A NEW SPECIES OF THE SAUROPTERYGIAN *CYMATOSAURUS* FROM THE LOWER MUSCHELKALK OF THURINGIA, GERMANY

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ABSTRACT. The sauropterygian *Cymatosaurus*, *C. minor* sp. nov., from the Lower Muschelkalk of Hetschburg near Bad Berka, Thuringia, Germany, is described. It differs from other species of its genus by its relatively small overall size, the development of a parietal sagittal crest, a comparatively long and narrow upper temporal fossa, the anterior extent of the parietals reaches to a level well in front of the posterior margins of the orbits, and the vomers are fused. The acid-prepared skull preserves some interesting anatomical detail, and documents for *Cymatosaurus* the same derived course of the internal carotid through the basicranium that has previously been described for *Nothosaurus* and *Simosaurus*. A detailed geographical and stratigraphical analysis of the occurrence of the genera *Nothosaurus* and *Cymatosaurus* in the Muschelkalk suggests competitive exclusion between the two genera.

CYMATOSAURUS first appears in the fossil record in the uppermost Buntsandstein of Rüdersdorf near Berlin (E. von Huene 1944). Additional material has come from the Lower Muschelkalk of eastern Germany (Halle/Saale: von Fritsch 1894) and Upper Silesia (now Poland: Gürich 1884, 1891; Koken 1893; Schrammen 1899). Early westward expansion through the Muschelkalk Basin may be documented by a humerus, possibly referable to the genus *Cymatosaurus*, from the Lower Muschelkalk of Winterswijk, Netherlands (Oosterink 1986; Rieppel 1994*a*; but see the discussion of the genus *Anarosaurus* in Rieppel and Lin 1995). The early invasion of the Alpine Triassic is documented by the appearance of the genus in the Lower Anisian of the Lechtaler Alps, Austria (F. von Huene 1958; Rieppel 1995*a*; Rieppel and Hagdorn 1996). The occurrence of the genus in the Lower Muschelkalk of Wadi Ramon, Israel, remains controversial at this time (Haas 1963; Sues 1987). The genus is not known from deposits younger than the Lower Muschelkalk.

Cymatosaurus has not previously been recorded from Thuringia. Jaekel (1911, p. 148, fig. 161; this specimen has not been located) figured a skull from the Lower Muschelkalk of Mühlhausen, which he referred to '*Nothosaurus* (*Cymatosaurus*) cf. *fridericianus*'. *Cymatosaurus fridericianus* von Fritsch, 1894, is the type species of the genus, but the skull figured by Jaekel (1911) represents *Nothosaurus marchicus* (Rieppel and Wild 1996), as is indicated by its proportions. All other sauropterygians from Thuringia (*Placodus*: Rieppel 1995*b*; Cyamodontoidea indet: Rieppel 1995*c*; *Nothosaurus*: Rieppel and Wild 1996) are from the Upper Muschelkalk of Bad Sulza. In this paper, we describe a recently located (by RW) incomplete skull from the Lower Muschelkalk of Hetschburg near Bad Berka, Thuringia. This skull lacks the rostrum, but can be referred to the genus *Cymatosaurus* on the basis of shared diagnostic characters (see description below).

A recent review of the genus *Cymatosaurus* (Rieppel 1997) showed that of all the species previously described, only three can be considered valid, viz. *Cymatosaurus fridericianus* von Fritsch, 1894, *Cymatosaurus latifrons* Gürich, 1884, and *Cymatosaurus multidentatus* (F. von Huene, 1958). All other previously described species of *Cymatosaurus* are considered to be junior synonyms of *Cymatosaurus latifrons* (*C. gracilis* Schrammen, 1899; *C. silesiacus* Schrammen, 1899), or a *nomen dubium* (*C. erythreus* E. von Huene, 1944). Although incomplete, the skull described here can be assigned to a separate species.
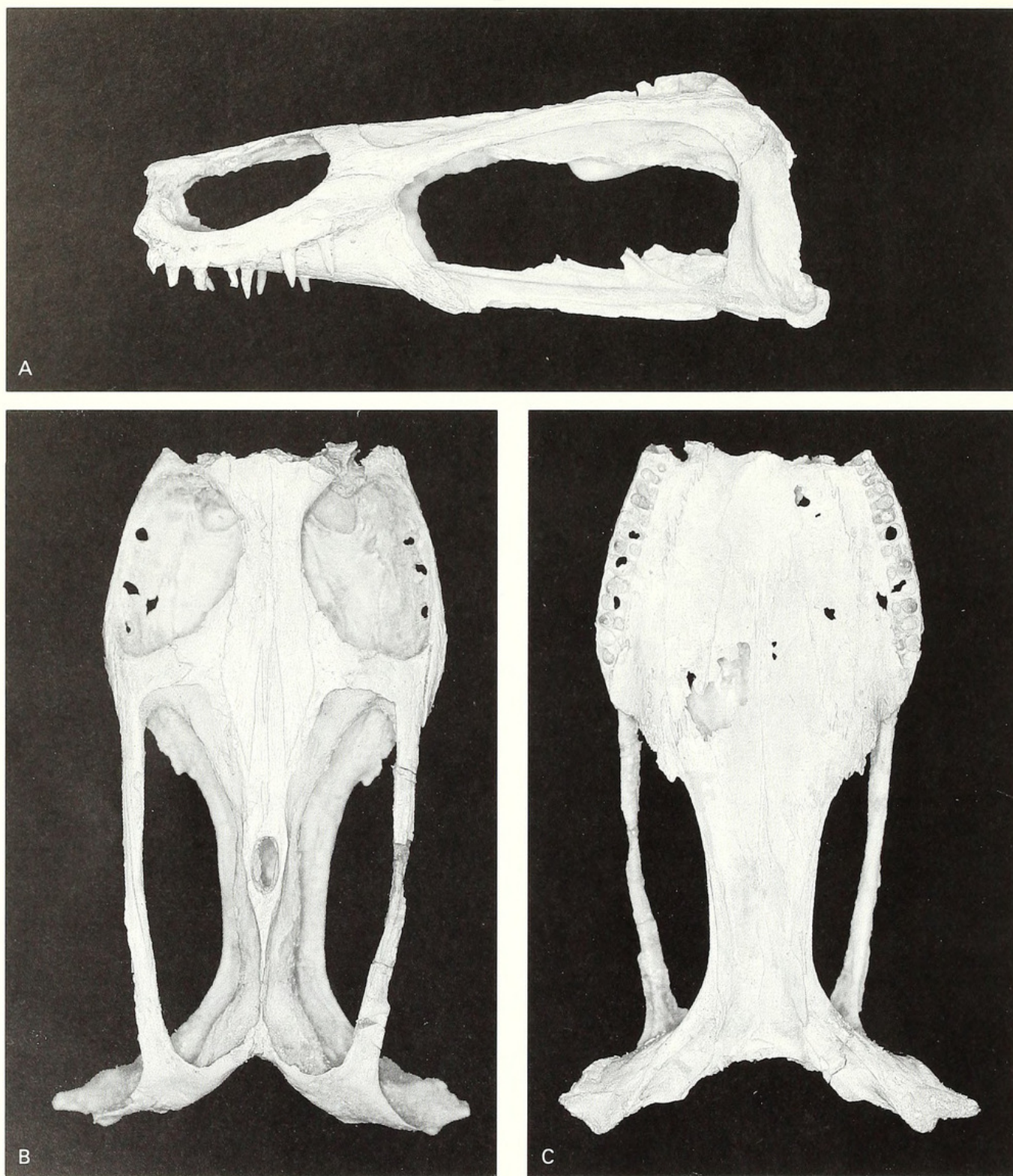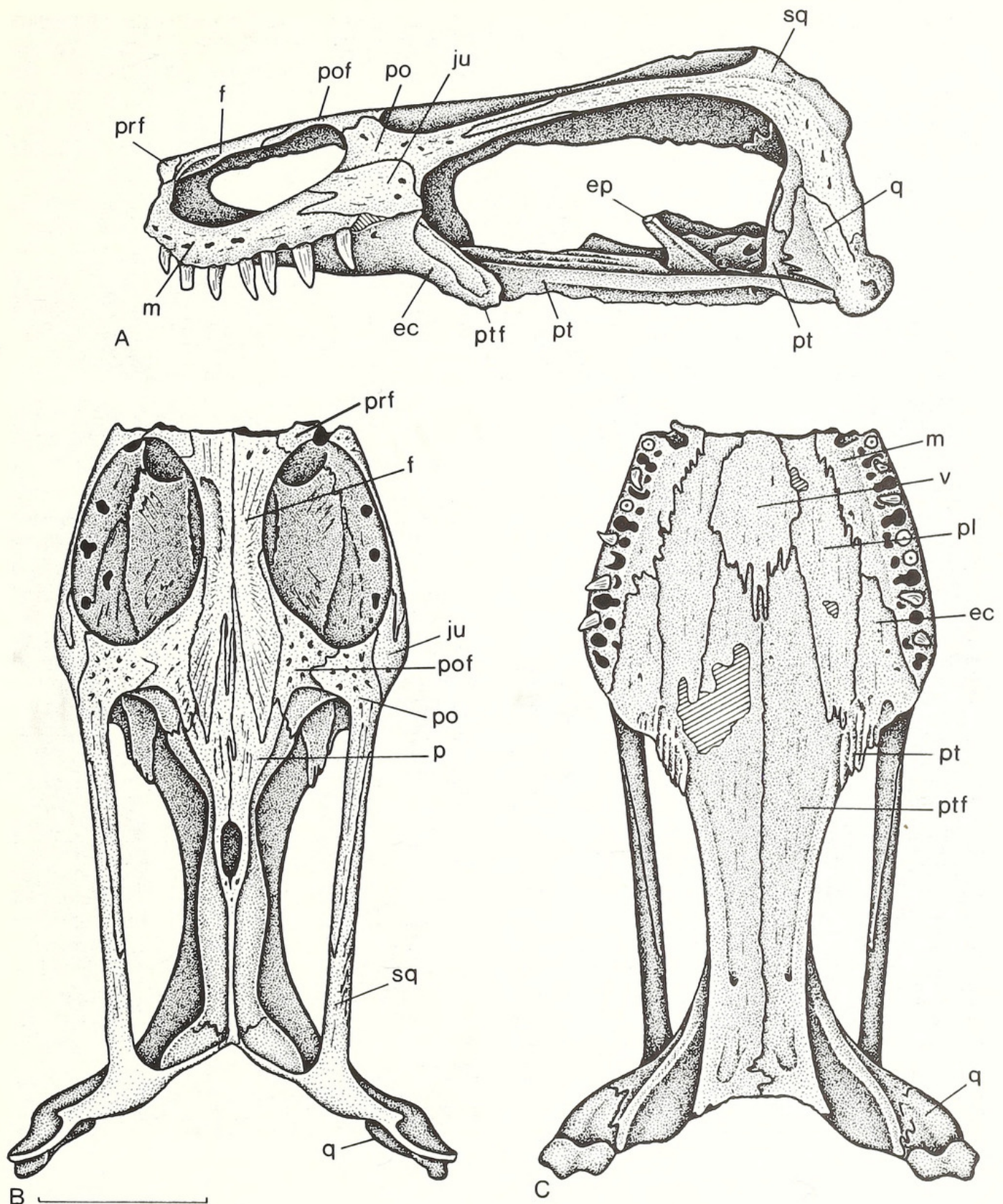
TEXT-FIG. 1. *Cymatosaurus minor* sp. nov.; holotype, NHMS-GT 21; skull in A, left lateral view; B, dorsal view; C, ventral view. All ×1·125.

TEXT-FIG. 2. The skull of *Cymatosaurus minor* sp. nov. A, left lateral view; B, dorsal view; C, ventral view. Scale bar represents 20 mm. Abbreviations: ec, ectopterygoid; ep, epipterygoid; f, frontal; ju, jugal; m, maxilla; p, parietal; pl, palatine; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; ptf, pterygoid flange; q, quadrate; sq, squamosal; v, vomer.

MATERIAL AND METHODS

The new species of *Cymatosaurus* described here is based on an incomplete skull kept at the Naturhistorisches Museum Schloss Bertholdsburg in Schleusingen, Thuringia, Germany (NHMS-GT 21). The specimen was located by one of us (RW) in the private collection of Paul Georgi, a teacher at the Schleusingen school, and was probably collected in the period between the years 1930 and 1950. The skull was enclosed in a block of limestone, with the rostrum already broken off. The back end of the skull was still covered by approximately 20 mm of matrix, but no part of the cervical vertebral column was attached to the skull. The skull must therefore have been disarticulated before being buried in sediment.

The skull was collected near Hetschburg, *c.* 2 km north-east of Bad Berka and 7 km south-south-west of Weimar in Thuringia. The limestone block containing the skull was most probably collected in the Ilm-valley near Hetschburg, where almost the entire *Wellenkalk* sequence (Lower Muschelkalk, Lower Anisian) crops out. The specimen derives from a bed of limestone about 50 mm thick, which cannot be attributed to any marker horizon of the Lower Muschelkalk. The limestone bed is densely packed with allochthonous bivalves (*Myophoria* cf. *vulgaris*) and gastropods (*Loxenema*), and probably represents a thin-bedded tempestite of the *Wellenkalk* facies.

The skull was completely removed from the surrounding matrix through chemical preparation, by exposing the specimen to 5 per cent. formic acid over a period of 4 weeks. Every time the exposure of bone had progressed by 2 mm, the specimen was thoroughly washed, dried, and the newly exposed bone stabilized by application of a thin film of resin. The only organic remains in the residue were teeth and scales of actinopterygians; it did not contain any bony elements that might have belonged to the endocranium or the postcranial skeleton of the *Cymatosaurus* specimen.

SYSTEMATIC PALAEONTOLOGY

Order SAUROPTERYGIA Owen, 1860
Suborder EOSAUROPTERYGIA Rieppel, 1994*a*
Family CYMATOSAURIDAE F. von Huene, 1948

Cymatosaurus von Fritsch, 1894

Type species. Cymatosaurus fridericianus von Fritsch, 1894, from the Lower Muschelkalk (lower Middle Triassic) of Halle/Saale, Germany.

Diagnosis. Eosauropterygians with a moderately depressed skull; snout constricted; postorbital skull distinctly elongated; occiput deeply concave; supraoccipital vertically oriented and in loose connection with the dermatocranium; distinctly reduced nasals that may or may not enter the external naris; frontals paired; posterolateral processes of frontals closely approach the upper temporal fossa and may enter its anteromedial margin; parietals incompletely or completely fused; jugal enters posterior margin of the orbit and remains excluded from upper temporal arch; quadratojugal absent.

Distribution. Uppermost Buntsandstein and Lower Muschelkalk, Lower Anisian, Middle Triassic, Europe.

Cymatosaurus minor sp. nov.

Text-figures 1–3

Holotype. NHMS-GT 21: incomplete skull (Text-fig. 1). The skull is the only material known for this taxon.

Locality and Horizon. Ilm-valley near Hetschburg, Thuringia, Germany. *Wellenkalk*, Lower Muschelkalk (Lower Anisian, Middle Triassic).

Diagnosis. A relatively small species of *Cymatosaurus* distinguished from all other species by a comparatively long and/or a relatively narrow upper temporal fossa, by the presence of a parietal

sagittal crest, by the anterior extent of the parietals, which reach to a level well in front of the posterior margins of the orbits, and by the fused vomers.

DESCRIPTION

General remarks and measurements. The new species is represented by an incomplete skull with the preorbital region missing due to transverse breakage just in front of the orbits. The basicranium (basisphenoid) is well preserved, but the remainder of the braincase is missing. For reasons discussed below, the skull is interpreted as that of a mature animal, and hence is indicative of a relatively small size for the new species as compared with the other species of *Cymatosaurus* from the Germanic Triassic (the neotype of *Cymatosaurus latifrons* (Gürich, 1884), is considered a juvenile for reasons discussed in Rieppel 1997, and below). Measurements of the specimen are given in Table 1.

Lateral view of skull (Text-fig. 2A). The skull appears moderately depressed, as is characteristic for *Cymatosaurus*. The orbits face dorsolaterally, the upper temporal arch is a delicate structure, and the cheek region is widely open. A fragment of the prefrontal can be located at the anterodorsal margin of the orbit. Its anterior edge is broken, indicating a relatively large dorsal exposure of the prefrontal as is characteristic of *Cymatosaurus*, but unlike *Nothosaurus* where the dorsal exposure of the prefrontal is distinctly reduced. The maxilla forms a relatively high ascending process at the anterior margin of the orbit, again with a broken anterior edge. As in *Nothosaurus*, the lacrimal foramen is located entirely within the maxilla. The maxilla defines most of the ventral edge of the orbit, and meets the jugal at the posteroventral corner of the orbit in a deeply interdigitating suture. The posterior tip of the maxilla is broken, but does not seem to have extended beyond the level of the anterior margin of the upper temporal fossa. The maxillary tooth row does not extend beyond the level of the posterior margin of the orbit, as is characteristic of *Cymatosaurus* (Rieppel 1997). The jugal is a rather broad element with a forked anterior end, one prong narrowly entering the posteroventral margin of the orbit, the second (ventral) prong interdigitating with the maxilla. Dorsally, the jugal contacts the postorbital. Posteroventrally, the jugal contacts the ectopterygoid on the lateral aspect of the prominent pterygoid-ectopterygoid flange. A similar contact of jugal and ectopterygoid is observed in the three dimensionally preserved skull of *Cymatosaurus latifrons* (SMNS 10977; Rieppel 1994b, fig. 11), but not in *Nothosaurus* (Rieppel 1993a, text-fig. 4), due to the backward extension of the maxilla and the reduction of the jugal.

Below the posterior end of the maxilla and of the jugal, the ectopterygoid gains prominent exposure due to the well developed ectopterygoid-pterygoid flange serving as the origin of the superficial pterygoideus muscle. The insertion of the pterygoid aponeurosis is marked by a distinct ridge on the lateral aspect of the ectopterygoid flange. This ridge creates the impression of a separate element sutured to the lateral aspect of the ectopterygoid-pterygoid flange.

The postorbital defines the posterior margin of the orbit and meets the squamosal in a broadly overlapping suture in the upper temporal arch. The anterior tip of the squamosal remains broadly separated from the jugal, as is characteristic of *Cymatosaurus* (*C. latifrons*, SMNS 10977), but unlike *Nothosaurus*, in which the squamosal closely approaches the jugal (*N. marchicus*: Rieppel and Wild 1996). The posterior end of the squamosal forms a broad flange which descends far down towards the ventral margin of the skull, embracing the tapering dorsal margin of the laterally exposed quadrate. The posterior end of the pterygoid forms an interdigitating suture with the anterior margin of the quadrate, and reaches up to contact the descending flange of the squamosal in front of the quadrate. Behind the laterally exposed quadrate, and below the descending flange of the squamosal, the bone surface is rugose, suggesting the possible presence of a quadratojugal. However, there is no positive evidence for the presence of a quadratojugal in *Cymatosaurus minor*, and the quadratojugal appears absent in the other skulls of *Cymatosaurus* well enough preserved to show structural details (BGR S44/3: Rieppel 1994a, fig. 39B).

Dorsal view of the skull (Text-fig. 2B). The prefrontal remains widely separated from the postfrontal along the dorsal margin of the orbit, which is formed by the concave lateral margin of the frontal. The presence or absence of a contact of prefrontal and postfrontal along the dorsal margin of the orbit is highly variable within the species of the genus *Cymatosaurus*, and cannot be used in the diagnosis of separate species (Rieppel 1997). The frontals remain separated (unfused). Their anterior edge is broken, such that the relation of the frontal to the premaxilla, the nasal, and the maxilla cannot be established. A distinct posterolateral lappet of the frontal

TABLE 1. Measurements for *Cymatosaurus minor* sp. nov.; holotype, NHMS-GT21; values in brackets are those of the right side of the skull; all measurements are in mm.

Length of the skull (as preserved)	85·5
Width across the mandibular condyles of the quadrate	52
Width across the posterior ends of the squamosals	27·5
Width across postorbital arches	41
Width at level of anterior margins of orbits	27·5
Width of postorbital arch	4·7 (4·7)
Width of frontal bridge between orbits	7
Longitudinal diameter of orbits	22 (—)
Transverse diameter of orbits	16·5 (17)
Longitudinal diameter of upper temporal fossa	43·9 (44·3)
Transverse diameter of upper temporal fossa	12·5 (11·5)
Longitudinal diameter of pineal foramen	6·3
Transverse diameter of pineal foramen	2·5

extends backwards to a level well beyond the anterior margin of the upper temporal fossa. It does not enter the anteromedial margin of the upper temporal fossa, however, as is the case in *Cymatosaurus fridericianus*, but remains narrowly separated from it by a contact of the postfrontal with the parietal.

The anteromedial margin of the upper temporal fossa is formed by the postfrontal, which also defines the posterodorsal margin of the orbit. Laterally, the postfrontal meets the postorbital in the middle of the postorbital arch, and with an elongate posterior process the postorbital meets the anterior process of the squamosal within the upper temporal arch. The squamosal defines the posterolateral and posterior margin of the upper temporal fossa, and meets the parietal in a slightly interdigitating suture at the posteromedial corner of the fossa.

The parietals remain paired (unfused) in front of the relatively large pineal foramen. A trace of a median suture is retained at the posterior margin of the pineal foramen, beyond which, however, the parietals are fused. The relatively large pineal foramen is located close to the midpoint of the parietal as is typical for *Cymatosaurus*, but not for *Nothosaurus*, where the pineal foramen is displaced backwards. The anterior end of the parietals is forked: a short anterolateral process meets the postfrontal in a narrow suture along the anteromedial margin of the upper temporal fossa, whereas narrow and elongated anteromedial processes of the parietals enter deeply between the posterior lappets of the frontals, reaching to a level in front of the posterior margin of the orbits. This degree of anterior extent of the parietal(s) is not known in other species of *Cymatosaurus*, and hence is a diagnostic feature of *Cymatosaurus minor*. The posterior part of the parietal skull table is elaborated into a narrow sagittal crest, unknown in any other species of *Cymatosaurus*, and hence is another diagnostic character of *Cymatosaurus minor*. The posterior corner of the upper temporal fossa is rounded, and the occiput is deeply excavated in dorsal view, as is characteristic for *Cymatosaurus*.

Ventral view of the skull (Text-fig. 2c). The palate is of typical eusauropterygian structure, with the exception of the fused vomers. The anterior end of the skull is broken just behind the internal nares, whose posterior margins can no longer be identified. However, the broad posterior part of the vomer can be seen to enter deeply between the palatines, meeting the pterygoids in a deeply interdigitating, more-or-less transversely oriented suture which lies level with the anterior end of the ectopterygoid. In other species of *Cymatosaurus*, the vomers remain separate. The palatine is located between the maxilla and vomer anteriorly, and between the ectopterygoid and pterygoid posteriorly. As in other sauropterygians, it appears to form a broad portion of the posterior margin of the internal nares, but it does not participate in the formation of the anterolaterally trending flange which serves as the origin of the superficial pterygoideus muscle. This flange is formed by the posterior end of the ectopterygoid, and the distinct transverse process of the pterygoid.

The pterygoids are paired (unfused) elements which extend backwards to the level of the basioccipital condyle (not preserved), thus covering the entire endocranial skull base in ventral view. The slightly concave lateral margin of the pterygoid defines the medial margin of the subtemporal fossa. Posterolaterally, the pterygoid extends into a distinct quadrate ramus with well-developed ventrolateral and ventromedial flanges

serving as the origin of the deep pterygoideus muscle. A small foramen on the ventral surface of the posterior part of the pterygoid may have served as the exit for a branch of the palatine artery that continued anteriorly in a shallow groove running along the lateral edge of the pterygoid.

Posterolaterally, the pterygoid meets the quadrate in an interdigitating suture. The prominent mandibular condyle of the quadrate, located somewhat behind the level of the occipital condyle (not preserved), shows a bipartite articular surface that would have fitted a saddle-shaped articular surface on the mandible.

Posterior view of the skull (Text-fig. 3A). The squamosal has a broad occipital exposure which meets the broad occipital exposure of the quadrate in a ventrolaterally trending suture. The braincase is missing, and must have dropped out from the dermatocranial framework before the skull was buried by sediment. Due to the reduction of the posterior skull table to a sagittal crest, the occipital exposure of the parietal is restricted to a narrow strip of bone located between the broad squamosals. The parietal broadens ventrally, but the ventral margin of the occipital exposure of the parietal is deeply concave, forming a notch which must have received the supraoccipital. The smooth edge of the parietal along this notch suggests that the supraoccipital was not fused to the parietal, but that the two bones met in a rather loose connection, much as in a metakinetic skull. Lateral to the parietal, the ventral margin of the occipital exposure of the squamosal shows a shallow yet distinct embayment (on both sides of the skull) with a smooth finished margin, representing the dorsal margin of a distinct notch which is also observed in other, adequately preserved *Cymatosaurus* skulls (BGR S44/3: Rieppel 1994a, fig. 39B). Further preparation of the holotype of *Corosaurus alcovensis*, from the Mid Triassic Alcova Limestone of Casper, Wyoming (Storrs 1991), revealed a similar notch in the squamosal, which receives the distal tip of the (articulated) paroccipital process in a loose articulation. A similar arrangement may be assumed to have been present in *Cymatosaurus*. The loose connection of the braincase with the dermatocranium explains why the otico-occipital segment is missing in all known *Cymatosaurus* skulls. This contrasts with pachypleurosaurs, *Simosaurus* and the *Nothosaurus–Lariosaurus* clade, in which the occiput is closed and plate-like, and the braincase is fused with the dermatocranium.

The basicranium (Text-fig. 3B). The skull described here is remarkable for its preservation of the basicranium which indicates that in spite of a loose suspension of the otico-occipital segment (supraoccipital, paroccipital process) from the parietal unit (parietal, squamosal), the palatobasal articulation was fused in *Cymatosaurus*, as in all other Sauropterygia, and the skull thus was akinetic. A rugose surface of unfinished bone on the posteromedial part of the pterygoid indicates the sutural facet for the basioccipital which, although not preserved here, forms the occipital condyle in other *Cymatosaurus* skulls (BGR S44/3: Rieppel 1994a, fig. 39B). In front of the sutural facet for the basioccipital, the sella turcica rises as a shallow yet prominent feature, separated in two halves by a distinct longitudinal furrow. Each half assumes the shape of an elevated oval platform. In front of the sella turcica lies the deeply recessed, narrow and elongated fossa hypophyseos with paired foramina in its posteriormost part, serving as the exit for the cerebral carotids. The cerebral carotids continued anteriorly in deep grooves within the fossa hypophyseos, separated from one another by a distinct ridge or septum, longitudinally subdividing the fossa hypophyseos. In front of the fossa hypophyseos, the bone surface is slightly damaged, but more anteriorly a distinct yet narrow longitudinal ridge is observed, running anteriorly on the dorsal surface of the pterygoids. This ridge must have supported the trabecula communis (the fused trabeculae cranii), which indicates a tropibasic skull.

Anterolateral to the sella turcica, rudiments of the epipterygoid are preserved on both sides of the skull. The epipterygoid has a broad base sutured to the dorsal surface of the pterygoid, but seems to have extended dorsally into a narrow strut, as both its anterior and posterior margins are strongly concave. A canal running between the sella turcica and the epipterygoid represents the cavum epiptericum, and must have accommodated the lateral head vein. This vein must have entered the cavum epiptericum through a deep recess or foramen located between the lateral margin of the pterygoid and the overhanging margin of the raised sutural facet on the pterygoid which received the basioccipital.

Of special interest are the grooves exposed on the posterodorsal surface of the quadrate ramus of the pterygoids, and bridging the transition from the smooth bone surface to the unfinished surface of the basioccipital facet. In the complete skull, these grooves served as the entry of the internal carotid into the basicranium, and must have opened on the posterodorsal surface of the quadrate ramus of the pterygoid half way between the basioccipital anteromedially and the quadrate posterolaterally. From there, the canal continued anteriorly to enter the sutural interface between the pterygoid and basioccipital, now exposed as a groove on the sutural surface of the pterygoid which received the basioccipital. More anteriorly, the canal pierces the basisphenoid to pass below the sella turcica, where it subdivides. The medial branch opens into the posterior part of the fossa hypophyseos, and served as the passage for the cerebral carotid into the brain cavity.
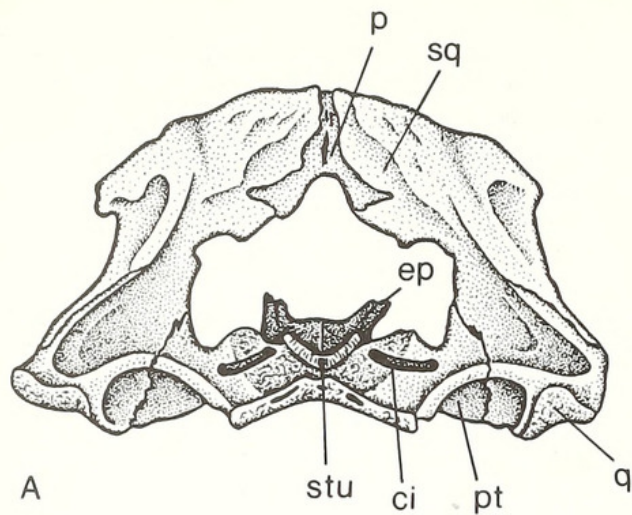
TEXT-FIG. 3. The skull of *Cymatosaurus minor* sp. nov. A, occipital view; B, dorsal view of basicranium. Scale bar represents 20 mm. Abbreviations: cc, foramen for cerebral carotid; ci, canal for internal carotid; ec, ectopterygoid; ep, epipterygoid; fhy, fossa hypophyseos; m, maxilla; p, parietal; pl, palatine; pt, pterygoid; q, quadrate; stu, sella turcica; sq, squamosal.
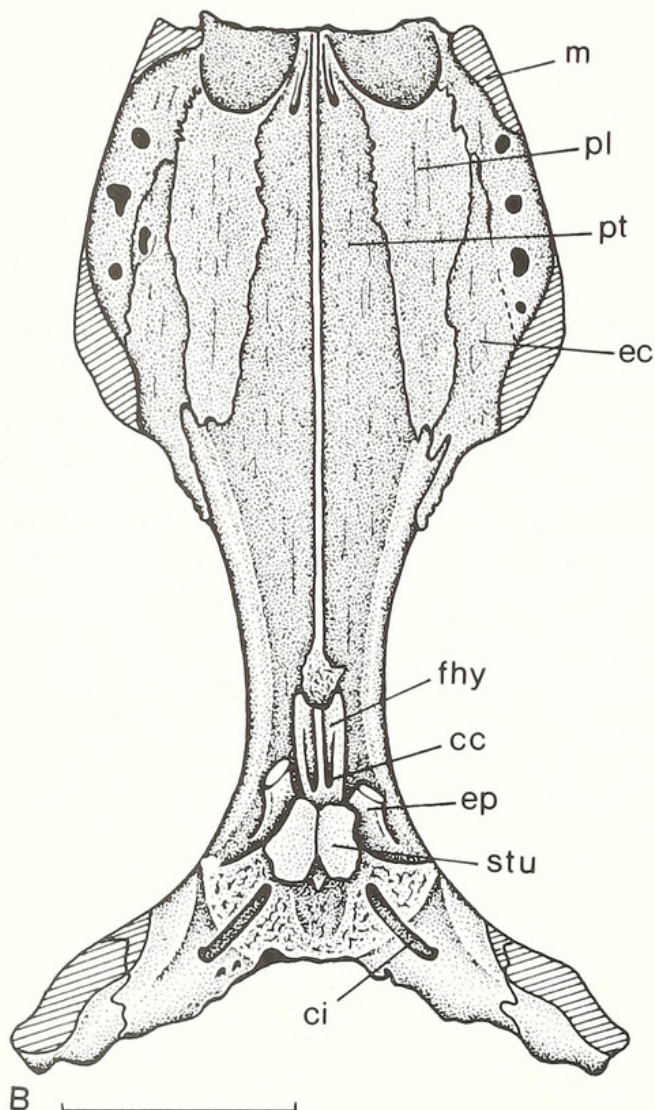
The lateral branch carried the palatine artery. The same unusual course of the internal carotid artery, piercing the quadrate ramus of the pterygoid and passing between pterygoid and basisphenoid on its way to the fossa hypophyseos, was previously reported for the eosauropterygian genera *Simosaurus* and *Nothosaurus* (Rieppel 1994b).
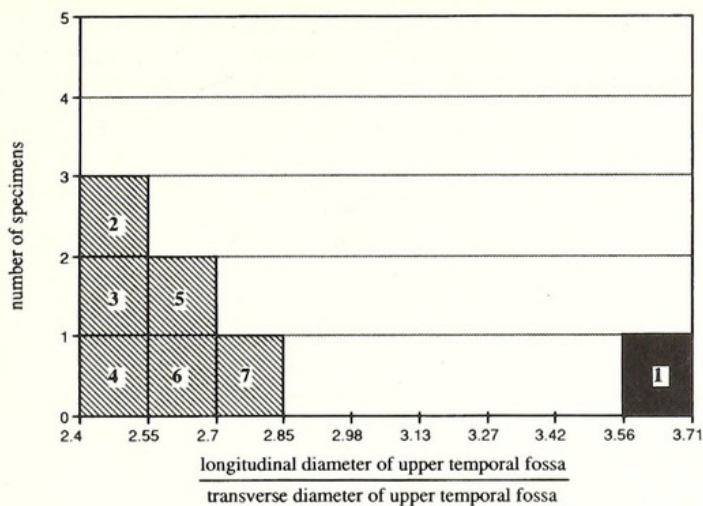
TEXT-FIG. 4. The relation of the longitudinal diameter to the transverse diameter of the upper temporal fossa in *Cymatosaurus*. The numbers refer to the following specimens: 1, *Cymatosaurus minor*, 2, 'specimen I' of *Cymatosaurus gracilis* described by Schrammen (1899; data taken from the literature); 3, 'specimen I' of *Cymatosaurus silesiacus* described by Schrammen (1899; data taken from the literature); 4, holotype of *Cymatosaurus fridericianus* von Fritsch, 1894; 5, neotype for *Cymatosaurus latifrons* (SMNS 10109; 'specimen II' of *Cymatosaurus gracilis* described by Schrammen 1899); 6, incomplete skull; BGR S44/3; 7, skull; SMNS 109877.

Skull proportions. The incomplete nature of the skull renders the assessment of a number of skull proportions impossible. In particular, *Cymatosaurus* (and *Germanosaurus*) have been shown to differ from *Nothosaurus* by a relatively more anterior position of the internal nares (Rieppel 1996), a character which cannot be ascertained for *Cymatosaurus minor*. Dividing the longitudinal diameter of the temporal fossa by the longitudinal diameter of the orbit yields a quotient of 1·3–2·0 for *Cymatosaurus* (including all skulls described in the literature, as well as the skull of *Cymatosaurus minor*), 1·87 for the only known skull of *Germanosaurus*, and 2·1–3·9 for *Nothosaurus* (all skulls deposited in public repositories). As this quotient is correlated with the relative size of the orbit and, therefore, with allometric growth of the orbit, further comments on its utility in taxonomic studies are in order.

The neotype for *Cymatosaurus latifrons* (Gürich, 1844) is the 'second specimen' referred to by Schrammen (1899) in his description of *Cymatosaurus gracilis* (SMNS 10109; see Rieppel 1997 for further discussion). In view of its relatively small size (skull length: 98 mm) relative to other skulls referred to the same species, the specimen may be considered to represent a juvenile. Indeed, the ratio of the longitudinal diameter of the upper temporal fossa to the longitudinal diameter of the orbit is 1·3, indicating relatively large orbits. In the holotype of *Cymatosaurus fridericianus* von Fritsch, 1894 (a large specimen with a skull length of 195 mm), the corresponding ratio is 1·9. The skull of *Cymatosaurus minor* is incomplete, but the specimen can be estimated to be somewhat larger than the neotype of *Cymatosaurus latifrons*, yet it is distinctly smaller than the holotype of *Cymatosaurus fridericianus*, and the corresponding ratio is 2·0. This indicates a relatively smaller orbit, or a relatively longer upper temporal fossa, but the high quotient (2·0, as compared to 1·3 for the juvenile neotype of *Cymatosaurus latifrons*) does not indicate a juvenile status.

The most significant relationship is the longitudinal diameter of the upper temporal fossa divided by its transverse diameter. The ratio for all the skulls of *Cymatosaurus* described in the literature ranges from 2·4 to 2·8, but it is 3·68 for *Cymatosaurus minor*. This indicates that *Cymatosaurus minor* has a comparatively long and narrow upper temporal fossa (Text-fig. 4), another diagnostic character of this new species.

DISCUSSION

Cymatosaurus minor is the smallest species of the genus in which the skull is known; the only species smaller than *Cymatosaurus minor*, if represented by an adult individual, is *Cymatosaurus multidentatus* (see Rieppel 1995a for a complete description). This raises the question of whether *Cymatosaurus minor* is represented by an adult individual. Whereas the orbit usually exhibits negative allometry with respect to skull length in sauropterygians, the relative size of the orbit is not indicative of a juvenile status of the holotype of *Cymatosaurus minor*. The adult status of the holotype of *Cymatosaurus minor* is further supported by the fusion of the vomers, and by the fusion of the parietals in their posterior part. Moreover, extant reptiles, which in the adult feature a sagittal crest, show a flat and broad parietal skull table in early developmental stages (*Sphenodon*: Rieppel 1992; *Chamaeleon*: Rieppel 1993b).

TEXT-FIG. 5. The phylogeny of stem-group Sauropterygia based on cladistic analysis (see Rieppel 1997 for further discussion).
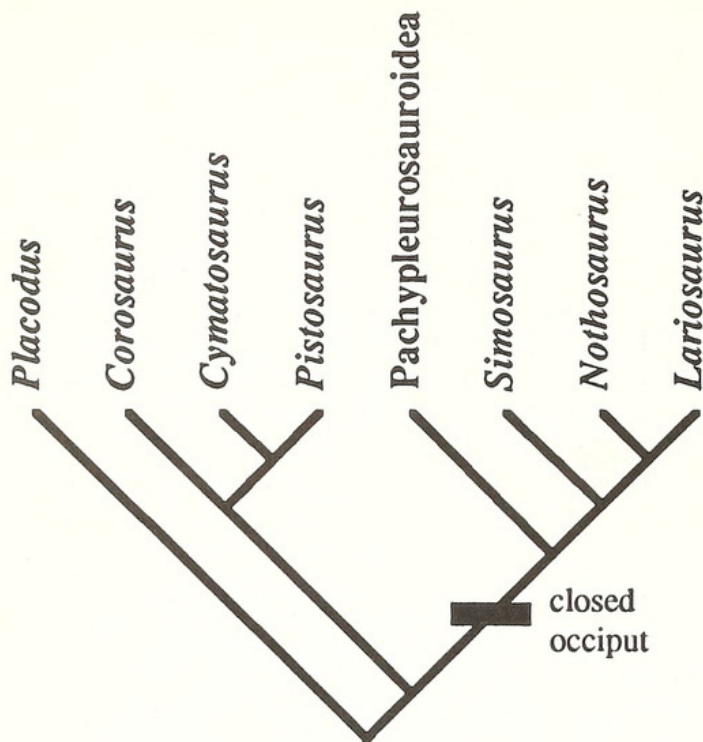
All of the skulls of *Cymatosaurus* currently accessible in public repositories (see Rieppel 1997) lack the posterior neurocranial elements, in particular the supraoccipital, the otic capsules, and the exoccipitals (the otico-occipital segment). In view of the exceptional preservation and preparation of the holotype of *Cymatosaurus minor*, and of the fact that it is represented by an adult individual, the loss of the otico-occipital segment in this specimen cannot be attributed to incomplete ossification in an immature specimen. In generalized reptiles, the skull is metakinetic, with the supraoccipital loosely connected to the parietal (as in *Cymatosaurus*), and the paroccipital process, composed of the opisthotic and exoccipital, loosely abutting against the quadrate suspension (against the squamosal in *Cymatosaurus*). This is not to say that *Cymatosaurus* retained a functionally metakinetic skull; only that it is less derived from the more generalized reptile skull than the skulls of pachypleurosaurs and nothosaurs in that it retains paroccipital processes in loose articulation with the dermatocranium, a loose connection of the supraoccipital with the parietal, and in all likelihood, a small but well-defined posttemporal fossa. Preservation of the endocranial basicranium, solidly fused to the underlying pterygoids, indicates complete fusion of the palatobasal articulation in *Cymatosaurus*, a prerequisite for metakinesis in a more generalized reptile skull. Closure of the dermal palate and fusion of the palatobasal articulation would therefore seem to have preceded fusion of the otico-occipital segment to the dermatocranium in the loss of metakinesis during the evolution of Sauropterygia. Alternatively, and depending on the phylogenetic interrelationships of *Cymatosaurus* and its fossil relatives, the open occiput might have to be considered a secondary development due to character reversal.

A distinct paroccipital process defining the ventral margin of a well defined posttemporal fossa (of variable size) is present in *Placodus* (Rieppel 1995b), *Corosaurus* (Storrs 1991; pers. obs.), and *Pistosaurus* (Edinger 1935) among Triassic stem-group Sauropterygia, and is also the pattern observed in plesiosaurs and pliosaurs (Brown 1981; Taylor 1992; Taylor and Cruickshank 1993). The previous revision of the genus (Rieppel 1997) showed *Cymatosaurus* to be the sister-taxon of *Pistosaurus*, supporting the concept of the Pistosauria proposed by Sanz (1983; see also Sues 1987; Storrs 1991, 1993; Alafont and Sanz 1996). *Pistosaurus*, on the other hand, has traditionally been interpreted as a sister-group or 'structural ancestor' of the Plesiosauroidea (Carroll and Gaskill 1985; Sues 1987; Storrs 1991). Indeed, both *Pistosaurus* (Edinger 1935) and plesiosaurs share the following characters: an open occiput with a well defined paroccipital process and a large

TEXT-FIG. 6. The stratigraphical distribution of the genus *Cymatosaurus* in the German Triassic.
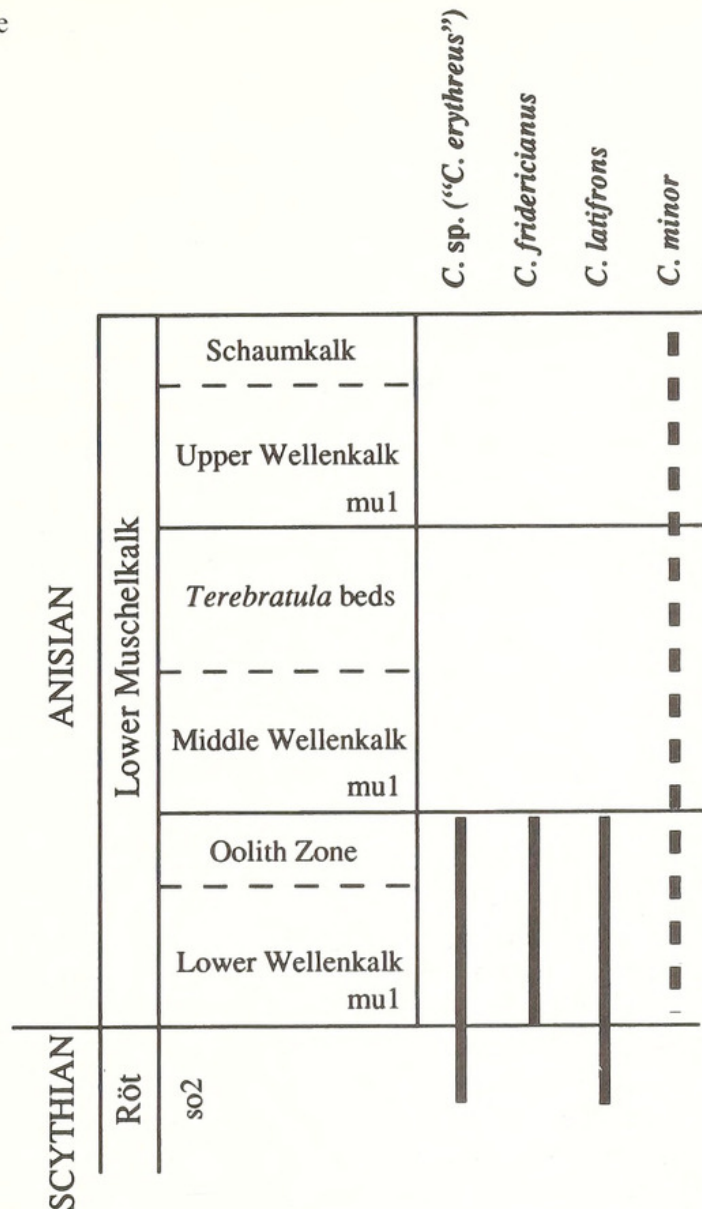
posttemporal fenestra, and a fused palatobasal articulation. The most recent cladistic analysis of the phylogenetic relationships of Sauropterygia (Rieppel 1997, based on 23 taxa and 119 characters) indicates a basal dichotomy within the Eosauropterygia, of which *Placodus* is the sister-group (Text-fig. 5). The one eosauropterygian lineage comprises *Corosaurus*, *Cymatosaurus*, *Pistosaurus* and, by extension, the plesiosaurs and pliosaurs. The second lineage comprises pachypleurosaurs, *Simosaurus* and the nothosaurs (*Germanosaurus*, *Nothosaurus* and *Lariosaurus*) (Text-fig. 5). Based on this pattern of relationships, closure of the occiput and fusion of the otico-occipital segment with the dermatocranium appears to be a synapomorphy of the second lineage, whereas the open occiput represents the generalized condition where it occurs among the Eosauropterygia. However, Testudines also show the fusion of the otico-occipital segment with the dermatocranial unit, and, as long as they continue to be found as the sister-group of the Sauropterygia, the interpretation of the status of the open occiput in the Eosauropterygia (generalized condition or secondarily derived) must remain equivocal.

Assuming that the otico-occipital segment fused with the dermatocranium independently in turtles, closure of the dermal palate and fusion of the palatobasal articulation would be the first step in the evolution of the akinetic skull of Sauropterygia. This development resulted in the derived condition, wherein the internal carotid passed through the basicranium. The entry of the internal

carotid into the quadrate ramus of the pterygoid, and its passage through the pterygoid-basioccipital suture on its way to the fossa hypophyseos, has previously been reported for the eosauropterygian genera *Simosaurus* and *Nothosaurus* (Rieppel 1994*b*), and is here documented for *Cymatosaurus*. Unfortunately, the pathway of the internal carotid is unknown in *Corosaurus*, pachypleurosaurs and lariosaurs (lack of adequate preservation), whereas the internal carotid follows the more generalized path through the cranioquadrate passage in *Placodus*, where the relationship of the basicranium to the dermal palate is drastically different (Rieppel 1995*b*). Unfortunately, lack of knowledge precludes any conclusion, at the present time, at which level of generality the derived course of the internal carotid would be synapomorphic within the Eosauropterygia.

Our current understanding of sauropterygian phylogeny and palaeobiology indicates that the clade entered the Germanic Basin during the period of deposition of the uppermost Buntsandstein and lowermost Muschelkalk (Lower Anisian) through an eastern gateway (Rieppel and Hagdorn 1986; Rieppel 1997). The genus *Cymatosaurus* diversified within the Germanic Basin, giving rise to three species (*C. fridericianus*, *C. latifrons*, and *C. minor*), but at the top of the Lower Muschelkalk, the genus disappears from the fossil record. Looking in more detail at the stratigraphical distribution of *Cymatosaurus* as documented by diagnostic cranial material (Text-fig. 6), its first occurrence is in the uppermost Buntsandstein of Rüdersdorf near Berlin ('*C. erythreus*': E. von Huene 1944) and Jenzig near Jena (SMNS 19077, referred to *C. latifrons*: Rieppel 1997). Most of the skull material comes from the Gogolin beds of Upper Silesia. Unfortunately, the exact stratigraphical correlation within the Lower Muschelkalk remains unknown for the skull of *Cymatosaurus minor*. Probable younger occurrences of the genus in the Germanic basin are documented by an isolated neural arch (MHI 1293/1), associated (but not articulated) with a centrum (MHI 1293/2), from the upper Lower Muschelkalk (*Spiriferina*-Bank, *decurtata* biozone) of Hettingen near Buchen, Badenia (Rieppel and Hagdorn 1996), and by a humerus from the *Schaumkalk* (uppermost Lower Muschelkalk) of Freyburg/Unstrut (Rieppel 1994*a*, fig. 57B). All the diagnostic *Cymatosaurus* material comes from the eastern part of the Germanic Basin, with the exception of the isolated vertebra from Badenia mentioned above (southern part of the Germanic Basin), and an isolated humerus from the Lower Muschelkalk of Winterswijk, Netherlands (western part of the Germanic basin), again probably referable to *Cymatosaurus* (Rieppel 1994*b*, fig. 57A).

The stratigraphical and geographical distribution of *Cymatosaurus* compares in an interesting way with the stratigraphical and geographical distribution of the genus *Nothosaurus*, which first appears in the Upper Buntsandstein ('*N. schimperi*' from Soultz-les-Bains, Alsace (France): von Meyer 1847–55; the specimen is now lost), and which is represented by rare and fragmentary material in the lower Gogolin beds (Kunisch 1888) of Upper Silesia (eastern part of the Germanic basin). Well preserved material of *Nothosaurus* comes from the Lower Muschelkalk of Winterswijk, Netherlands (Oosterink 1986), i.e. from strata of the western part of the Germanic basin which are geologically somewhat younger than Lower Muschelkalk deposits in the eastern part of the Germanic Basin (Rieppel and Hagdorn 1996). But, whereas the Lower Muschelkalk of Winterswijk yielded a fair abundance of *Nothosaurus* material (undescribed specimens in private collections), the possible occurrence of *Cymatosaurus* in that locality is documented only by an isolated humerus (Rieppel 1994*a*, text-fig. 57A; Rieppel and Lin 1995). In the eastern part of the Germanic basin, the fossil record of the genus *Nothosaurus* starts to improve in the uppermost Lower Muschelkalk (*Schaumkalk*) and lowermost Middle Muschelkalk (*orbicularis*-beds, now attributed to the Middle Muschelkalk) with a fair abundance of *Nothosaurus marchicus* (Rieppel and Wild 1996). Relatively large remains (undescribed) of *Nothosaurus* in the Schaumkalk deposits of Freyburg/Unstrut, as well as a specimen (MB.I.007.16, possibly referable to *N. mirabilis*) from the lower Middle Muschelkalk of Oberdorla, document the existence, at that time, of a second species of *Nothosaurus*, again in the eastern part of the Germanic Basin (Rieppel and Wild 1996). The frequency of occurrence of *Nothosaurus* in the eastern part of the Muschelkalk Basin, therefore, increased significantly at a time only (transition from the Lower to the Middle Muschelkalk) when the occurrence of *Cymatosaurus* had already declined. Also, the taxonomic diversification of the genus

Nothosaurus, most notable in the Upper Muschelkalk and beyond, occurred at a time when *Cymatosaurus* had become rare or extinct.

Given the provision that fragmentary sauropterygian remains from the Lower Muschelkalk are sometimes difficult or even impossible to identify, it appears on the basis of abundant material from well sampled localities (lower Lower Muschelkalk: Gogolin (Upper Silesia), Halle/Saale; Lower Muschelkalk: Winterswijk (Netherlands); upper Lower Muschelkalk: Freyburg/Unstrut, Rüdersdorf; lower Middle Muschelkalk: Rüdersdorf, Esperstädt, Jena, Querfurt), that the coexistence of *Cymatosaurus* and *Nothosaurus* was limited, and that the abundance and taxonomic diversity of *Nothosaurus* increased only in the absence of *Cymatosaurus*. This correlation possibly reflects the similar ecological requirements of the two genera. Indeed, the skull morphology of *Cymatosaurus* and early *Nothosaurus* (Winterswijk material, as well as *N. marchicus*) is very similar: both genera share an elongated and constricted rostrum bearing a procumbent dentition, the presence of maxillary fangs, and an elongated postorbital region of the skull characteristic of a dual jaw adductor system (Rieppel 1989, 1994*a*). Apart from the anatomical details pointed out in the descriptive section above, the main morphological changes distinguishing the genus *Nothosaurus* from *Cymatosaurus* are an increase in absolute size (in two species, *N. mirabilis* and *N. giganteus*), a further depression of the postorbital region of the skull, further relative elongation of the postorbital skull (dividing the distance from the tip of the snout to the posterior end of the parietal skull table by the distance from the tip of the snout to the posterior margin of the orbit yields a ratio of 1·4 for *Cymatosaurus*, and 1·7–2·1 for *Nothosaurus*), and the posterior extension of the maxillary tooth row beyond the level of the anterior margin of the upper temporal fossa. Further depression of the increasingly elongated postorbital skull required further differentiation of the dual jaw adductor system (Rieppel 1989), which, together with an elongated tooth row, may indicate increased efficiency of feeding mechanics in *Nothosaurus*.

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