

A NEW ANGUIMORPH LIZARD FROM THE LOWER MIOCENE OF NORTH-WEST BOHEMIA, CZECH REPUBLIC

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Abstract: The cranial remains of a new Lower Miocene anguimorph, *Merkurosaurus ornatus* gen. et sp. nov., are described from north-west Bohemia (Czech Republic). The animal is morphologically very similar to the Recent *Shinisaurus crocodilurus*, but it differs in several ways. The distinctive features of *Merkurosaurus* are: the nasal process of premaxilla is long and slender with a bilaterally constricted shaft and bilaterally broadened dorsal portion; the dorsal portion of the nasal process divides into three processes of which the median one is the longest; the ornamented surface of the parietal is subdivided into five pustule-like mounds on both right and left sides, with one further mound around the posterior and lateral margins of the parietal foramen. A close phylogenetic affinity to the angu-

imorph genera *Shinisaurus*, *Bahndwivici*, *Dalinghosaurus* and *Carusia*, and partially to *Xenosaurus*, is indicated by characters such as: frontal fused with deep cristae cranii; lateral border of frontals strongly constricted between orbits; double interorbital row of large mounds diverge posteriorly along orbital margin; sculptured postorbital ramus of jugal; small mounds on frontal and parietal with ornamented vermiculate structures; and parietal foramen within parietal but close to anterior margin. *Merkurosaurus* is the only taxon of this affinity known from the Cenozoic of Eurasia.

Key words: Anguimorpha, new genus, new species, cranial anatomy, Lower Miocene, Czech Republic.

THE locality of Merkur in north-west Bohemia in the Czech Republic has yielded abundant material of amphibians and reptiles (Vejvalka 1997; Ivanov 2002; Evans and Klembara 2005) and mammals (Fejfar and Kvacek 1993; Fejfar *et al.* 2003). Several specimens from the locality that are considered here were briefly described in the thesis of Vejvalka (1997). He concluded that this material might be attributed to the Recent lizard *Shinisaurus crocodilurus*, which lives in China and northern Vietnam and has no fossil record in Europe. However, there are several taxa in Asia that may have affinities with *Shinisaurus*. *Oxia karakalpakiensis* from the Cretaceous of Uzbekistan was assigned to 'Xenosauridae' (Nessov and Gao 1993), but subsequent revision of the material showed its phylogenetic position to be uncertain (Gao and Norell 1998; but see Alifanov 2000). According to Gao and Norell (1998), the best known Asiatic relative of *Shinisaurus* is *Carusia intermedia* from the Upper Cretaceous of Mongolia (Borsuk-Bialynicka 1985). In their revision of *Carusia*, Gao and Norell (1998) created a new clade, Carusioidea, which includes a basal *Carusia*, with *Shinisaurus*, *Xenosaurus* and possibly *Restes* and *Exostinus*. Recently, Evans and Wang (2005) redescribed an Early Cretaceous lizard

from China, *Dalinghosaurus longidigitus*, of probable carusioide affinity.

As for New World shinisaurids, Conrad (2006) described a new Eocene shinisaurid, *Bahndwivici ammoskii*, from the Green River Formation in Wyoming (USA), which is strikingly similar to Recent *Shinisaurus crocodilurus*. However, in his phylogenetic analysis *Carusia* is placed at the base of the whole anguimorph clade. Furthermore, the family Xenosauridae is excluded from the clade Anguiformes, which includes *Peltosaurus*, Anguidae and Platynota, with the family Shinisauridae placed within Platynota.

The aims of this paper are to: (1) provide a detailed description of the cranial material of a new anguimorph lizard from the Lower Miocene of north-west Bohemia, for which a shinisaurid affinity has been suggested previously (Vejvalka 1997); and (2) compare this new lizard with *Shinisaurus crocodilurus* and several other anguimorph taxa with the aim of deducing its possible taxonomic position.

The anatomical terminology of the individual skeletal elements used here is mostly that of Fejérváry-Lángh (1923), Oelrich (1956), Klembara (1979, 1981) and Conrad (2004).

MATERIAL AND METHODS

The material is disarticulated and the individual bones and osteoderms were either obtained by screen-washing or collected directly from the sediment layers. Within Recent anguimorph taxa, the bones and osteoderms are most similar to those of Recent *Shinisaurus crocodilurus*. They are attributed to a single taxon on the basis of the specific ornamentation of external surfaces (frontal, parietal and jugal), the morphology of the teeth (maxilla, premaxilla and dentary) and the overall similarity of individual bones (especially of the pterygoid), teeth and osteoderms to those of *Shinisaurus*.

The following specimens of Recent lizard taxa were used for comparison: (1) *Shinisaurus crocodilurus*, deposited in the University of Florida (UF 57112, 61139, 61685, 62316, 62355, 62497, 62578, 68203); (2) two uncatalogued specimens, *Shinisaurus crocodilurus* and *Elgaria multicarinata*, deposited in the private collection of Prof. Susan Evans (University College, London); (3) *Xenosaurus grandis*, CJB 570, deposited in the private collection of Dr Christopher Bell (University of Texas, Austin).

The following specimens are deposited in the Department of Ecology (DE), Faculty of Natural Sciences, Comenius University, Bratislava: *Pseudopus apodus* (DE 1–13, 29), *Ophisaurus harti* (DE 31), *O. koellikeri* (DE 30), *O. attenuatus* (DE 32–33), *O. ventralis* (DE 34–35, 38), *Anguis fragilis* (DE 14–21), *Varanus* sp. (39–40).

SYSTEMATIC PALAEOLOGY

Order SQUAMATA Opper, 1811
Infraorder ANGUIMORPHA Fürbringer, 1900

Genus MERKUROSAURUS gen. nov.

Generic diagnosis. As for *Merkurosauros ornatus*, the only species.

Type species. *Merkurosauros ornatus* sp. nov.

Derivation of generic name. After the Merkur locality in north-west Bohemia and Latin, *sauros*, lizard.

Merkurosauros ornatus sp. nov.
Text-figures 1–9

1997 cf. *Shinisaurus* Vejvalka, p. 48.

Derivation of specific name. Latin *ornatus*, after the pronounced ornamentation on the external surface of the skull roof bones, especially the parietal and the frontal.

Holotype. Specimen Pb 02045, parietal (Text-figs 3, 4D, H), deposited in the National Museum, Prague, Czech Republic.

Repository. National Museum, Prague (specimen numbers prefixed by Pb), and Geological Collection of the Bilina opencast mine (referred to in the form Ah, number, SGDB).

Referred specimens. Premaxilla (Pb 01852, 02018, Ah 843 SGDB, 930 SGDB); frontal (Pb 01813, 01820, 01874, Ah 790–815 SGDB); parietal (Pb 01814–01815, 01817–01819, 01867, 02019, Ah 775–789 SGDB, 816–819 SGDB, 823–838 SGDB); maxilla (Pb 01833, 01854, 01919, 01921, 02020, Ah 720–725 SGDB, 989 SGDB, 991–994 SGDB, 1015–1016 SGDB, 1018 SGDB, 1020 SGDB, 1022–1025 SGDB); jugal (Pb 01859, Ah 820–822 SGDB, 1026–1032 SGDB); pterygoid (Pb 02021–02022, Ah 839–842 SGDB); dentary (Pb 01796, 01823, 01844, 01847, 01850–01851, 01860–01861, 01897, 02023, Ah 747–770 SGDB, 934–938 SGDB, 978–980 SGDB, 995 SGDB, 997–999 SGDB, 1001–1002 SGDB, 1014 SGDB); osteoderms (Ah 716–719 SGDB).

Locality and horizon. Merkur-North opencast mine; base of Lower Miocene (Eggenburgian), Lower Orleanium, zone MN 3.

Specific diagnosis. A lizard of small adult size (as Recent *Shinisaurus*). Unique features are: (1) nasal process of premaxilla long, slender, with bilaterally constricted shaft and widened dorsal portion; dorsal portion terminates in three distinct processes of which the median one is the longest and most pointed; and (2) ornamented surface of parietal subdivided into five mounds on both right and left sides, with one mound around posterior and lateral margins of parietal foramen.

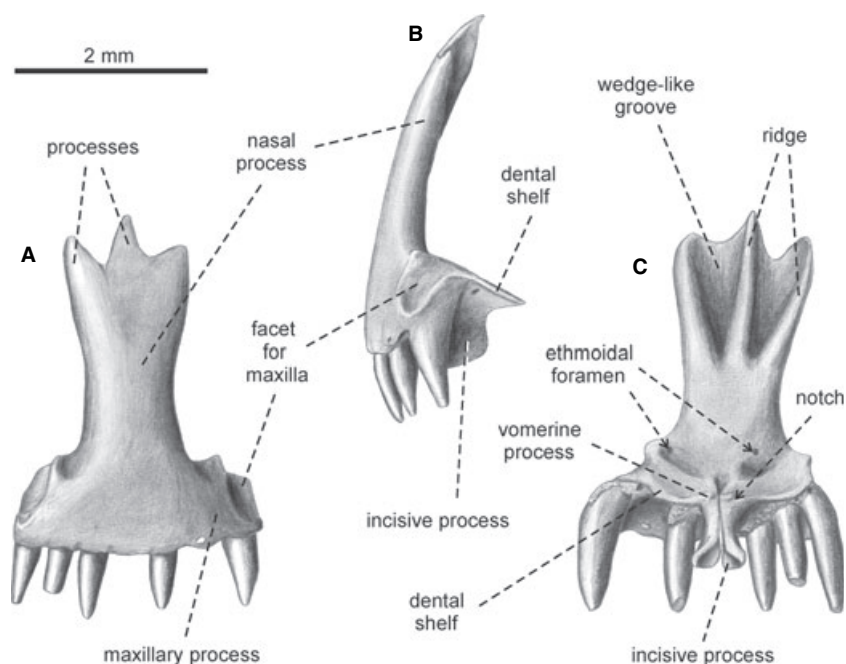
Description

Five different skull roofing bones are described, along with the pterygoid, dentary and osteoderms. The descriptions are based on the largest specimens preserved. Where a sequence of growth stages is available for a given bone, this is described at the end under 'Ontogenetic remarks'.

Premaxilla. Pb 02018 is a completely preserved premaxilla (Text-fig. 1). Its body extends into a stout nasal process dorsally and a maxillary process laterally, contributing to the ventromedial margin of the exonarial fenestra. Posteromedially, the premaxilla forms an anteroposteriorly broad dental shelf (horizontal lamina) that met the vomer and, presumably, also contacted the septomaxilla. It is an unpaired element but a distinct fissure between the parts bearing the vomerine facets provides evidence of its original paired nature. The external surface is smooth. Each premaxilla bears seven tooth positions.

The nasal process is long, about twice the dorsoventral length of the maxillary process. It is distinctly bilaterally constricted in its ventral portion and dorsally it gradually widens bilaterally. The constricted ventral portion is about three tooth positions

TEXT-FIG. 1. *Merkurosaurus ornatus* gen. et sp. nov., Pb 02018; premaxilla in A, anterior, B, left lateral, and C, internal views.



wide. The broadened dorsal portion divides into three processes, of which the median is the longest. Between the processes are distinct notches. These are marked internally by long, deep, wedge-like grooves bordered by massive ridges. The ventrally orientated point of each groove reaches the mid-length of the nasal process, and probably received a pointed anterior process of the nasal. On the inner surface of the premaxilla, an ethmoidal foramen is present at the junction of the nasal and maxillary processes. The position of this foramen corresponds to that in *Shinisaurus*, but it does not open on the external surface of the premaxilla as in this genus.

The maxillary process of the premaxilla narrows gradually laterally. Its lateral surface bears a crescent-shaped facet for the junction with the premaxillary process of the maxilla. The facet is orientated in an anteromedial–posterolateral direction.

The dental shelf extends back horizontally; dorsally it bears a slightly depressed facet for the vomer. Medially, the dental shelf forms a small vomerine process that meets its fellow in the median plane. The vomerine process, which also bears a slightly depressed facet, is separated from the rest of the dental shelf by a small, shallow notch. The incisive process is well developed, and represents a ventromedial fold of the dental shelf. The left and right incisive processes are divided by a very narrow fissure.

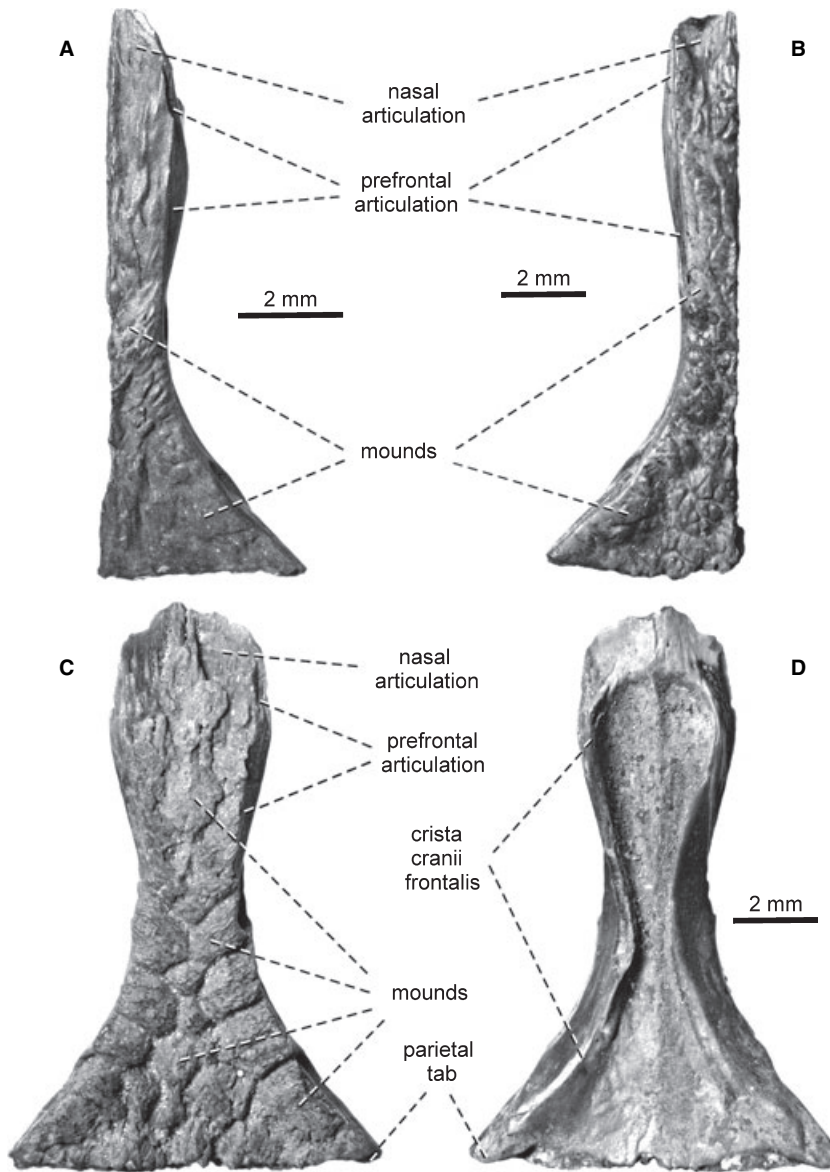
Frontal. Several fused frontals and several single frontals are present (Text-fig. 2). The frontal is subtriangular in shape and its lateral margin borders the orbit. It is clearly bilaterally constricted in its middle part, so that the orbital margin is distinctly arched. The posterior portion of the frontal is wide and sutured with the parietal along its entire posterior margin. The whole dorsal surface of the frontal is strongly ornamented (see below). On the anterior edge are two elongated, unornamented, ovoid surfaces divided by an anteroposteriorly elongated, ornamented median spur. The unornamented surfaces were overlapped by

the nasals and the median spur fitted as a wedge between them. Narrow prefrontal facets run anteroposteriorly along the lateral margins of the frontal, and extend to its mid-length. As a whole, the nasal portion of the frontal has a rounded margin. The posterior margin of the frontal is almost straight, with a small but distinct parietal tab at its lateralmost section in the largest specimens.

On the ventral surface, the crista cranii frontalis is well developed on each side. The crista is deepest in the anterior half of its length. Further to the posterior, it gradually becomes shallower. The ventral surface is smooth. The median line of fusion of conjoined frontals is always discernible.

Ontogenetic remarks. Ontogenetic changes are demonstrated by three size stages (Text-fig. 2), although several other frontals of intermediate length and robustness are present. Although there are no major proportional changes during growth, the individual growth stages clearly show the development of the mounds forming the ornament. The length of the smallest completely preserved frontal (Ah 810 SGDB) is 11 mm (Text-fig. 2A). It is a single, gracile, very slender bone that is only slightly ornamented. There are two pustule-like mounds, one in the region of the most constricted portion of the bone surface, and the other immediately posterior to it. They bear distinct grooves and ridges on their surfaces. Further to the posterior, three similar mounds lie one after the other along the orbital margin, but they are only slightly ornamented on their surfaces. Medial to these mounds, the surface of the large posterior portion of the bone is also covered by several small, smooth or only slightly anteroposteriorly ridged and grooved mounds. The anterior surface of the frontal bears ridges that run anteroposteriorly and grooves of varying intensity of development.

The second stage is represented by a single frontal (Ah 811 SGDB) 13.4 mm long (Text-fig. 2B). It is slightly more robust



TEXT-FIG. 2. *Merkurosaurus ornatus* gen. et sp. nov. A, Ah 810 SGDB, right frontal. B, Ah 811 SGDB, left frontal. C–D, Ah 812 SGDB, fused frontals. A–C, dorsal views; D, ventral view.

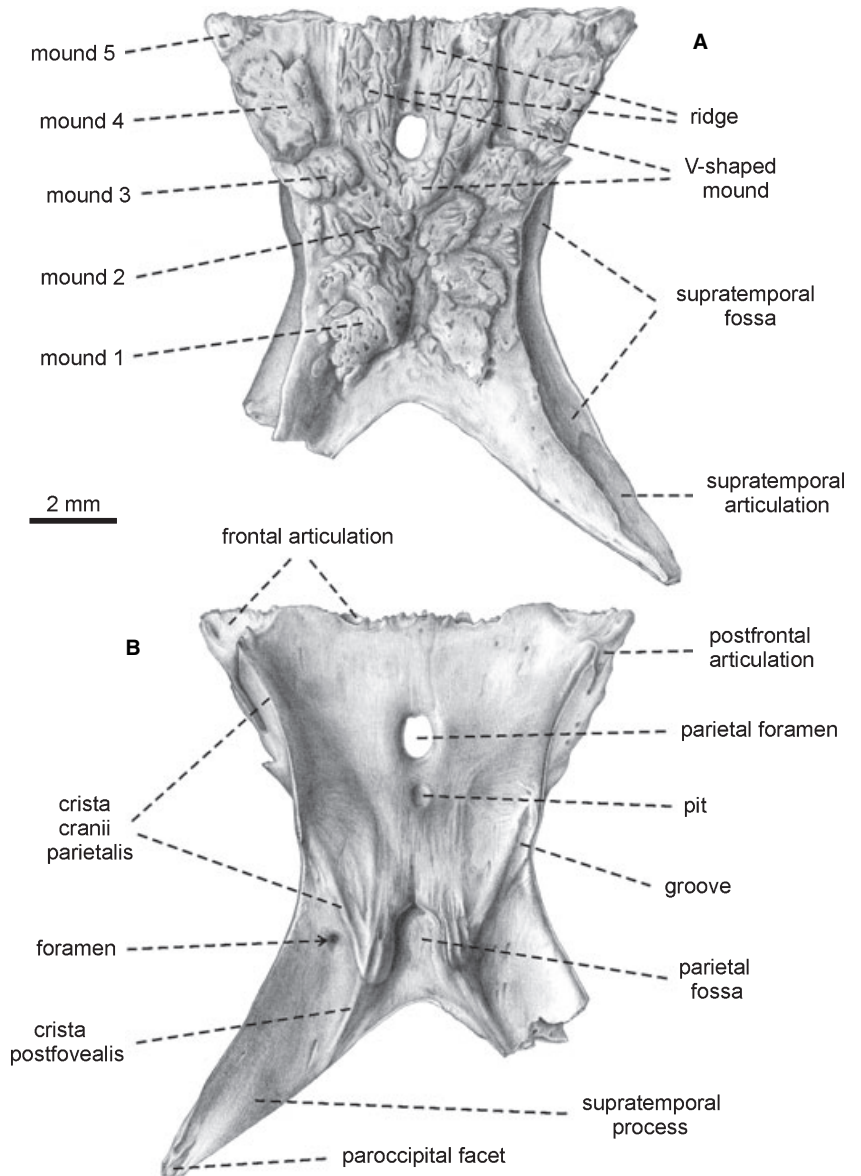
and its anterior end is more mediolaterally expanded. Along the posterior half of the orbital margin, there are distinct mounds with grooves and ridges on their surfaces. Medial to these, the posterior surface of the bone bears three further similar mounds and a small one close to the posteromedial margin. The anterior surface of the frontal bears more pronounced, anteroposteriorly elongated ridges divided by grooves, but no distinct mounds are present.

The third stage is represented by an already fused frontal Ah 812 SGDB (Text-fig. 2C–D). It is the same length as the preceding stage but more robust with much more strongly developed ornamentation consisting of high, well-developed mounds divided by deep grooves. The external surface of the mounds bears grooves, ridges and pits of various sizes. The mounds lie along the whole of the orbital margin, and are most robust in the posterior half of the frontal. The surface of the frontal between the orbital rows of mounds bears sev-

eral smaller mounds, some of these lying in the median plane.

Parietal. The parietal is a large median element consisting of the parietal plate with an ornamented surface, and two posterolaterally diverging supratemporal processes (Text-figs 3–4). The parietal plate is rectangular in shape with concave lateral margins. The supratemporal processes diverge posterolaterally and are curved posteroventrally in lateral view. The parietal houses the parietal foramen which lies at the border of the first and the second third of the parietal plate. The entire surface of the parietal plate is covered by dermal ornament consisting of one continuous V-shaped mound around the posterior and lateral margins of the parietal foramen and generally five oval distinct mounds or pustules on each side of the remaining surface of the plate. The surface of the mounds bears ridges, grooves and pits of different depths. The individual mounds are mostly separated by

TEXT-FIG. 3. *Merkurosaurus ornatus* gen. et sp. nov., Pb 02045 (holotype); parietal in A, dorsal, and B, ventral views.



distinct grooves and have basically a constant arrangement, but there is some variation (see below). The right and left rami of the mound around the parietal foramen form a strong, high margin to the parietal foramen that ends on the anterior margin; between the two rami and anterior to the parietal foramen, there is a more or less distinct median ridge, and bilaterally situated, anteroposteriorly orientated grooves are present.

Five pairs of mounds cover the remaining ornamented surface of the parietal plate. Of these, the posteriormost is the strongest and lies in the posterolateral corner of the plate, reaching the root of the supra-temporal process. The second mound lies immediately anteromedial to it and posterolateral to the parietal foramen. The third is lateral and slightly posterior to the parietal foramen, close to the lateral margin of the parietal plate. The fourth is anterolateral to the parietal foramen and close to the lateral margin of the plate. The last three mounds lie in a line orientated in a posteromedial–anterolateral direction. In the

largest specimens (e.g. Pb 02045), the anterolateral corner of the parietal plate may bear an extra, small, fifth mound. There are slight variations in the development of the ornament; they include either the fusion of neighbouring mounds or more or less distinct subdivision(s) of individual mounds (mostly first and second mounds). In Ah 825 SGDB, the fourth and fifth mounds are fused. In some specimens (e.g. Ah 777 SGDB and 824 SGDB), the anterior portions of the mound around the parietal foramen are separated from the rest of the mound.

The broad anterolateral surface of the parietal bears a wedge-like area for articulation with the postfrontal. This area is pointed posteriorly and extends back to the level of the anterior margin of the parietal foramen in the largest specimens. In the smallest specimens, it extends back to the level of the posterior margin of the parietal foramen. The lateral edge of the parietal contributes to the margin of a large, deeply embayed and anteroposteriorly long, supra-temporal fossa that extends from the

postfrontal articulation to the posterior tip of the supratemporal process. The supratemporal fossa is inclined ventrolaterally and is mediolaterally broadest at the level of the anterior portion of the supratemporal process. The supratemporal fossa is the place of the origin of the adductor musculature. The sharp edge of the ornamented dorsal surface of the parietal extends laterally above the supratemporal fossa. The lateral margin of the parietal forms the medial margin of the supratemporal fenestra.

On the ventral surface of the parietal, the crista cranii parietalis runs along the lateral margin of the parietal plate. The crista cranii is deepest at a level immediately posterior to the parietal foramen. Anteromedial to the crista cranii, there is a triangular facet that accommodated a small parietal tab from the frontal. The crista cranii is convex in the anterior half of its course, particularly at the level of the parietal foramen. From the level at which the whole parietal is most constricted, the crista cranii turns posteromedially; between this posterior section and the anterior section of the crista cranii, a groove is a more or less developed. The posterior section of the crista cranii has an almost straight course. In the largest specimens, the crista cranii does not reach the inner margin of the base of the supratemporal process. The anterior and lateral margins of the parietal fossa, which receives the processus ascendens of the synotic tectum, are distinctly developed. The posterolateral edge of the fossa is confluent with the posterior end of the crista cranii. This area is slightly elevated and bears distinct scars. From here, a well-developed crista postfovealis runs posterolaterally and merges with the inner margin of the base of the supratemporal process. In the smallest specimens, the crista postfovealis is absent or extremely short (see below). There is a small median pit immediately behind the parietal foramen. In most specimens, a relatively large foramen is located immediately lateral to the posteriormost section of the crista cranii parietalis (sometimes on the left side, sometimes on the right).

The supratemporal processes diverge posterolaterally and increase in length relative to the length of the parietal plate with age (see below). The angle between the long axes of the supratemporal processes is about 80 degrees in the largest specimens (Pb 02045; Text-figs 3, 4D, H), but in one of the smallest juvenile parietals preserved (Ah 819 SGDB; Text-fig. 4A, E), this angle is more acute, about 70 degrees. The distal tip of the supratemporal process bears two facets. The lateral supratemporal facet is large and elongate, with its anterior end extending almost to the posterior margin of the parietal plate. The ventral paroccipital facet is small and sometimes forms a small plate (well preserved in Pb 01867). The posterior margin of the parietal and the medial margins of the supratemporal processes bear narrow nuchal scars.

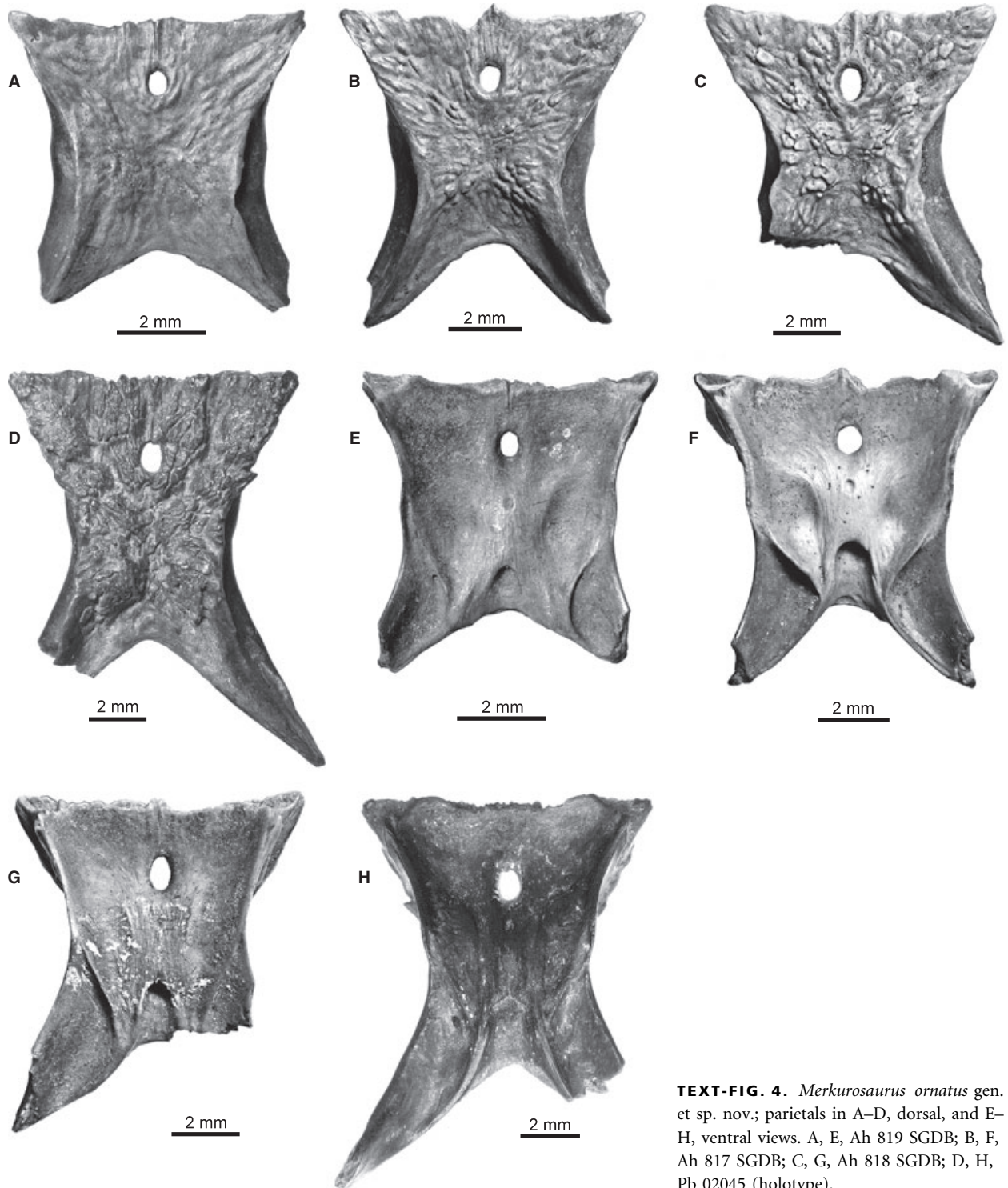
Ontogenetic remarks. The ontogeny of the parietal is demonstrated here by four growth stages, although several intermediate stages are also present. Besides the changes in size of individual portions of the parietal, the individual growth stages clearly show the gradual development of ornamentation, i.e. the gradual development of the individual mounds. The lengths of these four parietals are as follows: Ah 819 SGDB, 6.7 mm; 817 SGDB, 9 mm; 818 SGDB, 11 mm; and Pb 02045, 13.6 mm (Text-fig. 4). On the basis of comparison with the *Shinisaurus* parietals, the

smallest represents a juvenile animal and the largest, an adult. During growth, the following changes occur: (1) there is mediolateral narrowing of the supratemporal fossa in dorsal view; (2) the supratemporal processes become more elongate; (3) the angle between the long axes of the supratemporal processes increases; (4) a short, but distinct crista postfovealis develops; (5) strong ornamentation develops on the external surface of the parietal plate; and (6) there is overall bilateral narrowing and anteroposterior elongation of the parietal plate. In the smallest specimen the mound around the parietal foramen is already present. The posteriormost mound is the largest. The remaining three mounds are also already present but still relatively indistinct. With growth, all five pairs of mounds become stronger, the spaces between them deeper, and the grooves and ridges on their surfaces more distinct. The grooves and ridges run in (1) an anteroposterior direction on the mound around the parietal foramen; (2) an anteromedial–posterolateral direction on the posteriormost mound; and (3) an anterolateral–posteromedial direction on all four remaining mounds.

Maxilla. The best preserved maxillae are AH 1022–1023 SGDB, 1025 SGDB and 720 SGDB. The maxilla is subtriangular in shape and consists of a high, vertical facial (or nasal) process, a short premaxillary process and a stout suborbital ramus (Text-fig. 5). Unfortunately, in all maxillae the dorsalmost portion of the facial process is broken. The external surface of the facial process above the rows of labial foramina is ornamented by ridges, grooves and pits, and is most pronounced close to the margin of the fenestra exorarina.

The premaxillary process of the maxilla is perfectly preserved in Ah 720 SGDB (Text-fig. 5E–F). It bears an articular facet for the premaxilla that corresponds to the crescent-shaped facet on the latter. The dorsomedial corner of the premaxillary process extends into a short, pointed process running anteromedially immediately above the dental shelf and posterior to the nasal process of the premaxilla. This process, called here the septomaxillary process, contacted the dorsal surface of the dental shelf of the premaxilla and presumably also the septomaxilla, as in *Shinisaurus*. There is no premaxilla-maxilla aperture. The maxilla presumably articulated with the vomer but this cannot be confirmed. The lacrimal margin is deeply incised and the jugal margin is almost straight. Their junction lies at the level of the infraorbital foramen (see below), and is marked on the dorsal surface by a slight groove (i.e. Ah 1025 SGDB; Text-fig. 5C). The posterior end of the maxilla is perfectly preserved in Ah 724 SGDB, 1023–1024 SGDB and Pb 01854. It shows that the facet for the ectopterygoid is restricted to the posteromedial and terminal surfaces of the maxilla (Text-fig. 5C–D). Hence, the ectopterygoid would have been exposed on the external surface of the skull.

The inner surface of the maxilla bears a prominent dental shelf (Text-fig. 5B, F). At about the junction of the second and last third of its length, the shelf widens medially and develops a slight concavity. Its dorsal surface bears a distinct, elongate, palatine facet, and lateral to this is a large infraorbital foramen. The infraorbital canal branches at the level of the maxilla-palatine suture. One branch passes through a foramen that carried the maxillary artery and nerve into a long

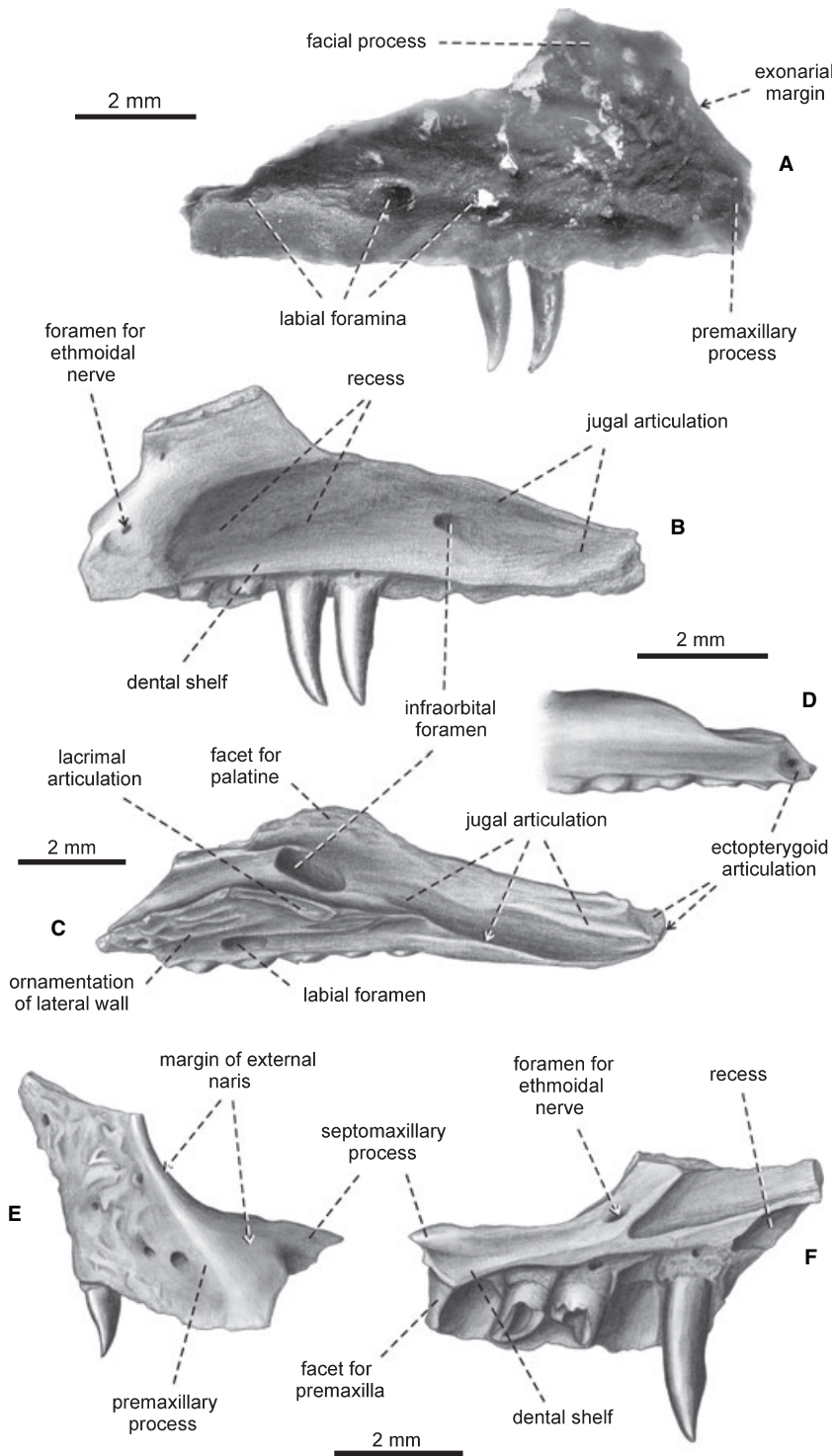


TEXT-FIG. 4. *Merkuosaurus ornatus* gen. et sp. nov.; parietals in A–D, dorsal, and E–H, ventral views. A, E, Ah 819 SGDB; B, F, Ah 817 SGDB; C, G, Ah 818 SGDB; D, H, Pb 02045 (holotype).

maxillary infraorbital canal (Oelrich 1956). This canal branched to give rise to the foramina that open on the labial surface of the bone. A small foramen for the ethmoidal nerve is present on the anteromedial surface of the maxilla, near the anterior end of the facial process. Immediately anterior to the infra-

orbital foramen, there is a large, deep, anteroposteriorly elongated recess that extends forward just short of the level of the ethmoidal nerve foramen.

A deep narrow groove runs along the dorsal surface of the suborbital ramus of the maxilla, close to its lateral wall. The



TEXT-FIG. 5. *Merkurosaurus ornatus* gen. et sp. nov. A–B, right maxilla of Ah 1023 SGDB in A, external, and B, internal views. C, posterior half of left maxilla of Ah 1025 SGDB in dorsal view. D, posterior end of maxilla of the same specimen in posterolateral view. E–F, anterior portion of right maxilla of Ah 720 SGDB in E, anterodorsal, and F, internal views.

groove extends from the infraorbital foramen to the posterior end of the maxilla, and accommodated a strong ridge on the ventral surface of the suborbital ramus of the jugal (Text-figs 5C–D, 6). The surface of the jugal lying lateral to the ridge abutted the inner surface of the lateral maxillary wall. The sur-

face of the jugal medial to the ridge articulated broadly with the dorsal surface of the maxilla. Hence, the maxilla-jugal articulation formed a strong tongue and groove joint.

There are usually 5–6 labial foramina (Text-fig. 5A). The largest foramen lies at the level of the infraorbital canal and the

maxilla-palatine junction, and is usually the last, but in Ah 1022 SGDB there is a smaller one posterior to it. All other foramina are orientated almost directly outward, although in Ah 1022 SGDB the anterior foramen is relatively large and directed forwards. The maxilla carried at least 14 teeth.

Jugal. Most of jugals are completely preserved. In lateral view, the jugal is L-shaped (Text-fig. 6). Its facets show that it contacted the maxilla, lacrimal, ectopterygoid and postfrontal. According to Conrad (2004), the jugal also sometimes contacts the prefrontal in *Shinisaurus*; but this cannot be confirmed in *Merkurosaurus*. It has two long processes, postorbital and suborbital, that contributed to the posteroventral margin of the orbit. From their junction, a third, short but distinct process extends posteroventrally. The whole external surface of the jugal is ornamented, especially in the largest specimens (i.e. Ah 822 SGDB), and is most pronounced at the junction of the three processes. This consists of grooves and ridges radiating from the body of the jugal; several foramina are also occasionally present between the grooves.

The suborbital and postorbital processes are triangular in cross-section. In each case, the external side is flat and a strong ridge is developed medially. The orbital lamina is sharp. The anterior end of the suborbital process is pointed, and its dorso-medial surface bears a distinct, dorsoventrally elongated articulation surface for the lacrimal. This broad articular facet bears two or three more or less distinct ridges on its surface. Immediately behind the posterior end of the maxillary articular surface, there is a relatively deep, roughened ovoid area for articulation with the ectopterygoid.

The postorbital process is more gracile than the suborbital process. It is slightly constricted at its mid-point, but its dorsal portion is anteroposteriorly wider and bears a dorsoventrally

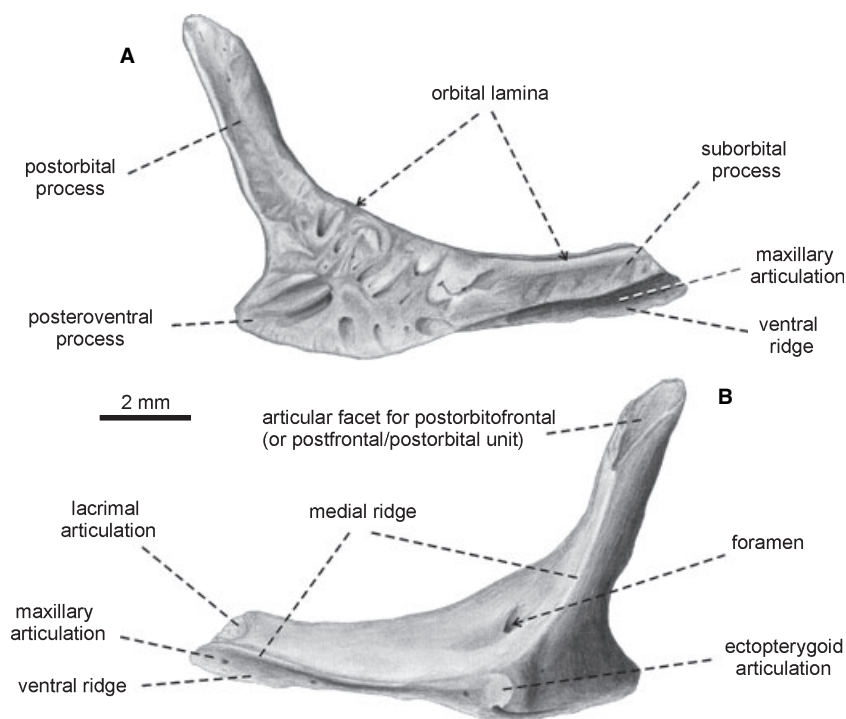
elongated articular facet on its medial surface. This facet lies immediately anterodorsal to the medial ridge. In *Shinisaurus*, the postfrontal is fused with the postorbital in adults, but the bones are separate in very young specimens (Conrad 2004). In the adult Eocene shinisaurid *Bahndwivici ammoskius* these two bones are still unfused (Conrad 2006). The condition in *Merkurosaurus* is unknown, but it is certain that the postorbital process of the jugal articulated either with the postorbitofrontal (as in *Shinisaurus*) or the postorbital/postfrontal unit (as in *Bahndwivici*).

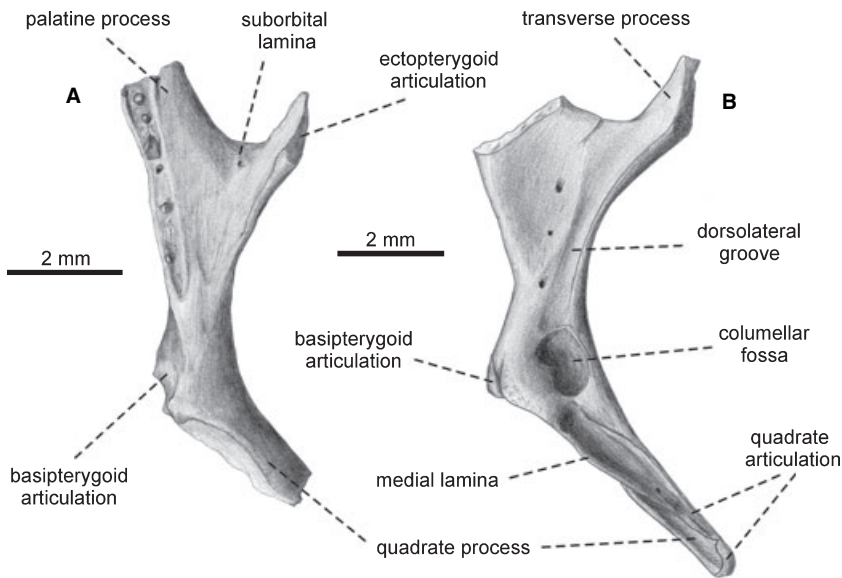
On the inner surface of the jugal, at the junction of the suborbital and postorbital processes, there are one or two relatively large foramina anterior to the medial ridge.

Pterygoid. The pterygoid is a triradiate structure, with palatine, transverse and quadrate processes extending from the main body (Text-fig. 7). Besides the palatine, ectopterygoid and quadrate, the pterygoid articulated with the basisphenoid, the epipterygoid and probably the vomer. The medial edge of the pterygoid is slightly concave and formed the lateral margin of the interpterygoid vacuity. Further laterally, the palatine and transverse processes formed the posteromedial margin of the suborbital fenestra.

In all pterygoids preserved, the anterior portion of the palatine ramus is broken. However, its preserved posterior portion in Ah 839 SGDB and Pb 02021 shows that the process was long (Text-fig. 7A). The posterior portion of the palatine process is mediolaterally broad and dorsoventrally narrow and flat. It gradually narrows mediolaterally towards the anterior end. The ventromedial margin of the palatine process and the body of the pterygoid bear a single row of teeth, the most posterior of which lie behind the root of the transverse process, on or close to the level of the pterygoid-ectopterygoid articulation.

TEXT-FIG. 6. *Merkurosaurus ornatus* gen. et sp. nov., Pb 01859; right jugal in A, lateral, and B, medial views.





TEXT-FIG. 7. *Merkurosaurus ornatus* gen. et sp. nov. A, left pterygoid, Ah 839 SGDB, in ventral view. B, right pterygoid, Ah 840 SGDB, in dorsal view.

The transverse process extends anterolaterally from the root of the palatine process. It is short and mediolaterally flat. Its distal portion is dorsoventrally expanded and bears two facets for articulation with the ectopterygoid. The dorsal facet is elongated; the ventral one is larger and roughly oval in shape. Between the two facets, there is a groove with elevated margins. A broad suborbital lamina joins the transverse and the palatine processes.

The quadrate process is preserved in Ah 840 SGDB and Pb 02022. It is long and mediolaterally narrowed, and the posterolateral surface bears an elongated facet for the quadrate.

The posterodorsal surface of the body of the pterygoid, immediately anterior to the root of the quadrate process, bears a deep, rounded columellar fossa that housed the ventral end of the epipterygoid. Immediately medial to the fossa, the wall of the pterygoid bears a deep depression for the basipterygoid process of the basisphenoid. The dorsal margin of this depression is thin and continues in the form of a thin lamina along the medial surface of the quadrate process. This medial lamina forms a shelf that divides the internal surface of the quadrate process into two, dorsal and ventral, surfaces. Further to the posterior, it gradually diminishes in height and fades out close to the tip of the quadrate process. A deep dorsolateral groove runs along the sharp lateral margin of the pterygoid body, terminating immediately anterior to the columellar fossa.

Dentary. This is a long, ventrally arched bone, with a slight medial curvature at its anterior end (Text-fig. 8). The symphyseal facets are kidney-shaped. In transverse section, the dentary is C-shaped with a smooth external surface. There are usually 5–6 mental foramina. Ah 934 SGDB and Pb 01796 both preserve a complete dental shelf and coronoid process. Pb 01796 also preserves a complete surangular process; between it and the coronoid process there is a relatively deep coronoid incisure (Text-fig. 8A).

None of the dentaries preserves the posteroventral portion. The dentary bears up to 20 teeth (20 tooth positions are present in Ah 934 SGDB). The lingual surface contains a deep groove

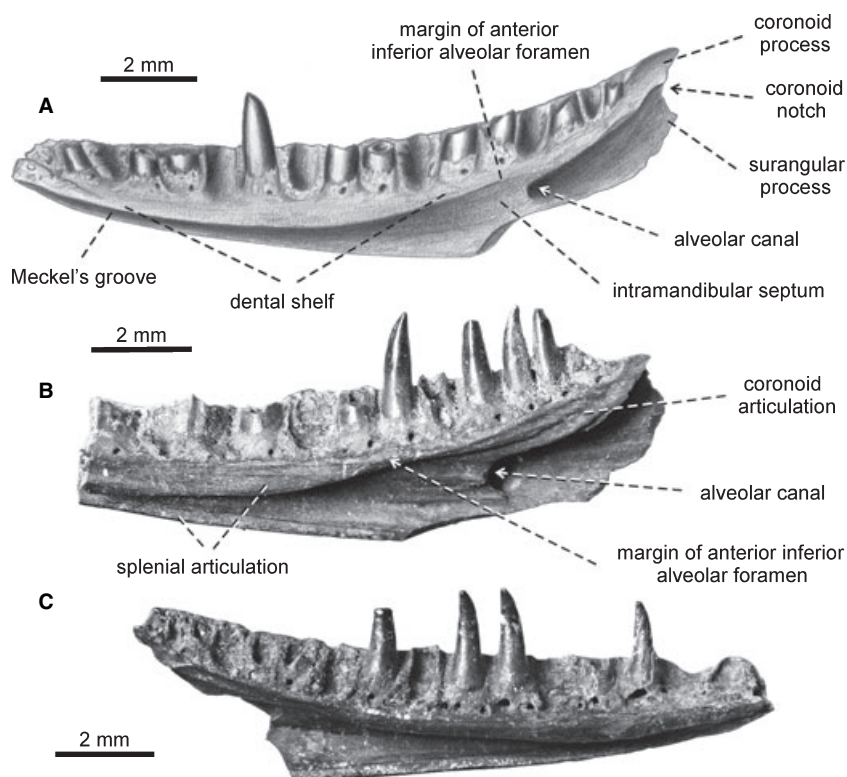
for Meckel's cartilage. This just enters the symphyseal facet and deepens in a posterior direction. Meckel's groove is roofed by the dental shelf (horizontal lamina), the medial margin of which bears a shallow notch, located anterior to the opening of the alveolar canal and posterior to the facet for the anterior process of the coronoid. This shallow notch is the dorsal margin of the anterior inferior alveolar foramen. The lingual surface of the posteroventral half of the dental shelf and the corresponding ventral margin of the dentary bear narrow facets for the splenial. A high intramandibular septum forms the lingual wall of the alveolar canal. The opening of the alveolar canal is large and lies at the level of the fourth tooth from the rear. The posteroventral margin of the intramandibular septum is sutured to the medial surface of the dentary.

Dentition. The marginal teeth are large, smooth, pointed and slightly recurved (Text-figs 1, 5A–B, 8). The tips of the crowns bear anterior and posterior cutting edges, pronounced in Ah 979 SGDB. The bases of the teeth are expanded lingually. The premaxilla has seven teeth and the maxilla had at least 14 teeth. The largest dentaries have up to 20 teeth or tooth positions. The maxillary and the dentary teeth are of similar size, but the premaxillary teeth are notably smaller. The premaxilla of Pb 01850 shows that the replacement teeth developed posterolingually. In most specimens, small resorption pits are present on the lingual sides of the tooth bases.

The pterygoid teeth are substantially smaller than the maxillary and dentary teeth. They are almost straight, pointed and inclined posteriorly. Specimen Ah 839 SGDB has nine tooth positions, but more teeth were present and the palatal process, which also bears teeth, is not completely preserved.

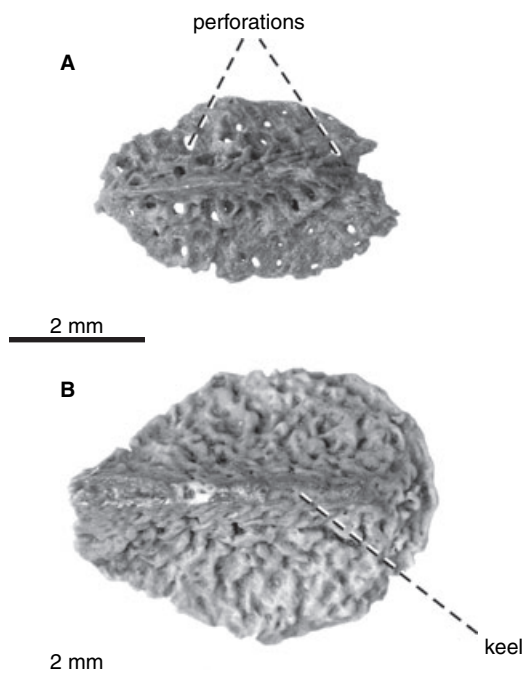
Osteoderms. Four osteoderms are preserved, ranging from 2–5.5 mm in length. They are ovoid and non-imbricate (Text-fig. 9), high, keeled, and have an inverted V-shape. Their surface is ornamented with high ridges, grooves of irregular shape and

TEXT-FIG. 8. *Merkurosaurus ornatus* gen. et sp. nov.; internal views of A, right dentary, Pb 01796, B, right dentary, Pb 01850, and C, left dentary, Pb 01851.



deep pits. In the osteoderm Ah 717 SGDB (Text-fig. 9A) the walls are completely perforated, but those of the largest osteoderm, Ah 718 SGDB (Text-fig. 9B), bear no perforations. The

inner surface of the osteoderms is grooved and pitted. The morphology of the osteoderms is very similar to those of *Shinisaurus* and *Bahndwivici* (Conrad 2006).



TEXT-FIG. 9. *Merkurosaurus ornatus* gen. et sp. nov.; external views of osteoderms A, Ah 717 SGDB, and B, Ah 718 SGDB.

COMPARISONS AND DISCUSSION

Comparison with shinisaurids

Some of the material discussed here was briefly described in the thesis of Vejvalka (1997). He attributed his material to cf. *Shinisaurus* Ahl, 1930, and suggested that these skeletal remains could be attributed to the Recent *Shinisaurus crocodilurus*. It is true that within Recent Anguimorpha, *Merkurosaurus ornatus* is morphologically most similar to *Shinisaurus* (Conrad 2004; pers. obs.), but it differs from the latter and from the recently described Eocene *Bahndwivici ammoskius* (Conrad 2006) in the following characters (not all data are available in *Bahndwivici*):

1. The nasal process of the premaxilla is long and slender with a bilaterally constricted shaft; its bilaterally widened dorsal portion terminates in three distinct processes of which the median process is the longest and most pointed. The nasal process of *Shinisaurus* is much shorter, more robust, and has parallel lateral margins. Its length is roughly equal to the height of the maxillary process of the premaxilla (measured in its medial portion).

2. Deep, wedge-like grooves on the internal surface of the nasal process of the premaxilla extend to its mid-length. In *Shinisaurus*, the corresponding structures form roughly oval depressions and extend to only about one-third of the length of the nasal process.
3. The frontal is bilaterally constricted at its midpoint. In *Shinisaurus* and *Bahndwivici*, the constriction between the orbits is absent and the interorbital margins are parallel in the middle section of the frontal.
4. The anterior margin of the frontal is rounded. In *Shinisaurus* it is pointed.
5. The frontals are not fused in subadult specimens. In subadult specimens of *Shinisaurus* (e.g. UF 61685), they are already fused into a median bone. In similar-sized specimens of *Merkurosaurus*, the frontals are not fused and the length of the largest single frontal is the same as that of the fused frontal. However, the fused frontal is much more massive and more strongly ornamented.
6. The angle between long axes of the parietal supratemporal processes increases during growth. In *Shinisaurus*, the angle between the supratemporal processes is obtuse in the smallest specimens, and there is a right angle between them in the largest specimens. In the adult specimen of *Bahndwivici*, the angle between the supratemporal processes is 90 degrees. The situation is reversed in *Merkurosaurus*: this angle is 70 degrees in the smallest specimens and about 80 degrees in the largest.
7. There is progressive narrowing of the supratemporal fossa and ornamented surface of the parietal plate in dorsal view during growth. With growth in *Shinisaurus*, the supratemporal fossa becomes broader and the ornamented portion of the parietal plate becomes markedly narrower.
8. In subadult specimens, the parietal foramen is large and lies at the border between the first and second thirds of the parietal. In similar ontogenetic stages of *Shinisaurus*, the parietal foramen is small and much further to the anterior, very close to the anterior margin of the parietal.
9. The dorsal surface of the parietal plate is strongly ornamented by five pustule-like mounds on the right and left sides and one mound around the posterior and lateral margins of the parietal foramen; the mounds are covered by ridges and grooves. In *Shinisaurus*, the ornamentation is much less developed, and is most pronounced in the region behind the parietal foramen. It consists of ridges and grooves that diverge anteriorly and laterally.
10. Anteroposteriorly short crista postfovealis is present in adult specimens. In *Shinisaurus* the crista postfovealis is very long in subadults as well as adults.
11. The recess on the internal surface of the maxilla is deep and anteroposteriorly long. It is much smaller in *Shinisaurus*.
12. The dentary bears up to 20 teeth. That of *Shinisaurus* commonly has 14–15 teeth, whereas *Bahndwivici* has an estimated 16–17.
13. The portion of dentary anterior to the level of the alveolar canal is longer and straighter. When the dentaries of the largest specimens of *Merkurosaurus* and *Shinisaurus* are aligned according to the position of the alveolar foramen,

the anterior portion of the dentary of *Merkurosaurus* is seen to be much longer.

It may be concluded that in spite of the many similarities between the taxa with respect to the morphology of individual bones, teeth and osteoderms, *Merkurosaurus* and *Shinisaurus* clearly represent different genera. As demonstrated by several structures of the parietal, they also exhibit reversed ontogenetic processes leading to the adult morphology of this bone.

Systematic assignment

The systematic assignment of *Merkurosaurus ornatus* is difficult because the material is disarticulated and the representative bones are limited in number. Nevertheless, *Merkurosaurus* exhibits several features (especially the type of ornamentation on the parietal and frontal) that (1) have not been previously recorded in any other Cenozoic taxon from Eurasia, and (2) indicate anguimorph affinity. In addition, frontal and parietal bones of various sizes from *Merkurosaurus* clearly document the ontogeny of these bones, including their pustule-like ornamentation, a feature characteristic of this new taxon.

The taxon Anguimorpha is defined as the most recent common ancestor of *Shinisaurus*, *Xenosaurus*, Anguinae, *Heloderma*, *Lanthanotus*, *Varanus*, and all of its descendants (Estes *et al.* 1988). Estes *et al.* (1988) listed 22 characters that define the Anguimorpha, with which *Merkurosaurus* shares the following:

1. Meckel's groove subdivided near posterior end of dentary tooth row with intramandibular septum well developed.
2. Meckel's groove opens ventrally anterior to anterior inferior alveolar foramen. Although there is no complete lower jaw present, the position of the facets for the splenial indicates this.
3. Replacement teeth develop posterolingually, small resorption pits present.

Other characters listed by Estes *et al.* (1988) concern mostly the postcranium and soft structures (similar to those of Rieppel 1988) and cannot be applied to the remains of *Merkurosaurus*: this differs from the anguimorph *Xenosaurus*, *Shinisaurus*, *Carusia*, *Pseudopus*, *Heloderma* and *Varanus* in the following features, which can serve as its autapomorphies:

1. Nasal process of premaxilla long, slender, with bilaterally constricted shaft and widened dorsal portion; dorsal portion of nasal process terminates in three distinct processes of which the median process is the longest and most pointed.
2. Ornamented surface of parietal subdivided into five pustule-like mounds on right and left sides and one mound around posterior and lateral margins of parietal foramen.

Gao and Norell (1998) introduced a new anguimorph clade, Carusioidea, which includes *Carusia intermedia* from Late Cretaceous deposits in the Gobi Desert, *Xenosaurus*, *Shinisaurus*, and possibly *Restes* and *Exostinus*. According to Evans and Wang (2005), the Early Cretaceous *Dalinghosaurus longidigitus* from China could represent an early carusioideid. However, in his phylogenetic analysis Conrad (2006) placed *Carusia* at the base of Anguimorpha.

Merkurosaurus shares with *Carusia* (Gao and Norell 1998) and *Dalinghosaurus* (Evans and Wang 2005) the following characters:

1. Frontal fused with deep cristae cranii.
2. Lateral border of frontals strongly constricted between orbits.
3. Double interorbital row of large mounds diverging posteriorly along orbital margin. This is also present in *Shinisaurus*, although the individual mounds are less pronounced.
4. Postorbital ramus of jugal ornamented.
5. Small mounds on frontal and parietal with ornamented vermiculate structures. In *Carusia* the parietal is covered with cranial osteoderms (dermal units) ornamented with vermiculate sculpture. The arrangement of the mounds in *Merkurosaurus* is very similar to that in *Dalinghosaurus*, although the number of mounds is higher in *Dalinghosaurus* and their arrangement is also slightly different in the latter genus. The type of ornamentation of the dorsal surface of the parietal plate in *Xenosaurus grandis* is similar in certain respects to that of *Merkurosaurus*. In *Xenosaurus*, the parietal plate is covered by rows of tubercles that diverge radially from its centre. The surfaces of the tubercles bear grooves and ridges. The parietals and frontals of the Late Cretaceous platynotans *Parviderma*, *Gobiderma* and *Proplatynotia* from the Gobi Desert, Mongolia, also bear osteodermal units sculptured by pits and furrows (Borsuk-Białynicka, 1984), but other morphological characters of these three genera with respect to equivalent skull and jaw bones, and teeth, are different from those in *Merkurosaurus*.
6. Parietal foramen within parietal but close to anterior margin.

Merkurosaurus shares the above characters 1, 3, 4 and 6 with *Shinisaurus* and *Bahndwivici*, and the morphology of the teeth and osteoderms is very similar in the three taxa. Characters 5 and 6 are also shared with xenosaurs, as is the suture between the posteroventral margin of the intra-mandibular septum and the medial surface of the dentary. All of these similarities suggest a close phylogenetic relationship between *Merkurosaurus*, *Shinisaurus*, *Bahndwivici*, *Carusia* and *Dalinghosaurus*, and partially with *Xenosaurus*. However, more complete material of *Merkurosaurus* is needed to confirm this.

Biogeography

With reference to the above, *Dalinghosaurus* is from the Lower Cretaceous of China (Evans and Wang 2005) and *Carusia* is from the Upper Cretaceous of Mongolia (Gao

and Norell 1998). Conrad (2006) described a new shinisaurid, *Bahndwivici ammoskius*, from the Lower Eocene of the USA, which, together with the Recent *Shinisaurus crocodilurus* from China and Vietnam, was included in the family Shinisauridae. In his phylogenetic analysis, Conrad (2006) separated Shinisauridae from Xenosauridae in which *Shinisaurus* was traditionally placed (see review in Conrad 2004). The Xenosauridae includes the Recent genus *Xenosaurus*, which is restricted to Mexico and Guatemala, and two North American fossil genera: *Exostinus* from the Upper Cretaceous and *Restes* from the Upper Paleocene and Lower Eocene (Gauthier 1982; Conrad 2006). The fragmentary fossil remains from Asia originally attributed to 'xenosaurs' (in the previous sense) now require revision. However, despite the fact that the shinisaur-xenosaur interrelationship has been resolved, Conrad (2006) concluded that at present it is not possible to determine whether shinisaurids were an Asian group that invaded North America before the end of early Eocene or vice versa. *Merkurosaurus* from the Lower Miocene of Europe represents the only anguimorph with a pustule-like ornamentation on the parietals and frontals recorded from the Cenozoic of Eurasia. Regardless, the similarities between *Merkurosaurus*, *Shinisaurus*, *Bahndwivici*, *Carusia* and *Dalinghosaurus*, as described above, strongly indicate the existence of a widespread group of these anguimorphs which survives in Eurasia, although its origin remains unknown. *Merkurosaurus* represents the youngest fossil member of this group and the only one recorded in Europe.

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