THE STATUS OF THE NOTHOSAURIAN REPTILE *ELMOSAURUS LELMENSIS*, WITH COMMENTS ON *NOTHOSAURUS MIRABILIS*

by OLIVIER RIEPPEL

ABSTRACT. The type and only known specimen of *Elmosaurus lelmensis* Huene was originally described as a pachypleurosauroid and plesiomorphic sauropterygian, but is here redescribed and identified as skull fragment of *Nothosaurus* cf. *mirabilis*. It shares with the Nothosauridae the presence of two caniniform teeth on the maxilla. *Elmosaurus* is compared with a newly prepared and as yet undescribed skull of *Nothosaurus mirabilis* Münster.

IN 1957, Huene described a new genus and species of sauropterygian reptile, *Elmosaurus lelmensis*, which had been found by H. Wehrmann in 1930 along a footpath west of Lelm, near Braunschweig, Germany. The specimen comes from the upper *Ceratites*-layers of the *Hauptmuschelkalk* (Upper Muschelkalk, Ladinian). It consists of a partial skull, broken anteriorly in a transverse plane just in front of the external nares, and posteriorly along an oblique line of fracture passing through the anterior corner of the left upper temporal fossa, continuing through the interorbital space and in front of the right orbit. During preparation of the fossil, impressions of the anteromedial margin of the left upper temporal fossa were noted in the surrounding matrix, as well as what Huene (1957, p. 92) interpreted to be the left lateral margin of the parietal foramen (Text-fig. 2A). These impressions were cast, and the cast subsequently attached to the fossil. The palate is exposed in ventral view, but badly eroded.

Huene (1957) recognized the sauropterygian affinities of the fossil, but noted problems in the analysis of its relationships within the group. He concluded (Huene 1957, p. 97) that the genus represents a 'primitive pachypleurosaurid', and 'the most primitive nothosaurian' known to be derived from a pelycosaurian ancestor. His conclusions notwithstanding, the systematic status of *Elmosaurus* continued to be problematical. Carroll (1988) treated the taxon as a nothosaur *incertae sedis*, while Storrs (1991, p. 135) considered it as a 'possible early offshoot of the Sauropterygia'.

In view of its allegedly plesiomorphic status within the Sauropterygia, a redescription of the specimen seems justified in order to assess its significance for the analysis of sauroptergyian interrelationships.

SYSTEMATIC PALAEONTOLOGY

Superorder SAUROPTERYGIA Owen, 1860
Family NOTHOSAURIDAE Baur, 1889
Genus NOTHOSAURUS Münster, 1834

Type species: *Nothosaurus mirabilis* Münster, 1834, from the Upper Muschelkalk, (Middle Triassic), Germany

Nothosaurus cf. *mirabilis*

Text-figs 1–4

1957 *Elmosaurus lelmensis*, Huene, p. 97.
1988 *Elmosaurus lelmensis*, Carroll, p. 619.
1991 *Elmosaurus lelmensis*, Storrs, p. 135.

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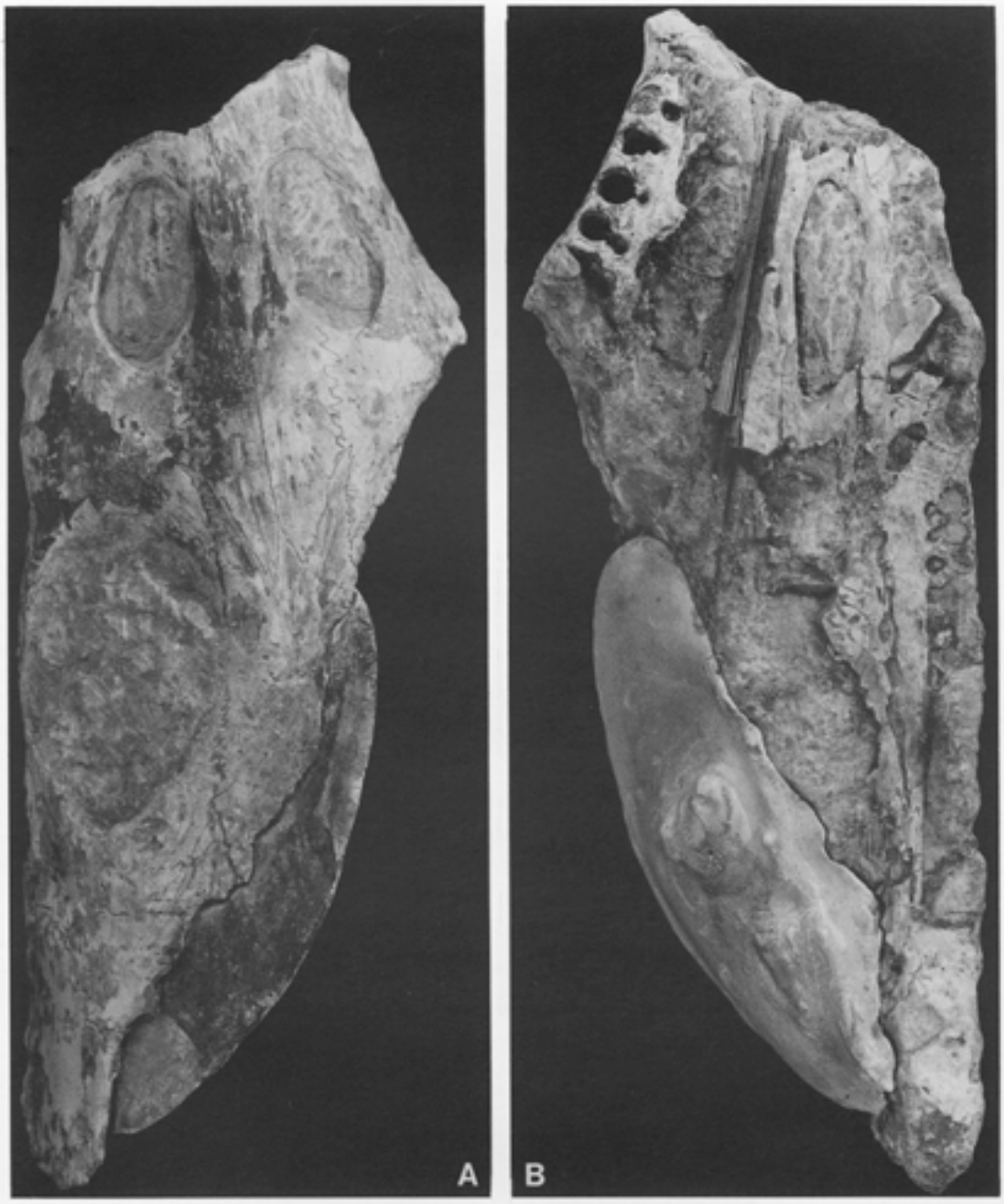
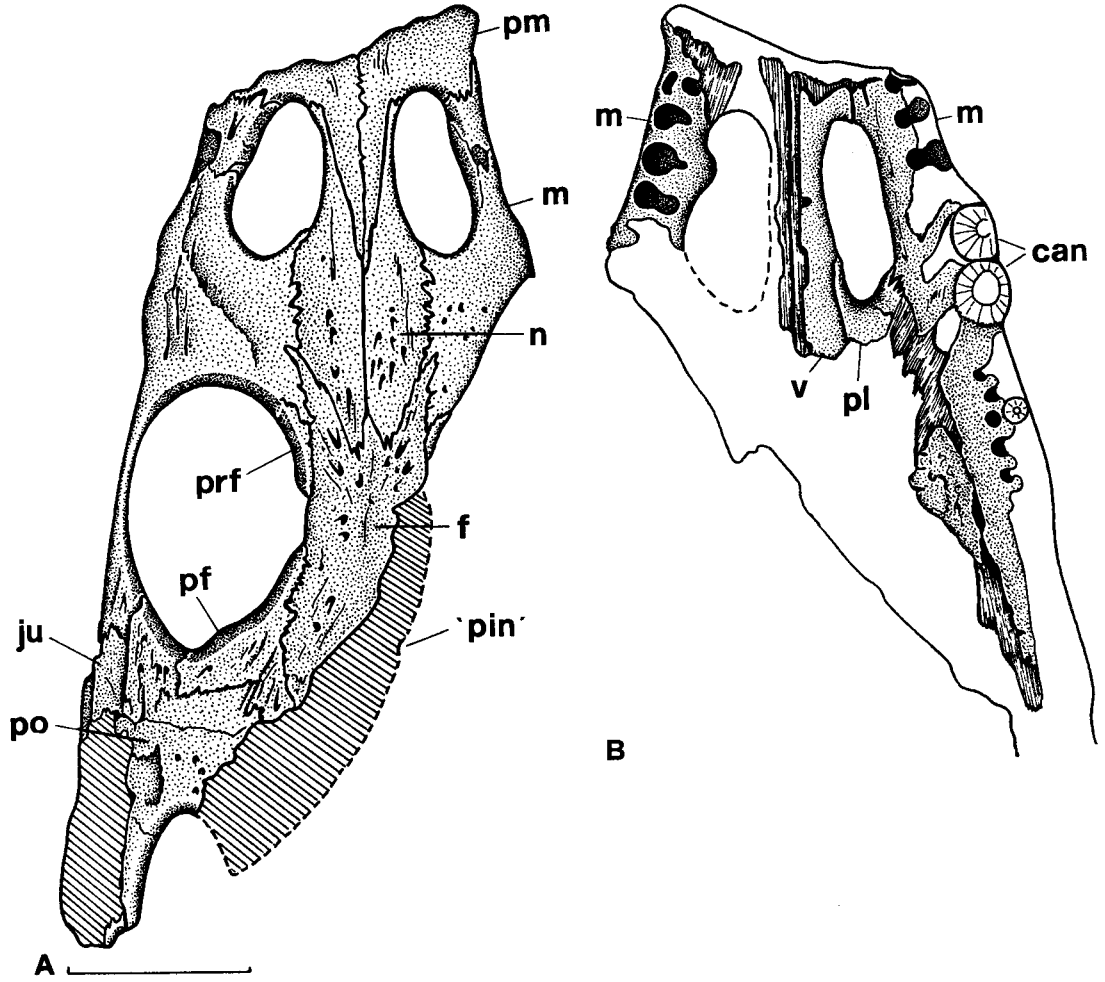


TEXT-FIG. 1. The holotype and only known specimen of *Elmosaurus lelmensis* Huene, 1957 (SMNS 59077); dorsal (A) and ventral (B) views ×1.

Material. Staatliches Museum für Naturkunde, Stuttgart (SMNS) 59077, a partial skull (Text-figs 1–3), the holotype of *Elmosaurus lelmensis* Huene. The specimen formerly belonged to the geological collections of the Technische Hochschule in Braunschweig. The original label attached to the specimen reads as follows: *1930*



TEXT-FIG. 2. The skull of *Elmosaurus lelmensis* Huene, 1957; dorsal (A) and ventral (B) views. The hatched part represents the plaster case of the natural mould left on the matrix by the eroded skull table. Abbreviations: can, caniniform teeth on maxilla; f, frontal; ju, jugal; m, maxilla; n, nasal; pf, postfrontal; 'pin', pineal foramen as identified by Huene 1957; pl, palatine; pm, premaxilla; p, postorbital; prf, prefrontal; v, vomer. Scale bar = 20 mm.

Mixosaurus. Ob. Muschelkalk, Ob. Ceratitenschichten, Lelm (Elm), Steinhaufen, Feldweg. Sammlung Wehrmann, Braunschweig; SMNS 59074, a previously undescribed skull (Text-fig. 4) referred to *Nothosaurus mirabilis* Münster.

Locality and horizon. SMNS 59077, upper *Ceratites*-layers, Upper Muschelkalk (Ladinian), Lelm near Braunschweig, Germany. SMNS 59074, *spinosus* zone, Upper Muschelkalk (Ladinian), Hegnabrunn near Kulmbach, Germany.

Description

The skull in dorsal view (Text-figs 1A, 2A). The preorbital region of the skull shows the fully preserved nasal bones, which meet along the dorsal midline of the snout in an extensive suture, thus broadly separating the posterior (nasal) processes of the premaxillae from the frontal bone. Between the external nares, the nasal

bones are reduced to slender anterior processes which form most of the medial margins of the external nares, terminating in their anteromedial corner. The premaxillae form pointed posterior (nasal) processes, entering between the nasal bones and extending to the level of the posterior margin of the external nares. Posteriorly, the nasal bones are drawn out into pointed tips reaching a level well behind the anterior margin of the orbits, and embracing between them a small anteromedial projection of the frontal bone.

The premaxilla enters the anterior margin of the external naris and meets the maxillary bone at the anterolateral edge of the external naris. The maxilla thus forms most of the lateral margin of the external naris, as well as the latter's posterior margin as it extends dorsally to meet the lateral edge of the nasal bone. More posteriorly, the maxilla enters the anterior margin of the orbit and extends further posteriorly below it to form its lower margin, meeting the postorbital bone in the posteroventral corner of the orbit. The snout on the whole appears slightly constricted at the level of the external naris.

The frontal bone is unpaired. It enters the dorsal margin of the orbit between the prefrontal and the postfrontal bones. Anterolaterally, the frontal forms an elongate and tapering process extending well beyond the level of the anterior margin of the orbit, thus entering deeply between the nasal and maxillary bones, separating the prefrontal from the nasal. The prefrontal bone lines the anterodorsal margin of the orbit. It gains a very limited exposure only on the dorsal surface of the skull.

The postfrontal bone participates broadly in the formation of the posterodorsal margin of the orbit. More posteriorly, however, it narrows abruptly to a slender posterior process which ends at the posterior oblique line of fracture. The relation of the postfrontal to the anteromedial margin of the upper temporal fossa remains unknown. Below the postfrontal, the postorbital participates in the formation of the posteroventral margin of the orbit. It extends posteriorly, forming a broad postorbital arch and can be observed to define the anterolateral margin of the upper temporal fossa. The ventral contact of the postorbital with the maxilla excludes the jugal bone from the posterior margin of the orbit. The jugal is represented by its anteriormost part only.

The supplementing cast, attached to the posterior end of the fossil along the posterior oblique line of fracture, shows the anteromedial margin of the upper temporal fossa in continuation with the postorbital. As preserved, the anterior corner of the upper temporal fossa appears narrow and distinctly smaller than the orbit. Huene's (1957) identification of the lateral margin of the pineal foramen in a very anterior position, at about the level of the posterior margins of the orbits, cannot be corroborated. All that can be seen is a small nick in the margin of the supplementing cast with no clear anatomical relation.

The skull in ventral view (Text-figs 1B, 2B). The bones of the ventral surface of the skull are badly eroded, but remains of both maxillae, of the vomers, and of the left palatine can be identified. The left internal naris and its surrounding bones are well preserved. The narrow vomer forms most of its medial margin, and meets the maxilla in a suture at the midline of its anterior margin. The maxilla lines the internal naris laterally, while the palatine bone is seen to enter the posterior margin of the choana. The broken roots of two distinctly enlarged, i.e. caniniform, teeth can be identified in the maxillary bone at a level of the posterior part of the internal naris.

TABLE 1. Measurements of the holotype of *Elmosaurus lelmensis* Huene (to the accuracy of 0·5 mm). Values in parentheses refer to the right side of the skull.

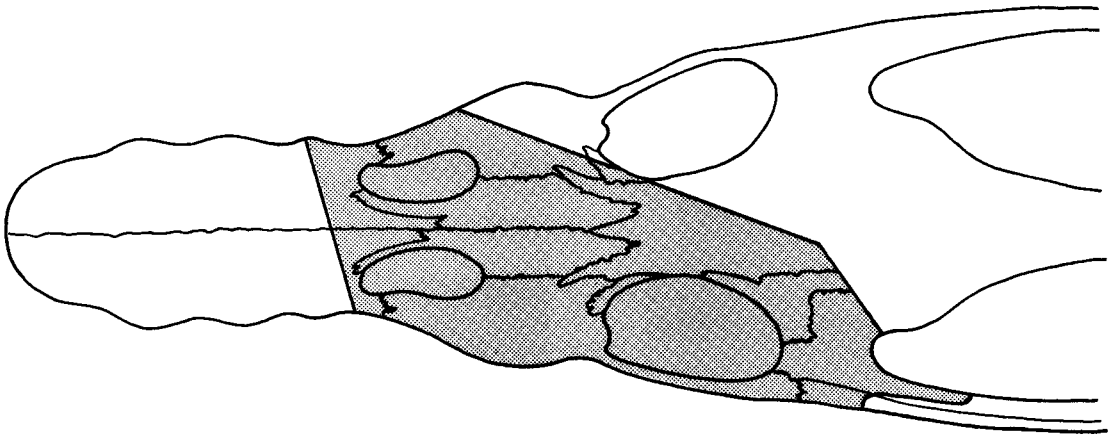
Total maximal length of skull fragment	100
Width of skull between external nares	32
Longitudinal diameter of external naris	16·5 (17)
Transverse diameter of external naris	9·5 (10)
Longitudinal diameter of internal naris	19
Transverse diameter of internal naris	6·5
Longitudinal diameter of orbit	28
Transverse diameter of orbit	22
Distance between external naris and orbit	14·5
Distance between orbit and upper temporal fossa	18
Width of bony bridge between external nares	7
Width of interorbital space (at posterior tips of prefrontals)	12·5

DISCUSSION

The description of SMNS 59077 given above, as well as the corresponding reconstruction (Text-fig. 3), differs markedly from Huene's (1957) description of *Elmosaurus lelmensis* and refutes the hypothesis of pachypleurosauroid relationships, as well as the assumption of a plesiomorphic status of the genus within the Sauropterygia.

SMNS 59077 differs from pachypleurosauroids (Carroll and Gaskill 1985; Rieppel 1989; Sander 1989) with respect to almost all aspects of its morphology, including the constriction of the snout, shape and relations of the nasal bones (which in pachypleurosaurs do not extend along the medial margin of the external naris), the small size of the prefrontal bones, the shape and relations of the postfrontal bone and of the jugal bone, the latter forming a slender and curved element defining most of the ventral and posterior border of the orbit in pachypleurosaurs. Indications of heterodonty, and in particular the presence of paired maxillary fangs, is additional evidence against pachypleurosauroid affinities and suggests nothosaur relationships instead.

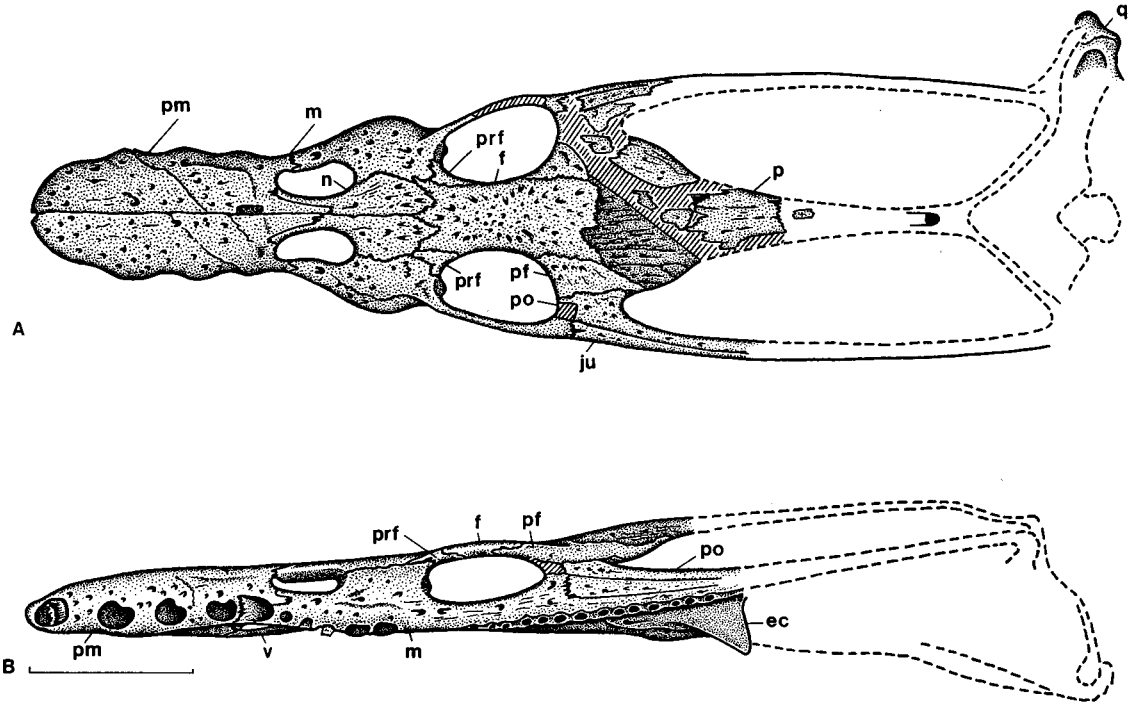
Indeed, the Nothosauridae (*sensu* Tschanz 1989), and *Nothosaurus* in particular (*Paranothosaurus* may well be congeneric with *Nothosaurus*: Kuhn-Schnyder 1966; Storrs 1991; Rieppel and Wild unpublished), are characterized by shared derived characters such as the exclusion of the jugal from the posterior margin of the orbit, and the presence of two caniniform teeth in the maxilla. In addition, SMNS 59077 shares with *Nothosaurus* the configuration of circumorbital bones, as well as the arrangement of elements around the external naris and the choana. It is therefore concluded that SMNS 59077 represents the partial skull of *Nothosaurus* sp. (Text-fig. 3).



TEXT-FIG. 3. Reconstruction of the skull of *Elmosaurus lelmensis* Huene, 1957, interpreted as a partly preserved skull of *Nothosaurus* sp.

The diagnosis of the genus *Nothosaurus*, and its systematics at the species level, remain problematical, which precludes the definitive assignment of SMNS 59077 to any particular nothosaur species at the present time. The problem originates with the introduction of the genus *Nothosaurus* by Münster (1834), who described the type species of the genus, *Nothosaurus mirabilis*, on the basis of a postcranial skeleton, associated with a fragment of the lower jaw. The only nothosaur with a complete skull associated to a postcranial skeleton in *Nothosaurus raabi* Schröder (1914; a junior synonym of *N. venustus* Münster, 1834; see Schultze 1970). The problems originating from this situation concern the diagnosis of, *Nothosaurus mirabilis* on the basis of skull characters, as well as the generic assignment of material known from skulls only. There is, however, a general consensus that *Nothosaurus* is represented by medium to large sized eusauropterygians with a longirostrine skull, constricted snout, large and elongated upper temporal fossae, posteriorly

displaced parietal foramen, and paired caniniform teeth in the maxilla (Tschanz 1989; Storrs 1991). H. V. Meyer (1847–1855, Pl. 1, fig. 1) figured a skull which he assigned to *Nothosaurus mirabilis* and which, in comparison to other nothosaur species, shows a distinctly elongated snout (Schultze, 1970, table 1). The relative length of the snout seems unique among the *Nothosaurus* species so far described, and is matched by the hitherto undescribed specimen SMNS 59074 from the Upper Muschelkalk (Text-fig. 4).



TEXT-FIG. 4. The skull of *Nothosaurus cf. mirabilis*; dorsal (A) and lateral (B) views. Abbreviations: ec, ectopterygoid; f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pf, postfrontal; pl. palatine; pm, premaxilla; po, postorbital; prf, prefrontal; q, quadrate; v, vomer. Scale bar = 50 mm.

The total length of the skull of SMNS 59074, measured from the tip of the snout to the right mandibular condyle (preserved *in situ*) is 324 mm. The distance from the anterior margin of the external naris to the tip of the snout is 72 mm; the longitudinal diameter of the external naris is 23·5 mm (left) and 24·5 mm (right); the longitudinal diameter of the orbit is 36 mm (right); the internarial space is 10 mm; the interorbital space is 19 mm; the distance between the orbit and the external naris is 23·5 mm (left) and 23 mm (right), the distance from the orbit to the upper temporal fossa is 21 mm (right). The relation of the diameter of the external naris to the longitudinal diameter of the orbit is 1 : 1·5; the relation of the distance of the orbit to the external naris to the distance from the orbit to the upper temporal fossa is 1·1 : 1. The relative length of the snout (distance from external naris to tip of snout as percentage of total skull length) in the species of *Nothosaurus* recognized by Schultze (1970, his Table 1) is as follows: *edingerae*: 65·4; *juvenilis*: 54; *venustus*; 67·2; *procerus*: 59·5; *andriani*: 61·6; *chelydrops*: 64·5; *mirabilis*: 47·7; SMNS 59074: 45. In conclusion, SMNS 59074 is here compared to *Nothosaurus mirabilis* Münster, 1834, a species provisionally diagnosed by the apomorphic elongation of the snout, pending future revision.

The last comprehensive review of *Nothosaurus* was conducted by Schultze (1970), who recognized two species from the Lower Muschelkalk (*N. venustus* Münster, 1834; *N. procerus* Schröder, 1914),

and four possible species from the Upper Muschelkalk; *N. mirabilis* Münster, 1834; *N. giganteus* Münster, 1834 (a skull which lacks diagnostic features according to Schultze, 1970); *N. andriani* Meyer, 1839; and *N. juvenilis* Edinger, 1921 (another problematical species, possibly a juvenile of *N. mirabilis*). Schultze (1970) identified features which consistently distinguish the species from the Lower and Upper Muschelkalk, some of which are also observable in SMNS 59077. *Nothosaurus* from the Lower Muschelkalk shows the separation of the prefrontal from the nasal bone by the frontal, and the distance between the external naris and the orbit is somewhat larger than the distance between the orbit and the upper temporal arch (1·1:1 to 1·4:1). Species from the Upper Muschelkalk usually show a larger exposure of the prefrontal on the dorsal surface of the skull, the element meeting the nasal bone; the distance between the external naris and the orbit is smaller than the distance between the orbit and the upper temporal fossa (0·8:1 to 0·9:1).

Measurements and relations involving the orbit are prone to ontogenetic variation, since the orbit usually grows negatively allometric (e.g. Sander 1989). This observation may bear on the interpretation of SMNS 59077, which is a relatively small skull as compared to the other species from the Upper Muschelkalk except for the even smaller *Nothosaurus juvenilis* (Edinger 1921). Schultze (1970, p. 213) addressed the problem of ontogenetic variation in *Nothosaurus* skulls, and found that the relative size of the orbit (as compared to the size of the external naris) is similar for small and large species except in *N. juvenilis*, which shows relatively much larger orbits than the other species. The ratio of the longitudinal diameter of the external naris to the longitudinal diameter of the orbit in SMNS 59077 (1:1·67) falls into the range of variation of other nothosaur species (Schultze 1970, p. 213, 1:1·5–1:1·94) and shows SMNS 59077 to have relatively much smaller orbits that *N. juvenilis* (1:2·7; Schultze 1970, p. 213). The ratio of the distance from the external naris to the orbit to the distance from the orbit to the upper temporal fossa is 0·8:1 in SMNS 59077, and hence corresponds to the values obtained by Schultze (1970) for the *Nothosaurus* species of the Upper Muschelkalk. *Nothosaurus juvenilis* (Edinger 1921; see also Haas 1963, pl. 12) differs from SMNS 59077 by its smaller size, the narrow postorbital arch (perhaps correlated with the large size of the orbit), and by the broad postfrontal bone.

In contrast to SMNS 59077, the prefrontals usually meet the nasals in the nothosaurs from the Upper Muschelkalk. However, Schultze (1970, p. 223) discussed variability of this character, as is further documented by the *Nothosaurus mirabilis* skull (SMNS 59074) from the Upper Muschelkalk, which shows the prefrontal meeting the nasal on the left side, whereas the two bones remain separated by the frontal on the right side of the skull (Text-fig. 4).

In his assessment of *Elmosaurus* as a pachypleurosauroid, Huene (1957) was intrigued by the anterior position of the parietal foramen (not corroborated), and by what appeared to him to be small and narrow upper temporal fossae. Only the anterior corner of the upper temporal fossa is preserved in SMNS 59077, and it does appear relatively narrow. However, the size and shape of the upper temporal fossa in *Nothosaurus mirabilis* (Text-fig. 4) and other species from the Upper Muschelkalk (Schultze 1970, figs 9–12) is entirely compatible with the observations on SMNS 59077. In these species, the upper temporal fossa is large and elongate, but its anterior corner is distinctly constricted due to a convex anterolateral margin of the parietal (this constriction of the anterior corner of the upper temporal fossa is absent in the species from the Lower Muschelkalk: Schultze 1970, figs 2–8). The narrow anterior corner of the upper temporal fossa therefore does not preclude the existence of large temporal fossae in SMNS 59077.

On the basis of the evidence discussed above, *Elmosaurus* Huene, 1957, is considered a junior synonym of *Nothosaurus* Münster, 1834. The skull as preserved differs from the Lower Muschelkalk species by the relative width of the postorbital arch and by the shape of the upper temporal fossa, but it is not diagnostic among the species of the Upper Muschelkalk. *Elmosaurus lelmensis* is therefore referred to *Nothosaurus* cf. *mirabilis* pending future revision of the genus.

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hospitality, workspace and access to the collection at the latter institution. The photographs of *Elmosaurus* were taken by H. Lumpe, also from the Staatliches Museum für Naturkunde in Stuttgart. I thank Drs S. E. Evans, A. R. Milner and an anonymous reviewer for comments on an earlier draft of the paper. This work was supported, in part, by NSF grant DEB – 9220540.

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