THE STATUS OF THE SAUROPTERYGIAN REPTILE *NOTHOSAURUS JUVENILIS* FROM THE MIDDLE TRIASSIC OF GERMANY

by OLIVIER RIEPPEL

ABSTRACT. The holotype and only known specimen of *Nothosaurus juvenilis* from the Hauptmuschelkalk of Germany is redescribed and compared with the type material of all other *Nothosaurus* species described from the Muschelkalk of central Europe. *N. juvenilis* proves to be a valid species diagnosed by morphological features and by cranial proportions, as well as by its small overall size. It overlaps in stratigraphical and geographical distribution with a medium-sized and a large species of the genus *Nothosaurus*, and thus provides the first evidence for niche partitioning among coexisting species of that genus.

NOTHOSAURUS juvenilis was first described by Edinger (1921*a*) in her unpublished Ph.D. thesis. The specimen was collected by R. H. M. König (1862–1921) from the Hauptmuschelkalk (Lower Trochitenkalk, mo1) in the Nusslocher Quarry along the road to Wiesloch near Heidelberg, Germany. Edinger (1921*a*, p. 47) described the skull as *Nothosaurus juvenilis* n. sp., but voiced concern that the specimen might represent a juvenile individual of *Nothosaurus mirabilis*. She asserted that if the status of *N. juvenilis* as a separate species was eventually corroborated, it should be re-named *N. koenigi*, honouring the collector of the fossil. In the same year, Edinger (1921*b*, fig. 4) published an excerpt of her thesis, in which she figured the anterior part of the palate of the specimen; in the figure caption, she referred to the specimen as *Nothosaurus juvenilis* sp. nov., without any further comment. No diagnosis was given for this new species. Her drawing of the palate of *N. juvenilis* was reproduced by Edmund (1960, fig. 11; 1969, fig. 51) in his discussion of tooth replacement in sauropterygians.

The photographs of *Nothosaurus juvenilis* published by Edinger (1921*a*) were reproduced by Haas (1963), who compared the specimen with *Micronothosaurus stensiöi* Haas, a partial skull from Israel (probably referable to *Cymatosaurus* – Schultze 1970) but offered no further statements on the taxonomic status of the specimen. Schultze (1970) redescribed the skull of a small nothosaur from the Lettenkeuper first mentioned by Edinger (1922), designating it the holotype of a new species, *Nothosaurus edingerae*. In so doing, he reviewed the synonymy of nothosaur species on the basis of published descriptions, indicating that a critical review of nothosaur systematics would have to be based on an examination of the original material (Schultze 1970, footnote 1 on p. 218). Nevertheless, Schultze (1970, pp. 225–226) provided the first diagnosis of *N. juvenilis*, arguing that the specimen should be considered a separate species rather than a juvenile specimen of a species already known.

The purpose of this paper is to redescribe the holotype of *Nothosaurus juvenilis* Edinger as preserved today, to corroborate its status as a separate species, and to diagnose it on the basis of homology (synapomorphy, autapomorphy) in comparison with other species of *Nothosaurus* from the Muschelkalk of central Europe (see Appendix for list of comparative material), particularly *N. mirabilis* and *N. 'münsteri'* (the latter species is generally thought to be represented by juvenile *Nothosaurus mirabilis* specimens – Edinger 1921*a*; Schultze 1970; Kruckow 1979). This is part of a research programme designed to identify the terminal taxa (species) within the genus *Nothosaurus* on an unambiguous basis (Rieppel and Wild 1994). The assessment of the phylogenetic relationships of *Nothosaurus juvenilis* will have to await the review of the status of other *Nothosaurus* species

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described to date. The diagnosis of the genus *Nothosaurus* will remain problematical until a better knowledge of the terminal taxa is attained.

SYSTEMATIC PALAEONTOLOGY

Order SAUROPTERYGIA Owen, 1860
Suborder EUSAUROPTERYGIA Tschanz, 1989
Family NOTHOSAURIDAE Baur, 1889
Genus NOTHOSAURUS Münster, 1834

Type species. *Nothosaurus mirabilis* Münster, 1834, from the Upper Muschelkalk, Middle Triassic, of Germany.

Diagnosis. Medium-sized to large eusauropterygians with a longirostrine skull, constricted snout, large and elongated upper temporal fossae, posteriorly displaced pineal foramen, paired fangs in the maxilla, enlarged fangs in the posterior symphyseal area of lower jaw, lower jaw symphysis distinctly elongated and distinctly set off from lower jaw ramus, vertebrae platycoelous and non-notochordal with short and stout transverse processes.

Distribution. Triassic (Anisian to uppermost Carnian) of Europe and Asia.

Nothosaurus juvenilis Edinger, 1921*b*

Text-figures 1–3, 7A

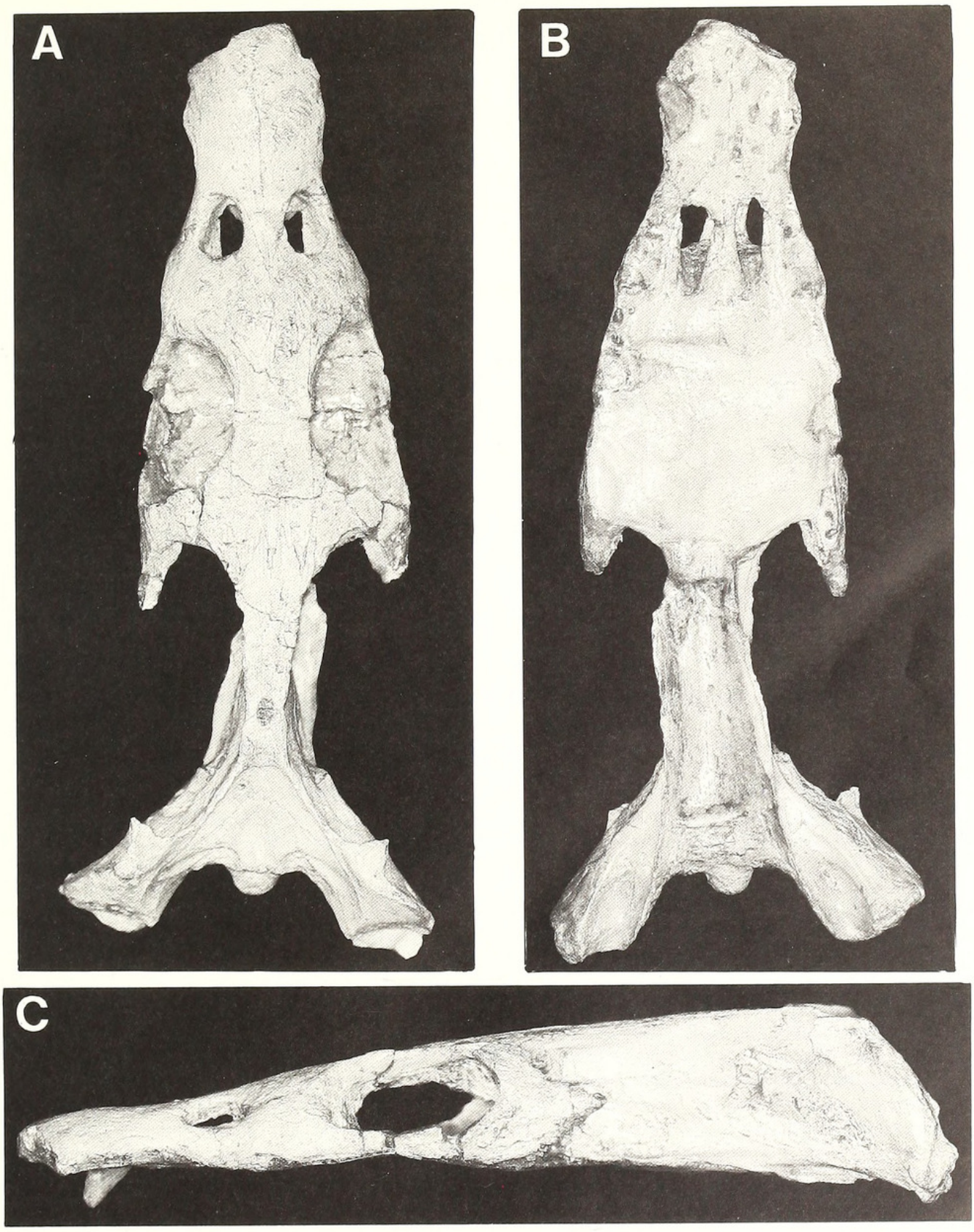
1921*a* *Nothosaurus juvenilis* Edinger, p. 47, figs 8–11 [unpublished].
1921*b* *Nothosaurus juvenilis* Edinger, fig. 4.
1963 *Nothosaurus juvenilis* Edinger; Haas, p. 37, pl. 12.
1970 *Nothosaurus juvenilis* Edinger; Schultze, p. 225, fig. 13.

Holotype. The holotype and only known specimen (Text-fig. 1) is kept at the Palaeontological and Geological Institute and Museum, University of Heidelberg (König Collection, K.8698–1).

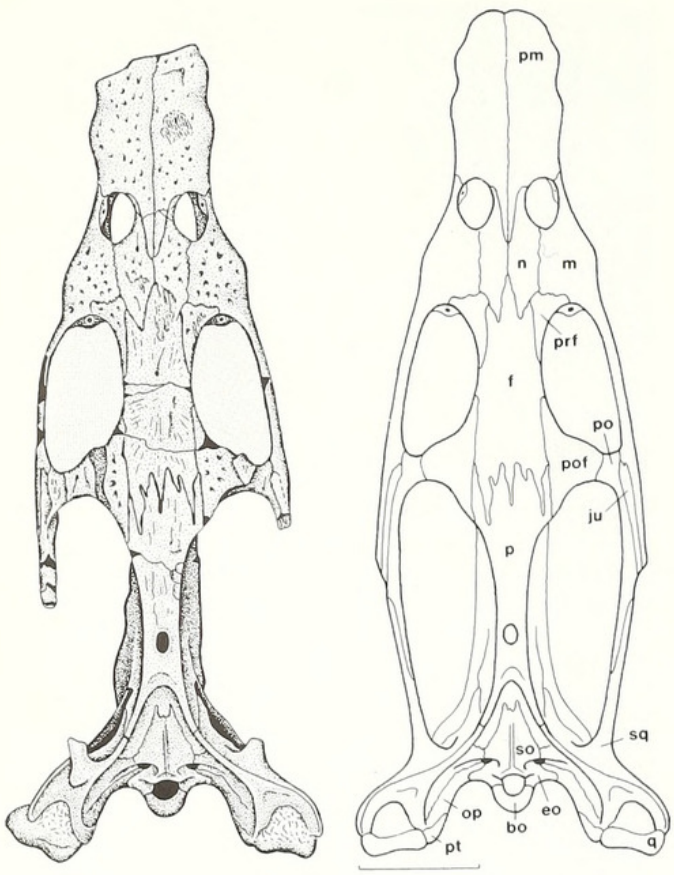
Locality and horizon. Nusslocher Zementbruch, Wiesloch near Heidelberg. Lower Trochitenkalk (mo1, Lower Hauptmuschelkalk, Anisian, Middle Triassic).

Diagnosis. A small species of *Nothosaurus* with relatively large orbits; relatively narrow postorbital arches; the pterygoids closely approach the internal nares; the paroccipital processes trend posterolaterally resulting in a distinct posterior displacement of the lower jaw joints to a level well behind the occipital condyle; the occiput is deeply concave.

Remarks. *Nothosaurus juvenilis* is known from a single skull only. The original condition of the skull of *Nothosaurus juvenilis* is well documented by the photographs included in Edinger's (1921*a*) thesis, and published by Haas (1963). These photographs allow the assessment of the damage suffered by the holotype as available today (Text-figs 1–3). Most importantly, the holotype suffered a break through the postorbital region, causing extensive damage to the upper temporal arches (now lost). The two parts of the skull were glued back together in an imperfect (oblique) manner (corrected for in Text-figs 3–4). The palate seems to have suffered severely, and has now been covered in its middle part by a thick layer of epoxy resin. The bone substance still preserved in this area is extremely thin, and does not allow the identification of morphological detail, nor any further preparation of the specimen.



TEXT-FIG. 1. *Nothosaurus juvenilis* Edinger. Paläontologisches und Geologisches Institut und Museum, Universität Heidelberg, König Collection, K.8698-1 (holotype); Nusslocher Zementbruch, near Heidelberg; Lower Trochitenkalk (Anisian, Middle Triassic). A, dorsal view. B, ventral view. C, lateral view. All $\times 1$.



TEXT-FIG. 2. *Nothosaurus juvenilis* Edinger. Dorsal views of holotype; scale bar equals 20 mm. Abbreviations: bo, basioccipital; ec, ectopterygoid; eo, exoccipital; f, frontal; ju, jugal; m, maxilla; n, nasal; op, opisthotic; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, squamosal; v, vomer.

DESCRIPTION

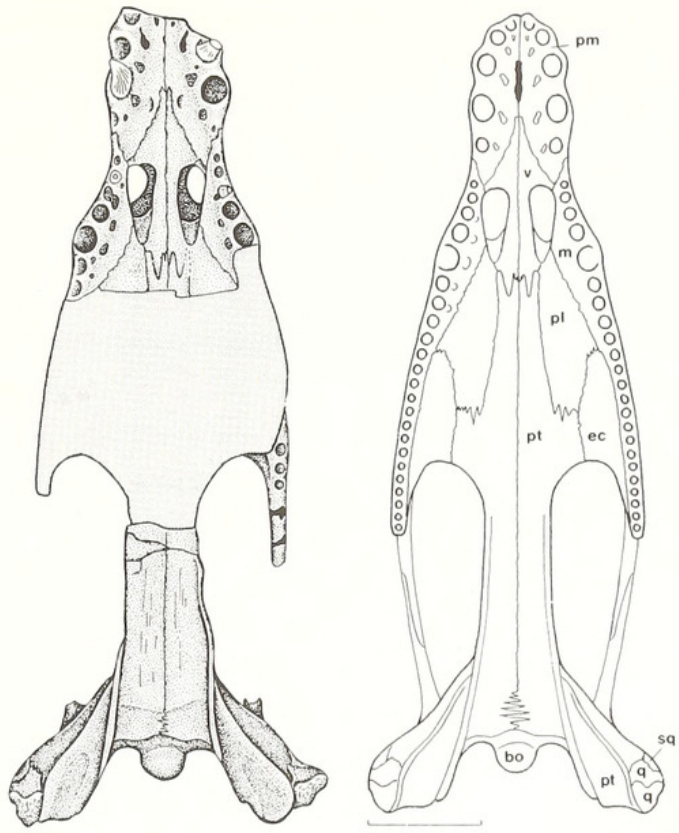
Dorsal view of the skull (Text-fig. 2). The elongated rostrum, characteristic for the genus *Nothosaurus*, is formed by the premaxillae. The premaxilla meets the maxilla at the anterolateral corner of the external naris. The posteromedial nasal process of the premaxilla enters between the external nares, extending somewhat beyond the level of their posterior margin. The premaxilla can be reconstructed to have five tooth positions, the second and fourth teeth being the largest. In between the corresponding tooth positions, the rostrum appears slightly constricted in dorsal view.

The external naris is of rounded, slightly elliptical contour. The nasal bone forms the posteromedial and, with a slender anteromedial process, the entire medial margin of the external naris. The nasal is a fairly broad, plate-like element tapering to a pointed tip posteriorly. It forms an extensive lateral contact with the maxilla, and meets the prefrontal along a well defined posterolateral contact, separating the maxilla from the anterolateral process of the frontal. The nasal bones of the two sides of the skull meet in a short suture along the dorsal midline of the skull, in between the posterior (nasal) processes of the premaxillaries and the anteromedial process of the frontal bone.

The ventral and posterolateral margin of the external naris is formed by the maxilla. In between the external naris and the orbit, the maxilla bulges laterally, indicating the position of the maxillary fangs. The maxilla defines the anterolateral and lateral margin of the orbit, the lacrimal foramen is situated entirely within the maxilla, as is characteristic for *Nothosaurus*.

The frontal bone is unpaired as a result of complete fusion of its progenitors. It enters the dorsal margin of the orbit between the prefrontal and postfrontal bones. Anteriorly, the frontal bears well defined anterolateral processes, entering between the prefrontal and the nasal bones, and an anteromedial process entering in between the paired nasals. Posteriorly, the frontal meets the parietal in a deeply interdigitating suture at the level of the postorbital arch, leaving the posterolateral processes of the frontal ill-defined.

The prefrontal bone defines the anteromedial margin of the orbit. It is well exposed in dorsal view and bears a distinct anteromedial lappet, which establishes a well defined contact with the nasal. The postfrontal bone defines the posteromedial margin of the orbit. It forms the dorsal part of a narrow postorbital arch and broadly enters the upper temporal fossa along its anteromedial margin. The postorbital bone completes the postorbital arch and defines the posterolateral margin of the orbit. Posteriorly, it extends into the (now broken) upper



TEXT-FIG. 3. *Nothosaurus juvenilis* Edinger. Ventral views of holotype; scale bar equals 20 mm. Abbreviations as in Text-fig. 2.

temporal arch. The jugal bone, situated between postorbital and maxilla, approaches the orbit rather closely but remains excluded from its posterior margin.

The parietal bone is unpaired (fused) and forms a flat and narrow parietal skull table. The pineal foramen is located at some distance from the posterior occipital crest formed by the parietal and the squamosal. The parietal gains a narrow occipital exposure, embracing the trapezoidal supraoccipital. Laterally, the parietal meets the squamosal which defines the posterior margin of the upper temporal fossa, extending anteriorly into the (now broken) upper temporal arch. The squamosal gains an occipital exposure, meeting the posterolateral corners of the supraoccipital posterior to the parietal.

Ventral view of the skull (Text-fig. 3). The palate in the holotype of *Nothosaurus juvenilis* is poorly preserved, in particular in its middle (suborbital) region. However, some important details are still discernible. The internal naris is enclosed between the vomer, maxilla, and palatine, as is characteristic for *Nothosaurus*. The vomer defines the entire anterior margin of the internal naris; the vomers enter deeply between the premaxillae with a combined anteromedial process. At the anterolateral corner of the internal naris, the vomer establishes a very narrow contact with the maxilla, apparently excluding the premaxilla from the anterolateral margin of the internal naris. However, preservation is such that a narrow entry of the premaxilla into the anterolateral margin of the internal naris cannot be entirely ruled out, although comparison with other nothosaurs supports exclusion.

The posterolateral margin of the internal naris is defined by the palatine bone which meets the vomer in the posterior margin of the choana. The posterior margin of the internal naris extends into a deep choanal groove. The pterygoid shows a bifurcated anterior tip, with its lateral prong closely approaching the posterior margin of the internal naris (choanal groove) without quite reaching it.

The morphology of the posterior part of the pterygoid is characteristic for the genus *Nothosaurus* (Rieppel 1994): deep flanges for the origin of the pterygoideus internus muscle extend all along the quadrate ramus of the pterygoid to the mandibular joint (partially broken in *Nothosaurus juvenilis*). Behind the pterygoids, the basioccipital is narrowly exposed in ventral view.

Posterior view of the skull. The occiput in the holotype of *Nothosaurus juvenilis* is not completely prepared, and the delicate condition of the skull does not allow further (acid) preparation. The detail that can be observed

corresponds to the standard nothosaur morphology (Rieppel 1994). The trapezoidal supraoccipital defines the dorsal margin of the foramen magnum. The element carries a low sagittal crest. Small but well defined posttemporal fossae are located in a deep recess at the posterolateral corners of the supraoccipital. They are bordered by the supraoccipital (dorsally), squamosal (dorsolaterally), opisthotic (laterally) and exoccipital (ventrally and medially). The posterior surface of the occiput is formed by squamosal (dorsally), opisthotic and pterygoid (ventrally). The exoccipitals define the lateral margins of the foramen magnum, but they do not meet dorsal to the basioccipital. The occipital condyle, defining the ventral margin of the foramen magnum, is formed by the basioccipital only. Lateral to the occipital condyle, the basioccipital carries distinct basioccipital tubers. An eustachian foramen may open between the basioccipital tuber and the pterygoid, or the basioccipital tuber may meet the pterygoid in a closed suture (Rieppel 1994). The condition in the holotype of *Nothosaurus juvenilis* remains unclear due to incomplete preparation. Nevertheless it can be ascertained that the diameter of the basioccipital tuber is distinctly less than that of the occipital condyle.

The cranioquadrate passage is not cleared from matrix in the holotype of *Nothosaurus juvenilis*. Nevertheless, the mandibular condyle of the quadrate, defining its ventral margin, is well exposed. It is important to note that the paroccipital processes in *Nothosaurus juvenilis* trend posterolaterally to a degree which causes the displacement of the mandibular joint to a level well behind the occipital condyle.

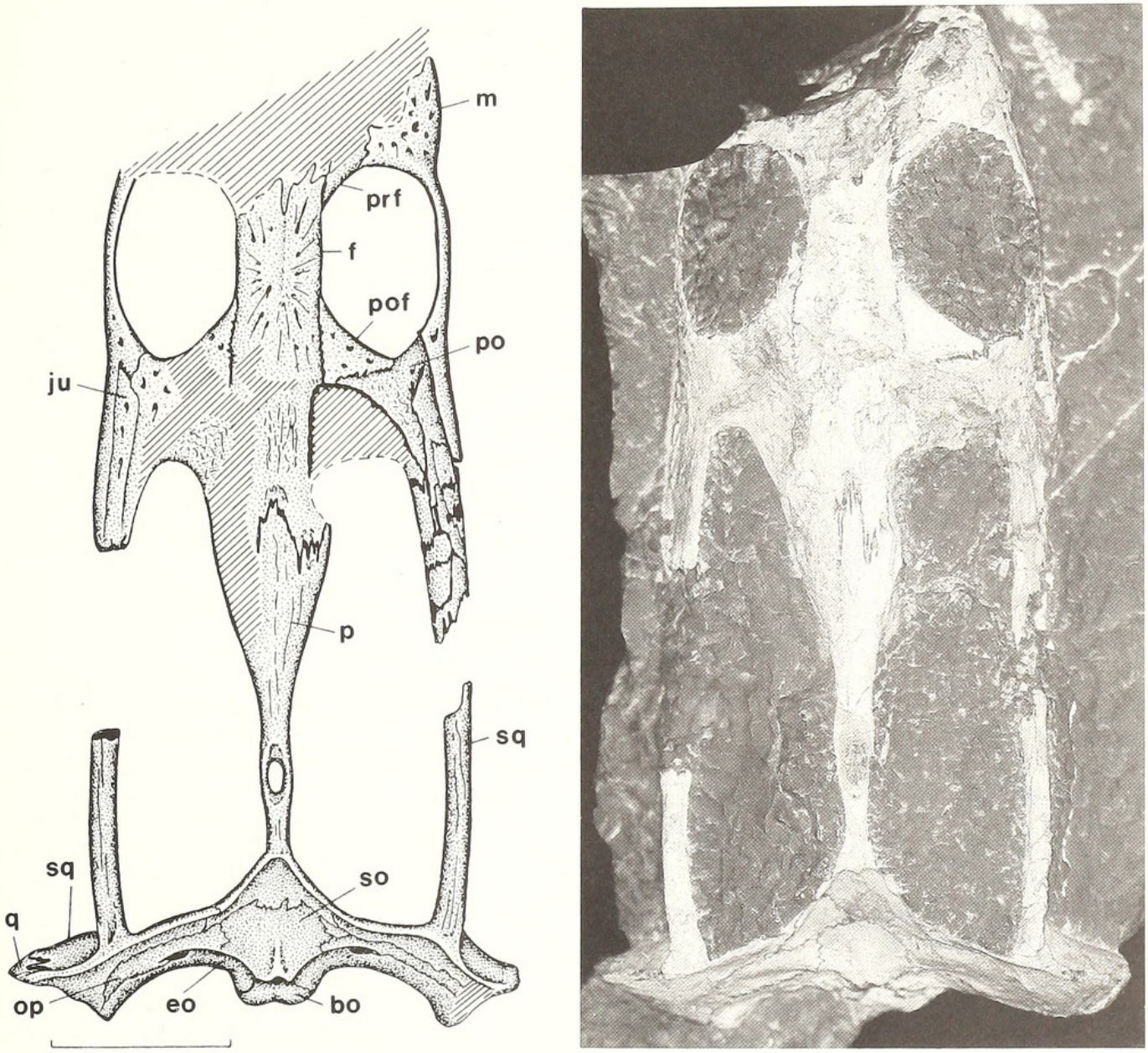
Lateral view of the skull (Text-fig. 1). Again, the lateral view of the skull would require further (acid) preparation to allow the identification of relevant detail, which is impossible due to the condition of the specimen. Nevertheless, the broad-based epipterygoid characteristic of *Nothosaurus* (Rieppel 1994) is well exposed, with deeply recessed anterior and posterior margins and a broad dorsal contact with the laterally descending flange of the parietal.

DISCUSSION

Among the described nothosaur species from the Upper Muschelkalk, *Nothosaurus juvenilis* is exceptional in its small size (apart from *N.* '*münsteri*' discussed below) and its relatively large orbits. This explains why the specimen was considered a possible juvenile of a species already known, such as *Nothosaurus mirabilis* (Edinger 1921*a*). This interpretation was disputed by Schultze (1970) on the basis of a number of morphological features characterizing *N. juvenilis* as a separate species. Indeed, the degree of ossification of the skull of *N. juvenilis* does not suggest an immature status for the specimen. The frontals have completely fused, the margins of the pineal foramen are well defined as are the sutures between braincase elements. The postfrontals enter the anteromedial margins of the upper temporal fenestrae broadly, admittedly a plesiomorphic feature but shared by no other species of *Nothosaurus* from the Upper Muschelkalk. A narrow entry of the postfrontal into the margin of the upper temporal fossa is known in some specimens from the Lower Muschelkalk (Schröder 1914), as well as in *Nothosaurus edingerae* (Schultze 1970; Rieppel and Wild 1994) from the Keuper. Derived features which distinguish *N. juvenilis* from other described species of *Nothosaurus* are, (1) the anterior extent of the pterygoid which closely approaches the posterior margin of the internal naris, in correlation with the differentiation of a deep choanal groove, and (2) the posterior displacement of the mandibular condyles of the quadrates to a level well behind the occipital condyle, resulting in a deeply excavated occiput. Other features diagnostic of *N. juvenilis* are the relatively large orbits, correlated with a relatively narrow postorbital arch. Since these characters are liable to be subject to ontogenetic variation, a close comparison of the holotype of *N. juvenilis* with other nothosaurs, particularly small specimens from the Upper Muschelkalk, seems to be in order.

The most widespread species from the Upper Muschelkalk is *Nothosaurus mirabilis* Münster (1834; see also Meyer 1847–1855) which is of intermediate size among all nothosaurs known from the Upper Muschelkalk, but adults are distinctly larger than *N. juvenilis*. In view of the problematical status of *N. mirabilis* (diagnosed by Münster 1834 on the basis of postcranial remains and a lower jaw fragment), the specimens of that taxon primarily used for comparison in this paper are from the historical material described and figured by Meyer (1847–1855). *Nothosaurus* '*münsteri*' (Meyer, 1847–1855) is of distinctly smaller size than *N. mirabilis*, and generally considered to be represented by juvenile specimens of the latter species (Edinger 1921*a*; Schultze 1970; Kruckow 1979). However, because of its small size, the comparison of the syntypes of *N.*

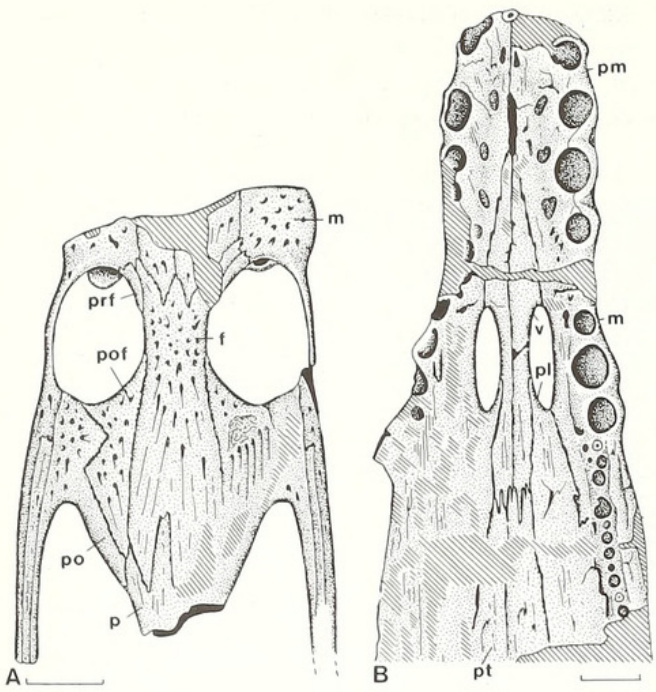
'*münsteri*' (i.e. the specimens figured by Meyer 1847–1855, pl. 9) with the holotype of *N. mirabilis* is important. *Nothosaurus edingerae* is a small nothosaur from the Middle Keuper (Schultze 1970; Rieppel and Wild 1994). Finally, an as yet undescribed small nothosaur skull will be used for comparison (Text-fig. 4). It comes from the Upper Trochitenkalk (Upper Muschelkalk) of



TEXT-FIG. 4. *Nothosaurus* sp. Paläontologisches und Geologisches Institut und Museum, Universität Heidelberg, König Collection, K.3881; dorsal view; drawing with abbreviations as in Text-fig. 2; Steinsfurt; Upper Trochitenkalk (Anisian, Middle Triassic); scale bar equals 20 mm.

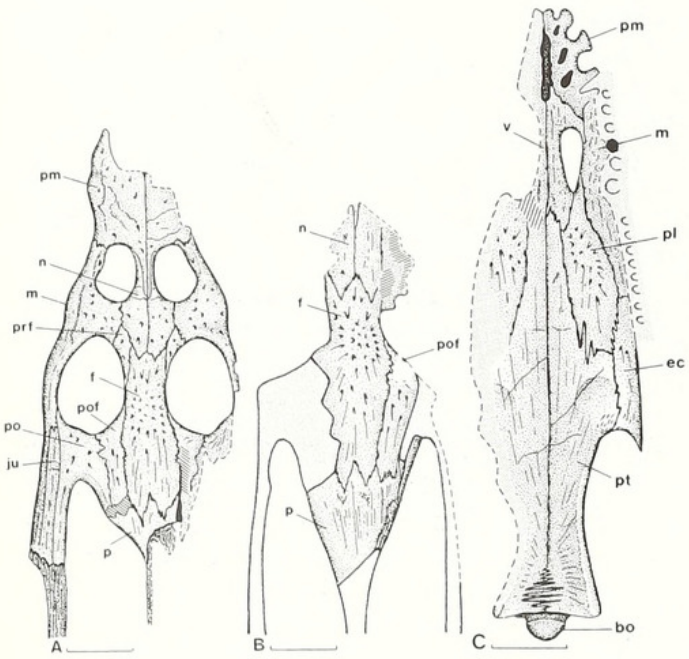
Steinsfurt, and was collected by R. H. M. König (König Collection, K-3881) who also collected the holotype of *N. juvenilis*.

In *N. mirabilis* (Text-fig. 5A–B), the prefrontal usually gains only a limited dorsal exposure and frequently remains separate from the nasal bone; the postfrontal is always excluded from the upper temporal fossa; interdigitation of the fronto-parietal suture may be less complex; the posterolateral lappets of the frontal bone are well defined; the vomer is relatively longer and the pterygoid widely separated from the internal nares, which show no differentiation of a choanal groove; and the



TEXT-FIG. 5. *Nothosaurus mirabilis* Münster. A, BSP 1935.I.16; anterior part of skull in dorsal view; Bayreuth; Upper Muschelkalk (Anisian, Middle Triassic). B, SMNS 56286; anterior part of palate; Berlichingen; Upper Muschelkalk (Anisian, Middle Triassic). Abbreviations as in Text-fig. 2; scale bars equal 20 mm.

mandibular condyles of the quadrate are not displaced as far back as they are in *N. juvenilis*. *N.* '*münsteri*' closely resembles *N. mirabilis* in these features (Text-fig. 6), although one specimen (Meyer 1847–1855, pl. 9, fig. 4; see also Text-fig. 6A of this paper) shows broadly exposed prefrontals establishing a broad contact with the nasal bones, and the vomer is relatively short in another (Meyer, 1847–1855, pl. 9, fig. 2; see also Text-fig. 6C of this paper). The small *Nothosaurus*

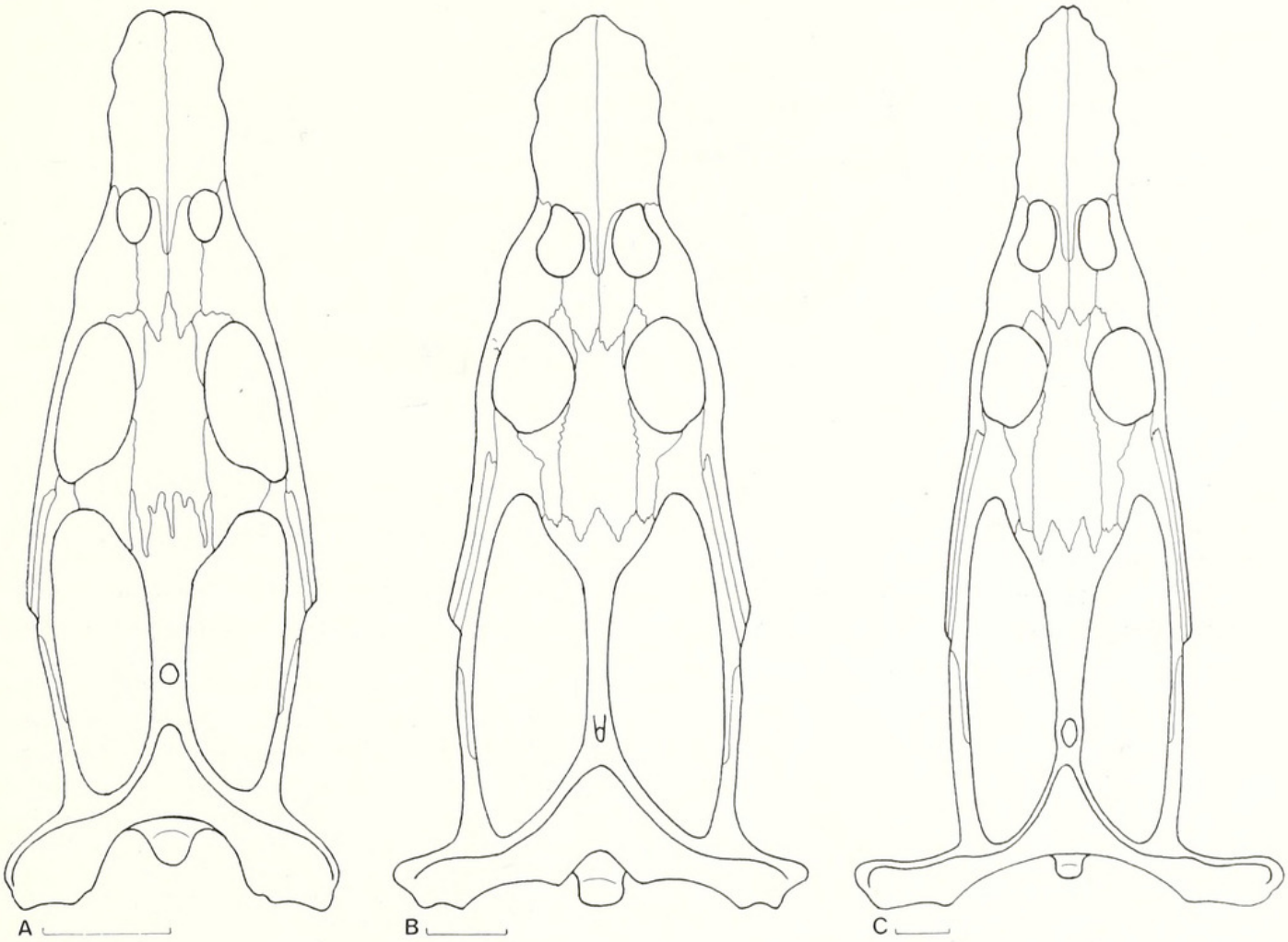


TEXT-FIG. 6. *Nothosaurus* '*münsteri*' (Meyer). Oberfränkisches Erdgeschichtliches Museum, Bayreuth, uncatalogued; Bayreuth; Upper Muschelkalk (Anisian, Middle Triassic). A, anterior part of skull in dorsal view; original of Meyer (1847–1855, pl. 9, fig. 4). B, skull as preserved in dorsal view; original of Meyer (1847–1855, pl. 9, fig. 6). C, skull as preserved in ventral view; original of Meyer (1847–1855, pl. 9, fig. 2). Abbreviations as in Text-fig. 2; scale bars equal 20 mm.

specimen from the König Collection (K-3881) also shares the same characteristics as far as preservation allows to identify them (Text-fig. 4). *N. edingerae* resembles *N. juvenilis* with respect to the narrow postorbital arch (Schultze 1970, p. 227) but otherwise differs from the latter species with respect to several characters, including a less deeply excavated occiput; the differentiation of a distinct sagittal crest formed by the parietal posterior to the pineal foramen, which lies in a deep

groove; and the much larger basioccipital tubers, the diameters of which exceed that of the occipital condyle (Schultze 1970; Rieppel and Wild 1994).

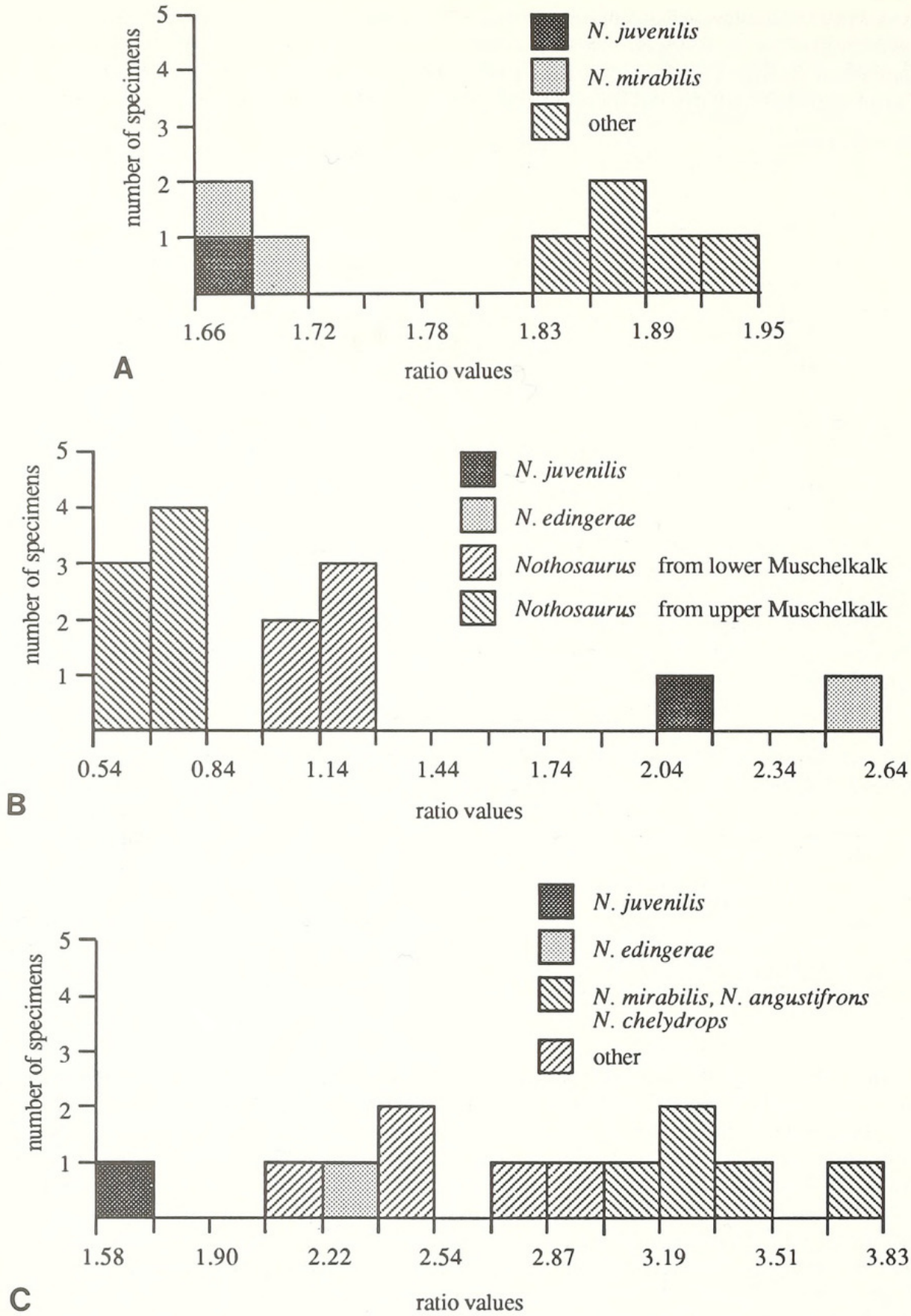
Proportional relations add support to the recognition of *N. juvenilis* as a separate species (Text-fig. 7), although these are often difficult to obtain because of incomplete or poor preservation of the



TEXT-FIG. 7. Reconstructions of nothosaur skulls in dorsal view. A, *N. juvenilis* Edinger. B, *N. 'münsteri'* (Meyer). C, *N. mirabilis* Münster (based on Meyer, 1847–1855, pl. 2, fig. 1). Scale bars equal 20 mm.

cranial material. The rostrum in the holotype of *N. juvenilis* is broken at its anterior tip; if this damage is corrected for by the addition of 5 mm, the relative length of the rostrum falls into the range of variation of the material referred to *N. mirabilis* by Meyer (1847–1855; Text-fig. 8A). Unfortunately, the relative rostrum length remains unknown for *N. 'münsteri'* (due to incomplete preservation). Relative rostrum length distinguishes *N. juvenilis* from the small nothosaurs of the Lower Muschelkalk described by Schröder (1914), some of which show the plesiomorphic entry of the postfrontal into the margin of the upper temporal fossa, but which all show a distinctly shorter rostrum. A relatively shorter rostrum is also characteristic of the holotype of *Nothosaurus chelydrops*, and appears to be shared by the holotype of *Nothosaurus angustifrons* (the rostrum of which is, however, incompletely preserved).

The ratio (distance from external naris to orbit:distance from orbit to upper temporal fossa) segregates the specimens compared here into three groups (Text-fig. 8B). The first group, with values ranging from 0·55 to 0·81, comprises the historical material of *N. mirabilis* and *N. 'münsteri'*, as well



TEXT-FIG. 8. Proportional relations in the skulls of *Nothosaurus* listed in Appendix 2. A, ratio (distance from tip of snout to anterior margin external naris : distance from tip of snout to anterior margin external orbit). B, ratio (distance from external naris to orbit : distance from orbit to upper temporal fossa). C, ratio (longitudinal diameter upper temporal fossa : longitudinal diameter orbit). For further discussion see text.

as the holotypes of *N. angustifrons* Meyer and *N. chelydrops* Fraas. The second group, with values ranging from 1·03 to 1·27, comprises the small nothosaurs from the Lower Muschelkalk described by Schröder (1914). (It should be noted that inclusion of other, as yet undescribed, *Nothosaurus* skulls from the Upper Muschelkalk causes a narrow overlap in that ratio between *N.* cf. *mirabilis* and the Lower Muschelkalk species – personal observation). The value of 2·1 reflects the narrow postorbital arch in *N. juvenilis*, approached only by *N. edingerae* with a value of 2·5–2·7 (Schultze 1970).

The narrow postorbital arch of *N. juvenilis* may be a consequence of its large orbits, as is the low value (1·58) of the ratio (longitudinal diameter upper temporal fossa: longitudinal diameter orbit). All other specimens compared here show continuous variation between values of 2·13 to 3·43 (Text-fig. 8c). It is interesting to note that the small specimens or species of *Nothosaurus* from the Lower Muschelkalk described by Schröder (1914), *N.* '*münsteri*', *N. edingerae* and the *Nothosaurus* sp. from the König Collection (K-3381) fall into the lower range of these values (2·13–2·98) while *N. mirabilis*, *N. angustifrons* and *N. chelydrops* range from 2·72–3·43, thus indicating a negative allometric growth of the orbit. However, even the small species of *Nothosaurus* from both the Lower and Upper Muschelkalk, and *N. edingerae* from the Keuper, some very close to *N. juvenilis* in absolute size, show relatively smaller orbits and (with the exception of *N. edingerae*) a relatively broader postorbital arch. This indicates that ontogenetic variation alone is not a sufficient explanation for the relative size of the orbits in *N. juvenilis*.

CONCLUSION

The recognition of *Nothosaurus juvenilis* as a separate taxon on the basis of morphological characteristics as well as skull proportions indicates the presence of a small species of *Nothosaurus* in the Upper Muschelkalk, different from the medium-sized species *Nothosaurus mirabilis* and a large species of as yet problematic synonymy (*Nothosaurus* '*andriani*' Meyer, *N.* '*baruthicus*' Geissler, *N.* '*giganteus*' Münster, '*Paranothosaurus*' Peyer; cf. Schultze 1970, for a discussion). A similar pattern of taxic diversity is observed in the Lower Muschelkalk, with the small species of *Nothosaurus* described by Schröder (1914) coexisting with a large species known from as yet undescribed, very incomplete material (personal observation). Likewise in the Keuper, the small *Nothosaurus edingerae* (Upper Keuper) may have overlapped in geographical and temporal distribution with the large *Nothosaurus chelydrops* (Lower Keuper), if some incompleteness of the fossil record is assumed. A better diagnosis of all the terminal taxa within the genus *Nothosaurus* is still required, as is a well supported cladogram indicating their phylogenetic interrelationships. However, the general pattern which only just begins to emerge from the revision of the genus *Nothosaurus* is one of niche-partitioning, the coexisting species segregating into different size classes with presumably different trophic preferences.

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APPENDIX I

Measurements of *Nothosaurus juvenilis* (König Collection, K.8698-1). The tip of the rostrum is incomplete (broken); 5 mm have been added to rostrum length for the computation of the proportional relations discussed in the text and Text-figure 8. Measurements given below refer to the rostrum as preserved on the right side of the skull. All measurements are given in mm; values in parentheses are for the left side of the skull.

Tip of the snout to posterior margin of the mandibular condyle of quadrate:	137·2
Tip of the snout to occipital condyle:	126·2
Tip of the snout to posterior margin of supraoccipital:	121·0
Tip of the snout to posterior margin of occipital crest of parietal:	105·1
Tip of the snout to anterior margin of upper temporal fossa:	74·0 (75·0)
Tip of the snout to anterior margin of the orbit:	44·5 (47·2)
Tip of the snout to anterior margin of the external naris:	24·5 (26·4)
Tip of the snout to the anterior margin of internal nares:	27·5 (27·1)
Longitudinal diameter of external naris:	8·7 (8·5)
Transverse diameter of external naris:	6·4 (6·2)
Longitudinal diameter of orbit:	26·5 (25·9)
Transverse diameter of orbit:	16·0 (14·4)
Longitudinal diameter of upper temporal fossa:	42·0 (41·0)

Longitudinal diameter of internal naris:	12·5 (13·0)
Transverse diameter of internal naris:	4·2 (41·0)
Distance from posterior margin of external naris to anterior margin of orbit:	11·5 (12·0)
Distance from posterior margin of orbit to anterior margin of upper temporal fossa:	5·7 (5·5)
Mid-dorsal bridge between external nares:	6·0
Mid-dorsal bridge between orbits (minimal width)	11·2
Mid-dorsal bridge between upper temporal fossae (behind the pineal foramen):	6·5
Longitudinal diameter of pineal foramen:	4·3
Transverse diameter of pineal foramen:	2·7
Distance from pineal foramen to posterior edge of parietal:	6·3
Vertical diameter of foramen magnum:	6·5
Horizontal diameter of foramen magnum:	8·5

APPENDIX 2

Comparative material included in this study and used in the computation of Text-figure 8. Institutional abbreviations are as follows: Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich – BSP; Museum für Naturkunde, Humboldt Universität, Berlin – MB.R.; Oberfränkisches Erdgeschichtliches Museum, Bayreuth – BT; Senckenberg Museum, Frankfurt a.M. – SMF; Staatliches Museum für Naturkunde, Stuttgart – SMNS.

Nothosaurus angustifrons Meyer: SMNS 51972 (holotype).

Nothosaurus chelydrops Fraas: SMNS 7162 (holotype).

Nothosaurus edingerae Schultze: SMF R-4035 (holotype); referred material: SMNS 59072.

Nothosaurus marchicus Koken: MB.R. 2 (counterpart of holotype).

Nothosaurus mirabilis Münster: BT uncatalogued: original to Meyer (1847–1855, pl. 2, fig. 1–2; pl. 3, fig. 1); original to Meyer (1847–1855, pl. 3, fig. 2; pl. 34, fig. 1); original to Meyer (1847–1855, pl. 6, figs 1–3; pl. 7, fig. 1); BT uncatalogued, undescribed; BSP 1935.I.16.

Nothosaurus '*münsteri*' (Meyer): BT uncatalogued: original to Meyer (1847–1855, pl. 9, figs 1–3); original to Meyer (1847–1855, pl. 9, fig. 4); original to Meyer (1847–1855, pl. 9, figs 6–7).

Nothosaurus oldenburgi Schroeder: MB.R. 1 (holotype).

Nothosaurus procerus Schroeder: MB.R. 4 (holotype).

Nothosaurus procerus var. *parva*: MB.R. 5 (holotype).

Nothosaurus raabi Schroeder: MB.I. 007.18 (holotype).

Nothosaurus cf. *raabi*: MB.R. 24 (undescribed specimen).

Nothosaurus sp.: Geologisch–Paläontologisches Institut, Ruprecht-Karls-Universität, Heidelberg, König Collection, K-3881.