *Nothosaurus*, but it is widely present in small-sized eosauropterygians of the Luoping Fauna, such as *Diandongosaurus*, *Dianopachysaurus*, *Dianmeisaurus*, and *Dawazisaurus*. These hind limb characters appear to be related to aquatic adaptation (habitat use), but it is difficult to give a functional interpretation right now due to the lack of comparable living species with similar structures.

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7 Conclusions

The Luoping Fauna (Anisian) has been yielding a remarkable taxonomic diversity of eosauropterygians, to which the new species is added, *Nothosaurus luopingensis.* This results in a total of five genera and six species of eosauropterygians known from the Luoping Fauna. Except for the incomplete and large-sized *N. zhangi*, all of the other five species are relatively small to medium-sized and their hind limbs are equipped with markedly expanded ungular phalanges. This convergence may have been related to a shallow marine habitat commonly shared by them.

With the addition of *Nothosaurus luopingensis*, our phylogenetic analyses support the monophyly of both *Nothosaurus* and *Lariosaurus* when *Lariosaurus sanxiaensis* is excluded. However, the new taxon does not increase the fit of the phylogenetic relationships of the species of *Nothosaurus* to their stratigraphic occurrences. *N. luopingensis* from the Luoping Fauna is the sister group of *N. yangjuanensis* from the Panxian Fauna. A suite of relatively plesiomorphic characters of *Nothosaurus* is present in the skull of *N. luopingensis* but absent in *N. yangjuanensis*, which may correspond to their stratigraphic occurrence. The Luoping Fauna is slightly older than the Panxian Fauna, though both are considered to be within the *Nicoraella kockeli* Zone of the Anisian age.

Acknowledgements. We are very grateful to Chen Yinfang and Ding Jinzhao for the preparation of the materials and to Gao Wei for the photographs. This study was financially supported by the Strategic Priority Research Program (B) of the Chinese Academy of Sciences (grants XDB26000000) and the National Natural Science Foundation of China (NSFC grants 41772006, 41372028).

Chinese Abstract

A New Species of Nothosaurus (Sauropterygia) from the Anisian, Middle Triassic of Luoping, Yunnan Province, China

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Abstract: Based on a marine reptile skeleton from Member II of the Guanling Formation (Middle Triassic) in Luoping, Yunnan, a new species of the eosauropterygian genus *Nothosaurus*—*Nothosaurus luopingensis* n. sp.—is established and described. The skeleton comprises a complete skull with tightly occluded upper and lower jaws and an incomplete postcranial skeleton, including all cervical vertebrae, most dorsal vertebrae, the first two caudal vertebrae, and most of the pectoral and pelvic girdle elements as well as limb bones. The new specimen exhibits a long and flattened skull, large temporal fenestrae, a relatively posteriorly positioned pineal foramen, maxillary fang-like teeth, and a closed, horizontally exposed supraoccipital, indicating affinities with the sauropterygian Nothosauria. Cranial features such as the maxillary tooth row extending posteriorly beyond the level of the anterior margin of the upper temporal fenestra, and the upper temporal fenestra being more than twice the length of the orbit, suggest a closer relationship to the genus *Nothosaurus*. Compared with *Lariosaurus*, the pectoral girdle and limb structures of the new specimen also exhibit *Nothosaurus* characteristics, including: markedly expanded anterolateral corners of the clavicles, a curved humerus with a straight preaxial angle, a distinct deltopectoral crest on the humerus, absence of hyperphalangy in the manus, and lack of pachyostosis in the vertebrae. On the other hand, the postcranial skeleton also displays some features previously considered diagnostic of *Lariosaurus*, such as: more than three ossified carpals, four or more sacral vertebrae, and an interclavicle with a straight posterior margin lacking a posterior process. These postcranial characters can no longer be used to distinguish *Lariosaurus* from *Nothosaurus*. *Nothosaurus luopingensis* is distinguished from other *Nothosaurus* species by the following derived characters: the jugal entering the orbit, separated nasals, a bifurcated posterior end of the frontal, pedal digit V being subequal in length to digit IV, and markedly expanded ungual phalanges. Phylogenetic analysis supports the new species as a member of the *Nothosaurus* clade, with it being the sister taxon to *N. yangjuanensis*, and confirms *Nothosaurus* as a monophyletic group; however, the phylogenetic position of the *N. luopingensis*-*N. yangjuanensis* clade does not correspond to their stratigraphic occurrence.

Key words: Luoping, Yunnan; Middle Triassic; Anisian; Eosauropterygia; *Nothosaurus*

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Appendix

Appendix 1A. Revised two scores in two taxa in the data matrix of Hinz et al. (2019: Supplemental Data2). In *N. marchicus*, the code of character 15 is changed from 1 to {0, 1}, based on Albers, 2011. In *N. yangjuanensis*, the code of character 27 is changed from 0 to 1, based on Yin et al., 2014 (15: Pineal foramen: 0. close to the middle of the parietal skull table; 1. displaced posteriorly; 27: Upper temporal fenestra, constriction of anterior corner: 0. Absent; 1. Present.)

Appendix 1B. Scores for two newly added taxa based on the matrix in Hinz et al. (2019: Supplemental Data2)

N. luopingensis 22?1100101 000110?211 00?1101??1 2?????10?? 11020???01 0011010?00 201020??11 01

L. sanxiaensis ?????????? ?????????? ?????????? ?????????? ???????11? 0110211020 211021???? ??

Brevicaudosaurus 2100100101 0000100211 01?11000?1 1????10?1 ?110000111 ???1?-10-1 211030???1 01

Note: Figure translations are in progress. See original paper for figures.

Source: ChinaXiv —Machine translation. Verify with original.