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A Revision of the Genus *Nothosaurus* (Reptilia: Sauropterygia) from the Germanic Triassic, with Comments on the Status of *Conchiosaurus clavatus*

Olivier Rieppel

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A Revision of the Genus *Nothosaurus* (Reptilia: Sauropterygia) from the Germanic Triassic, with Comments on the Status of *Conchiosaurus clavatus*

Olivier Rieppel **Rupert Wild**

Abstract

The systematic revision of the genus *Nothosaurus* from the Germanic Triassic (Muschelkalk, lower and middle Keuper) results in the recognition of five valid species. These are *N. edingerae, N. giganteus, N. juvenilis, N. marchicus,* and the genotypical species, *N. mirabilis.* The holotype of *Conchiosaurus clavatus* from the base of the middle Muschelkalk is unequivocal evidence of the synonymy of *Conchiosaurus* with *Nothosaurus.* Since *Conchiosaurus* has priority, it must be declared a nomen oblitum to preserve the genus name *Nothosaurus.* Intrageneric relationships of the species as reconstructed by cladistic analysis match the stratigraphic distribution of the species. The first occurrence of the genus is *Nothosaurus* cf. *N. marchicus* in the early lower Muschelkalk; the latest occurrence is *Nothosaurus edingerae* from the middle Keuper (Gipskeuper). *Paranothosaurus* is a junior synonym of *Nothosaurus* and supports faunal interchange between the Germanic and Alpine Triassic at the time of the Anisian–Ladinian boundary.

Zusammenfassung

Bei der systematischen Revision der Gattung *Nothosaurus* von der Germanischen Trias (Muschelkalk, Unterer und Mittlerer Keuper) erweisen sich fünf Arten als valid. Diese sind *N. edingerae, N. giganteus, N. juvenilis, N. marchicus,* und die genotypische Art *N. mirabilis.* Der Holotypus von *Conchiosaurus clavatus* von der Basis des Mittleren Muschelkalkes weist nach, dass *Conchiosaurus* ein älteres Synonym von *Nothosaurus* ist. Eine Petition, *Conchiosaurus* als Gattungsname zu unterdrücken, wurde der Internationalen Kommission für Nomenklaturfragen eingereicht. Die Verwandtschaftsverhältnisse der Arten, wie sie sich aus der kladistischen Analyse ihrer Merkmale ergibt, spiegelt die stratigraphische Verbreitung der Arten wider. Das erste Auftreten der Gattung im Fossilbeleg ist *Nothosaurus* cf. *N. marchicus* im frühen Unteren Muschelkalk; das letzte Auftreten der Gattung ist *Nothosaurus edingerae* vom Mittleren Keuper (Gipskeuper). *Paranothosaurus* ist ein jüngeres Synonym von *Nothosaurus* und belegt einen Faunenaustausch zwischen der Germanischen und der Alpinen Trias zu einem Zeitraum um die Anis–Ladin Grenze.

Introduction

The history of the investigation of sauropterygians from the Germanic Triassic goes back to the beginning of the 19th century. Large, black, shiny tooth plates have been reported from the upper Muschelkalk of Bayreuth (Bavaria, southern Germany) since 1809 (Weiss, 1983; 1806 following Müller, 1979), the year when Count Georg von Münster (1776–1844) started the systematic collection of vertebrate fossils from these deposits. The first skull was collected in 1824, described by

Münster in 1830, and named by Agassiz (1833–1845) as a new genus of pycnodont fish, *Placodus.* It was left to Owen (1858) to discover the reptilian affinities of that genus. Only after 25 years of collecting efforts did Münster obtain the first articulated, albeit incomplete, skeleton of a saurian (Weiss, 1983), unfortunately lacking the skull, but associated with a tooth-bearing fragment of the lower jaw. Münster (1834) described this fossil under the name *Nothosaurus mirabilis,* thereby making *mirabilis* the type species of its genus.

The only other fossil reptile that had previously been described from the Muschelkalk of Bayreuth (as Münster and Meyer originally thought) was *Conchiosaurus clavatus* (Meyer, 1834a,b). Although Meyer (1847–1855: 106) dates the original description of *Conchiosaurus clavatus* to 1833, the publication bears the printed date of 1834. The fossil, which Count Münster had turned over to H.v. Meyer for study, consists of an incomplete skull, badly crushed and split horizontally, exposing the posterior part of the skull roof and the anterior part of the dermal palate in dorsal view. Because it was part of the Münster collection, Meyer (1834) believed the fossil to be from the upper Muschelkalk of Bayreuth. However, Münster had not collected this skull himself, but had received it from another collector. Later, Münster claimed to have found the counterpart of the specimen in a collection in Halle (the fossil can no longer be located at the Institut für Geowissenschaften, Martin-Luther-Universität, Halle). The counterpart indicated that the fossil came from the Saurierkalk of Esperstädt, which corresponds to the base of the middle Muschelkalk (Meyer, 1847–1855: 106). In his redescription of *Conchiosaurus clavatus,* Meyer (1847–1855: 107) recognized the similarity to *Nothosaurus,* particularly to *Nothosaurus venustus* from the same deposits, and added: "Should the two genera concur, I would retain the name *Nothosaurus* although it is younger, because it has been widely accepted in the meantime." In his description of *Nothosaurus venustus,* Meyer (1847–1855) in fact referred to the specimen as "*Conchiosaurus* or *Nothosaurus clavatus.*"

Quenstedt (1852) listed *Conchiosaurus clavatus* as a valid taxon and emphasized similarities of tooth morphology shared with *Simosaurus.* He was followed by Zittel (1887–1890) and Huene (1948), who included *Conchiosaurus* in the Simosauridae (see also Huene, 1956). Lydekker (1889) treated *Conchiosaurus clavatus* as a senior synonym of *Nothosaurus venustus,* whereas Edinger (1921a) followed Meyer's (1847–1855) suggestion and treated *Nothosaurus venustus* as a valid name for *Conchiosaurus clavatus* (also in Arthaber, 1924, and Schmidt, 1928). Kuhn (1934) finally listed *Nothosaurus clavatus* as a valid species, but resurrected *Conchiosaurus* as a valid genus name in a later edition of the Fossilium Catalogus (Kuhn, 1964), noting that if *Conchiosaurus* and *Nothosaurus* were synonymous, the latter name would have to become a nomen conservandum (Kuhn, 1964: 7). In his review of the genus *Nothosaurus,* Schultze (1970) listed *Nothosaurus venustus* as a valid species but did not refer to *Conchiosaurus clavatus* (see also Kruckow, 1979).

The name *Nothosaurus venustus* (first used by Münster, 1834, with no description, no diagnosis, and no illustration) referred to another skull from the Saurierkalk (lower middle Muschelkalk) of Esperstädt, smaller than that of *Conchiosaurus clavatus,* and described as well as figured by Meyer (1847–1855: 107, Pl. 10, Fig. 5; the figure is reproduced in Schultze, 1970, Fig. 2). The specimen, which can no longer be located today, was split horizontally, exposing part of the skull roof in ventral (medial) view. Meyer (1847–1855: 107) noted that the specimen had been labeled by Münster as *Nothosaurus venustus,* but that Münster also used that name to refer to postcranial remains from the same and other deposits. After a thorough discussion of all the specimens referred to that species by Münster, Meyer (1847–1855: 109) concluded: "In fact, Münster referred to *Nothosaurus venustus* specimens which cannot possibly belong to the same species. It is therefore difficult to assess the significance of that name."

Although the "holotype" of *Nothosaurus venustus* (Meyer, 1847–1855, Pl. 10, Fig. 5) can no longer be located, recent survey of sauropterygians from the Germanic Muschelkalk in public repositories resulted not only in the rediscovery of the holotype of *Conchiosaurus clavatus* described by Meyer (1834), but also in the discovery of a number of skull fragments that carry historical labels identifying them as *Nothosaurus venustus.* It is the purpose of this paper to assess the taxonomic validity of these names in the context of a revision of the genus *Nothosaurus.*

INSTITUTIONAL ABBREVIATIONS—Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin: BGR; The Natural History Museum, London: BMNH; Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich: BSP; Ob-

erfränkisches Erdgeschichtliches Museum, Bayreuth: BT; Naturkundemuseum Erfurt: Er; Institut und Museum für Geologie und Paläontologie, Georg-August-Universität, Göttingen: Gö; Museum der Natur, Gotha: Got; Institut für Geowissenschaften, Martin-Luther-Universität, Halle: Ha; Museum für Naturkunde, Humboldt University, Berlin: MB; Institute of Geological Sciences, University of Wraclaw: MGU; Muséum National d'Histoire Naturelle, Paris: MHNP; Phyletisches Museum Jena: P; Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a.M.: SMF; Staatliches Museum für Naturkunde, Stuttgart: SMNS.

Systematic Paleontology

Sauropterygia Owen, 1860
Eosauropterygia Rieppel, 1994a
Eusauropterygia Tschanz, 1989
Nothosauridae Baur, 1889

DEFINITION—A monophyletic taxon that includes the genera *Germanosaurus* Nopcsa, 1928, and the Nothosaurinae Nopcsa, 1923.

DIAGNOSIS—Small to large eusauropterygians with a distinctly constricted snout, pineal foramen displaced posteriorly; jugal excluded from posterior margin of orbit; maxillary tooth row extending to level of anterior margin of upper temporal fenestra or beyond; reduced dorsal exposure of prefrontal.

DISTRIBUTION—Lower to Upper Triassic, Europe and Israel.

Nothosaurinae Nopcsa, 1923

DEFINITION—A monophyletic taxon that includes the genera *Nothosaurus* Münster, 1934, *Ceresiosaurus* Peyer, 1931, and *Lariosaurus* Curioni, 1847 (*Silvestrosaurus* Kuhn-Schnyder, 1990, is here considered a junior synonym of *Lariosaurus* [Rieppel, 1993]).

DIAGNOSIS—Frontals fused; parietal skull table strongly constricted; maxillary fangs present; occipital crest of parietal and squamosal well developed; posttemporal fenestrae rudimentary or closed; pterygoid–ectopterygoid flange reduced or absent; medioventral flange extends to posterior tip of quadrate ramus of pterygoid.

DISTRIBUTION—Lower to lower Upper Triassic, Europe and Israel.

***Nothosaurus* Münster, 1834**

1834 *Nothosaurus*, Münster, p. 525.
1834 *Conchiosaurus*, Meyer, p. 8 (nomen oblitum).
1834 *Dracosaurus*, Münster, p. 526.
1847–55 *Opeosaurus*, Meyer, p. 82.
1893 *Kolposaurus*, Skuphos, p. 14.
1894 *Oligolycus*, Fritsch, p. 7.
1911 *Cymatosaurus*, Jaekel, p. 148, Fig. 161.
1939 *Paranothosaurus*, Peyer, p. 1.
1957 *Elmosaurus*, Huene, p. 97.

TYPE SPECIES—*Nothosaurus mirabilis* Münster, 1834, from the upper Muschelkalk, Middle Triassic, Germany.

DEFINITION—A monophyletic taxon that includes the following species: *edingerae, giganteus, juvenilis, marchicus,* and *mirabilis.*

DIAGNOSIS—Small to large eusauropterygians of the family Nothosauridae; maxillary tooth row extending well beyond level of anterior margin of upper temporal fenestra; paired maxillary fangs followed by a palisade of densely set, distinctly smaller, conical teeth; longitudinal diameter of the upper temporal fenestra between two and four times the longitudinal diameter of the orbit; never more than three ossifications in carpus or tarsus of adult.

DISTRIBUTION—Middle and lower Upper Triassic, Europe and Israel.

***Nothosaurus edingerae* Schultze, 1970**

1922 *Nothosaurus* sp., Edinger, p. 37 *ff.*, Fig. 1.
1928 *Nothosaurus* sp., Schmidt, p. 402. Fig. 1129.
1970 *Nothosaurus edingerae*, Schultze, p. 226 *f.*, Figs. 1, 14, Pl. 1.
1983 *Nothosaurus* sp., Weiss, p. 37.
1993b *Nothosaurus edingerae*, Rieppel, p. 972.
1994 *Nothosaurus edingerae*, Rieppel and Wild, p. 1 *ff.*, Figs. 1–4, 5C,D.

HOLOTYPE—Skull (SMF R-4035).

LOCUS TYPICUS: Middle Keuper (associated with *Estheria* [now *Palaeoestheria*: Warth, 1969] *laxitexta*: A. Grossmann, in lit. 10.6.1920), Bodenmühle im Rotmaintal near Bayreuth (Weiss, 1983: 37).

DIAGNOSIS—A species of *Nothosaurus* of small size (total length of skull not exceeding 140 mm); posterior (nasal) processes of the premaxillae

reach to a level well behind the posterior margin of the external nares; upper temporal fenestrae broad anteriorly; elongated pineal foramen located in a deep trough at two thirds of the parietal; a sagittal crest present behind the pineal foramen; basioccipital tubers equal in size to occipital condyle.

DISTRIBUTION—Middle Keuper (lower Upper Triassic), southern and southwestern Germany (Bayreuth, Upper Bavaria; Affaltrach, North-Württemberg).

REFERRED SPECIMEN—Skull (SMNS 59072, upper Gipskeuper [Estherienschichten, Anatinenbank], Affaltrach).

COMMENTS—This species was revised by Rieppel and Wild (1994).

Nothosaurus giganteus Münster, 1834

1834 *Nothosaurus giganteus,* Münster, p. 525.
1837 *Nothosaurus mirabilis* (partim), Bronn, p. 189, Pl. 13, Figs. 14a–d.
1839 *Nothosaurus andriani,* Meyer, p. 559.
1840 *Nothosaurus andriani,* Braun, p. 80, Pl. 5, Figs. 1–2.
1840 *Nothosaurus giganteus,* Braun, p. 80, Pl. 6.
1844 *Nothosaurus angustifrons,* Meyer and Plieninger, p. 47, Pl. 10, Fig. 2.
1847 *Nothosaurus andriani,* Giebel, p. 160.
1847 *Nothosaurus angustifrons,* Giebel, p. 160.
1847 *Nothosaurus giganteus,* Giebel, p. 160.
1847–55 *Nothosaurus aduncidens,* Meyer, p. 85, Pl. 67, Figs. 1–3.
1847–55 *Nothosaurus andriani,* Meyer, pp. 21, 61; Pl. 12, Fig. 1; Pl. 12, Figs. 2–3.
1847–55 *Nothosaurus angustifrons,* Meyer, p. 84, Pl. 8, Figs. 1–3.
1847–55 *Nothosaurus giganteus,* Meyer, p. 22, Pl. 11, Figs. 1–3, Pl. 14, Figs. 1-3.
1847–55 ?*Opeosaurus suevicus,* Meyer, p. 82, Pl. 14, Figs. 7–9.
1852 *Nothosaurus angustifrons,* Quenstedt, p. 134.
1853 *Nothosaurus aduncidens,* Meyer, p. 162.
1859 *Nothosaurus andriani,* Gervais, p. 476, Pl. 55, Fig. 4.
1864 *Nothosaurus aduncidens,* Alberti, p. 222.
1864 *Nothosaurus andriani,* Alberti, p. 221.
1864 *Nothosaurus angustifrons,* Alberti, p. 223.
1864 *Nothosaurus giganteus,* Alberti, p. 222.
1864 ?*Opeosaurus suevicus,* Alberti, p. 226.
1889 *Nothosaurus aduncidens,* Lydekker, p. 293.
1889 *Nothosaurus andriani,* Lydekker, p. 299.
1889 *Nothosaurus giganteus,* Lydekker, p. 293.
1895 *Nothosaurus aduncidens,* Geissler, p. 336.
1895 *Nothosaurus andriani,* Geissler, p. 336, 340.
1895 *Nothosaurus baruthicus* partim, Geissler, p. 333 *ff.*; Pl. 13, Fig. 1.
1895 *Nothosaurus giganteus,* Geissler, p. 336.
1896 *Nothosaurus aduncidens,* Fraas, p. 9.
1896 *Nothosaurus andriani,* Fraas, p. 11, Fig. 2.
1896 *Nothosaurus angustifrons,* Fraas, p. 10 *f.*, Fig. 3.
1896 *Nothosaurus chelydrops,* Fraas, p. 12, Pl. 4.
1896 *Nothosaurus giganteus,* Fraas, p. 9.
1899 *Nothosaurus andriani,* Schrammen, Pl. 24, Fig. 4a.
1924 ?*Opeosaurus,* Arthaber, pp. 470, 473.
1928 *Nothosaurus aduncidens,* Schmidt, p. 401, Fig. 1125.
1928 *Nothosaurus andriani,* Schmidt, p. 401, Fig. 1126.
1928 *Nothosaurus angustifrons,* Schmidt, p. 401, Fig. 1127.
1928 *Nothosaurus chelydrops,* Schmidt, p. 402, Fig. 1128.
1928 *Nothosaurus giganteus,* Schmidt, p. 400 *f.*, Fig. 1124.
1928 ?*Opeosaurus suevicus,* Schmidt, p. 403, Fig. 1132.
1928 *Nothosaurus andriani,* Corroy, p. 120.
1928 *Nothosaurus angustifrons,* Corroy, p. 120 *f.*; Pl. 3, Figs. 3–6; Pl. 4, Fig. 5.
1928 *Nothosaurus giganteus,* Corroy, p. 119.
1934 *Nothosaurus aduncidens,* Kuhn, p. 32 *f.*
1934 *Nothosaurus andriani,* Kuhn, p. 30.
1934 *Nothosaurus angustifrons,* Kuhn, p. 30 *f.*
1934 *Nothosaurus baruthicus* partim, Kuhn, p. 31.
1934 *Nothosaurus chelydrops,* Kuhn, p. 32.
1934 *Nothosaurus giganteus,* Kuhn, p. 31 *f.*
1934 ?*Opeosaurus suevicus,* Kuhn, p. 40.
1938 *Nothosaurus chelydrops,* Peyer, p. 237.
1939 *Nothosaurus andriani,* Peyer, p. 9 *ff.*

1939 *Nothosaurus baruthicus* partim, Peyer, p. 8 *ff.*
1939 *Paranothosaurus amsleri,* Peyer, p. 1 *ff.*, Figs. 1–7; Pls. 66–71.
1949 *Nothosaurus baruthicus* partim, E.v. Huene, p. 135
1949 *Paranothosaurus amsleri,* E.v. Huene, p. 123, Fig. 19.
1955 *Paranothosaurus amsleri,* Saint-Seine, p. 424, Fig. 6.
1956 *Nothosaurus andriani,* Huene, p. 338.
1956 *Nothosaurus angustifrons,* Huene, p. 338.
1956 *Nothosaurus giganteus,* Huene, p. 338.
1956 *Paranothosaurus amsleri,* Huene, p. 387 *f.*, Figs. 426a–b.
1956 ?*Opeosaurus,* Huene, p. 390.
1964 *Nothosaurus aduncidens,* Kuhn, p. 7.
1964 *Nothosaurus andriani,* Kuhn, p. 7.
1964 *Nothosaurus angustifrons,* Kuhn, p. 7.
1964 *Nothosaurus baruthicus* partim, Kuhn, p. 7 *f.*
1964 *Nothosaurus chelydrops,* Kuhn, p. 8.
1964 *Nothosaurus giganteus,* Kuhn, p. 8.
1964 ?*Opeosaurus suevicus,* Kuhn, p. 18.
1966 *Nothosaurus aduncidens,* Kuhn-Schnyder, p. 534.
1966 *Nothosaurus andriani,* Kuhn-Schnyder, p. 534.
1966 *Nothosaurus angustifrons,* Kuhn-Schnyder, p. 534.
1966 *Nothosaurus baruthicus* partim, Kuhn-Schnyder, p. 534.
1966 *Nothosaurus chelydrops,* Kuhn-Schnyder, p. 534.
1966 *Nothosaurus giganteus,* Kuhn-Schnyder, p. 534.
1966 *Paranothosaurus amsleri,* Kuhn-Schnyder, p. 517 *ff.*; Figs. 1–2, Pls. 1–2.
1970 *Nothosaurus aduncidens,* Schultze, pp. 221, 223.
1970 *Nothosaurus andriani,* Schultze, pp. 221, 223 *f.*; Fig. 11.
1970 *Nothosaurus angustifrons,* Schultze, p. 221.
1970 *Nothosaurus baruthicus* partim, Schultze, p. 221.
1970 *Nothosaurus chelydrops,* Schultze, p. 226, Fig. 12.
1970 *Nothosaurus giganteus,* Schultze, pp. 221, 223.
1974 *Paranothosaurus amsleri,* Kuhn-Schnyder, p. 57 *ff.*, Figs. 36–38.
1979 *Nothosaurus aduncidens,* Kruckow, p. 63.
1979 *Nothosaurus andriani,* Kruckow, p. 63.
1979 *Nothosaurus angustifrons,* Kruckow, p. 63.
1979 *Nothosaurus baruthicus* partim, Kruckow, p. 63.
1979 *Nothosaurus giganteus,* Kruckow, p. 63.
1993b *Nothosaurus andriani,* Rieppel, p. 972.
1993b *Nothosaurus chelydrops,* Rieppel, p. 972.

HOLOTYPE—Skull fragments (BT, uncatalogued); originals of Meyer, 1847–55, Pl. 11, Fig. 1 (left orbit); Pl. 11, Fig. 2 (skull fragments); Pl. 11, Fig. 3 (partial occiput).

PARATYPE—Posterior part of left lower jaw (BT, uncatalogued); original of Meyer, 1847–1855, Pl. 14, Figs. 1–3.

LOCUS TYPICUS—Upper Muschelkalk (mo_1), Oschenberg near Laineck (also referred to as Lainecker Berg) east of Bayreuth, Bavaria, Germany.

DIAGNOSIS—A species of *Nothosaurus* of large size, with an adult condylobasal skull length of up to 750 mm; premaxillary rostrum relatively short and broad; four fangs on each premaxilla, followed by a distinctly smaller fifth premaxillary tooth; length to width ratio of mandibular symphysis ranging from 1.0 to 1.3; postorbital with a narrow entry into the posteroventral margin of the orbit; ectopterygoid flanges at the anterior margin of the subtemporal fossa strongly developed.

DISTRIBUTION—Upper Muschelkalk (mo_1 to mo_3) and lower Keuper, Germanic Triassic, central and western Europe; Grenzbitumenzone (Anisian–Ladinian boundary), southern Alps.

REFERRED MATERIAL—BT, uncatalogued (skull, upper Muschelkalk, Bayreuth; holotype of *Nothosaurus andriani* Meyer, 1839, and original of Meyer, 1847–1855, Pl. 12, Fig. 1); BT, uncatalogued (skull fragments, upper Muschelkalk, Bayreuth; holotype of *Nothosaurus giganteus* Münster, 1834, originals of Meyer, 1847–1855, Pl. 11, Figs. 1–3, Pl. 14, Figs. 1–3). MHNP 9115 (skull, Muschelkalk, Lunéville, France; original of Gervais, 1859, Pl. 55, Fig. 4). SMF, R-uncatalogued (lower jaw, upper Muschelkalk, Bayreuth; original of Geissler, 1895, Pl. 13, Fig. 2); SMF R-475 (skull, upper Muschelkalk, Bayreuth; holotype of *Nothosaurus baruthicus* Geissler, 1895); SMF R-503 (skull fragment, upper Muschelkalk, Bayreuth; original of Edinger, 1921a, Fig. 7); SMF R-504 (lower jaw fragment, upper Muschelkalk, Bayreuth); SMF R-563 (skull fragment, upper Mu-

schelkalk, Bayreuth); SMF R-811 (skull fragment, upper Muschelkalk, Bayreuth; SMF R-1062 (mandibular symphysis, upper Muschelkalk, Bayreuth); SMF R-4542 (skull fragment, upper Muschelkalk, Bayreuth). SMNS 4141 (lower jaw, upper Muschelkalk, Stuttgart-Zuffenhausen; holotype of *Opeosaurus suevicus* Meyer, 1847–1855); SMNS 4200 (premaxillary rostrum, upper Muschelkalk, Crailsheim; holotype of *Nothosaurus aduncidens* Meyer, 1853); SMNS 7162 (upper lower Keuperdolomit, Hoheneck near Ludwigsburg; holotype of *Nothosaurus chelydrops* Fraas, 1896: 12); SMNS 80205 (upper lower Keuperdolomit, Hoheneck near Ludwigsburg; syntype of *Nothosaurus chelydrops* Fraas, 1896: 12); SMNS 7214b (lower jaw, upper lower Keuper, Hoheneck near Ludwigsburg); SMNS 7537 (lower jaw, upper Muschelkalk, Crailsheim); SMNS 7860 (skull, upper Muschelkalk, Crailsheim; original of Fraas, 1896, Fig. 2 [specimen "Allmendinger" of *Nothosaurus andriani*]); SMNS 8549 (skull, upper Muschelkalk, Crailsheim; original of Fraas, 1896, Fig. 2 [specimen "Blezinger" of *Nothosaurus andriani*]; SMNS 8872 (skull, upper Muschelkalk, Crailsheim; original of Fraas, 1896, Fig. 3 ["Blezinger" specimen of *Nothosaurus angustifrons*]); SMNS 10506 (lower jaw, upper lower Keuper, Hoheneck near Ludwigsburg); SMNS 10806 (mandibular symphysis, upper Muschelkalk, Crailsheim); SMNS 17674 (lower jaw fragment, upper Muschelkalk, Tiefenbach near Crailsheim); SMNS 18001 (skull, upper Muschelkalk [*Discoceratites* layers], Tiefenbach near Crailsheim); SMNS 18058 (lower jaw fragment, upper Muschelkalk, Heldenmühle near Crailsheim); SMNS 18210 (lower jaw fragment, upper Muschelkalk, Heldenmühle near Crailsheim); SMNS 18475 (skull, upper Muschelkalk [*Discoceratites* layers], Tiefenbach near Crailsheim); SMNS 18515 (rostrum, upper Muschelkalk [*Discoceratites* layers], Heldenmühle near Crailsheim); SMNS 51972 (skull, upper Muschelkalk, Crailsheim; holotype of *Nothosaurus angustifrons* Meyer and Plieninger, 1844); SMNS 56685 (lower jaw, uppermost Muschelkalk [top layer underlying the Grenzbonebed], Gundelsheim); SMNS 57047 (skull, upper Muschelkalk [*Discoceratites* layers], Heimsheim).

POSTCRANIUM—BMNH R-42830 (humerus, upper Muschelkalk, Württemberg). Got, uncatalogued (vertebra, upper Muschelkalk [mo_2], Grossenbehringer near Gotha). MB R. 143 (vertebra, upper Muschelkalk [mo_1], Bad Sulza); MB R. 202 (vertebra, upper Muschelkalk [mo_1], Bedheim–Ehrlichsgraben). MHNP 1882-17 (vertebra, "Muschelkalk," Montdessus, Neurthé, France); MHNP 9115 (neural arch, Muschelkalk, Lunéville, France). P 48 (vertebra, upper Muschelkalk [mo_2], Kleinromstedt near Weimar); P 1110 (ischium, upper Muschelkalk [mo_2?], Bad Sulza); P 1149 (pectoral girdle, upper Muschelkalk [mo_2?], Bad Sulza); P 1205 (ilium, upper Muschelkalk [mo_2?], Bad Sulza). SMF R-47 (cervical vertebra, upper Muschelkalk, Bayreuth); SMF R-276 (sacral vertebra, upper Muschelkalk, Bayreuth; original of Huene, 1902, p. 41, Fig. 44a; Schmidt, 1928, Fig. 1112d); SMF R-863 (vertebra, upper Muschelkalk, Bayreuth); SMF R-938 (vertebra, upper Muschelkalk, Bayreuth); SMF R-871 (vertebra, upper Muschelkalk, Bayreuth); SMF R-4556 (sacral vertebra, upper Muschelkalk, Bayreuth); SMF R-4557 (two articulated vertebrae, upper Muschelkalk, Bayreuth); SMF R-33 (coracoid, upper Muschelkalk, Bayreuth); SMF R-36 (scapula and parts of clavicle, upper Muschelkalk, Bayreuth). SMNS 17438 (vertebra, upper Muschelkalk [Trochitenkalk], Stengelberg, Neidenfels near Crailsheim); SMNS 18285 (vertebra, upper Muschelkalk [*Discoceratites* layers], Heldenmühle near Crailsheim; original of Huene, 1952, p. 176 *ff.*, Figs. 76a–c); SMNS 50819 (vertebra, upper Muschelkalk, Bettenfeld near Rothenburg); SMNS 54825 (vertebra, upper Muschelkalk, Eschenau); SMNS 55298 (vertebra, upper Muschelkalk [*Discoceratites* layers], Schmalfelden); SMNS 56273 (vertebra, upper Muschelkalk, Berlichingen); SMNS 58457 (vertebra, upper Muschelkalk [*Discoceratites* layers], Schmalfelden); SMNS 58804 (vertebra, upper Muschelkalk [*Discoceratites* layers], Rüblingen); SMNS, uncatalogued (several vertebrae, upper Muschelkalk, Hegnabrunn near Kulmbach, Tiefenbach near Crailsheim, Schmalfelden; Grenzbonebed Crailsheim); SMNS, uncatalogued, coll. M. Wild nos. 733, 826, 907, 2060, 2062, 2091, and 2176 (vertebrae, upper Muschelkalk [*spinosus* biozone], Hegnabrunn); SMNS, uncatalogued, coll. M. Wild nos. 993, 1583, 1667, and 1770 (vertebra, upper Muschelkalk [*nodosus* biozone], Hegnabrunn); SMNS, uncatalogued, coll. M. Wild nos. 941, 1327, and 1957 (vertebrae, upper Muschelkalk [*enodis–laevigatus* biozone], Hegnabrunn); SMNS, uncatalogued, coll. M. Wild no. 1874 (vertebra, upper Muschelkalk [*evolutus* biozone], Hegnabrunn); SMNS, uncatalogued, coll. M. Wild no. 14 (vertebra, upper Muschelkalk [*spinosus* biozone], Rugendorf); SMNS, uncatalogued, coll. M. Wild no. 49 (vertebra, upper Muschelkalk [*spinosus* biozone], Forstlahm-Herlas); SMNS 12160 (coracoid, upper Muschelkalk, Höfingen near Leonberg); SMNS

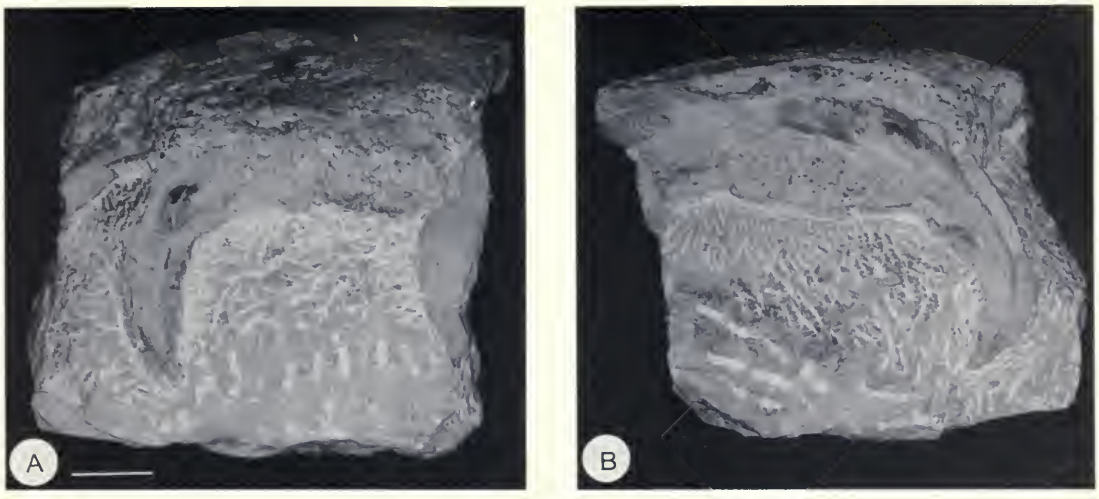


FIG. 1. *Nothosaurus aduncidens* Meyer (holotype; SMNS 4200); upper Muschelkalk, Crailsheim. **A,** Left lateral view; **B,** right lateral view. Scale bar = 20 mm.

17326 (coracoid, upper Muschelkalk, Stuttgart-Zuffenhausen); SMNS 18689c (coracoid, upper Muschelkalk, Heldenmühle near Crailsheim); SMNS, uncatalogued (coracoid, upper Muschelkalk, Crailsheim); SMNS uncatalogued (coracoid, upper Muschelkalk [Grenzbonebed], Crailsheim); SMNS 11336 (pubis, upper Muschelkalk, Sattelweiler); SMNS 50821 (ilium, lower Keuper, Zwingelhausen); SMNS, uncatalogued (ischium, upper Muschelkalk, Crailsheim); SMNS 15957 (humerus, upper Muschelkalk, Tiefenbach near Crailsheim); SMNS 16250b (humerus, upper Muschelkalk, Bindlach near Bayreuth); SMNS 17224 (humerus, upper Muschelkalk, Heldenmühle near Crailsheim); SMNS 17822c (humerus, upper Muschelkalk [*Discoceratites* layers], Heldenmühle near Crailsheim); SMNS, uncatalogued, coll. M. Wild no. 1797 (humerus, upper Muschelkalk [*spinosus* biozone], Hegnabrunn near Kulmbach); SMNS 15892b (femur, upper Muschelkalk, Tiefenbach near Crailsheim); SMNS 18694 (femur, upper Muschelkalk [*Discoceratites* layers], Heldenmühle near Crailsheim); SMNS 80204 (dorsal vertebrae, Middle Triassic, Belogradcik, NW Bulgaria).

COMMENTS—Following his description of the holotype of *Nothosaurus mirabilis,* Münster (1834: 259) mentioned similar bones collected at the same locality but four to five times the size of the genotypical species. These large fragments, later figured by Meyer (1847–1855), were named *Nothosaurus giganteus* by Münster (1834: 259).

In 1853, Meyer mentioned a fragmentary skull even larger than *Nothosaurus giganteus* from the upper Muschelkalk of Crailsheim, and characterized by a recurved premaxillary fang (Fig. 1). The specimen was named *Nothosaurus aduncidens* and later figured and described in more detail (Meyer, 1847–1855: 85, Pl. 67, Figs. 1–3). It consists of an incomplete premaxillary rostrum, a fragment of the middle portion of the skull, and the partial impression of the occiput (SMNS 4200). The anterior part of a large lower jaw from the same locality (SMNS 7537) was referred to the same species. The synonymy of *Nothosaurus aduncidens* with *Nothosaurus giganteus* was recognized by Fraas (1896), Lydekker (1889: 293), and Edinger (1921a).

Summarizing the then current knowledge of *Nothosaurus,* Meyer (1839: 559) mentioned *Nothosaurus andriani,* a new species based on a large skull from the upper Muschelkalk of Bayreuth, prepared in ventral view and later described and figured in detail (Meyer, 1847–1855: 21, Pl. 12, Fig. 1). A similar skull from the upper Muschelkalk of Lunéville (Lorraine, France), again prepared in ventral view and slightly larger than the holotype, was referred to the same species (Meyer, 1847–1855: 61, Pl. 12, Figs. 2–3). Both skulls are figured with four premaxillary tooth positions, but personal inspection of the holotype of *Nothosaurus andriani* (Fig. 2; arrow points to fifth premaxillary tooth) confirms the presence of the usual four premaxillary fangs followed by a distinctly smaller, fifth premaxillary tooth (see also Gervais, 1859, Pl. 55, Fig. 4; in his drawing, Meyer, 1847–1855, did not include the anteriormost

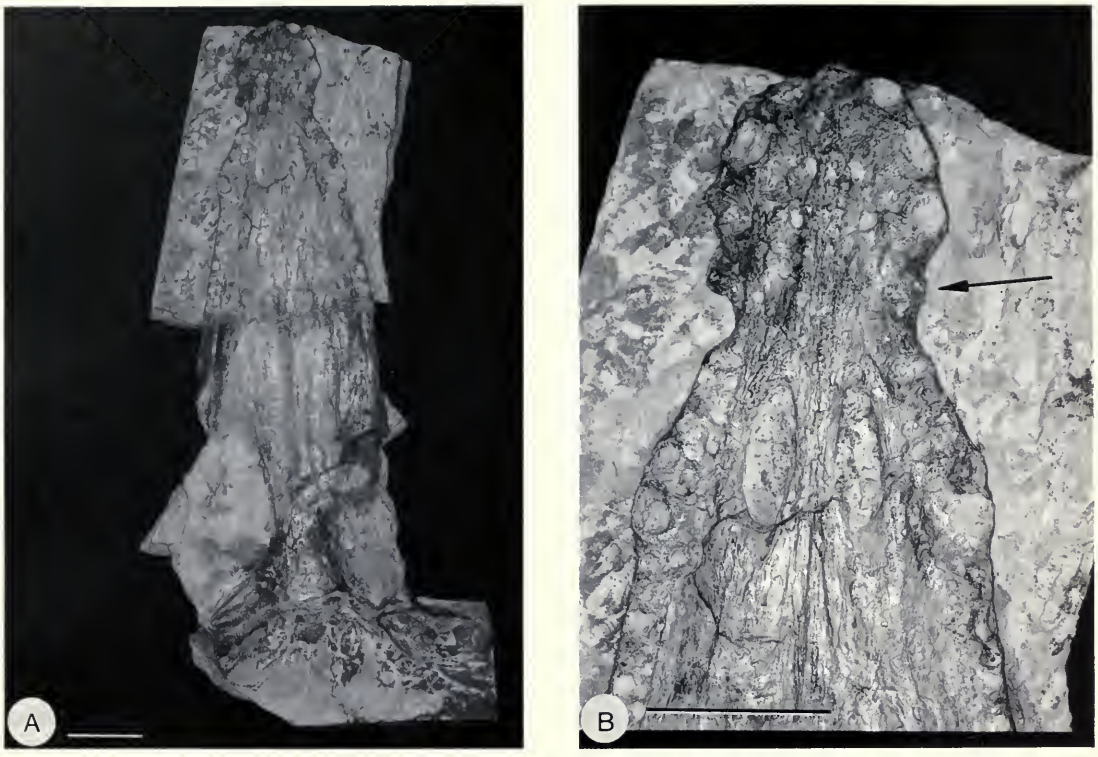


FIG. 2. *Nothosaurus andriani* Meyer (holotype; BT, uncatalogued); upper Muschelkalk, Bayreuth. **A,** Skull in ventral view; **B,** premaxillary rostrum in ventral view. Arrow points to fifth premaxillary tooth. Scale bar = 50 mm.

alveolus facing straight foward and hence not exposed in ventral view). The characters used by Meyer (1847–1855: 21) to distingusih *Nothosaurus andriani* from *Nothosaurus mirabilis* are all due to variation or subject to deformation by dorsoventral compression of the skull, with the exception of the relatively shorter rostrum in the first species. The dorsal surface of the skull was described by Fraas (1896, Fig. 2) on the basis of two further skulls ("Allmendinger" specimen, SMNS 7860a,b; "Blezinger" specimen, SMNS 8549, posterior part of skull only) from the upper Muschelkalk of Crailsheim. Both specimens are in rather poor condition, and the best indication of the sutural pattern on the dorsal surface of the skull is on a crude metal cast (Fig. 3A) made from the counterpart (natural mold) of the "Allmendinger" specimen (SMNS 7860b). Edinger (1921a) considered *Nothosaurus andriani* a valid species (subspecies of *Nothosaurus giganteus*?) because of its somewhat smaller size compared to *Nothosaurus giganteus*; the condylobasal skull length is 428 mm for the holotype of *Nothosaurus andriani* (BT, uncatalogued) and an estimated 600–700 mm for *Nothosaurus giganteus* (Edinger, 1921a). Edinger (1921a) also noted that the skull of *Nothosaurus baruthicus* Geissler, 1895 (condylobasal skull length 608 mm) shows fused cranial sutures that are still visible in the slightly larger *Nothosaurus giganteus* and concluded that *Nothosaurus baruthicus* Geissler (1895) is an old individual and a junior synonym of *Nothosaurus andriani* Meyer. Schultze (1970) tentatively accepted *Nothosaurus andriani* as a separate species on the assumption that the sutural pattern indicated by Fraas (1896) is correct. As will be discussed in greater detail below, some of the characters considered important by Schultze (1970), such as the relation between nasal and frontal, or between premaxilla and frontal, are quite variable, whereas sutures remain very indistinct in the original material used by Fraas (1896, SMNS 7860b), especially in the preorbital region of the skull. The left postfrontal is well delineated, but whether it did, in fact, broadly enter the medial margin of the upper temporal fenestra remains doubtful. Where the postfrontal does seem to enter the medial margin of the upper temporal fenestra, the cast shows

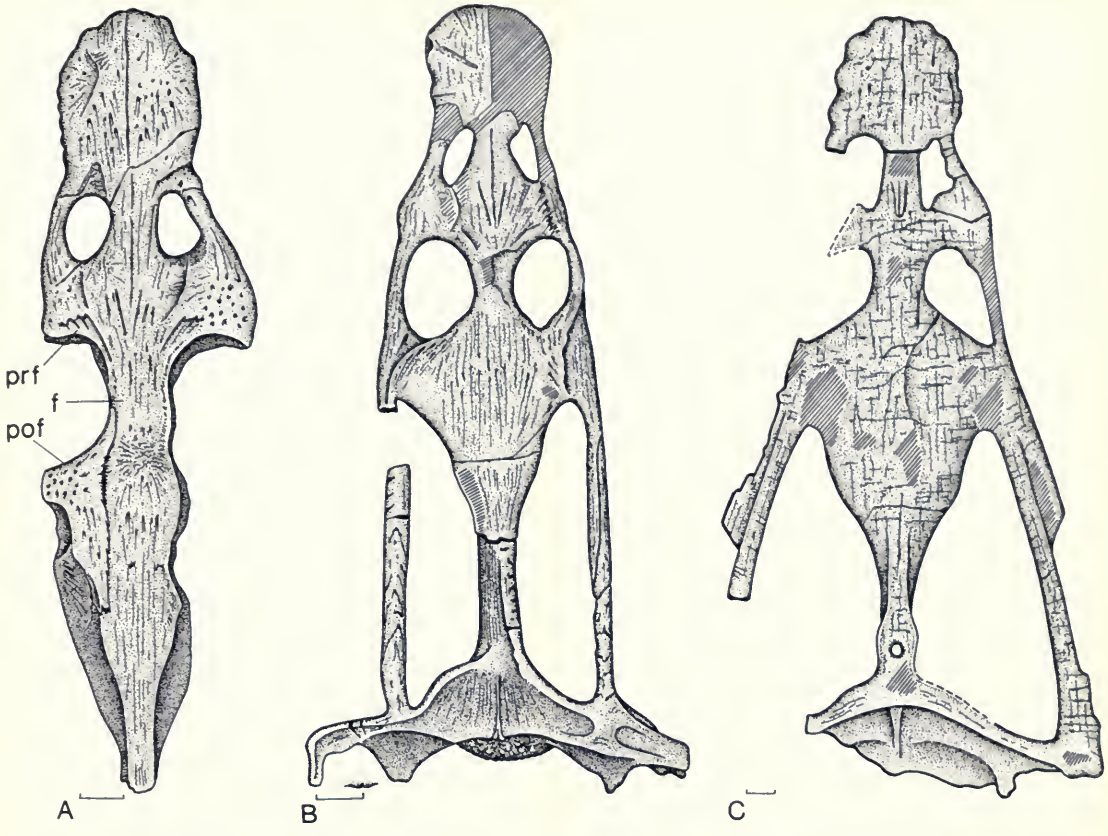


FIG. 3. **A,** Metal cast of the skull of *Nothosaurus andriani* Meyer (SMNS 7860b; original of Fraas, 1896 ["Allmendinger" specimen]); upper Muschelkalk, Crailsheim. **B,** *Nothosaurus angustifrons* Meyer and Plieninger (holotype; SMNS 51972); upper Muschelkalk (mo_2), Crailsheim. **C,** *Nothosaurus chelydrops* Fraas (holotype; SMNS 7162); lower Keuper, Hoheneck near Ludwigsburg. Scale bar = 20 mm. Abbreviations: f, frontal; pof, postfrontal; prf, prefontal.

an unusual and most probably artifactual concavity in the otherwise convex lateral margin of the parietal. In summary, *Nothosaurus andriani* cannot be distinguished from *Nothosaurus giganteus* except by its somewhat smaller size, which may well reflect ontogenetic variation.

The holotype of *Nothosaurus angustifrons* (SMNS 51972) from the upper Muschelkalk of Crailsheim (Fig. 4) was first described and figured by Meyer and Plieninger (1844: 47, Pl. 10, Fig. 2), and redescribed by Meyer (1847–1855: 84, Pl. 8, Figs. 1–3). Characters considered diagnostic for the new species other than those resulting from distortion of the skull during fossilization were the relatively short and rounded rostrum and the relatively broad frontal bones. Inspection of the holotype reveals the incomplete nature of the rostrum, which has lost its natural margins as a consequence of crude preparation. Relative length and shape of the rostrum cannot be determined in the holotype. Fraas (1896: 10, Fig. 3) identified a second specimen (SMNS 8872, "Blezinger" specimen). The width of the frontal bones between the orbits divided by the width of the dorsomedial bony bridge between the external nares yields a ratio of 1.3 in the holotype of *Nothosaurus angustifrons* (SMNS 51972) and 1.1 in the second specimen (SMNS 8872). This ratio is again highly variable; it ranges from 0.8 to 2.1 in *Nothosaurus mirabilis*, it is 2.5 in *Nothosaurus "muensteri"* (original of Meyer, 1847–1855, Pl. 9, Fig. 4), and it ranges from 1.2 to 4.3 in *Nothosaurus marchicus*. The same ratio is 1.4 in the "Allmendinger" specimen of *Nothosaurus andriani* (SMNS 7860), 1.2 in an undescribed skull of *Nothosaurus giganteus* (SMNS 57047; see below), and 1.6 in the holotype of *Nothosaurus baruthicus* (Geissler, 1895). The average value for this ratio in the

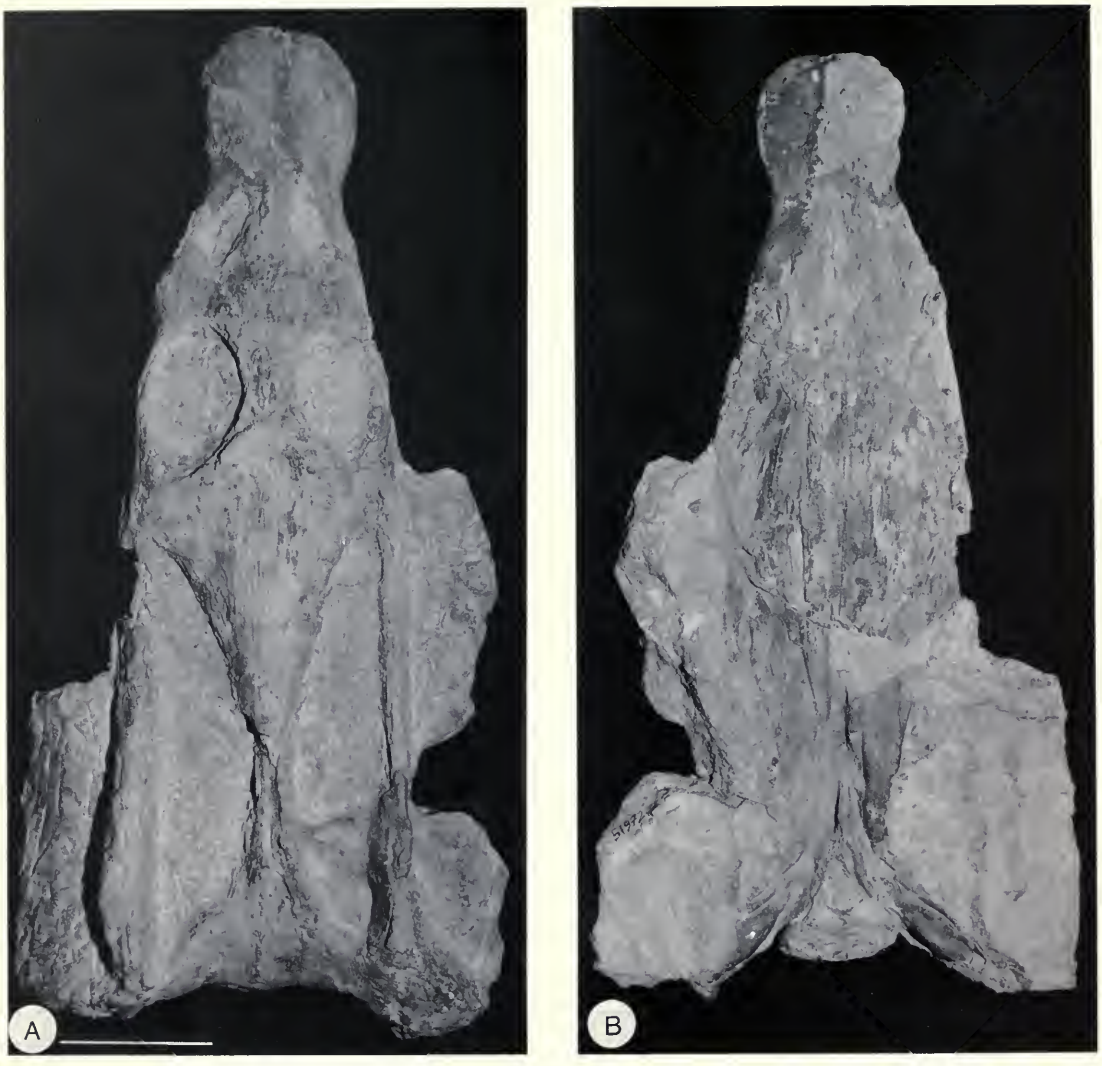


FIG. 4. *Nothosaurus angustifrons* Meyer and Plieninger (holotype; SMNS 51972); upper Muschelkalk, Crailsheim. **A,** The skull in dorsal view; **B,** the skull in ventral view. Scale bar = 50 mm.

above-mentioned taxa indicates that the relative width of the frontal bone between the orbits is size dependent. The average value is 2.52 for the relatively small skulls of *Nothosaurus marchicus,* 1.65 for the intermediate skulls of *Nothosaurus mirabilis* (excluding the one specimen of *Nothosaurus muensteri* with a ratio of 2.5), and 1.3 for the relatively large skulls of *Nothosaurus giganteus* (including *andriani, angustifrons,* and *baruthicus*). The holotype of *Nothosaurus angustifrons* (SMNS 51972; Fig. 5) is somewhat smaller than typical *Nothosaurus andriani* skulls, but the second specimen of *Nothosaurus angustifrons* identified by Fraas (1896; SMNS 8872, "Blezinger" specimen) is larger than the holotype and closely approaches the "Allmendiger" specimen of *Nothosaurus andriani* identified by Fraas (1896; SMNS 7860) in size. In essence, the skulls of *Nothosaurus angustifrons* cannot be distinguished from those of *Nothosaurus andriani* (Figs. 3A,B); this corroborates the synonymy of the two species (Edinger, 1921a; see also Quenstedt [1852: 134], who compared *Nothosaurus angustifrons* with *Nothosaurus cuvieri*).

Nothosaurus baruthicus (Fig. 6), from the upper Muschelkalk of Bayreuth, was first described

FIG. 5. *Nothosaurus angustifrons* Meyer and Plieninger (SMNS 8872; original of Fraas, 1896 ["Blezinger" specimen]); upper Muschelkalk, Crailsheim. Anterior part of skull in dorsal view. Scale bar = 20 mm.

by Geissler (1895). The holotype (SMF R-475; condylobasal skull length: 608 mm) consists of a beautifully preserved skull that shows little sutural detail, however. Edinger (1921a: 14) initially considered it unlikely that two species of *Nothosaurus*, both larger in size than *Nothosaurus mirabilis*, could have coexisted. But with reference to the fused sutures in *Nothosaurus baruthicus*, she accepted *Nothosaurus andriani* as a valid species (including *angustifrons* and *baruthicus*); it is distingly larger than *Nothosaurus mirabilis* yet remains smaller than *Nothosaurus giganteus* (including *aduncidens*). This hypothesis is very attractive and might be supported by the unique shape of the fronto-parietal suture in a skull (SMNS 57047) described in detail below and attributed to *Nothosaurus giganteus*. However, if that character were used as an autapomorphy diagnostic of the latter species, SMNS 57047 would be the only representative of *Nothosaurus giganteus* to show that character, and *Nothosaurus andriani* (including *baruthicus*) would have no diagnostic characters of its own, other than size. Furthermore, although available material does not allow the course of the fronto-parietal suture in SMNS 57047 to be assessed and a determination made of whether it is, in fact, a species-specific character or an individual variation, *Nothosaurus baruthicus* does provide a link in the size range between *Nothosaurus andriani* and *Nothosaurus angustifrons*, on the one hand, and between *Nothosaurus giganteus* and *Nothosaurus aduncidens* on the other. Indeed, if all the cranial material of *Nothosaurus* from the Germanic Basin and deposited in public repositories is taken into account, all intermediate sizes exist between the smallest (holotype of *Nothosaurus angustifrons*, SMNS 51972) and the largest (holotype of *Nothosaurus aduncidens*, SMNS 4200) skull; this is why all these taxa are here considered junior synonyms of *Nothosaurus giganteus* Münster and their size differences are treated as ontogenetic variation.

The occurrence of a large species of *Nothosaurus* beyond the Muschelkalk is indicated by a large ilium from the lower Keuper of Zwingelhausen (SMNS 50821), as well as by two large lower jaw fragments (SMNS 7214b and SMNS 10506), both from the lower Keuper of Hoheneck near Ludwigsburg and hence from a deposit that has also yielded two skulls of approximately 450 mm and 550 mm length (Edinger, 1921a: 16). These skulls, which match the mandibular fragments in size, also perfectly bridge the size gap between the holotypes of *Nothosaurus andriani* (condylobasal skull length: 428 mm) and *Nothosaurus baruthicus* (condylobasal skull length: 608 mm), and they were described by Fraas (1896: 12, Pl. 4) as those of a separate species, *Nothosaurus chelydrops* (Figs. 3C, 7). Most subsequent workers

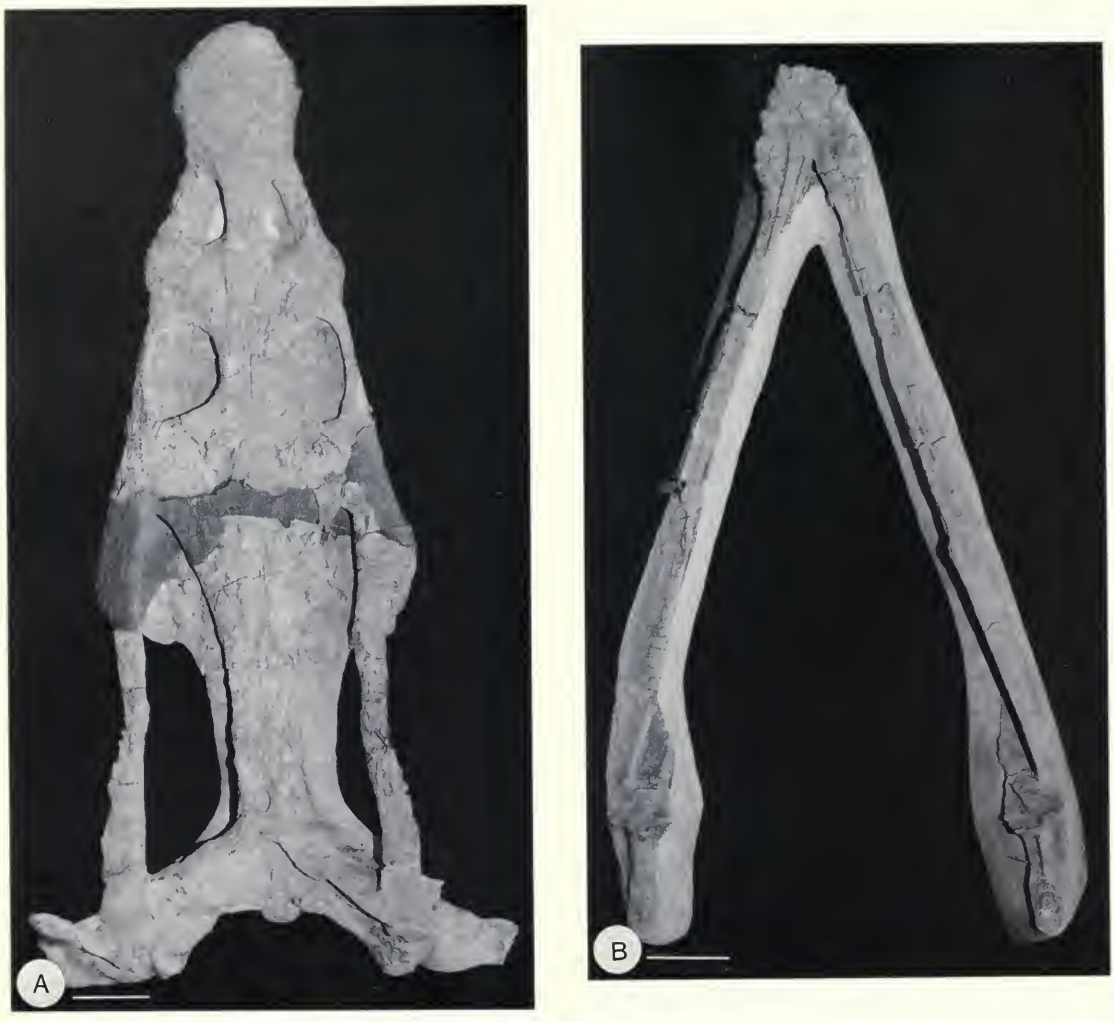


FIG. 6. *Nothosaurus baruthicus* Geissler; Muschelkalk, Bayreuth. **A,** The holotype (SMF R-475) in dorsal view; **B,** lower jaw (SMF R-uncatalogued; original of Geissler, 1895, Pl. 1, Fig. 2).

(e.g., Edinger, 1921a; Schultze, 1970) have accepted *Nothosaurus chelydrops* as a separate species, not only because of stratigraphic considerations (which may have influenced Fraas [1896]), but also because of its distinct morphology. The species was said to be characterized by its broad and distinctly triangular skull shape; the broad anterior expansion of the parietals and, correlated therewith, the strong anterior constriction of the upper temporal fenestrae; the oblique position of the orbits and external nares; and the fact that the bony bridge between the orbit and the upper temporal fenestra is much wider than the bridge between the external naris and the orbit. Because of its greater width, the skull of *Nothosaurus chelydrops* also conveys the impression of being relatively shorter than in other species. It must be noted, however, that the holotype of *Nothosaurus chelydrops* (SMNS 7162) was subject to severe dorsoventral compression during fossilization. Preservation of vertebrate fossils in the lower Keuper is generally less perfect than in the Muschelkalk, and the holotype of *Nothosaurus chelydrops* (SMNS 7162) shows finely broken bone in a generally poorly preserved and strongly compressed skull. Comparison of the skull of *Nothosaurus chelydrops* and the skull of *Nothosaurus giganteus* should therefore emphasize longitudinal rather than transverse length ratios. The only diagnostic character not directly influenced by dorso-

FIG. 7. *Nothosaurus chelydrops* Fraas (holotype; SMNS 7162); lower Keuper, Hoheneck near Ludwigsburg. The skull in dorsal view. Scale bar = 50 mm.

ventral compression of the skull is the relative width of the bony bridge between the orbit and the upper temporal fenestra, on the one hand, and between the orbit and the external naris on the other. However, neither one of the external nares preserves its original contours, and although the left external naris appears to permit a direct measurement of its longitudinal diameter, its posterior margin is, in fact, broken. Dividing the distance from the orbit to the upper temporal fenestra by a conservative estimate (37 mm) for the distance between the external naris and the orbit yields a ratio of 1.6 for the holotype of *Nothosaurus chelydrops*, indicating a somewhat broader postorbital arch than is typical for other skulls of *Nothosaurus giganteus*. The same ratio varies from 1.1 to 1.3 in other skulls of *Nothosaurus giganteus* (see list of synonymy above), from 0.8 to 1.3 in *Nothosaurus marchicus*, from 1.2 to 1.4 in *Nothosaurus* "*muensteri*," and from 0.9 to 1.8 in *Nothosaurus mirabilis*. Dividing the longitudinal diameter of the upper temporal fenestra by the longitudinal diameter of the orbit yields a ratio of 3.4 for the holotype of *Nothosaurus chelydrops* (SMNS 7162), compared to 3.0–3.7 in other skulls of *Nothosaurus giganteus*, 2.9–3.8 in *Nothosaurus mirabilis*, and 2.1–3.0 in *Nothosaurus marchicus*. Dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris results in an index of 2.0 for *Nothosaurus chelydrops* and 1.6–1.9 for *Nothosaurus giganteus*. Dividing the distance from the tip of the snout to the anterior margin of the upper temporal fenestra by the distance from the tip of the snout to the anterior margin of the external naris yields a ratio of 3.4 for *Nothosaurus chelydrops* and 2.6–3.2 for *Nothosaurus giganteus*. Dividing the distance from the tip of the snout to the anterior margin of the upper temporal fenestra by the distance from the tip of the snout to the anterior margin of the orbit yields a ratio of 1.7 for *Nothosaurus chelydrops* and 1.6–1.7 for *Nothosaurus giganteus*. These values indicate that the skull of the holotype of *Nothosaurus chelydrops* (SMNS 7162) shows no distinct shortening of overall proportions, but it does have a rostrum slightly shorter than the other skulls of *Nothosaurus giganteus*. The ratio obtained by dividing the distance from the tip of the snout to the anterior margin of the external naris either by the width of the skull at the constricted snout (0.9, compared to 1.1–2.5 in all other nothosaur skulls) or by the maximal width of the premaxillary rostrum (0.8, compared to 1.0–2.2 in all other nothosaur skulls) is unusually low in *Nothosaurus chelydrops*. This indicates a relatively broader rostrum in *Nothosaurus chelydrops* (Edinger, 1921a: 16), which may be another consequence of the strong dorsoventral compression of its skull. Considering the poor preservation of the holotype of *Nothosaurus chelydrops*, it seems questionable at this time to use slight proportional differences of the skull as characters diagnostic of a separate species. The left premaxilla of the holotype of *Nothosaurus chelydrops* (SMNS 7162) shows alveoli

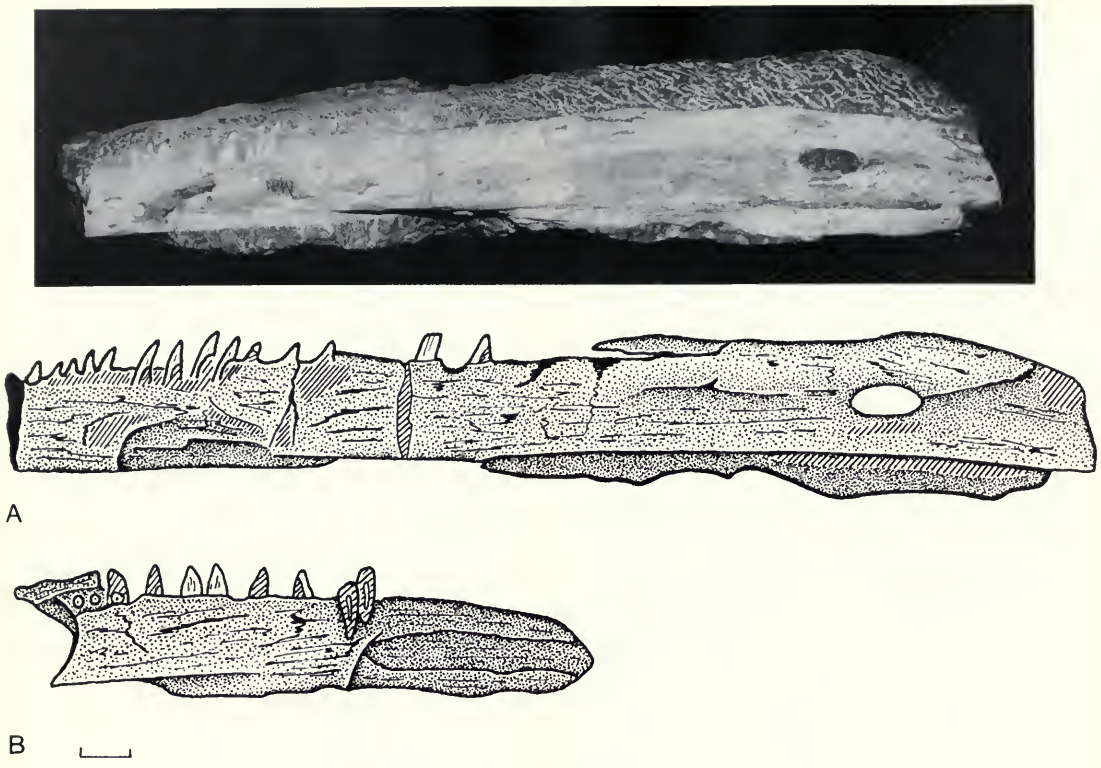


FIG. 8. *Opeosaurus suevicus* Meyer (holotype; SMNS 4141); upper Muschelkalk, Stuttgart-Zuffenhausen. **A,** Left lateral view; **B,** right lateral view. Scale bar = 20 mm.

for only four fangs, but not for a succeeding yet distinctly smaller fifth premaxillary tooth, as is typical for *Nothosaurus giganteus.* Such a small fifth premaxillary tooth may have been present on the left premaxilla, which is less well preserved, however. The second skull mentioned by Fraas (1896: 12; SMNS 80205) is very incomplete and difficult to interpret. Nevertheless, the preserved posterior part of the right squamosal indicates that the shape of the upper temporal fenestra was more closely comparable to that of other species of *Nothosaurus* than is true for the holotype of *Nothosaurus chelydrops* (SMNS 7162). On the basis of the presence of four (rather than five) premaxillary fangs, the species is here considered a junior synonym of *Nothosaurus giganteus. Nothosaurus chelydrops* would only become valid should new and better preserved skulls confirm the unusual triangular outlines of the skull, the marked anterior constriction of the temporal fenestrae, and the oblique orbits as real phenomena, not merely the result of preservational distortion.

Opeosaurus suevicus Meyer (1847–1855: 82, Pl. 14, Figs. 1–3) is represented by the fragmentary lower jaw of a large nothosaur (SMNS 4141) from the upper Muschelkalk of Stuttgart-Zuffenhausen (Fig. 8). It was considered a separate taxon because of a "mandibular fenestra" which is, in fact, an artifact of preparation or preservation. The specimen consists of a larger part of the left dentary (215 mm long) and a smaller part of the right dentary. In the absence of the mandibular symphysis, the specimen is not diagnostic, but its size corroborates Fraas's (1896: 9) conclusion that *Opeosaurus suevicus* is a junior synonym of *Nothosaurus aduncidens* (see also Schrammen, 1899: 408; Romer, 1956: 662), which in turn is a junior synonym of *Nothosaurus giganteus* Münster, 1834.

Paranothosaurus amsleri is a large nothosaur from the Grenzbitumenzone (Anisian–Ladinian boundary, corresponding to the boundary between mo_1 and mo_2) of the southern Alps (Monte San Giorgio, Switzerland), first described by Peyer (1939; see also Kuhn-Schnyder [1966] for a more complete description of the skull). Peyer (1939) emphasized the difference between the vertebrae of *Paranothosaurus* with a low neural spine and

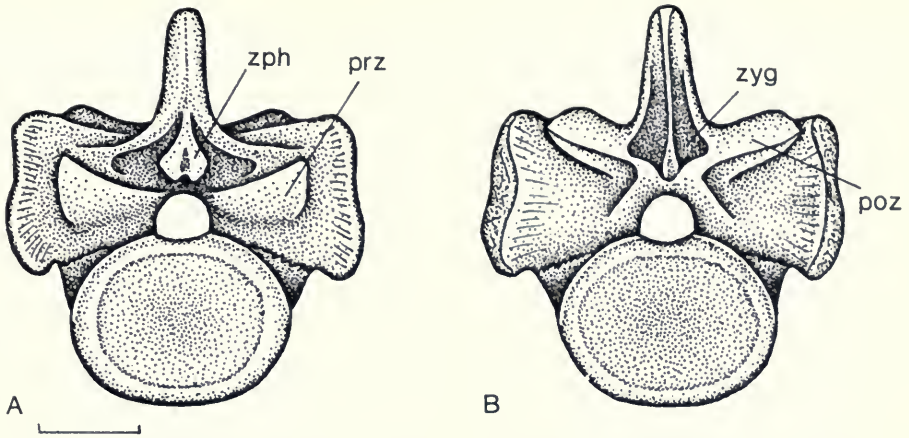


FIG. 9. *Nothosaurus giganteus* Münster (SMNS 58453; cast of original of Della Veccia, 1993, Figs. 6–7); Ladinian, southern Alps. **A,** Dorsal vertebra in anterior view; **B,** same in posterior view. Scale bar = 20 mm. Abbreviations: poz, postzygapophyses; prz, prezygapophyses; zyg, zygantrum; zph, zygosphene.

those of the genotypical species *Nothosaurus mirabilis* with a high neural spine. He also noted the occurrence of nothosaur-like vertebrae in the lower Muschelkalk with a low neural spine, but he did not discuss further the taxonomic implications of these observations. This was left to Kuhn-Schnyder (1966), who stressed the detailed similarity of skull structure in *Paranothosaurus* and *Nothosaurus* and considered the possibility that the neural spines in the holotype of *Paranothosaurus* might have been compressed during fossilization. The latter option may now be disregarded, since perfectly preserved large dorsal vertebrae with a low neural spine are known from the Alpine Triassic (Ladinian, Fusea, Province Udine, Italy: Dalla Veccia, 1993; Fig. 9) and from upper Muschelkalk desposits (see below). By comparison with outgroups (Rieppel, 1994a), as well as with nothosaurs from the lowermost Muschelkalk (see discussion of *Nothosaurus marchicus,* below) and possibly China (Young, 1965), the low neural arch on the dorsal vertebrae would seem to represent the plesiomorphic condition. Morphology indicates that the genus *Paranothosaurus* is a junior synonym of *Nothosaurus*; moreover, its size, skull proportions, and stratigraphic occurrence (upper Muschelkalk equivalent) indicate that *Paranothosaurus amsleri* Peyer, 1939, is a junior synonym of *Nothosaurus giganteus* Münster, 1834. It seems highly unlikely that different species of large nothosaurs would have existed at the same time in the Germanic Basin and in the southern Alpine intraplatform basin facies, and the description of the holotype of *Paranothosaurus amsleri* (currently not available for study) does not indicate any diagnostic characters for a spearate species.

Morphological Description

THE SKULL: The most conspicuous diagnostic feature of *Nothosaurus giganteus* is its large size (Münster, 1834), with the condylobasal skull length estimated to reach 700–800 mm by Edinger (1921a). The largest complete skulls are the holotype of *N. baruthicus* (SMF R-475; Fig. 10) with a condylobasal skull length of 608 mm, and the undescribed specimen SMNS 18475, with a condylobasal skull length of 625 mm (adding 25 mm for the missing tip of the rostrum). *Nothosaurus giganteus* differs from the genotypical species *N. mirabilis* not only by its size, but also by its relatively short and rounded rostrum, set off from the remaining skull by a distinct rostral constriction (except in the holotype of *N. chelydrops,* in which the rostral constriction is obscured by dorsoventral flattening of the skull). It is difficult, in general, to use morphometric indices in the analysis of nothosaur skulls because of incomplete preservation and distortion, in particular dorsoventral compression. Longitudinal measures appear less affected by preservational artifacts. Dividing the distance from the tip of the snout to the anterior margin of the external naris by the width of the skull at the rostral constriction yields a value of 1.2–1.6 for *N. giganteus* (0.9 for *N. chelydrops*—see discussion above; the corre-

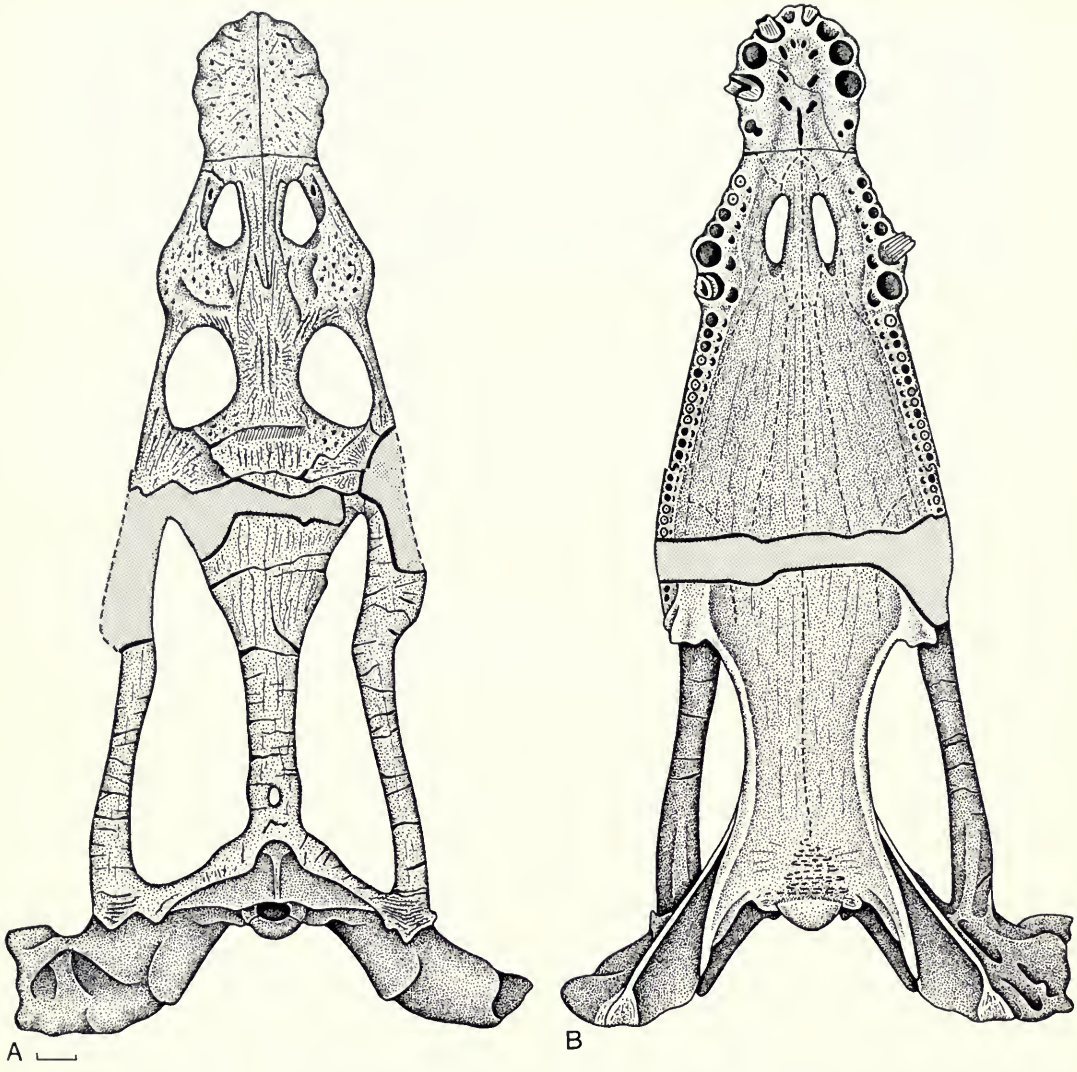


FIG. 10. *Nothosaurus giganteus* Münster (holotype of *Nothosaurus baruthicus* Geissler; SMF R-475); upper Muschelkalk, Bayreuth. **A,** The skull in dorsal view; **B,** the skull in ventral view. Scale bar = 20 mm.

sponding values for *N. mirabilis* are listed in the species description below). Dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris results in an index of 1.6–2.0. Dividing the distance from the tip of the snout to the anterior margin of the upper temporal fenestra by the distance from the tip of the snout to the anterior margin of the external naris yields a ratio of 2.6–3.4. Finally, dividing the longitudinal diameter of the external naris by its transverse diameter yields a ratio of 1.3–1.4 for juveniles (SMNS 7860, SMNS 8872) and 1.7–1.85 for adults (SMNS 57047, SMF R-475).

The specimen SMNS 57047 (Figs. 11, 12), from the uppermost Muschelkalk of Heimsheim, is a skull not previously described that has been acid prepared. The skull is incomplete, lacking the rostrum as well as the left part of the occiput. Both temporal arches are missing, and the lateral margins of the parietal show distinctive tooth scars caused by some scavenger. The maxillary–premaxillary suture can be identified at the anterolateral corner of the (right) external naris. Lateral to the external naris, the maxilla shows a distinct depression, but the foramen commonly observed in this depression in other nothosaur skulls cannot be identified. The holotype of *N. baruthicus* (SMF

R-475) shows the maxillary tooth row extending backward well beyond the orbit to a level between the first and the second third of the longitudinal diameter of the upper temporal fenestra.

The nasals are rather slender elements that define the posteromedial and (with a slender anterior process) medial margin of the external nares. The premaxillae form a posterior (nasal) process that separates the nasals and establishes a contact with the anteromedial process of the frontal. The premaxillary processes also appear to reach the frontal in the holotype of *N. baruthicus* (SMF R-475), whereas the nasals meet in a dorsomedial suture in "*Paranothosaurus amsleri*" (Kuhn-Schnyder, 1966), thus separating the premaxillaries from the frontal. As discussed below, this character is variable within the genotypical species, *N. mirabilis*. As is typical for the genus, the prefrontals are small elements situated at the anterodorsal margin of the orbit, and they have only a limited dorsal exposure. Slender anterolateral processes of the frontal contact the ascending process of the maxilla and thereby separate the prefrontal from the nasal. In "*Paranothosaurus amsleri*" (Kuhn-Schnyder, 1966), the prefrontal contacts the nasal on the right side but not on the left side. The same individual variation of this character is observed in the genotypical species, *N. mirabilis* (Rieppel, 1993b, Fig. 4).

The frontal is unpaired and forms a strongly interdigitating suture with the parietal at a level well behind the anterior margin of the upper temporal fenestra. SMNS 57047 shows an unusual anterolateral process of the parietal that enters deeply between the frontal and postfrontal, extending anteriorly up to a level just behind the posterior margin of the orbit. This character has not been observed in any other nothosaur skull, in particular because all other skulls referred to *N. giganteus* do not preserve enough morphological detail to assess the nature of the fronto-parietal suture. An initial development of anterolateral processes of the parietal is observed in "*Paranothosaurus amsleri*" (Kuhn-Schnyder, 1966), however, and their greater extent in SMNS 57047 could well be an expression of individual variation. It should be noted that a similar anterolateral process of the parietal, entering deeply between the frontal and postfrontal, is also observed in one skull of *Nothosaurus* sp. (SMNS 56618).

The postorbital shows a narrow entry into the posteroventral margin of the orbit. The jugal is excluded from the posterior margin of the orbit. Most of the posterior and posterodorsal margin of the orbit is defined by the broad postfrontal, which gradually narrows behind the orbit. The postfrontal lacks the distinct postorbital indentation of its lower (lateral) margin observed in *N. marchicus*. The posterior relation of the postfrontal to the anteromedial margin of the upper temporal fenestra is difficult to establish because of the incomplete preservation of the medial margin of the upper temporal fenestra. As far as they are preserved, however, the postfrontals show a slight lateral deflection of their posterior extremity, rendering it likely that they entered the medial margin of the upper temporal fenestra behind the postorbital, which defined the entire anterior margin of the temporal fenestra. A similar sutural pattern has been postulated for *N. andriani* by Fraas (1896, Fig. 2; see discussion above), but the postfrontals remain excluded from the upper temporal fenestra in "*Paranothosaurus amsleri*" (Kuhn-Schnyder, 1966). The upper temporal fenestra is relatively larger than in *N. marchicus*, and its anterior margin is constricted by a lateral convexity of the parietal, as in *N. mirabilis*, with an upper temporal fenestra of comparable size.

The parietal is unpaired, and the pineal foramen is shifted to a posterior position. The dorsal aspect of the right squamosal is severely damaged and shows no structural detail.

The occiput is partially preserved in SMNS 57047 and resembles in all details that of *N. mirabilis* (Rieppel, 1994b). The occipital condyle is formed by the basioccipital alone. The exoccipitals define the lateral margin of the foramen magnum and the medial margin of the jugular (metotic) foramen; they do not meet dorsal to the occiput. Basioccipital tubers are distinct, and the eustachian foramen is open.

The palate of *N. giganteus* is well exposed in another as yet undescribed specimen (SMNS 18475) from the upper Muschelkalk of Tiefenbach near Crailsheim (Figs. 13, 14), as well as in the holotypes of *N. baruthicus* (SMF R-475) and *N. andriani* (BT, uncatalogued). Each premaxilla bears four fangs followed by a distinctly smaller fifth tooth. The same premaxillary dentition is observed in "*Paranothosaurus amsleri*" (Kuhn-Schnyder, 1966). Four small maxillary teeth precede the paired maxillary fangs. The total number of maxillary teeth cannot be established in any of the specimens; in SMF R-475, a total of 19 small teeth can be counted behind the maxillary fangs, and the total number of postcanine maxillary teeth cannot have exceeded 24–26.

The sutural pattern is difficult to establish in all

FIG. 11. *Nothosaurus giganteus* Münster (SMNS 57047); upper Muschelkalk, Heimsheim. The skull in dorsal view. Scale bar = 100 mm. SMNS negative no. 8322.

available specimens. SMNS 18475 shows the premaxillary–maxillary suture on the lateroventral edge of the skull, as well as the entry of the palatine into the posterior margin of the internal naris. The ectopterygoid is relatively broad and short as in *N. mirabilis,* unlike the anteriorly extended ectopterygoid of *N. marchicus.* And as in *N. mirabilis,* the transverse (lateral) process of the pterygoid is weakly developed. The anterior margin of the subtemporal fossa, defined by the ectopterygoid, forms a distinctly projecting flange that is much more strongly developed than in the smaller species. Similarly strongly developed (ecto-)pterygoid flanges are observed in the holotypes of *N.*

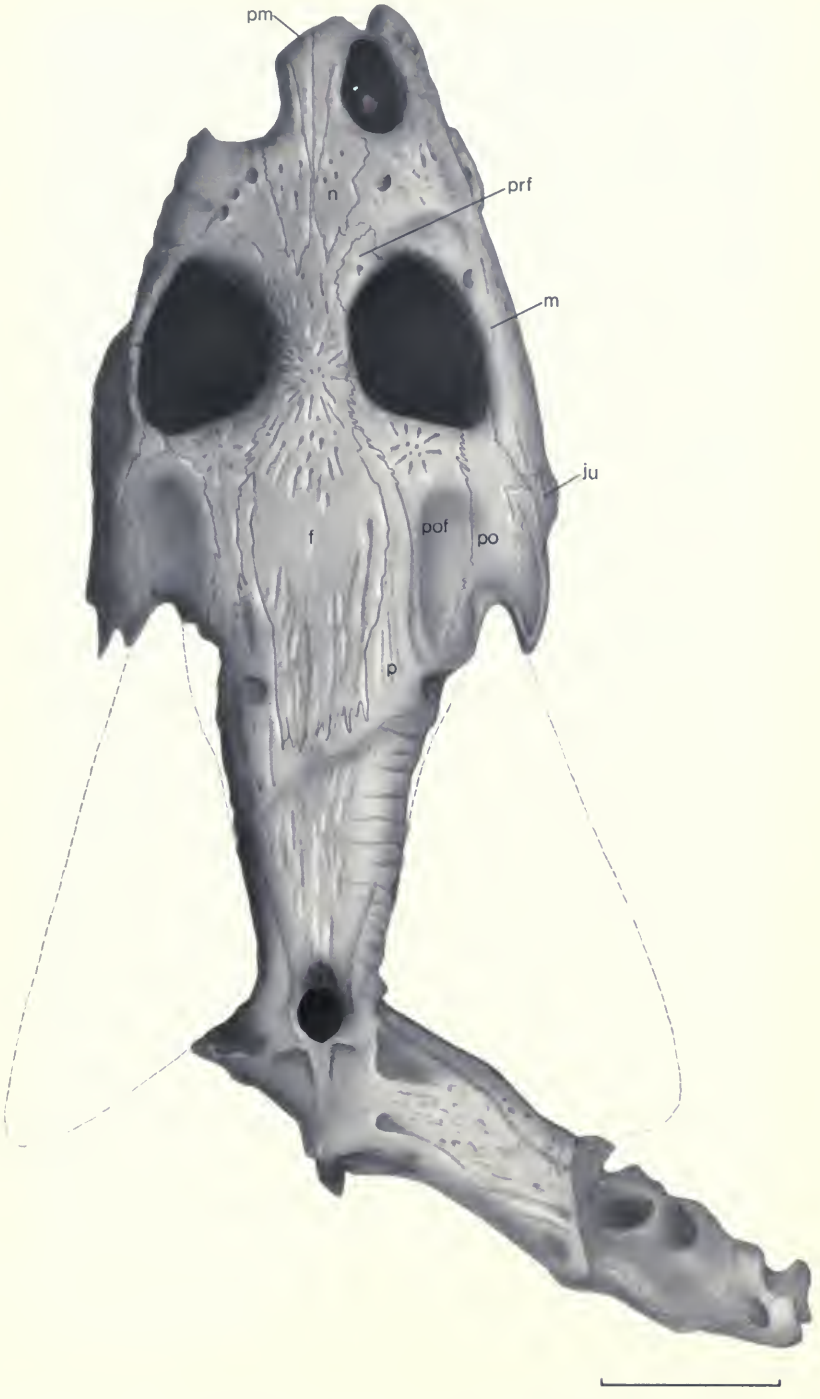


FIG. 12. *Nothosaurus giganteus* Münster (SMNS 57047); upper Muschelkalk, Heimsheim. The skull in dorsal view. Scale bar = 100 mm. Abbreviations: f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal.

FIG. 13. *Nothosaurus giganteus* Münster (SMNS 18475); upper Muschelkalk, Tiefenbach near Crailsheim. The skull in ventral view. Scale bar = 100 mm. SMNS negative no. 8541.

baruthicus and *N. andriani,* and they were noted in the holotype of "*Paranothosaurus amsleri*" by Peyer (1939). The strong development of these ectopterygoid flanges may relate to the strong development of the pterygoideus musculature in these large skulls. The quadrate ramus of the pterygoid again shows very well-developed medially and laterally descending flanges that extend up to its posterior tip, as in *Nothosaurus* in general (Rieppel, 1994b), and this arrangement again probably relates to the strongly developed pterygoideus musculature.

FIG. 14. *Nothosaurus giganteus* Münster (SMNS 18475); upper Muschelkalk, Tiefenbach near Crailsheim. The skull in ventral view. Scale bar = 100 mm. Abbrevations: ec, ectopterygoid; m, maxilla; pl, palatine; pm, premaxilla; pt, pterygoid; q, quadrate; v, vomer.

FIG. 15. *Nothosaurus giganteus* Münster (SMNS 56685); upper Muschelkalk, Gundelsheim. Mandibular symphysis, dorsal view. Scale bar = 20 mm.

LOWER JAW—Except for the specimen described and figured by Geissler (1895, Pl. 1, Fig. 2; SMF, R-uncatalogued; Fig. 6B this paper), SMNS 56685 from the uppermost Muschelkalk of Gundelsheim (Fig. 15) is the only completely preserved (and as yet undescribed) lower jaw of *N. giganteus*. In the latter specimen, the right ramus measures 590 mm and the left ramus measures 585 mm. The length of the symphysis is 88.5 mm and its maximal width is 68 mm. Symphyseal proportions mirror the relatively short and rounded rostrum (Figs. 15, 16). For all the jaws referred to *N. baruthicus* that preserve the mandibular symphysis, division of its length by its maximal width results in a ratio of 1.0–1.3. The mandibular symphysis carries five fangs on either side, with the posteriormost fang lying completely or incompletely within the symphysis. The symphysis itself is well set off from the remainder of the lower jaw. The teeth are set in a distinct ridge on the dorsal surface of the dentary. The left dentary of SMNS 56685 carries a total of 48 distinctly smaller teeth behind the five symphyseal fangs. The symphyseal fangs as well as the postsymphyseal teeth show lateral replacement.

Sutures are virtually impossible to identify on any of the lower jaws available. SMNS 56685, as well as Geissler's (1895) specimen, shows the absence of a coronoid process. The lateral surface of the surangular forms a distinctly projecting shelf for the insertion of superficial fibers of the jaw adductor musculature. Similarly, the prearticular forms a medially projecting shelf, located anteroventral to the mandibular joint on the inner side of the lower jaw ramus, into which may have inserted deep layers of the jaw adductor musculture (m. adductor mandibulae externus profundus, m. pterygoideus internus). The articular surface is saddle shaped to accommodate the mandibular condyle of the quadrate. Both the anterior and the posterior margins of the articular facet are distinctly raised, thus locking the lower jaw against the anterior and posterior pull of the jaw adductors (see Rieppel, 1994a, for a discussion of the dual jaw adductor system of Eusauropterygia). The dorsal surface of the distinctly developed retroarticular process is subdivided by a longitudinal ridge. The chorda tympani foramen cannot be identified in SMNS 56685 (see Rieppel, 1994a, for further discussion).

POSTCRANIAL SKELETON—The postcranial skeleton of *N. giganteus* is exceptionally well known from Peyer's (1939) description of "*Paranothosaurus amsleri.*" The postcranial remains associated with the second skull of *N. chelydrops* (Fraas, 1896: 12; SMNS 80205) are very incomplete and poorly preserved; identifiable elements include a coracoid, an isolated ulna, and rib fragments. The only other articulated material is a partial postcranium from the Middle Triassic of Belogradcik, northwestern Bulgaria (Fig. 17, SMNS 80204). The specimen comprises 11 articulated dorsal vertebrae, fragments of adjacent vertebrae, and fragments of dorsal and gastral ribs. Both the anteriormost and the posteriormost elements of the string of articulated vertebrae lack the centrum, and a disarticulated centrum is located at the level of the seventh and eighth elements of the string of vertebrae. Disarticulation of the centrum and neural arch indicates an unfused neurocentral suture. In general, the centra are slightly constricted, and their articular surface is slightly

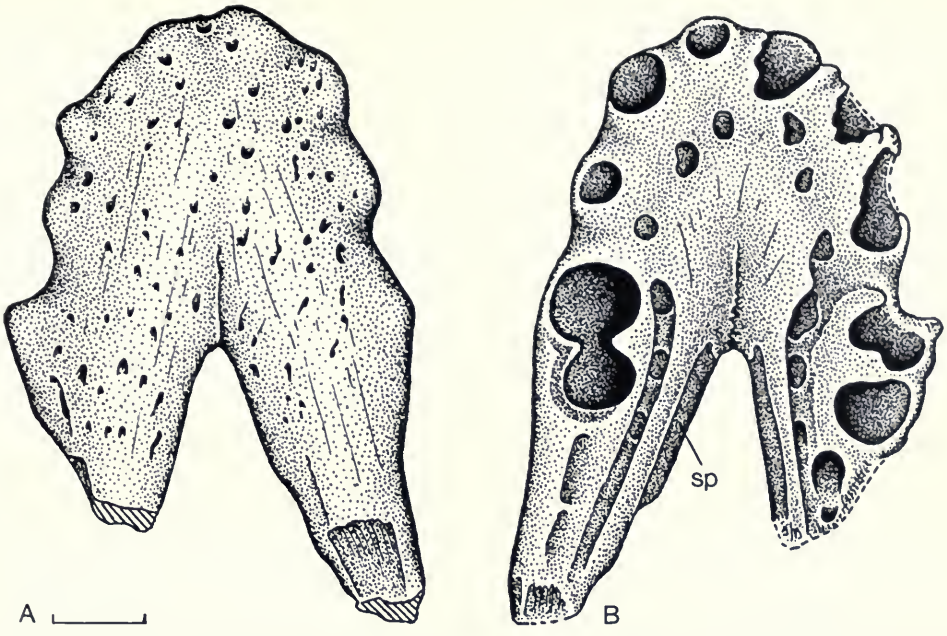


FIG. 16. *Nothosaurus giganteus* Münster (SMF R-1062); upper Muschelkalk, Bayreuth. Mandibular symphysis. **A,** Ventral view; **B,** dorsal view. Scale bar = 20 mm. Abbreviation: sp, splenial.

amphicoelous or platycoelous. The disarticulated centrum shows the horizontally oriented and "butterfly-shaped" or "cruciform" facet for the reception of the pedicels of the neural arch, which is diagnostic for the Eosauropterygia (Rieppel, 1994a).

The neural arches (Fig. 18) are characteristic for *N. giganteus* ("*Paranothosaurus*"). The neural spines are low throughout the vertebral column (Peyer, 1939), although their dorsal margin is slightly eroded in the specimen described here. The neural arches have a massive appearance, with large, "swollen" (pachyostotic) and "domed" postzygapophyses. The large postzygapophyses are set off from the deep transverse processes by a deep notch. The orientation of the articular surfaces of pre- and postzygapophyses is close to horizontal. A deep and broad trough (zygantrum), divided by an internal vertical septum, is located between the postzygapophyses. In comparison, the neural arches of *N. mirabilis* are characterized by distinctly higher neural spines (Fig.

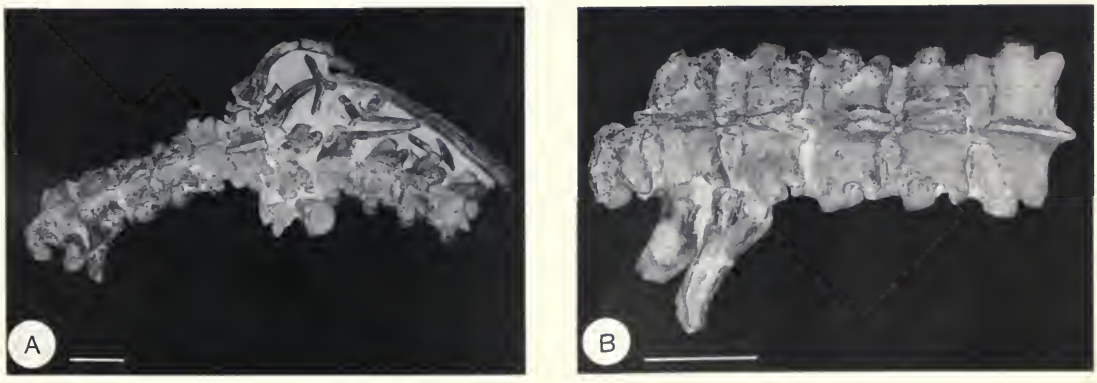


FIG. 17. *Nothosaurus giganteus* Münster (SMNS 80204); Anisian–Ladinian, Bulgaria. Incomplete postcranium. **A,** Overview; **B,** anterior vertebrae, dorsal view. Scale bar = 50 mm.

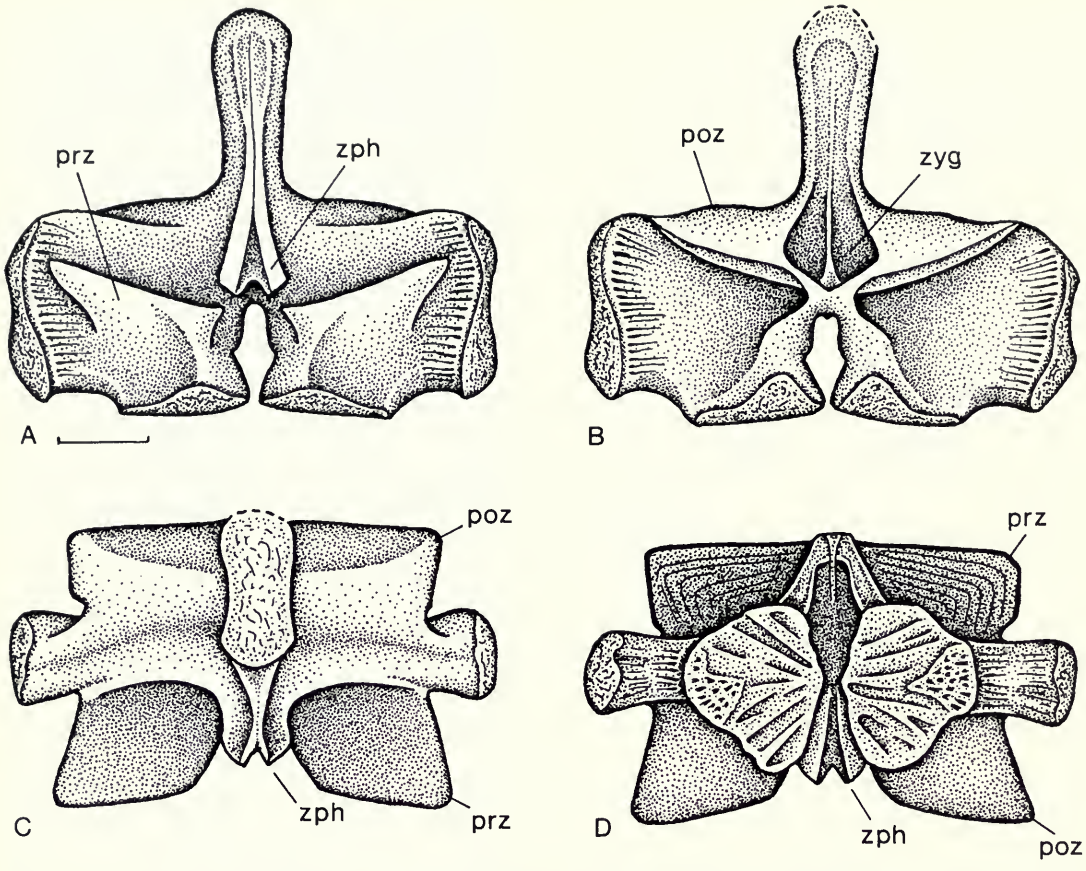


FIG. 18. *Nothosaurus giganteus* Münster (SMNS 55298); upper Muschelkalk, Schmalfelden. Dorsal neural arch. **A,** Anterior view; **B,** posterior view; **C,** dorsal view; **D,** ventral view. Scale bar = 20 mm. Abbreviations: poz, postzygapophyses; prz, prezygapophyses; zyg, zygantrum; zph, zygosphene.

19); the zygantrum is narrower but higher. The zygosphene, located between the broad prezygapophyses, shows a partially bifurcated anterior tip. In *Nothosaurus giganteus,* the strong transverse processes extend down all along the pedicels of the neural arch and take part in the formation of the neurocentral suture (Fig. 18). In comparison, the transverse processes of *N. mirabilis* have a more slender appearance and do not take part in the formation of the neurocentral suture in the dorsal region. Also, the pre- and postzygapophyses are broader and/or the transverse processes are relatively shorter in *N. giganteus* than in *N. mirabilis,* where the transverse processes project more distinctly beyond the zygapophyses (Fig. 20). Within the string of articulated vertebrae (SMNS 80204), the length of the centrum increases along an anteroposterior gradient from 34 mm (third element) to 37.5 mm (10th element). Similarly, the width of the neural arch (measured across the transverse processes) increases from 79.3 mm (second element) to 83 mm (10th element).

The preserved parts of the dorsal ribs show a single proximal articular head associated with the first and second elements of the articulated string of vertebrae and a distinct curvature in the proximal third of the rib. A well-preserved medial element of a gastral rib shows a distinctly developed anterior tip, as is generally present in the gastral ribs of *Nothosaurus.* No fusion of gastral ribs is reported for *N. giganteus,* as is known for cf. *N. marchicus* and cf. *N. mirabilis* (Koken, 1893; Rieppel, 1994a).

A number of isolated postcranial remains have been referred to *N. giganteus* on the basis of their large size (see discussion under Referred Material, above). These include a large coracoid of 380 mm

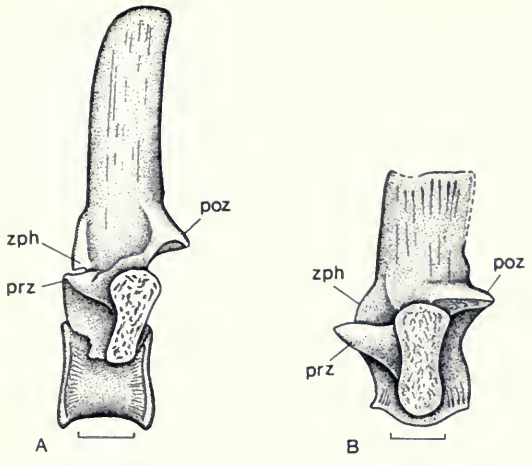


FIG. 19. Dorsal neural arch, left lateral view. **A,** *Nothosaurus mirabilis* Münster (SMNS uncatalogued, coll. M. Wild no. 1211); upper Muschelkalk, Bindlach. **B,** *Nothosaurus giganteus* Münster (SMNS 55298); upper Muschelkalk, Schmalfelden. Scale bar = 20 mm. Abbreviations: poz, postzygapophyses; prz, prezygapophyses; zph, zygosphene.

total length from the upper Muschelkalk of Crailsheim (SMNS, uncatalogued). In an articulated skeleton of *Nothosaurus* sp. (SMNS 56618), a coracoid of 101 mm total length is combined with a skull (prepared in dorsal view) measuring 157 mm from the tip of the snout to the back end of the parietal skull table and 175 mm from the tip of the snout to the back end of the squamosal. Assuming an isometric growth of the coracoid, the large specimen from Crailsheim would indicate a skull length of approximately 590 mm (tip of snout to back end of parietal skull table) or 660 mm (tip of snout to back end of squamosal), respectively, i.e., an individual falling into the size range of *N. giganteus*. Peyer (1939) described an incomplete enclosure of the coracoid foramen between the coracoid and scapula in "*Paranothosaurus amsleri*" that is a potentially diagnostic feature of *N. giganteus*. The large coracoid from Crailsheim shows a well-developed articular facet for the scapula on both sides of the incisure that marks the location of the coracoid foramen, as in the other species of *Nothosaurus*.

Humerus morphology has been shown to be subject to allometric growth changes and sexual variation in pachypleurosaurs (Rieppel, 1989, 1993c; Sander, 1989), and its proportions have diagnostic significance in the distinction of *Placodus*, *Simosaurus*, and *Nothosaurus* (Rieppel, 1995). A number of isolated humeri, referred to *N. giganteus* primarily on the basis of their size (Fig. 21; see also Rieppel, 1994a, Fig. 59B), have been compared to a range of smaller humeri. The total number of humeri compared is 34; the total size ranges from 66.8 mm to 365 mm. No clear-cut distinctions were found in proportional values for the larger as compared to the smaller humeri. Length divided by distal width yields a value ranging from 3.3 to 4.8 (3.6–3.7 for specimens >300 mm); proximal width divided by distal width yields a ratio of 0.7–1.2 (0.8–0.9 for specimens >300 mm); minimal (mid-diaphyseal) width divided by distal width yields a ratio of 0.6–0.9 (0.6–0.7 for specimens >300 mm).

Discussion

Nothosaurus giganteus is restricted to the upper Muschelkalk. Its first appearance is in the mo_1 of Bayreuth, and it most frequently occurs in the mo_2 of the southwestern Germanic Basin. Within the Germanic Basin, it persists into the lower Keuper. By the Anisian–Ladinian boundary (Grenzbitumenzone, Monte San Giorgio), the species had invaded the southern Alpine intraplatform basin facies ("*Paranothosaurus amsleri*" Peyer, 1939). *Nothosaurus giganteus* differs from the contemporaneous but smaller species *Nothosaurus mirabilis* by a number of relatively plesiomorphic features, such as the relatively short and rounded rostrum, the relatively short mandibular symphysis, four (rather than five) maxillary teeth preceding the paired maxillary fangs, and the lesser posterior extension of the maxillary tooth row. *Nothosaurus giganteus* shares with *Nothosaurus mirabilis* some derived features, such as the relatively large upper temporal fenestra (three to four times as long as the diameter of the orbit), the anterior constriction of the upper temporal fenestra, the posterior location of the fronto-parietal suture, the broad entry of the postorbital into the anterior margin of the upper temporal fenestra, and the broad postfrontal, which interdigitates posteriorly with the parietal.

Nothosaurus juvenilis Edinger, 1921b

1921a *Nothosaurus juvenilis*, Edinger, p. 47, Figs. 8–12.
1921a *Nothosaurus königi*, Edinger, p. 48.
1921b *Nothosaurus juvenilis*, Edinger, p. 197, Fig. 4.

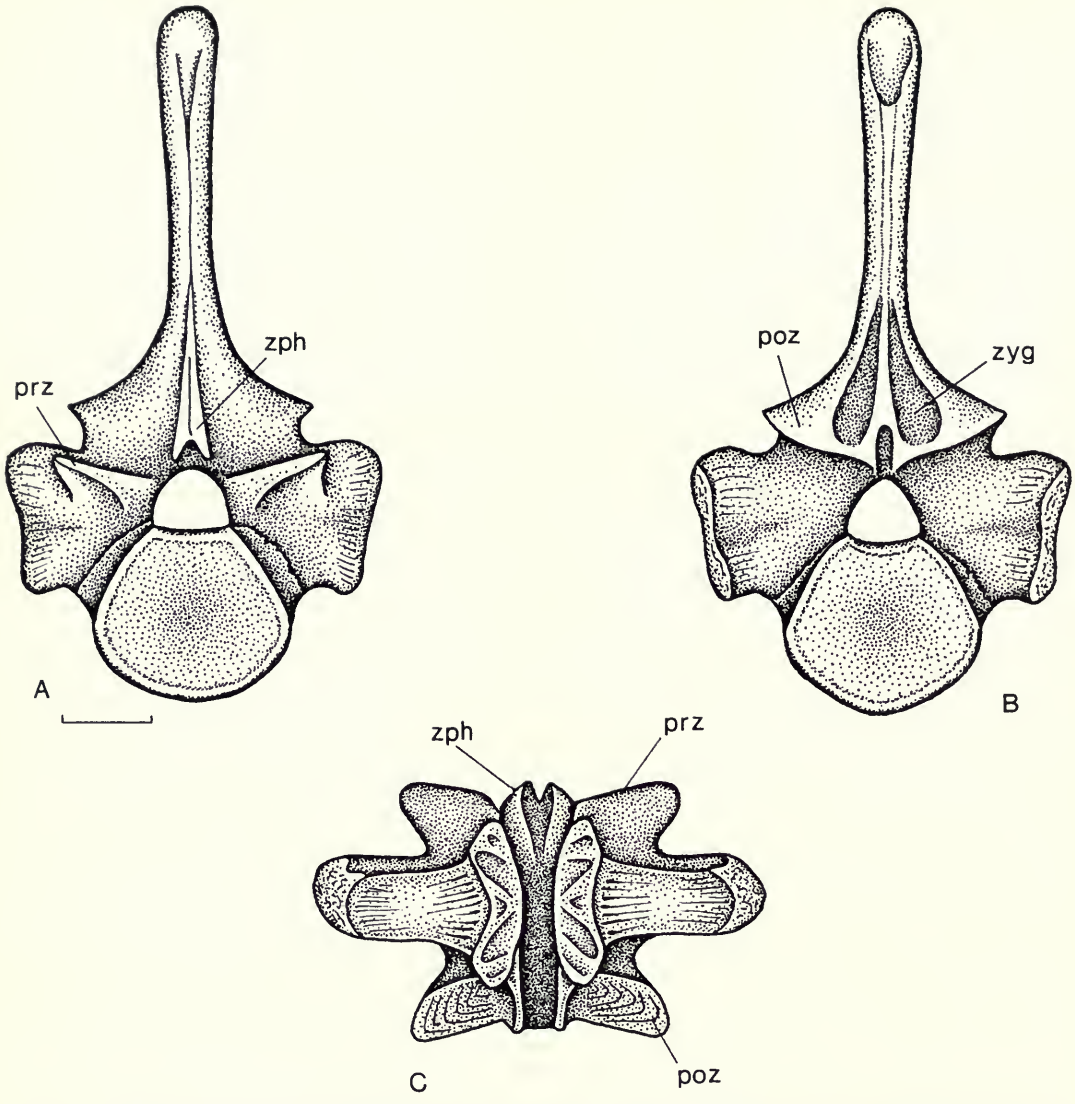


FIG. 20. *Nothosaurus mirabilis* Münster (SMNS, uncatalogued, coll. M. Wild no. 1211); upper Muschelkalk, Bindlach. Dorsal vertebra. **A,** Anterior view; **B,** posterior view; **C,** ventral view. Scale bar = 20 mm. Abbreviations: poz, postzygapophyses; prz, prezygapophyses; zph, zygosphene; zyg, zygantrum.

1960 *Nothosaurus juvenilis,* Edmund, p. 52, Fig. 11.
1963 *Nothosaurus juvenilis,* Haas, p. 37, Pl. 12.
1966 *Nothosaurus juvenilis,* Kuhn-Schnyder, p. 534.
1969 *Nothosaurus juvenilis,* Edmund, p. 192, Fig. 51.
1970 *Nothosaurus juvenilis,* Schultze, p. 225, Fig. 13.
1993b *Nothosaurus juvenilis,* Rieppel, p. 972.
1994c *Nothosaurus juvenilis,* Rieppel, p. 733*ff.*
1994 *Nothosaurus juvenilis,* Rieppel and Wild, p. 10.

HOLOTYPE—The holotype and only known specimen is kept in the Paläontologisches und Geologisches Institut und Museum, Universität Heidelberg (König Collection, K.8698-1).

LOCUS TYPICUS—Upper Muschelkalk (lower Trochitenkalk, mo_1), Nusslocher Zementbruch, Wiesloch near Heidelberg.

DIAGNOSIS—A species of *Nothosaurus* of small size (condylobasal skull length 126 mm); orbits

FIG. 21. *Nothosaurus giganteus* Münster (SMNS 1797); upper Muschelkalk, Schmalfelden. Isolated humerus. Scale bar = 50 mm.

relatively large; postorbital arches relatively narrow; pterygoids closely approaching the internal nares; paroccipital processes trend posterolaterally, which results in a distinct posterior displacement of the lower jaw articulation to a level well behind the occipital condyle; and occiput deeply concave.

DISTRIBUTION—Lower upper Muschelkalk (Anisian, Middle Triassic), western Europe.

COMMENTS—This species was revised by Rieppel (1994c).

Nothosaurus cf. *N. marchicus* Koken, 1893

Synonymy for this material:

1834a *Conchiosaurus clavatus*, Meyer, p. 8, Pl. I, Figs. 3–4.
1834b *Conchiosaurus clavatus*, Meyer, p. 114.
1847–55 *Conchiosaurus clavatus*, Meyer, p. 106, Pl. X, Figs. 2–3.
1864 *Nothosaurus* (*Conchiosaurus*) *clavatus*, Alberti, p. 222.
1852 *Conchiosaurus clavatus*, Quenstedt, p. 135.
1887–90 *Conchiosaurus clavatus*, Zittel, p. 484.
1889 *Conchiosaurus clavatus*, Lydekker, p. 295.
1934 *Nothosaurus clavatus*, Kuhn, p. 33.
1948 *Conchiosaurus clavatus*, Huene, p. 43.
1956 *Conchiosaurus clavatus*, Huene, pp. 389, 412.
1964 *Conchiosaurus clavatus*, Kuhn, p. 17.
1966 *Conchiosaurus clavatus*, Kuhn-Schnyder, p. 534.

HOLOTYPE—Bayerische Staatssammlung für Paläontologie und historische Geologie, BSP AS I 1446; incomplete skull (Fig. 22).

LOCUS TYPICUS—Saurierkalk (*orbicularis* layers, lower middle Muschelkalk), Esperstädt, Sachsen-Anhalt, Germany.

COMMENTS—In his original description of *Conchiosaurus clavatus*, Meyer (1834, Pl. I, Fig. 4) emphasized the striated tooth crown, which is distinctly set off from the constricted tooth base. This has led several workers to compare *Conchiosaurus* with *Simosaurus* (Quenstedt, 1852; Zittel, 1887–1890) or to include *Conchiosaurus* in the Simosauridae (Huene, 1948, 1956). Informally, *Conchiosaurus* has also been considered a possible senior synonym of *Cymatosaurus* (Fritsch, 1894).

Tooth morphology has led to the identification of two lower jaw fragments from the Saurierkalk of Esperstädt, and from the *orbicularis* beds (also lower middle Muschelkalk) of Querfurt, as *Conchiosaurus* in museum collection catalogues. Both specimens are now lost, but casts are preserved in the Staatliches Museum für Naturkunde in Stuttgart (SMNS 80082–3) and in the Natural History Museum in Berlin (MB R. 61–62). The specimens were first reported by Meyer (1838) under the name of *Charitosaurus tschudii*, but they were later redescribed as lower jaws of fishes (Meyer, 1851) and renamed as *Charitodon tschudii*. Although tooth morphology of *Charitosaurus* (*Charitodon*) *tschudii* resembles the pachypleurosaur *Anarosaurus* (Dames, 1890) more closely than *Conchiosaurus*, the dentaries are not diagnostic, and *Charitosaurus*, *Charitodon*, and *tschudii* are considered nomina dubia.

Other jaw fragments referred to as *Conchiosaurus* on museum collection labels come from the lowermost lower Muschelkalk (Gogolin beds) of

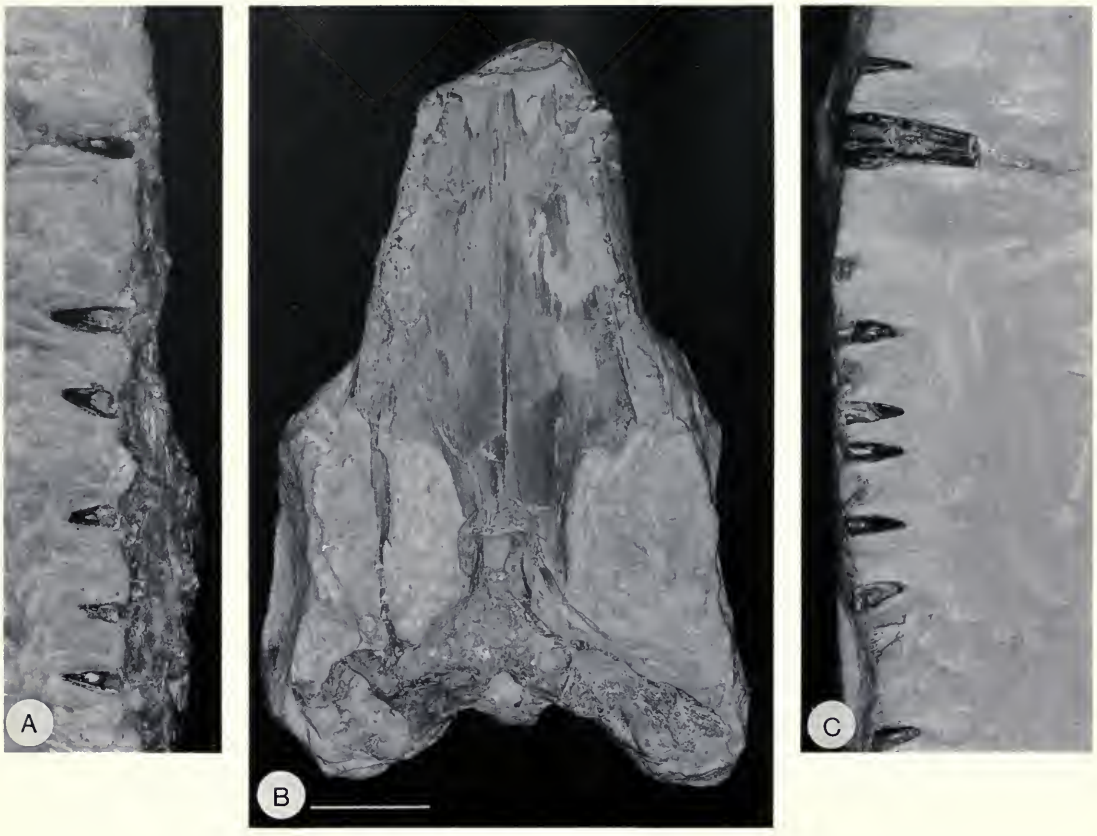


FIG. 22. *Conchiosaurus clavatus* Meyer (holotype; BSP AS I 1446); lower middle Muschelkalk, Esperstädt. **A,** Left maxillary dentition (not to scale); **B,** the skull as preserved (scale bar = 20 mm); **C** right maxillary dentition (not to scale).

Gogolin, Upper Silesia (BGW, S 44/1). The specimens are thus considerably older than the holotype of *Conchiosaurus,* and a fragment from Chorzow (Upper Silesia) has originally been described by Meyer (1847: 575; 1851: 236, Pl. 28, Fig. 16) as representative of a fossil fish named *Hemilopas mentzeli.* Jaekel (1907, Fig. 14) identified a similar fragment kept at the Humboldt Museum, Berlin (MB R. 1978), as representing the anterior dentition of the enigmatic genus *Tholodus,* of probable ichthyosaur affinities (Sander & Mazin, 1993). In fact, the remains of *Hemilopas mentzeli* are not diagnostic, and the name must remain a nomen dubium.

An isolated humerus (original of Lydekker, 1889, Fig. 84) and femur, both from the "Muschelkalk of Nürnberg" and housed in the Natural History Museum, London (BMNH 40052–53), although labeled as *Chonchiosaurus clavatus,* clearly represent proximal limbs bones of *Nothosaurus.*

Morphological Description

The holotype of *Conchiosaurus clavatus* (Meyer, 1834, Pl. I, Fig. 3) consists of an incomplete skull that is missing the rostrum. The anterior part of the palate, from the posterior margin of the internal nares to the anterior margin of the subtemporal fossa, is exposed in dorsal view. Further back, the posterior part of the parietal and the paroccipital processes are again exposed in dorsal view, but in a badly crushed or eroded condition. Remnants of the left upper temporal arch persist, but the right upper temporal arch is completely missing. The total length of the fossil (as preserved) is 118 mm; the width of the skull measured across the paroccipital processes (as preserved) is 76.5 mm. The general contours of the skull suggest synonymy of *Conchiosaurus* with *Nothosaurus* rather than with *Simosaurus* or *Cymatosaurus* (see discussion below).

As far as they can be identified, sutural details

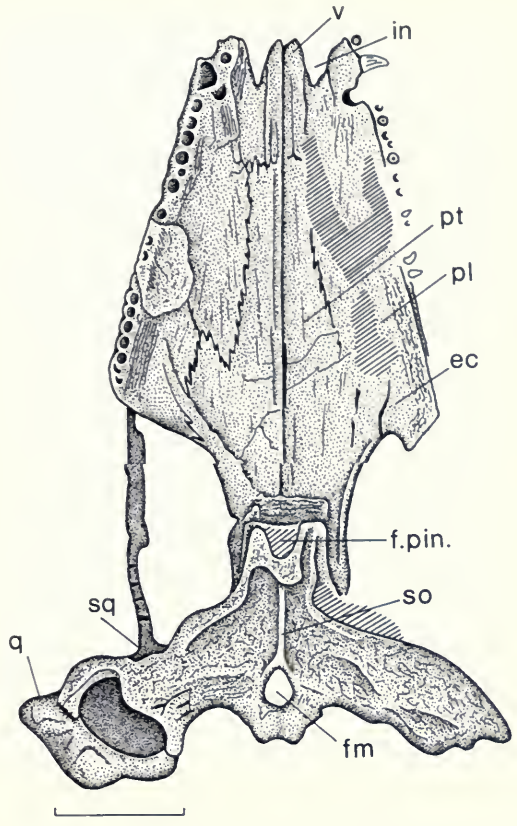


FIG. 23. *Conchiosaurus clavatus* Meyer (holotype; BSP AS I 1446); lower middle Muschelkalk, Esperstädt. Scale bar = 20 mm. Abbreviations: ec, ectopterygoid; fm, foramen magnum; f.pin., pineal foramen; in, internal naris; pl, palatine; pt, pterygoid; q, quadrate; so, supraoccipital, sq, squamosal; v. vomer.

in the dermal palate correspond closely to the pattern observed in *Nothosaurus* and *Cymatosaurus* (Fig. 23). The palatines define the posterior margins of the internal nares, which are separated from one another by the slender vomers. The exact relations between the posterior tips of the vomers and the anterior tips of the pterygoids are difficult to ascertain. Behind the palatine, the pterygoid extends laterally to meet the ectopterygoid. The transverse process of the pterygoid is well developed, a plesiomorphic trait. The anterior extent of the ectopterygoid cannot be ascertained. The two elements define the anterior margin of the subtemporal fossa without expanding ventrally into a distinct pterygoid flange. The latter is reduced in small and medium-sized specimens of *Nothosaurus,* but not in *Cymatosaurus* (Rieppel, 1994b).

The posterior part of the skull is strongly dorsoventrally flattened. The supraoccipital is easily identified by its low median crest; posteriorly, it enters the dorsal margin of the foramen magnum (Fig. 23). Anteriorly, the supraoccipital and the occipital exposure of the parietal is set off from the posterior margin of the skull roof by a distinct step that represents the crushed occipital crest characteristic of *Nothosaurus,* but not of *Cymatosaurus* (Rieppel, 1994b). Immediately in front of the damaged occipital crest, the posterior margin of the pineal foramen can be identified; it therefore has been displaced posteriorly, as is characteristic for *Nothosaurus* but not for *Cymatosaurus.* No detail can be reported on the structure of the paroccipital processes, except that the posterior opening into the cranioquadrate passage is well exposed on the left side (Fig. 23).

The position of two maxillary canines can be identified on both maxillae, a character shared with *Cymatosaurus* and *Nothosaurus.* Only one right canine tooth is (incompletely) preserved, however, and it shows the distinct striation of the enamel surface (Fig. 22). The canine teeth are followed by a palisade of distinctly smaller teeth (11 on the right side and 9 on the left side, but on neither side can the exact tooth count be established). Meyer (1834) emphasized the separation of the bulbous and distinctly striated crown from the constricted tooth base without striation, but close inspection of those few posterior maxillary teeth that remain intact shows considerable variation in tooth shape, but no particular resemblance to the teeth of *Simosaurus.* In particular, not all of the teeth show the constricted tooth base, and those with an unconstricted tooth base may have an upright or a slightly recurved crown. Indeed, the variation in tooth morphology observed in the holotype of *Conchiosaurus clavatus* is exactly matched by the variation in tooth morphology in the holotype of *Nothosaurus raabi* (Schröder, 1914) from the *orbicularis* beds (lower middle Muschelkalk) of Rüdersdorf. As already stated by Edinger (1921a), there is no clear-cut distinction between the posterior maxillary dentition of the holotype of *Conchiosaurus* and *Nothosaurus.*

Discussion

The morphological description identified a number of characters that the holotype of *Conchiosaurus clavatus* shares with *Nothosaurus* but

not with *Cymatosaurus.* These include the reduced pterygoid flanges, the displacement of the pineal foramen to the posterior margin of the parietal skull table, and the presence of an occipital crest.

The holotype of *Conchiosaurus clavatus* is identified as *Nothosaurus* by additional characteristics of the occiput. In *Cymatosaurus,* the occiput is vertically oriented, such that the occipital condyle comes to lie on level with the posterior margins of the upper temporal fenestrae. A dorsoventrally compressed skull of *Cymatosaurus* therefore shows a deeply concave, V-shaped posterior demarcation of the occiput. In *Nothosaurus,* the paroccipital processes extend further laterally than in *Cymatosaurus,* carrying the mandibular joints to a position distinctly lateral to the posterior end of the upper temporal arch, as in *Conchiosaurus.* The occiput is less vertically oriented in *Nothosaurus,* such that the supraoccipital extends posteriorly beyond the posterior margin of the parietal skull table in a dorsoventrally flattened skull, and the occipital condyle is exposed at the posterior end of the less excavated occiput, as is the case in *Conchiosaurus.*

Conchiosaurus can unequivocally be identified as *Nothosaurus,* but because of its incomplete preservation it is not diagnostic at the species level. The species name *clavatus* is a nomen dubium. The genus name *Conchiosaurus* is a senior synonym for *Nothosaurus* but has not been used as such other than by Lydekker (1889); it may therefore be treated as a nomen oblitum. A formal petition has been submitted to the International Commission for Zoological Nomenclature (ICZN) to suppress *Conchiosaurus* Meyer, 1834.

Nothosaurus cf. *N. marchicus* Koken, 1893

Synonymy for this material:

1834 *Nothosaurus venustus,* Münster, p. 525.
1847–55 *Nothosaurus venustus,* Meyer, p. 107, Pl. X, Figs. 5–6.
1889 *Nothosaurus venustus* (partim), Lydekker, p. 295.
1893 *Nothosaurus venustus,* Skuphos, p. 15.
1928 *Nothosaurus venustus,* Schmidt, p. 398, Fig. 1116.
1934 *Nothosaurus venustus,* Kuhn, pp. 32, 34.
1964 *Nothosaurus venustus,* Kuhn, p. 9.
1966 *Nothosaurus venustus,* Kuhn-Schnyder, p. 534.
1970 *Nothosaurus venustus* (partim), Schultze, p. 219, Fig. 2.

HOLOTYPE—An incomplete skull (Meyer, 1847–1855, p. 107, Pl. X, Fig. 5) that can no longer be located.

LOCUS TYPICUS—Saurierkalk (lower middle Muschelkalk), Esperstädt, Sachsen-Anhalt, Germany.

COMMENTS—As discussed above, Meyer (1847–1855) considered *Nothosaurus venustus* Münster a nomen dubium. He did include this name, in parentheses, in the figure caption for Pl. X, Fig. 5, which shows a fragmentary skull of 110 mm length (as preserved) from the lower middle Muschelkalk. The specimen can no longer be located and is presumed lost. It showed little detail except for the ventral (medial) view of the postorbital region of the skull roof, with the postfrontals clearly excluded from the anteromedial margin of the upper temporal fenestra. The Natural History Museum in Berlin holds two casts of the original material: MB R. 25 is the specimen figured by Meyer, 1847–1855, Pl. X, Fig. 5; MB R. 19 is the counterpart to MB R. 25, figured by Meyer, 1847–1855, Pl. X, Fig. 6. Both casts carry an original hand-written label that reads "*Conchiosaurus Germani* Münst., Muschelkalk, Querfurt, Coll. Münster." We were unable to find a published reference to the latter name, and the different locality data compared to those indicated by Meyer (1847–1855) remains unexplained.

Nothosaurus venustus was treated as a valid species name by Schultze (1970). Few other remains of *Nothosaurus* have so far been described from the middle Muschelkalk other than the specimens from the *orbicularis* beds of Rüdersdorf published by Schröder (1914; see discussion below). A fragmentary and incompletely prepared skull from the middle Muschelkalk of Göttingen (Gö 1202-50) was referred to as *Nothosaurus* sp. by Schultze and Möller (1986). Isolated teeth from the lower Muschelkalk of Helgoland were referred to *Nothosaurus venustus* by Kruckow (1979).

A survey of sauropterygians from the Germanic Muschelkalk kept in public repositories throughout Germany has produced two specimens from various localities and stratigraphic ages that have historically been labeled as *Nothosaurus venustus.* One of these specimens is a small but incomplete skull kept at the Phyletisches Muse-

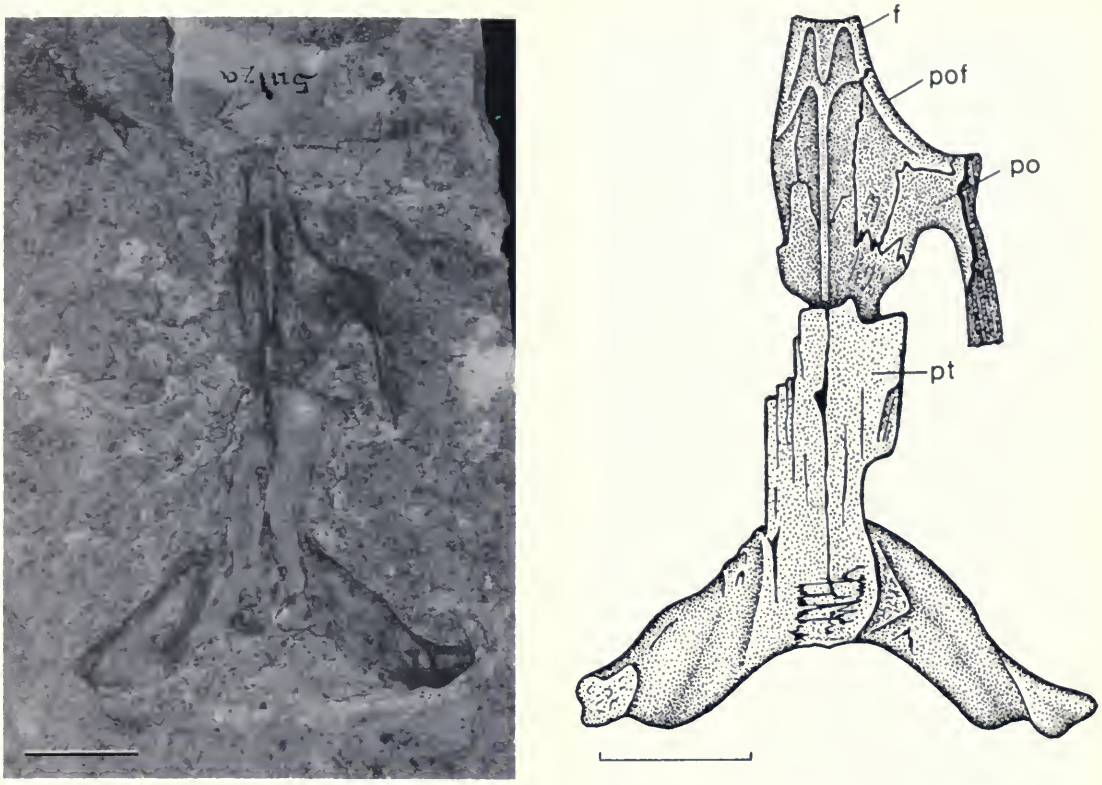
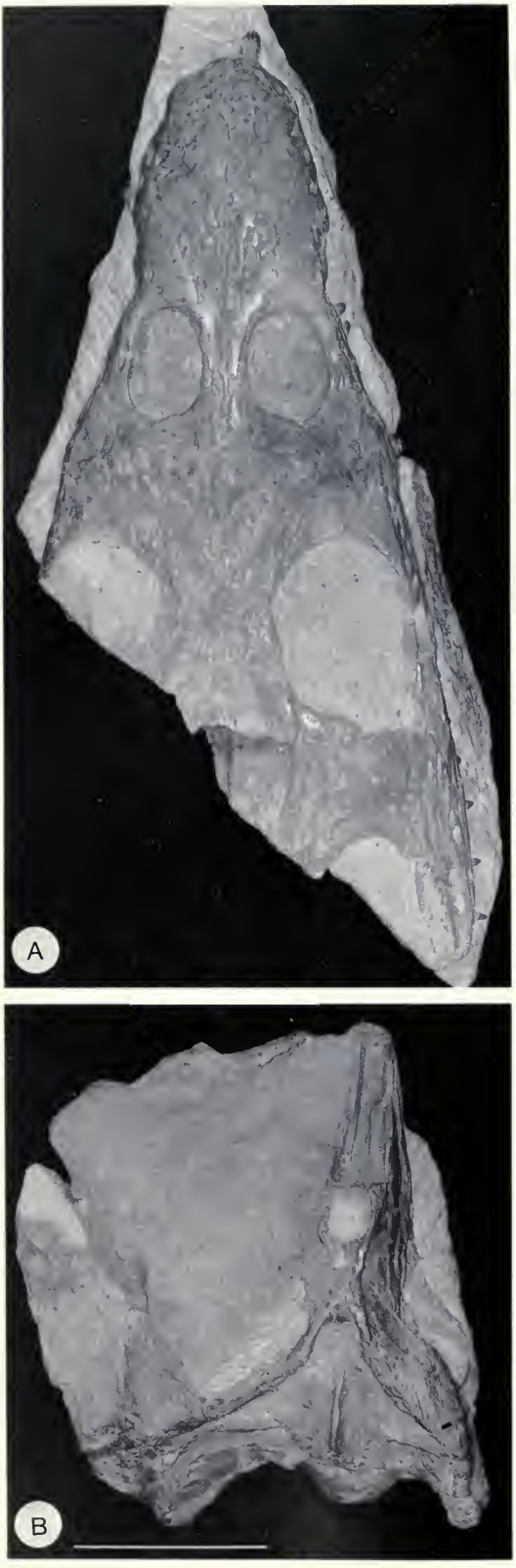


FIG. 24. *Nothosaurus* cf. *N. marchicus* Koken (P 1132); upper Muschelkalk, Bad Sulza. Scale bar = 20 mm. Abbreviations: f, frontal; po, postorbital; pof, postfrontal; pt, pterygoid.

um, Jena (P 1132). The specimen (Fig. 24) is from the Krähenhütte quarry in Bad Sulza, Thuringia, which has produced a number of fairly well-preserved skulls of *Nothosaurus* (and postcranial remains) kept at the Naturkundemuseum Erfurt (see below). The fossils of Bad Sulza are generally labeled as coming from mo_2, but more probably come from the lower upper Muschelkalk (Trochitenkalk, mo_1, H. Hagdorn, in lit. 7 Dec. 1994). The total length of the specimen P 1132 (as preserved) is 83 mm. Its total width measured across the paroccipital processes is 68.5 mm. The type of preservation of the specimen (Fig. 24) is closely similar to the holotype of *Nothosaurus venustus*. The main feature is again the exclusion of the postfrontal from the anteromedial margin of the upper temporal fenestra, as seen in the ventral (medial) view of the skull roof. The postfrontal is also excluded from the anteromedial margin of the upper temporal fenestra in the other skulls from Bad Sulza (described in more detail below).

The second specimen is an almost complete skull, preserved in two parts (Figs. 25, 26), labeled as coming from the Schaumkalk of Oberdorla, Thuringia (SMF R-4537a–b; the same institution also holds a partial and articulated postcranial skeleton from the same locality and now on permanent exhibit). The age of reptile fossils from Oberdorla is controversial. In contrast to the museum label indicating the Schaumkalk (upper lower Muschelkalk), fossil vertebrates at this locality generally appear to have come from the *orbicularis* layers, now attributed to the lower middle Muschelkalk (H. Hagdorn, pers. commun.). The skull is practically identical to that of the holotype of *Nothosaurus procerus* from the *orbicularis* beds of Rüdersdorf, both in size and morphology. Breakage of SMF R-4537 renders it impossible to determine the exact relations of the postfrontal bone to the anteromedial margin of the upper temporal fenestra, although it is probable that the bone narrowly entered the fenestra. The postfrontal broadly enters the anteromedial margin of the upper temporal fenestra in the holotype of *Nothosaurus procerus*, but the skulls from the *orbicularis* beds of Rüdersdorf, all of similar size but



referred to different species by Schröder (1914), show all intermediate stages between inclusion and exclusion of the postfrontal from the upper temporal fenestra.

For reasons discussed in detail below, it is here concluded that the skulls from the lower middle Muschelkalk of Rüdersdorf and from Oberdorla, as well as those from the lower upper Muschelkalk (mo_1) of Bad Sulza (and Bayreuth: "*Nothosaurus* sp." of Edinger, 1921a: 37 *ff.*), all belong to the same taxon, for which the name *Nothosaurus marchicus* Koken (1893) has priority. The (lost) holotype of *Nothosaurus venustus* was too poorly preserved to be diagnostic at the species level. Exclusion of the postfrontal from the margin of the upper temporal fenestra is a plesiomorphic trait that is variable within the nothosaurs described by Schröder (1914). It is therefore concluded that *venustus* is a nomen dubium.

Nothosaurus marchicus Koken, 1893

1893 *Nothosaurus marchicus,* Koken, p. 347, text figs. 1, 2, 3A; Pl. 10, Figs. 1–3.
1899 *Nothosaurus marchicus,* Schrammen, Pl. 24, Figs. 4d–e.
1902 *Nothosaurus marchicus,* Huene, p. 40, Fig. 43.
1911 *Nothosaurus (Cymatosaurus)* cf. *friedericianus,* Jaekel, p. 148, Fig. 161.
1914 *Nothosaurus crassus,* Schröder, p. 64, Fig. 12.
1914 *Nothosaurus marchicus,* Schröder, p. 63, Fig. 11.
1914 *Nothosaurus oldenburgi,* Schröder, p. 60, Fig. 10.
1914 *Nothosaurus procerus,* Schröder, p. 2, Figs. 1–4.
1914 *Nothosaurus procerus,* var. *parva,* Schröder, p. 23, Fig. 5.
1914 *Nothosaurus raabi,* Schröder, p. 26, Figs. 6–9.
1924 *Nothosaurus raabi,* Arthaber, p. 465 *ff.*, Figs. 4–6.
1924 *Nothosaurus procerus,* Arthaber, Figs. 2a–c.

←

FIG. 25. *Nothosaurus marchicus* Koken (SMF R-4537 a–b); Schaumkalk (*?orbicularis* layers), Oberdorla. **A,** Preorbital skull (SMR R-4537a); **B,** occiput (SMF R-4537b). Scale bar = 20 mm. See Figure 26.

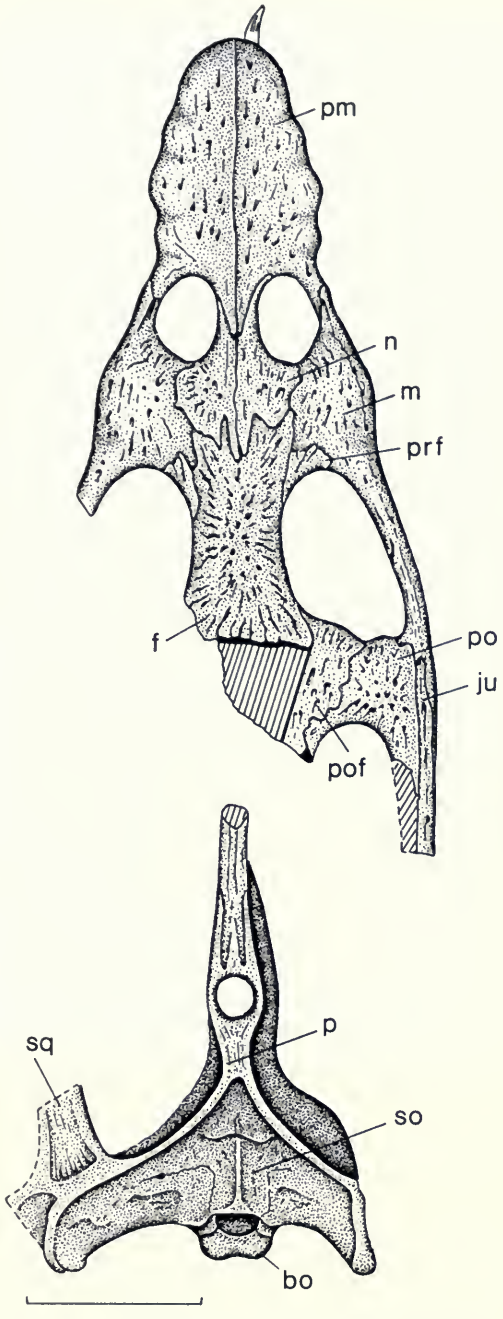


FIG. 26. *Nothosaurus marchicus* Koken (SMF R-4537a–b); Schaumkalk (*?orbicularis* layers), Oberdorla. Preorbital skull and occiput. Scale bar = 20 mm. Abbreviations: bo, basioccipital; f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; so, supraoccipital; sq, squamosal. See Figure 25.

1924 *Nothosaurus procerus* var. *parva,* Arthaber, Fig. 2d.
1925 *Nothosaurus raabi,* Schuster and Bloch, p. 60, Fig. 1.
1928 *Nothosaurus crassus,* Schmidt, p. 398, Fig. 1118.
1928 *Nothosaurus marchicus,* Schmidt, p. 398, Fig. 1117.
1928 *Nothosaurus oldenburgi,* Schmidt, p. 400, Fig. 1122.
1928 *Nothosaurus procerus,* Schmidt, p. 399, Fig. 1120.
1928 *Nothosaurus procerus* var. *parva,* Schmidt, p. 400, Fig. 1121.
1928 *Nothosaurus raabi,* Schmidt, p. 399, Fig. 1119.
1931 *Nothosaurus raabi,* Peyer, p. 57 *f.*
1934 *Nothosaurus crassus,* Kuhn, p. 34.
1934 *Nothosaurus marchicus,* Kuhn, p. 35.
1934 *Nothosaurus procerus,* Kuhn, p. 35.
1934 *Nothosaurus procerus* var. *parva,* Kuhn, p. 35.
1934 *Nothosaurus raabi,* Kuhn, p. 36.
1934 *Nothosaurus oldenburgi,* Kuhn, p. 37.
1938 *Nothosaurus raabi,* Peyer, p. 226.
1939 *Nothosaurus crassus,* Peyer, p. 9 *ff.*
1939 *Nothosaurus oldenburgi,* Peyer, p. 9 *ff.*
1939 *Nothosaurus procerus,* Peyer, p. 10 *ff.*
1939 *Nothosaurus raabi,* Peyer, p. 16 *ff.*
1944 *Nothosaurus schroederi,* E.v. Huene, p. 202, Fig. 4.
1949 *Nothosaurus raabi,* E.v. Huene, p. 139.
1955 *Nothosaurus procerus,* Saint-Seine, Fig. 5.
1955 *Nothosaurus raabi,* Saint-Seine, Fig. 25.
1956 *Nothosaurus crassus,* Huene, p. 338.
1956 *Nothosaurus marchicus,* Huene, p. 338.
1956 *Nothosaurus oldenburgi,* Huene, p. 338.
1956 *Nothosaurus procerus,* Huene, p. 338.
1956 *Nothosaurus raabi,* Huene, p. 338.
1961 *Nothosaurus marchicus,* Kuhn-Schnyder, p. 105.
1964 *Nothosaurus crassus,* Kuhn, p. 8.
1964 *Nothosaurus marchicus,* Kuhn, p. 8.
1964 *Nothosaurus oldenbourgi,* Kuhn, p. 8.
1964 *Nothosaurus procerus,* Kuhn, p. 9.
1964 *Nothosaurus raabi,* Kuhn, p. 9.
1964 *Nothosaurus schroederi,* Kuhn, p. 9.
1966 *Nothosaurus crassus,* Kuhn-Schnyder, p. 534.
1966 *Nothosaurus marchicus,* Kuhn-Schnyder, p. 534.
1966 *Nothosaurus parva,* Kuhn-Schnyder, p. 534.

1966 *Nothosaurus procerus,* Kuhn-Schnyder, p. 534.
1966 *Nothosaurus raabi,* Kuhn-Schnyder, pp. 517, 534.
1970 *Nothosaurus venustus* (partim), Schultze, p. 219, Figs. 2–5.
1970 *Nothosaurus procerus,* Schultze, p. 221, Figs. 6–8.
1974 *Nothosaurus raabi,* Kuhn-Schnyder, p. 61.
1979 *Nothosaurus crassus,* Kruckow, p. 55.
1979 *Nothosaurus marchicus,* Kruckow, p. 55.
1979 *Nothosaurus oldenburgi,* Kruckow, p. 55.
1979 *Nothosaurus procerus,* Kruckow, p. 55.
1979 *Nothosaurus procerus* var. *parva,* Kruckow, p. 55.
1979 *Nothosaurus raabi,* Kruckow, p. 55.
1992 *Nothosaurus raabi,* Alafont, p. 67, Fig. 3.13.
1993b *Nothosaurus procerus,* Rieppel, p. 972.
1993b *Nothosaurus venustus,* Rieppel, p. 972.
1994 *Nothosaurus* cf. *venustus,* Rieppel and Wild, Fig. 5A.

HOLOTYPE—The specimen figured by Koken (1893, text figs. 1, 2, 3A; Pl. 10, Figs. 1–3) can no longer be located today. The counterslab, showing the impressions of the dorsal aspect of the skull, is kept at the Natural History Museum, Humboldt University, Berlin (MB R. 2).

LOCUS TYPICUS—*Orbicularis* beds (lower middle Muschelkalk), Rüdersdorf near Berlin.

DIAGNOSIS—A species of *Nothosaurus* of small overall size (skull with condylobasal length not exceeding 200 mm in the adult); rostrum relatively short and broad, rounded; five fangs in each premaxilla, the fifth slightly smaller than the preceding fangs; five small maxillary teeth preceding the paired maxillary fangs; external nares relatively short and broad, kidney-shaped; nasals broad and leaf-shaped, with radiating ornamentation; postfrontal with a distinct postorbital constriction; squamosal closely approaching or contacting the posterior end of the jugal; quadratojugal absent; ectopterygoid reaching far forward up to half the length of palatine.

DISTRIBUTION—?Lowermost lower Muschelkalk of ?Gogolin (Upper Silesia, now Poland), ?Halle/Saale (Germany) and ?Winterswijk (Netherlands); upper lower Muschelkalk (Schaumkalk) and lowermost middle Muschelkalk (*orbicularis* beds) of Rüdersdorf near Berlin and Oberdorla; lowermost middle Muschelkalk (Saurierkalk) of Esperstädt (Germany); lower upper Muschelkalk (mo_1) of Bad Sulza and Bayreuth (Germany). Anisian, central and western Europe.

FIG. 27. *Nothosaurus* cf. *N. marchicus* Koken (MB R. 6; original of Schuster and Bloch, 1925, Fig. 1); lower middle Muschelkalk, Rüdersdorf. Mandibular symphysis, ventral view. Scale bar = 20 mm.

REFERRED MATERIAL—BGR 611 (holotype of *Nothosaurus schroederi* E.v. Huene, 1944; Schaumkalk, Rüdersdorf); BGR, uncatalogued (skull fragment, Schaumkalk, Rüdersdorf). MB R. 1 (holotype of *Nothosaurus oldenburgi* Schröder, 1914; *orbicularis* beds, Rüdersdorf); MB R. 3.1–3 (holotype of *Nothosaurus crassus* Schröder, 1914; Schaumkalk, Rüdersdorf); MB R. 4 (holotype of

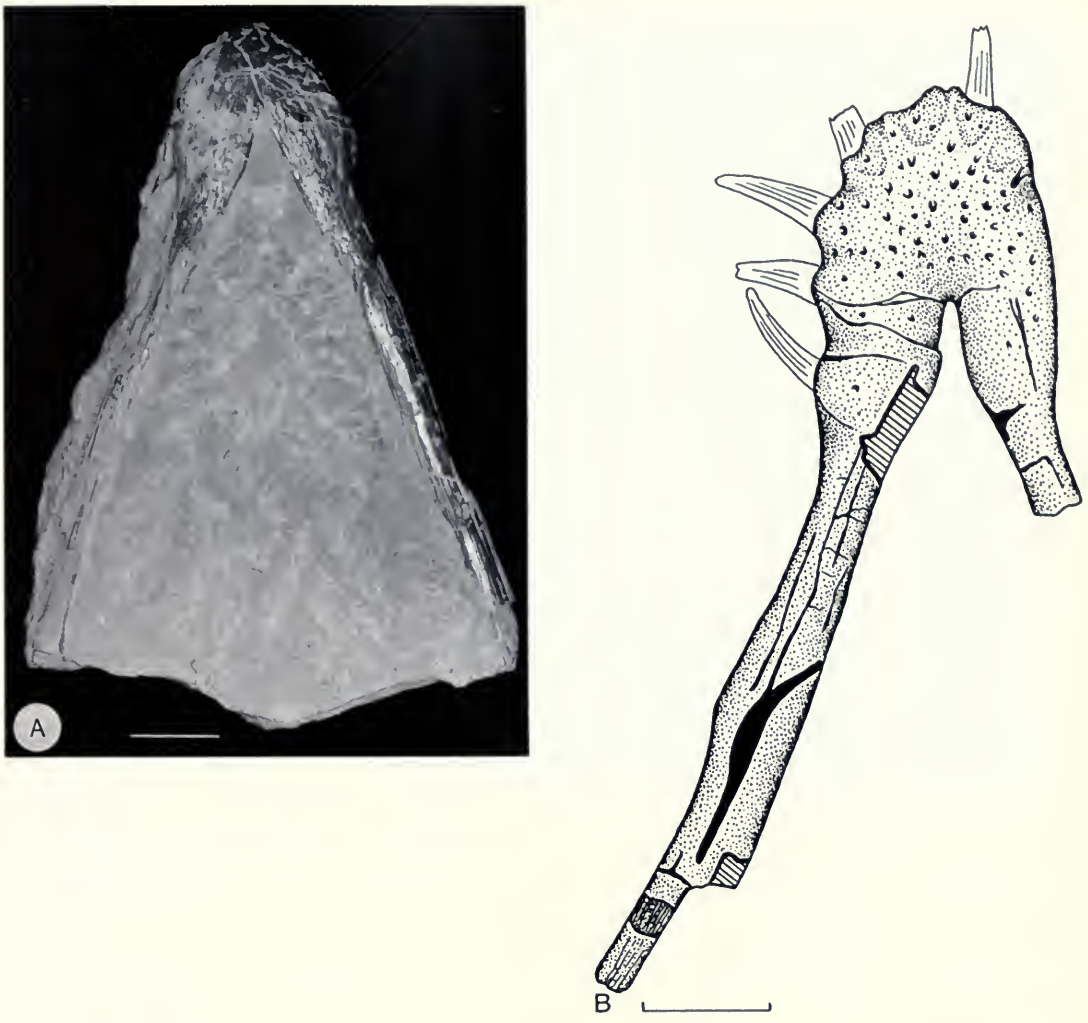


FIG. 28. **A,** *Nothosaurus* cf. *N. marchicus* Koken (BGR 56/7); lower Muschelkalk, Rüdersdorf. Mandibular symphysis, ventral view. **B,** *Nothosaurus* cf. *N. marchicus* Koken (MGU Wr 3865s); lower Muschelkalk, Gogolin, Upper Silesia. Mandibular symphysis, ventral view. Scale bar = 10 mm.

Nothosaurus procerus Schröder, 1914; *orbicularis* beds, Rüdersdorf); MB R. 5 (holotype of *Nothosaurus procerus* var. *parvus* Schröder, 1914; *orbicularis* beds, Rüdersdorf); MB R. 6 (lower jaw, original of Schuster & Bloch, 1925; *orbicularis* beds, Rüdersdorf); MB I. 007.18 (holotype of *Nothosaurus raabi* Schröder, 1914; *orbicularis* beds, Rüdersdorf); MB R. 24 (undescribed skull from the Schaumkalk [?*orbicularis* layers], Oberdorla); SMF R-4537 a–b (undescribed skull from the Schaumkalk [?*orbicularis* layers], Oberdorla); SMF R-4572 (original of Edinger, 1921a: 37; lower upper Muschelkalk, Bayreuth). Phyletisches Museum Jena, P 1132 (lower upper Muschelkalk, Bad Sulza). Er 2302 (cast of skull, the original can no longer be located; lower upper Muschelkalk, Bad Sulza); Er 78/510 (partial skull; lower upper Muschelkalk, Bad Sulza); Er 78/541 (partial skull; lower upper Muschelkalk, Bad Sulza); Er, uncatalogued (skull; lower upper Muschelkalk, Bad Sulza); Er 78/233 (lower jaw; lower upper Muschelkalk, Bad Sulza).

POSTCRANIUM—The only articulated skeleton is that of the holotype of *Nothosaurus raabi* (MB I. 007.18). The following isolated material is specifically referred to that species: Er 78/231 (vertebra, upper Muschelkalk, Bad Sulza); Er 78/245 (vertebra, upper Muschelkalk, Bad Sulza); Er 78/

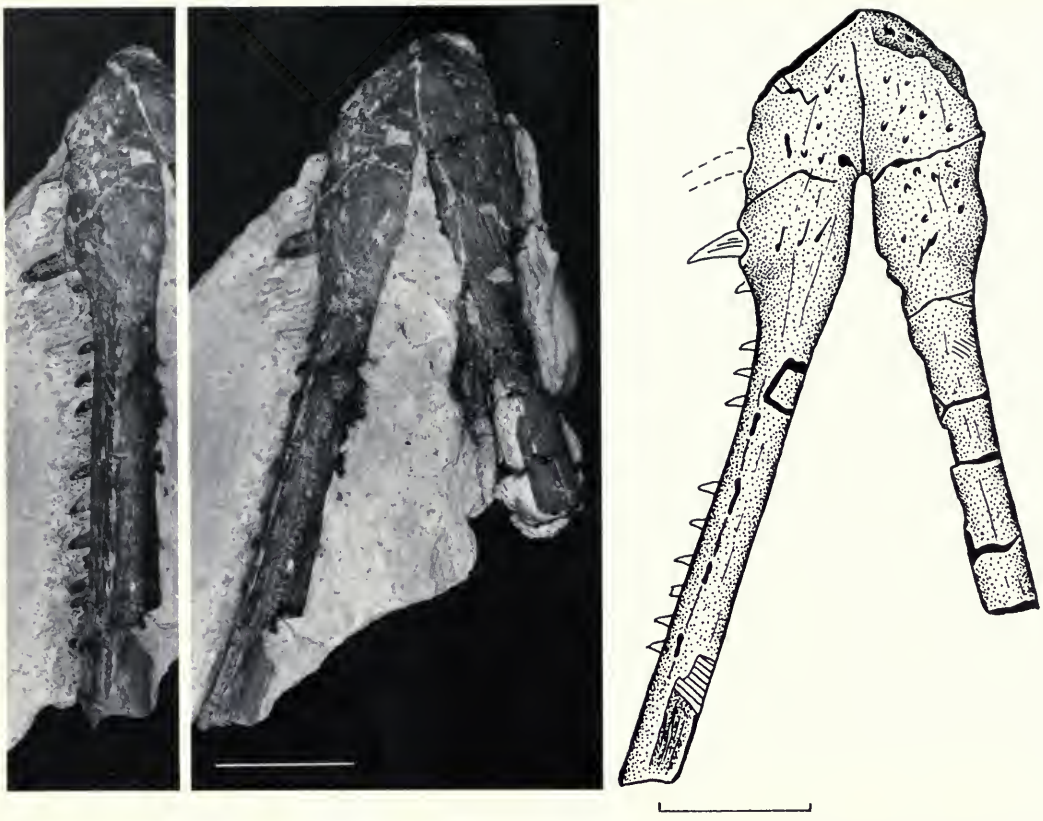


FIG. 29. *Nothosaurus* (*Oligolycus*) *hecki* v.Frisch (holotype; Ha 12/41); lower Muschelkalk, Halle/Saale. Scale bar = 10 mm.

247 (vertebra, upper Muschelkalk, Bad Sulza); Er 78/250 (vertebra, upper Muschelkalk, Bad Sulza); Er 78/251 (vertebra, upper Muschelkalk, Bad Sulza); Er 78/269 (vertebra, upper Muschelkalk, Bad Sulza); Er 78/287 (vertebra, upper Muschelkalk, Bad Sulza); Er 78/288 (vertebra, upper Muschelkalk, Bad Sulza); Er 78/509 (caudal rib, upper Muschelkalk, Bad Sulza); Er 78/530 (vertebra, upper Muschelkalk, Bad Sulza); Er 93/89 (vertebra, upper Muschelkalk, Erfurt-Drosselberg); Er 93/89 (vertebra, upper Muschelkalk, Erfurt-Tiefthal). MB R. 137.1–3 (vertebrae, upper Muschelkalk, Bad Sulza); MB R. 149 (vertebra, Schaumkalk, Oberdorla; original of Peyer, 1939, his Fig. 22); MB R. 150 (partial postcranial skeleton, Schaumkalk, Oberdorla; original of Peyer, 1939, his Figs. 23, 24).

COMMENTS—In the most recent review of the genus *Nothosaurus,* Schultze (1980) treated *Nothosaurus procerus* Schröder and *Nothosaurus marchicus* Koken (treated as a junior synonym of *Nothosaurus venustus* by Schultze, 1970; Figs. 25, 26) as separate species. The main characters considered to differentiate between the two species were the relation of the postfrontal to the margin of the upper temporal fenestra, the position of the posterior tips of the nasals with respect to the orbit, the contours of the upper temporal fenestra, and the degree of concavity of the occiput. The first character shows continuous variation within the sample referred to *Nothosaurus marchicus* in the list of synonymy above (see further discussion below). The position of the posterior tips of the nasals is closely comparable in *Nothosaurus raabi* and *Nothosaurus procerus,* referred to different species by Schultze. The last two characters are variable again throughout the specimens described by Schröder (1914; see description below) and/or distorted by preservation. For example, the occiput (as preserved) appears more distinctly concave in the holotypes of *Nothosaurus procerus* and *Nothosaurus oldenburgi* than in the holotype of *Nothosaurus raabi.* However, the first two "species" were synonymized

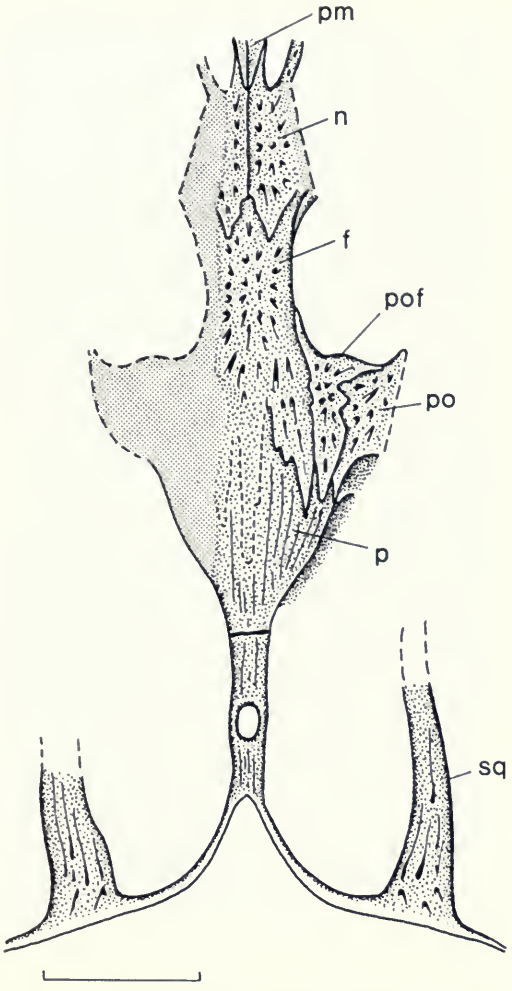


FIG. 30. *Nothosaurus marchicus* Koken (MB R. 2; latex peel of counterpart of holotype); lower middle Muschelkalk, Rüdersdorf. Scale bar = 20 mm. Abbreviations: f, frontal; n, nasal; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; sq, squamosal.

with *Nothosaurus procerus* by Schultze (1970: 221), said to be characterized by a weakly excavated occiput, whereas *Nothosaurus marchicus* ("*venustus*" in Schultze, 1970), said to be characterized by a deeply excavated occiput (Schultze, 1970: 220), would include the latter species ("*raabi*").

The lower jaw from the lower middle Muschelkalk of Rüdersdorf, first described by Schuster and Bloch (1925) and referred to "*Nothosaurus raabi*" (Fig. 27), shows features that clearly distinguish it from the genotypical species *Nothosaurus mirabilis*. The mandibular symphysis is relatively short (ratio maximal length/maximal width: 0.79), such that the posteriormost (fifth) fang is located behind the mandibular symphysis. Another lower jaw fragment (Fig. 28A) from the Schaumkalk (mu_2) of Rüdersdorf (BGR S 56/7) is closely comparable to the specimen of Schuster and Bloch (1925). It is somewhat distorted and shows a symphyseal ratio (maximal length/maximal width) of 0.86. A lower jaw from Bad Sulza (Er 78/233), which matches the skulls from the same locality in size, shows a symphyseal ratio (maximal length/maximal width) of 0.84. Compared to sauropterygian outgroups, a short mandibular symphysis is the plesiomorphic condition, and within the Sauropterygia a relatively short mandibular symphysis with a length/width ratio of 0.7–1 is relatively plesiomorphic compared to *Nothosaurus mirabilis*, with a length/width ratio of 1.5 or more (SMNS 59817; SMNS, uncatalogued, coll. M. Wild nos. 546 and 2074) and with the fifth (and last) fang located within the symphysis. Relative shortness of the symphysis will therefore not allow the unequivocal assignment of isolated lower jaw fragments to *Nothosaurus marchicus*. This has important consequences for the interpretation of specimens from the lowermost Muschelkalk of Gogolin, Halle/Saale, and Winterswijk.

The relative shortness of the mandibular symphysis was used as a diagnostic character of *Nothosaurus* (*Oligolycus*) *hecki* (Fig. 29) from the lowermost lower Muschelkalk of Halle/Saale by Fritsch (1894). Edinger (1921a: 13) synonymized *Nothosaurus hecki* with *Cymatosaurus* sp., not on the basis of morphology but on the basis of the provisional assumption that only *Cymatosaurus* occurs in the lower Muschelkalk of the eastern Germanic Basin (she considered the fragment too incomplete to be diagnostic of a separate species). The holotype of *Nothosaurus hecki* Fritsch, 1894 (Ha no. 12/41) is of relatively small size and probably represents a juvenile, but its proportions are very similar to those of Schuster and Bloch's (1925) specimen, with a ratio (maximal length/maximal width) of 0.71 (confirmed by personal observation). A similar lower jaw fragment (Ha, uncatalogued), with a symphyseal ratio (maximal length/maximal width) of 0.73, comes from the Schaumkalk (upper lower Muschelkalk) of Freyburg/Unstrut. A lower jaw fragment (Fig. 28B) from the lowermost lower Muschelkalk (Gogolin beds) of Gogolin, Upper Silesia (now Poland), housed in the Institute of Geological Sciences, University of Wroclaw (MGU Wr 3865s), is closely comparable to, if somewhat larger than, the holotype of *Nothosaurus hecki*. The symphyseal ratio

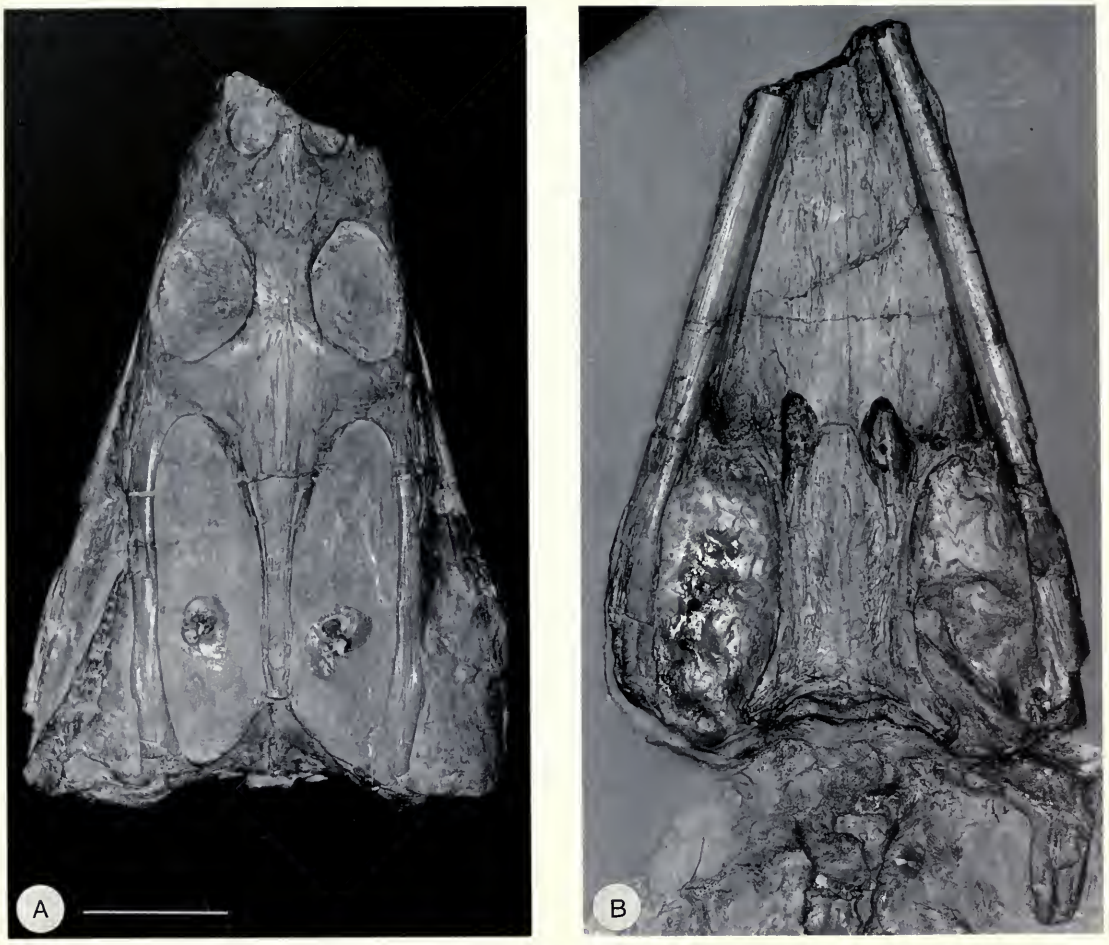


FIG. 31. *Nothosaurus raabi* Schröder (holotype; MB I. 007.18); lower middle Muschelkalk, Rüdersdorf. **A,** The skull in dorsal view; **B,** the skull in ventral view. Scale bar = 20 mm.

(maximal length/maximal width) as preserved is 0.87, but it may have been as low as 0.7 if the eroded left margin is corrected for. From the same deposit comes a partial rostrum (SMNS 16248), which almost exactly matches the holotype of *Nothosaurus schroederi* E.v. Huene, 1944, from the Schaumkalk of Rüdersdorf. A left premaxilla from Gogolin (MGU Wr 3943s) may perhaps also be referred to the same taxon. Whether these early remains from the eastern part of the Muschelkalk Basin may all be referred to *Nothosaurus marchicus* Koken (rendering *Nothosaurus hecki* Fritsch, 1894, a junior synonym of this species) must remain an open question in the absence of shared derived characters. In view of the incomplete nature of the holotype, *Nothosaurus* (*Oligolycus*) *hecki* Fritsch, 1894, remains a nomen dubium.

Kunisch (1888) described fragmentary remains of *Nothosaurus* from the lowermost lower Muschelkalk (Gogolin beds) of Gogolin, Upper Silesia, which he compared to *Nothosaurus* "*venustus.*" Skuphos (1893: 14) referred the specimen to a new genus and species, *Kolposaurus dichthadius,* claiming that it differed from *Nothosaurus* in vertebral structure. Comparison with *Nothosaurus mirabilis,* which shows a derived vertebral structure (see discussion below), may have misled Skuphos (1893). More important, however, Skuphos's (1893) description of a supposedly bipartite transverse process of the vertebrae of "*Kolposaurus dichthadius*" appears to be based on a misidentification of the postzygapophyses. Indeed, comparison of Kunisch's (1888) specimen (MGU Wr 3934s) with the holotype of *Nothosaurus raabi* (MB R. 007.18), or with the partially preserved postcranial skeleton from the Schaumkalk

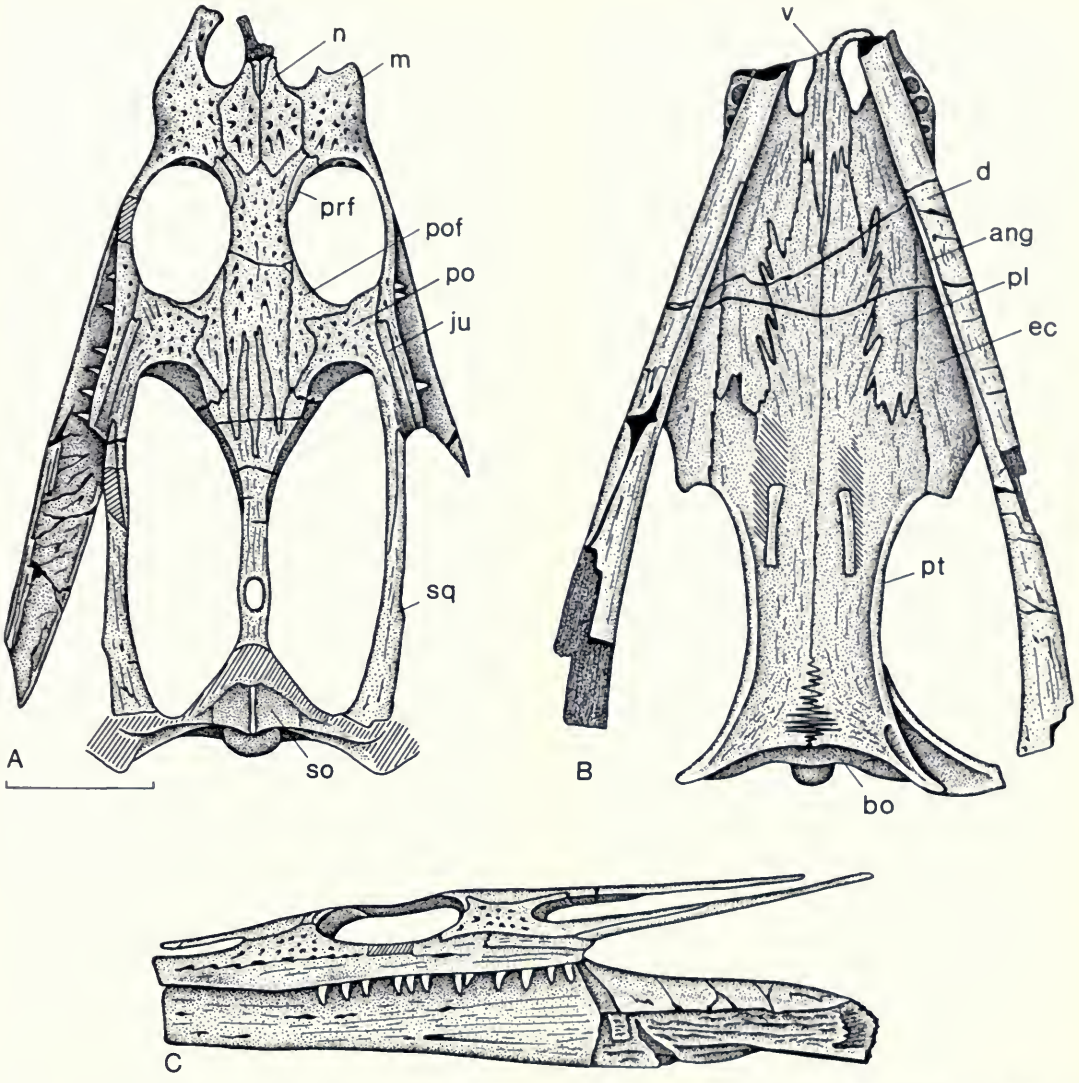


FIG. 32. *Nothosaurus raabi* Schröder (holotype; MB I. 007.18); lower middle Muschelkalk, Rüdersdorf. **A,** The skull in dorsal view; **B**, the skull in ventral view; **C**, the skull in left lateral view. Scale bar = 20 mm. Abbreviations: ang, angular; bo, basioccipital; d, dentary; ec, ectopterygoid; f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; so, supraoccipital; sq, squamosal; v, vomer.

(upper lower Muschelkalk; or *orbicularis* layers, lower middle Muschelkalk—see comments above) of Oberdorla (MB R. 150) first described by Peyer (1939, Figs. 23, 24), reveals close similarity of all three specimens. Since isolated postcranial remains cannot be diagnostic for *Nothosaurus marchicus,* the species name *dichthadius* must be treated as a nomen dubium, although synonymy with *Nothosaurus marchicus* is likely.

"*Nothosaurus* cf. *raabi*" has been recorded from the lower Muschelkalk of Winterswijk (the Netherlands) on the basis of a lower jaw fragment (Hoojer, 1959). It again shows the characteristically short mandibular symphysis, as does an undescribed lower jaw from the same deposit (kept in a private collection) with a symphyseal ratio (maximal length/maximal width) of 0.78. Because the base of the Muschelkalk is geologically somewhat younger in the western part of the Muschelkalk Basin than in the eastern part (Hagdorn,

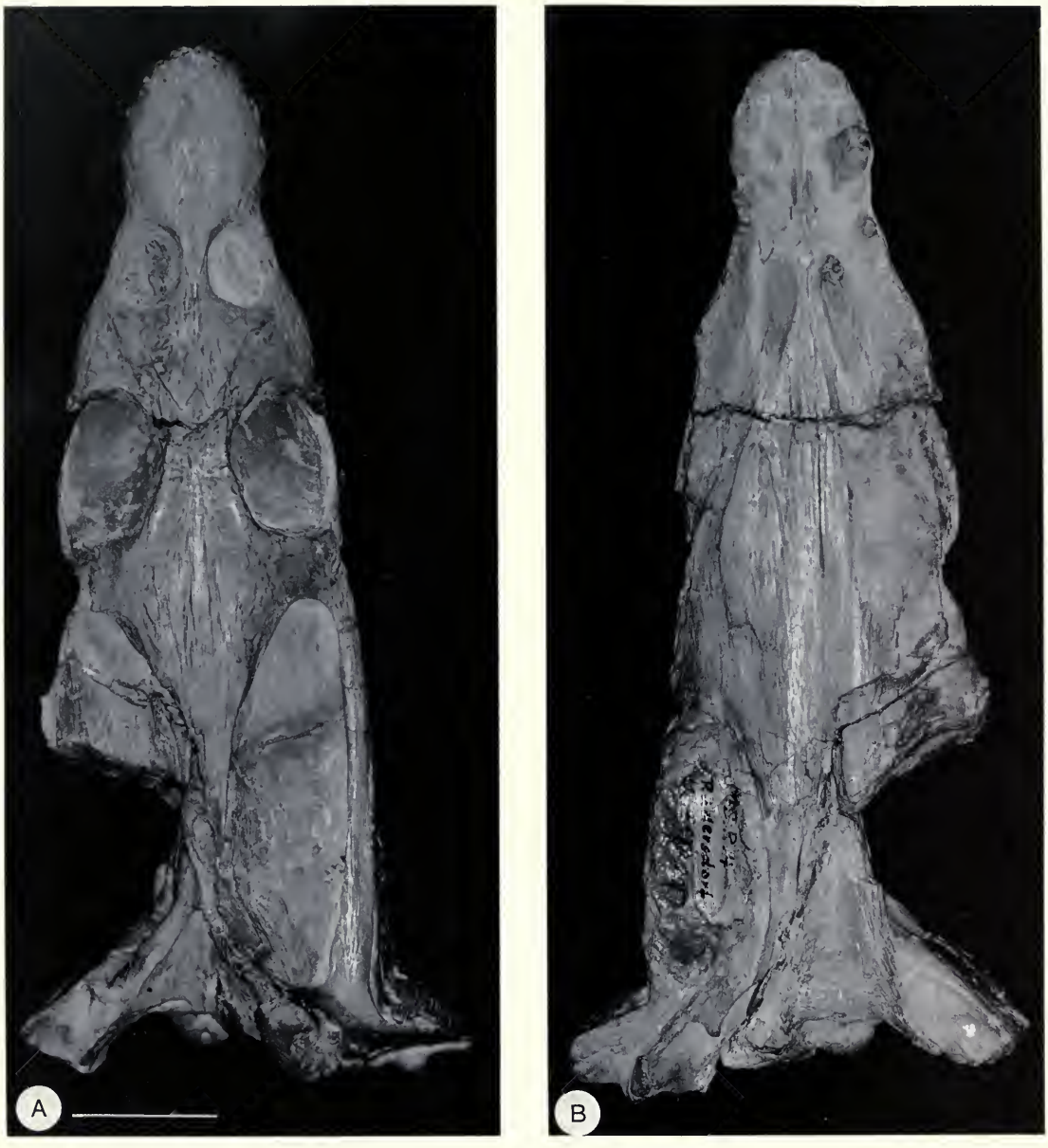


FIG. 33. *Nothosaurus procerus* Schröder (holotype; MB R. 4); lower middle Muschelkalk, Rüdersdorf. **A,** The skull in dorsal view; **B,** the skull in ventral view. Scale bar = 20 mm.

1991), the Winterswijk material is somewhat younger than the specimens from Gogolin and Halle/Saale. Nothosaur skulls from Winterswijk have been referred to "*Nothosaurus venustus*" (Oosterink, 1986; Oosterink & Diepenbroek, 1990) and again are closely comparable to those from Rüdersdorf and Bad Sulza. Personal inspection of the material (kept in private collections) showed the jugal to enter the posteroventral margin of the orbit, a plesiomorphic trait, yet a significant difference from *Nothosaurus marchicus,* where the jugal remains excluded from the posterior margin of the orbit. It should be noted, however, that this character is variable within the genotypical species *Nothosaurus mirabilis* (Rieppel, 1994a; and below). Also, the Winterswijk skulls

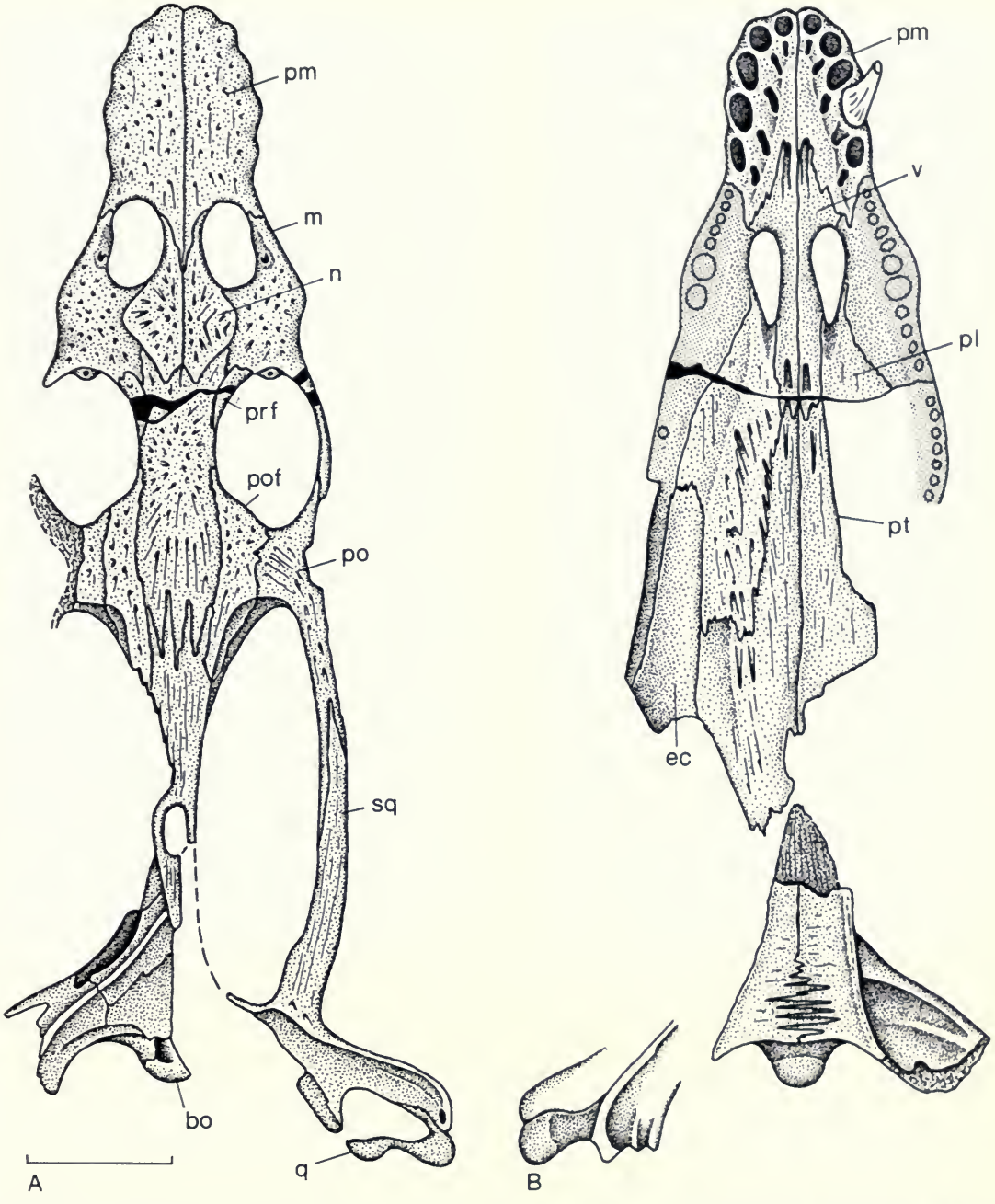


FIG. 34. *Nothosaurus procerus* Schröder (holotype; MB R. 4); lower middle Muschelkalk, Rüdersdorf. **A,** The skull in dorsal view; **B,** the skull in ventral view. Scale bar = 20 mm. Abbreviations: bo, basioccipital; ec, ectopterygoid; m, maxilla; n, nasal; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; sq, squamosal; v, vomer.

FIG. 35. **A,** *Nothosaurus procerus* var. *parva* Schröder (holotype; MB R. 5); lower middle Muschelkalk, Rüdersdorf. **B,** *Nothosaurus oldenburgi* Schröder (holotype; MB R. 1); lower middle Muschelkalk, Rüdersdorf. Scale bar = 20 mm.

show the pineal foramen in the plesiomorphic position almost at the center of the parietal (Oosterink & Diepenbroek, 1990, Fig. 10), rather than shifted back toward the posterior margin of the parietal skull table, as is the case in *Nothosaurus marchicus* and other species of the genus. The Winterswijk skulls share with *Nothosaurus marchicus* the relatively short but rounded rostrum (plesiomorphic), the limited posterior extent of the maxillary tooth row (plesiomorphic), the short and broad external nares (apomorphic), and the broad and leaf-shaped nasals (plesiomorphic). The presence or absence of the quadratojugal in the Winterswijk material remains unknown. All that can be concluded at the present time is that all the traits that differentiate the Winterswijk skulls from those of *Nothosaurus marchicus* are plesiomorphic and hence not diagnostic of a separate species. In this context it is interesting to note that Jaekel (1911, Fig. 161) figured a *Nothosaurus* skull from the lower Muschelkalk of Mühlhausen (Thuringia) that appears to share with the Winterswijk material the entry of the jugal into the posterior margin of the orbit, as well as the relatively forward position of the pineal foramen (the skull can no longer be located).

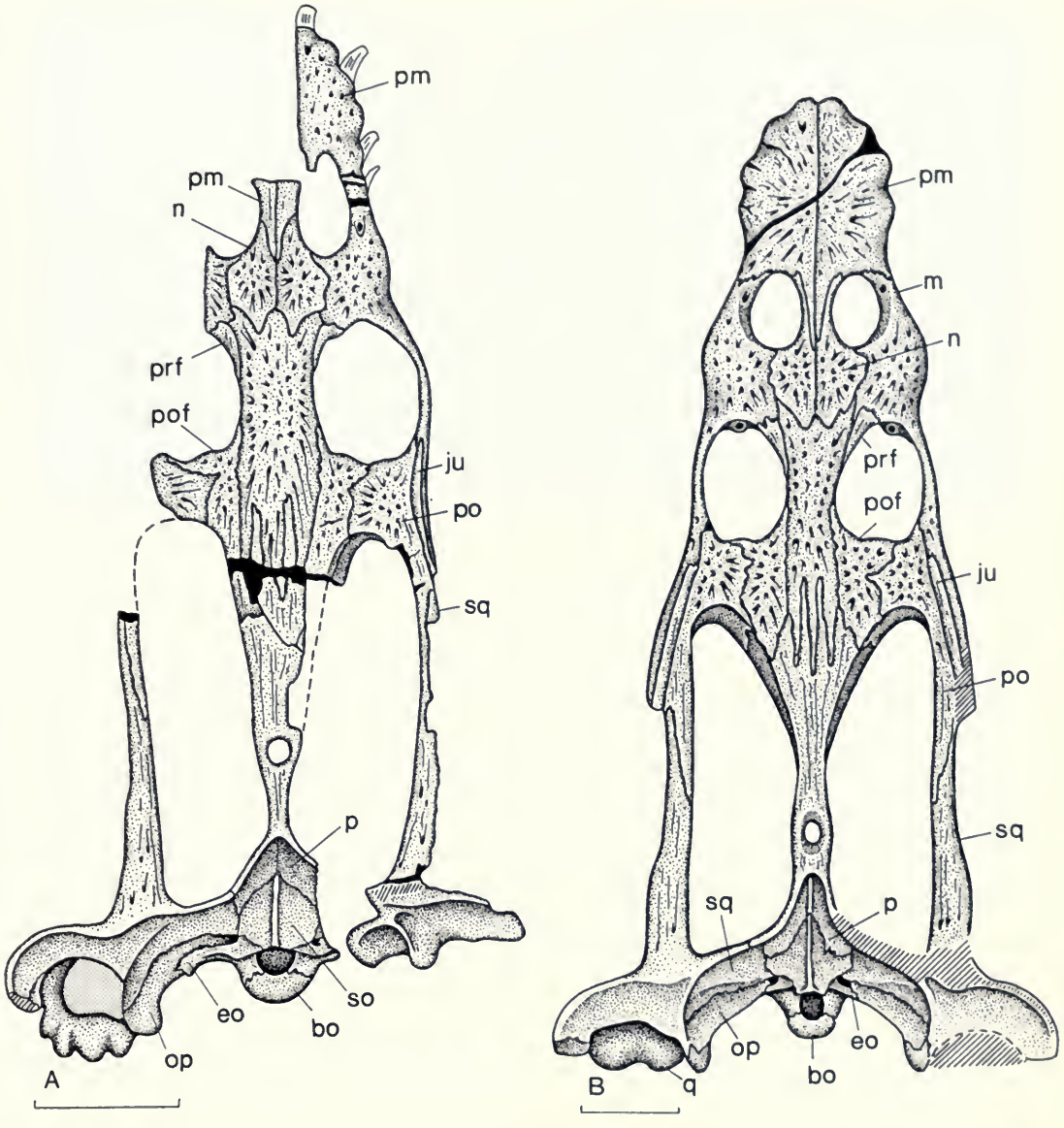


FIG. 36. **A,** *Nothosaurus procerus* var. *parva* Schröder (holotype; MB R. 5); lower middle Muschelkalk, Rüdersdorf. **B,** *Nothosaurus oldenburgi* Schröder (holotype; MB R. 1); lower middle Muschelkalk, Rüdersdorf. Scale bar = 20 mm. Abbreviations: bo, basioccipital; eo, exoccipital; ju, jugal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; q, quadrate; so, supraoccipital; sq, squamosal.

Morphological Description

THE SKULL—The holotype of *N. marchicus* today is represented only by the counterpart. A latex peel (Fig. 30) shows the posterior tips of the nasals located well behind the level of the anterior margin of the orbit, a character that is variable within the species. The fronto-parietal suture is deeply interdigitating and located at the level of the anterior margin of the upper temporal fenestra. The postfrontal broadly enters the posterodorsal margin of the orbit, shows a characteristic constriction in its anterior part, and has a tapering posterior tip that remains excluded from the upper temporal fenestra. The pineal foramen is displaced posteriorly but still lies clearly in front of the pos-

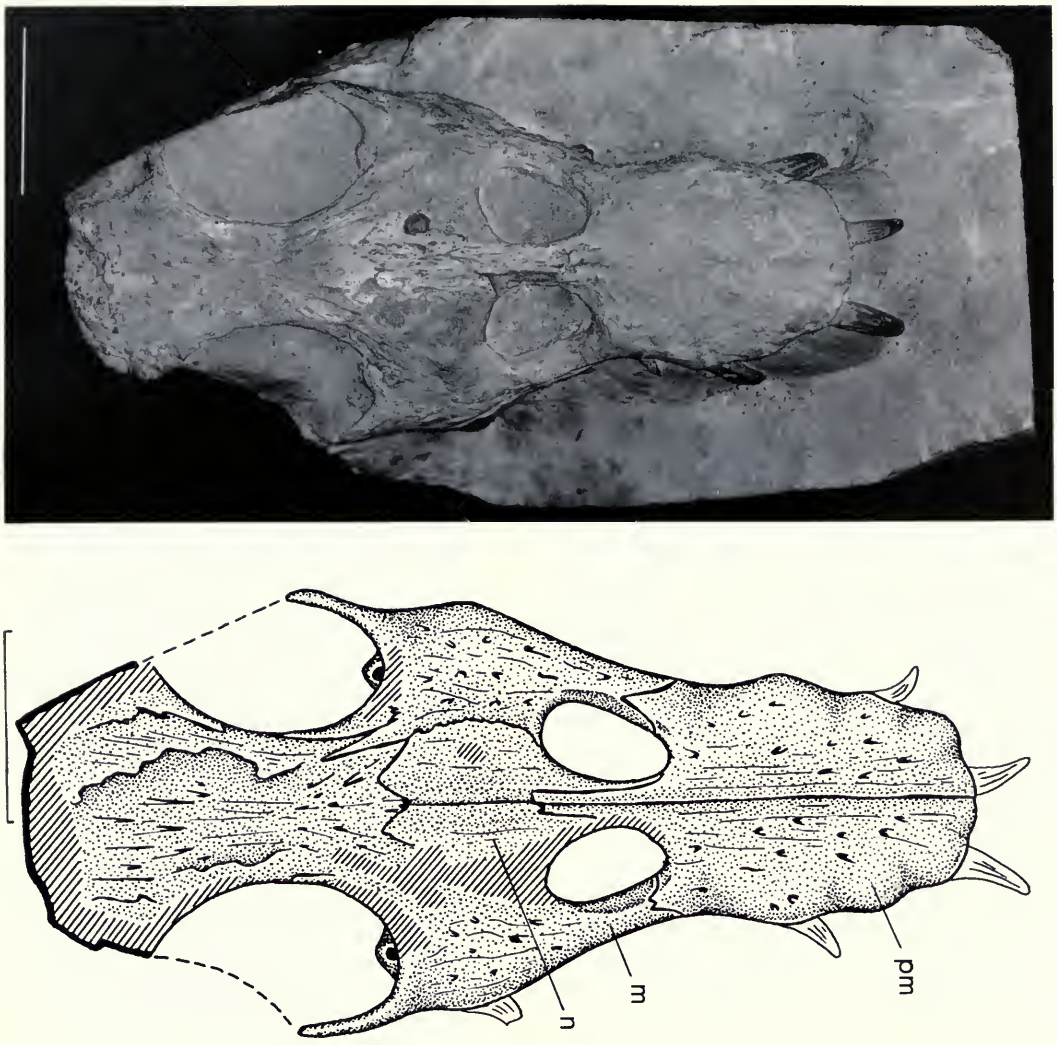


FIG. 37. *Nothosaurus schroederi* E.v.Huene (holotype; BGR 611); upper lower Muschelkalk, Rüdersdorf. The skull in dorsal view. Scale bar = 20 mm. Abbreviations: m, maxilla; n, nasal; pm, premaxilla.

terior margin of the parietal skull table (in the genotypical species *N. mirabilis,* the pineal foramen generally lies closer to the posterior margin of the skull table). The posterolateral corners of the upper temporal fenestra are not distinctly pointed. In some or all of its characters, supplemented by Koken's (1893) description of the original material, *N. marchicus* matches all the specimens referred to that species (Figs. 31–42).

In general, *N. marchicus* shows a relatively short and broad rostrum with rounded contours, set off from the preorbital skull by a distinct rostral constriction. The external nares are relatively short and broad, and distinctly kidney-shaped. In contrast, the genotypical species *N. mirabilis* shows a relatively longer and slender rostrum with almost parallel lateral edges, set off by a less distinct rostral constriction. Its external nares are relatively longer and narrower. Dividing the distance from the tip of the snout to the anterior margin of the external naris by the width of the skull at the rostral constriction yields a value of 1.1–1.4 for *N. marchicus.* Dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris results in an

index of 1.8–2.0. Dividing the distance from the tip of the snout to the anterior margin of the upper temporal fenestra by the distance from the tip of the snout to the anterior margin of the external naris yields a ratio of 2.9–3.4. Finally, dividing the longitudinal diameter of the external naris by its transverse diameter yields a ratio of 1.0–1.4 (1.6). The one specimen of *N. marchicus* with an index of 1.6 (close to *N. mirabilis*) is SMF R-4537, which also shows a slightly less rounded rostrum than seems otherwise typical for the species (Figs. 25, 26). The difference is minor, however, and accounted for by individual variation.

As in other nothosaurs, the rostrum is formed by the premaxillae. These carry a posterior nasal process that enters between the external nares and may or may not reach beyond the level of the posterior margin of the external nares. In all specimens, however, the nasals meet in a dorsomedial suture, thus separating the premaxilla from the frontal (this character is variable in *N. mirabilis*). The nasal is a broad element with a radiating ornamentation of pits and ridges (rather than longitudinal as in *N. mirabilis*); its lateral edge may be straight or convex. Posteriorly the nasals end in a blunt tip, with an anteromedial process of the frontal entering between them.

The maxillae show a distinct lateral expansion in front of the orbits to accommodate the roots of the maxillary fangs. This accentuates the rostral constriction, which is most pronounced at the level of the anterior margin of the external nares, where the maxilla meets the premaxilla. As in all nothosaurs, the prefrontal has a limited dorsal exposure at the anterodorsal margin of the orbit. The lacrimal foramen is located entirely within the maxilla. The frontal bears anterolateral processes that contact the maxilla. None of the available skulls shows the prefrontal in contact with the nasal, thus separating the maxilla from the frontal (this character is variable in *N. mirabilis*). An incomplete skull from Bad Sulza (Er 78/541; Fig. 41B) shows a longitudinal slit (or fontanelle) at the anterior margin of the parietal, aligned with what looks like a suture separating the two frontals. Paired frontals have not been recorded for *Nothosaurus* before, but they could conceivably constitute a juvenile character (not recorded in *N. muensteri* or *N. juvenilis*; Rieppel, 1994c). The specimen in question is no smaller than the other skulls of *N. marchicus* available, and the paired frontal bones may be an expression of individual variation (if not an artifact of preservation).

The maxillary tooth row extends posteriorly well beyond the orbit to a level between the first and the second third of the longitudinal diameter of the upper temporal fenestra. Along this posterior process of the maxilla extends the narrow jugal, which remains excluded from the posterior margin of the orbit, as described by Schröder (1914). The degree to which the maxillary tooth row extends below the upper temporal fenestra varies with different species and specimens of *Nothosaurus*. In *N. mirabilis*, the tooth row extends backward to about the level of the midpoint of the upper temporal fenestra. Dividing the longitudinal diameter of the upper temporal fenestra by the distance from the level of the anterior margin of the upper temporal fenestra to the posterior end of the maxilla yields values between 5.4 and 4.6 for *N. mirabilis* (original specimen figured in Meyer, 1847–1855, Pl. 2, Fig. 1; and BMNH R-42829). The corresponding ratio varies from 3.4 to 3.6 in *N. marchicus*, with the exception of the holotype of *N. raabi* (MB I. 007.18: Figs. 31–32), for which the corresponding value is 4.5. In that respect, the latter specimen approaches the undescribed skulls from the lower Muschelkalk of Winterswijk, with values of 4.2 and 4.8, respectively.

The posteroventral margin of the orbit is lined by the postorbital, which extends backward into the upper temporal arch, where it meets the squamosal in an oblique suture. The squamosal reaches far anteriorly, very nearly approaching the posterior end of the jugal; whether the jugal actually contacts the squamosal is difficult to establish unequivocally in Schröder's (1914) specimens because of breakage, but a contact of squamosal and jugal is indicated in the Erfurt cast (Er 2302, right side of skull; Figs. 40A, 41A).

The postfrontal broadly lines the posterodorsal margin of the orbit, behind which it shows a distinct constriction due to a V-shaped indentation of its lateral (ventral) margin. Posterior to that constriction the bone widens again, and it may or may not enter the anteromedial margin of the upper temporal fenestra. The posterior end of the postfrontal may be tapering to a blunt tip (holotype of *N. raabi*, MB I. 007.18 [Fig. 32A], and the undescribed skull MB R. 24 [Fig. 39A]) or remain rather broad (all other skulls). The postfrontal remains clearly excluded from the upper temporal fenestra in the holotypes of *N. raabi* (MB I. 007–18 [Fig. 32A]) and *N. crassus* (MB R. 3.2 [Fig. 42A]), in the skull MB R. 24 (Fig. 39A), and in all the Bad Sulza specimens (Fig. 41). In a skull fragment from the Schaumkalk of Rüdersdorf (BGR, uncata-

FIG. 38. *Nothosaurus marchicus* Koken (MB R. 24); upper lower Muschelkalk or lower middle Muschelkalk, Oberdorla. Scale bar = 20 mm.

logued; Fig. 42B), the posterior end of the postfrontal is broad and follows the outline of the anteromedial margin of the upper temporal fenestra without quite reaching it. In the holotype of *N. oldenburgi* (MB R. 1; Figs. 35B, 36B), the postfrontal reaches the margin of the upper temporal fenestra, but it does not contribute to the lateral descending flange that lines the medial margin of the temporal fenestra and serves as an area for the origin of jaw adductor muscle fibers. In the holotype of *N. procerus* var. *parva* (MB R. 5; Figs. 35A, 36A), the postfrontal just barely enters the lateral descending flange, whereas in the holotype of *N. procerus* (MB R. 4; Figs. 33A, 34A), the participation of the postfrontal in the lateral descending flange is substantial. Another way to describe the progressive participation of the postfrontal in the formation of the anteromedial margin of the upper temporal fenestra is to visualize a progressive expansion of the attachment for the

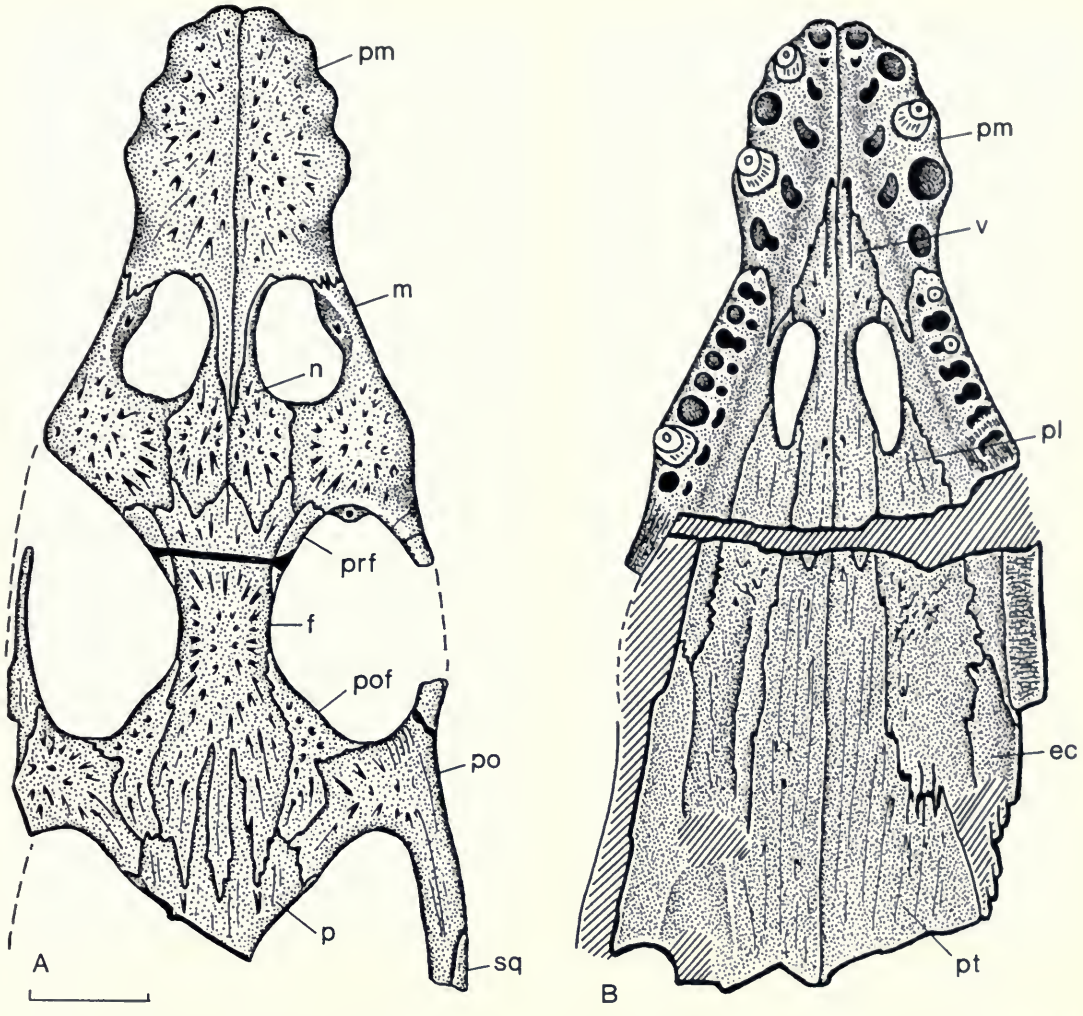


FIG. 39. *Nothosaurus marchicus* Koken (MB R. 24); upper lower Muschelkalk or lower middle Muschelkalk, Oberdorla. **A,** The skull in dorsal view; **B,** the skull in ventral view. Scale bar = 20 mm. Abbreviations: ec, ectopterygoid; f, frontal; n, nasal; m, maxilla; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; sq, squamosal; v, vomer.

jaw adductor muscles onto the skull roof, i.e., a progressive widening of the upper temporal fenestra. Unfortunately, incomplete preservation and lack of data on ontogenetic variation render it difficult to specify numerical values for a progressive widening of the upper temporal fenestra. Nevertheless, division of the longitudinal diameter of the upper temporal fenestra by its transverse diameter yields a quotient of 2.85 for the holotype of *N. raabi* (MB I. 007.18), with the postfrontal widely separated from the temporal fenestra, as opposed to 3.12 for the holotype of *N. oldenburgi* (MB R. I), with the postfrontal bordering on the upper temporal fenestra. In general, the upper temporal fenestra is shorter relative to the orbit in *N. marchicus* as compared to *N. mirabilis*; division of the longitudinal diameter of the upper temporal fenestra by the longitudinal diameter of the orbit yields a ratio of 2.1–3.0 for *N. marchicus* and 2.9–3.8 for *N. mirabilis*.

As far as exposed in the skulls available, the occiput corresponds to the pattern observed in *Nothosaurus* in general (see Rieppel, 1994b, for a detailed description). The posterior end of the upper temporal arch is slightly broadened before it blends into the occipital crest. The parietal gains

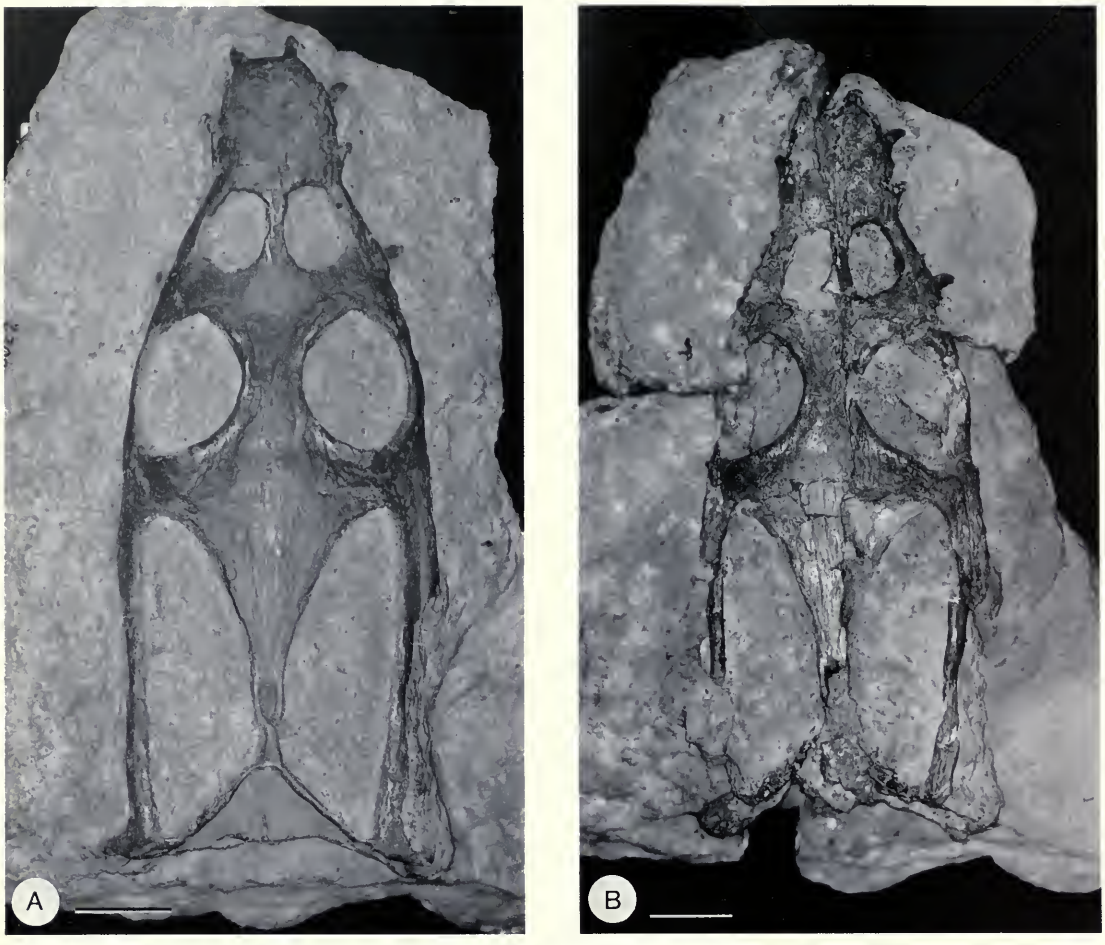


FIG. 40. *Nothosaurus marchicus* Koken; upper Muschelkalk, Bad Sulza. **A,** Cast (Er 2302); **B,** original (Er, uncatalogued). Scale bar = 20 mm.

a limited occipital exposure behind the latter, meeting the squamosal laterally and the supraoccipital posteriorly. The supraoccipital carries a weak sagittal crest and forms the dorsal margin of the foramen magnum, which is lined laterally by the exoccipitals. The latter do not meet on the dorsal aspect of the occipital condyle, which is formed by the basioccipital only. The holotype of *N. procerus* var. *parva* (MB R. 5; Fig. 36A) shows the much reduced posttemporal fenestra bordered by the exoccipital, squamosal, and opisthotic; the supraoccipital remains narrowly excluded. All adequately preserved skulls show an open eustachian foramen (Koken, 1893; Rieppel, 1994b) and a basioccipital tuber with a diameter close to half the horizontal diameter of the occipital condyle.

The posterior opening into the cranioquadrate passage is bordered by the squamosal dorsally, the pterygoid medially, and the quadrate laterally. The lateral aspect of the quadrate is covered, in its dorsal part, by a laterally descending flange of the squamosal. A quadratojugal was identified on the lateral edge of the quadrate below the squamosal in a nothosaur braincase that, on the basis of its size and stratigraphic provenance, can be referred to *N. mirabilis* (Rieppel, 1994b). A quadratojugal was also unequivocally identified in the same position in a large braincase from the Schaumkalk of Freyburg/Unstrut (MB R. 1775) that is discussed in more detail below. The well-prepared material from Rüdersdorf (Schröder, 1914) shows the quadratojugal to be unequivocally absent in *N. marchicus.*

The palate is exposed only in some of the avail-

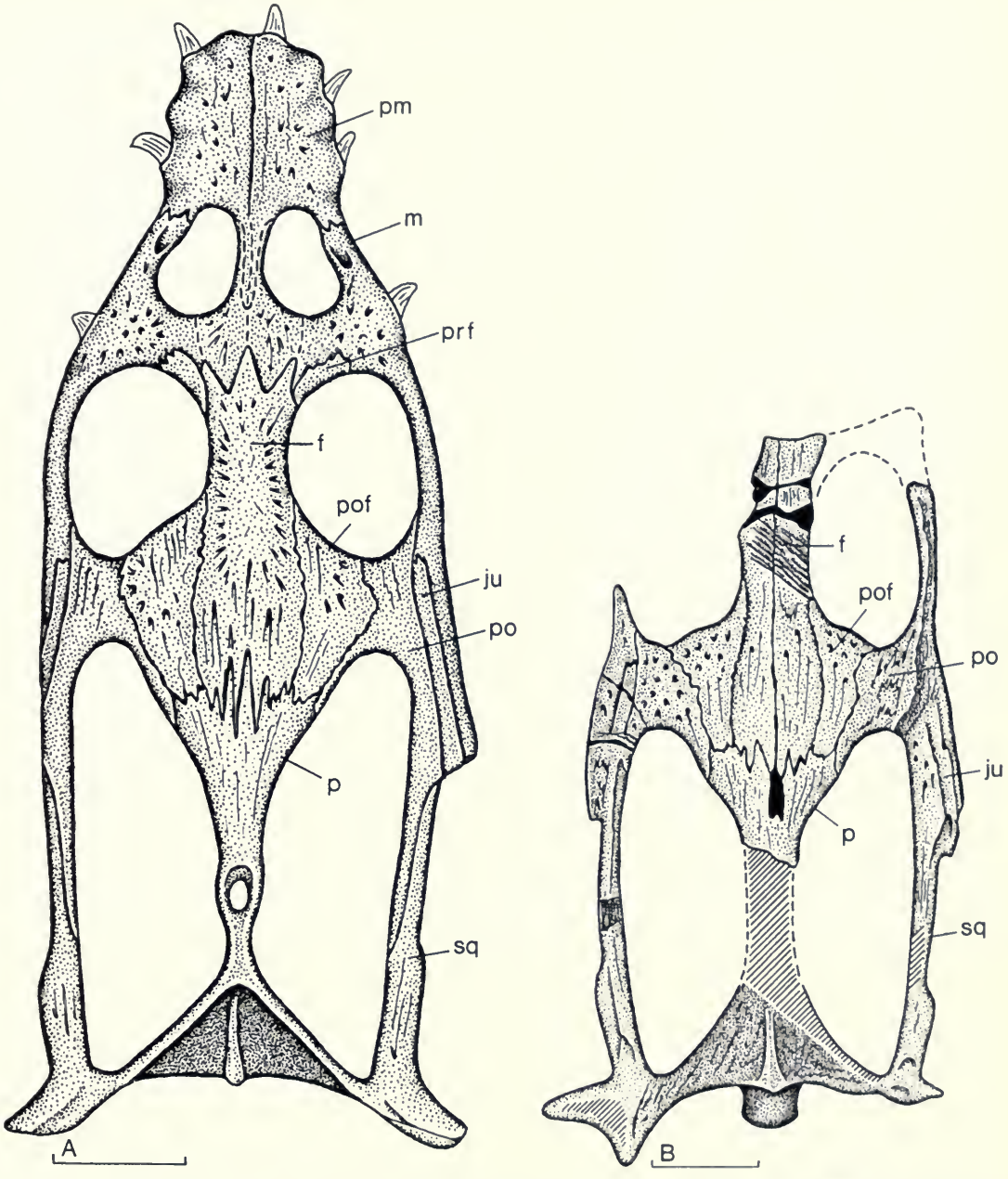


FIG. 41. *Nothosaurus marchicus* Koken; upper Muschelkalk, Bad Sulza. **A**, Cast (Er 2302); **B**, incomplete skull (Er 78/541). Scale bar = 20 mm. Abbreviations: f, frontal; ju, jugal; m, maxilla; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; sq, squamosal.

able specimens (Figs. 31B, 32B, 33B, 34B, 38B, 39B). The premaxilla carries five fangs, the fifth being slightly smaller than the preceding ones. Five small teeth precede the two maxillary fangs. The full maxillary tooth count cannot be established on any of the available specimens. In the holotype of *N. raabi* (MB I. 007.18), 12 postcanine teeth are preserved in the left maxilla and 14 postcanine teeth in the right maxilla; the total number of postcanine tooth positions is approximately 23.

As in all *Nothosaurus* (with the possible exception of *Nothosaurus juvenilis*: Rieppel, 1994c),

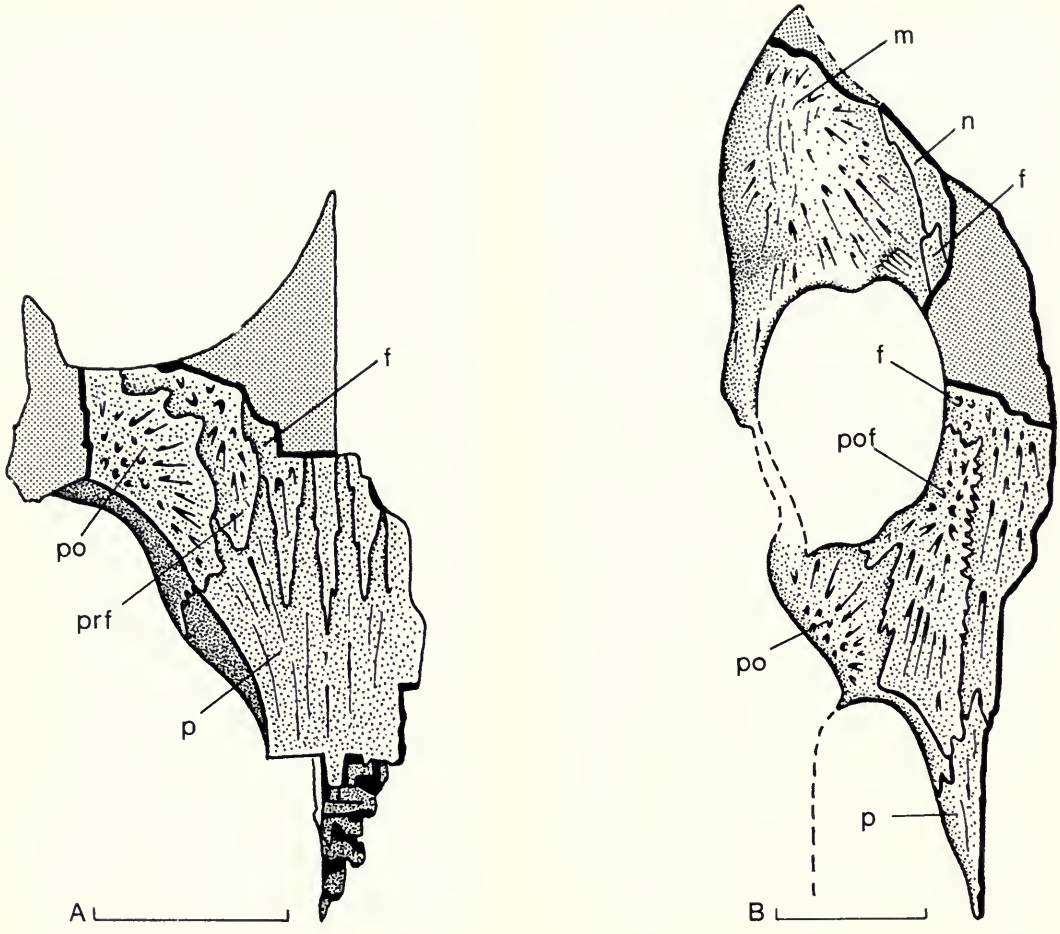


FIG. 42. **A,** *Nothosaurus crassus* Schröder (part 2 of holotype; MB R. 3.2.); upper lower Muschelkalk, Rüdersdorf. **B,** *Nothosaurus marchicus* Koken (BGR, uncatalogued), upper lower Muschelkalk, Rüdersdorf. Scale bar = 20 mm. Abbreviations: f, frontal; m, maxilla, n, nasal; p, parietal; po, postorbital; pof, postfrontal.

the premaxilla is excluded from the internal naris. The vomers are elongate paired elements, separating the internal nares from one another and entering between the premaxillaries anteriorly and between the pterygoids posteriorly. Incisive foramina are located in the contact zone between premaxillaries and vomers. The lateral margin of the internal naris is formed by the maxilla, and the posterior margin is formed by the palatine. *N. marchicus* differs from *N. mirabilis* (and other nothosaurs) in the shape and size of the ectopterygoid, which tapers to a blunt tip anteriorly and reaches to about the level of the midpoint of the palatine. The palatine–pterygoid suture is deeply interdigitating. The pterygoid flange is very weakly developed.

LOWER JAW—The only lower jaw associated with a skull is that of the holotype of *N. raabi* (MB I. 007.18; Figs. 31, 32). It is incomplete in that it lacks the mandibular symphysis (see discussion above) and the mandibular articulation. The surangular is well exposed in lateral view. It shows a distinct lateral ridge, which defines the ventral margin of a marked dorsolateral facet that served as a site of insertion for superficial jaw adductor muscle fibers. In ventral view, the angular can be seen to extend far anteriorly along the ventromedial edge of the mandible, wedged in between the dentary and the splenial. In medial view, the splenial is seen to define the anterior margin of the adductor fossa, from where it extends anteriorly, closing the Meckelian canal medially. The splenial does not gain a ventrolateral exposure on the mandible (see also Rieppel,

1994a). The coronoid is not fully exposed, but it can be identified at the anterodorsal margin of the adductor fossa on the medial side of the lower jaw.

An incompletely prepared lower jaw from the lower upper Muschelkalk of Bad Sulza (Er 78/233; Fig. 43) may be referred to *N. marchicus* on the basis of its size and the fact that the latter species is the most frequently encountered one in the these deposits. It shows the characteristically short symphysis (maximal length/maximal width: 0.84), with the fifth and last fang located behind the symphysis. Sutures cannot be unequivocally identified on the specimen (which is exposed in ventral view), but there is a distinct broadening of the mandibular ramus in the area below the mandibular joint, supporting the expanded medial articular facet (as in *N. mirabilis*: Rieppel, 1994a).

POSTCRANIAL SKELETON—The only postcranial skeleton associated with a skull is that of the holotype of *N. raabi* (MB I. 007.18). Measurements are given in Table 1. A total of 38 presacral vertebrae can be identified (not 36 as stated by Schröder, 1914). Of these, 18 lie in front of the interclavicular–clavicular complex; the 19th lies below that complex. The anteriormost cervical rib that can be identified is associated with the 11th cervical vertebra, and it shows a distinct free-ending anterior process. The rib associated with the 18th cervical retains the same morphology, such that 18, maximally 19, cervical vertebrae can be counted. This leaves a maximum of 20 (minimum of 19) dorsal vertebrae. Three sacral vertebrae can be identified; the following four centra show paired posteroventral facets for articulation with the chevrons, identifying them as caudal elements.

The centrum of the dorsal vertebrae is not constricted in ventral view; some of the centra (including the third sacral) have dissociated from their neural arches, indicating that the neurocentral suture remained unfused. Dissociated centra show the butterfly-shaped or cruciform sutural facet, which received the pedicels of the neural arch characteristic for eosauropterygians (Rieppel, 1994a). The pre- and postzygapophyses of the neural arch are wider than the centrum.

The dorsal ribs show a broad, slightly pachyostotic "shoulder" region and a slight distal expansion. The three sacral ribs show broad proximal ends, but they remain unfused from their respective centra. The distal end of the sacral ribs is not expanded. The caudal ribs again do not fuse with their respective centra. The first caudal rib mimics a sacral rib and appears to have converged on the posterior aspect of the ilium. The gastral ribs are composed of five elements each. The angular medial element bears a distinct anterior tip; the lateral element is slightly curved and shows a blunt distal tip.

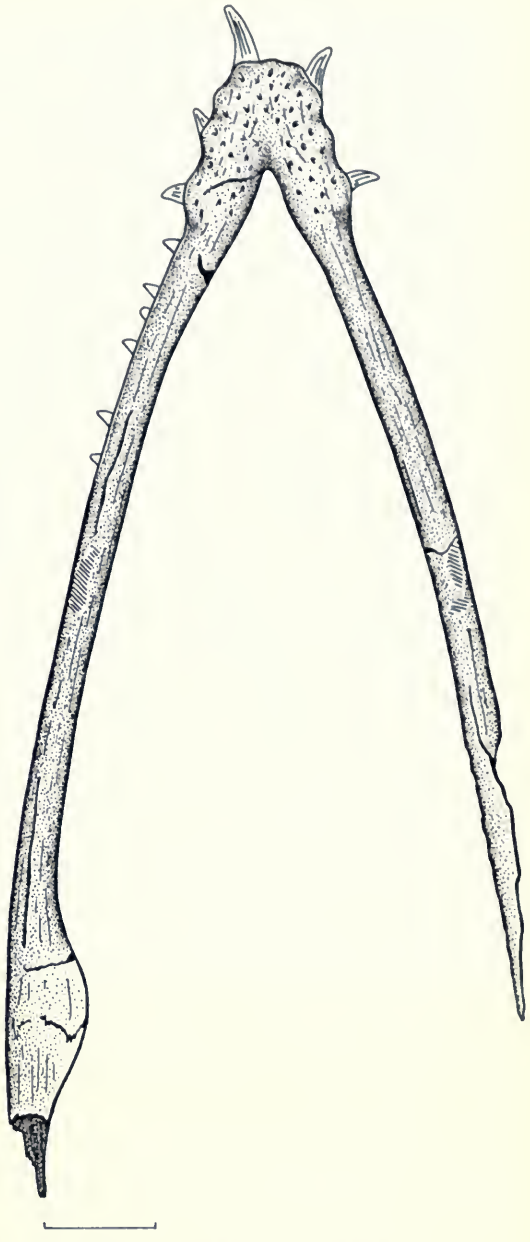


FIG. 43. *Nothosaurus marchicus* Koken (Er 78/233); upper Muschelkalk, Bad Sulza. Lower jaw, ventral view. Scale bar = 20 mm.

The interclavicular–clavicular complex is par-

TABLE 1. Measurements (in mm) for the postcranial skeleton of the holotype of *Nothosaurus raabi* (MB I. 007.18).

measurements in mm	length	proximal width	minimal width	distal width
humerus, left	64	11.8	13.2	17.6
humerus, right	62.3	12.3	12.6	17.8
radius, right	34.5	9.1	5.5	7.5
ulna, right	48.4	15.1	8	10
pubis, left	48.4	27.4	19.1	32.6
ischium, left	51.3	18.2	19	ca. 45
femur, left	ca. 72	15.8	7.5	--
femur, right	74.5	15.9	7	12.3
tibia, right	36	9.2	6.9	9.7
fibula, right	36.9	7.5	--	9.6
metatarsal I	--	--	--	--
metatarsal II	17.8	--	--	--
metatarsal III	ca. 25	--	--	--
metatarsal IV	22.5	--	--	--
metatarsal V	16.1	--	--	--

tially preserved but badly crushed. In particular, it cannot be established unequivocally whether the clavicles meet in a suture anteroventral to the interclavicle, as is typical for pachypleurosaurs and eusauropterygians (Rieppel, 1994a), with the interesting exception of the *Nothosaurus* from the lower Muschelkalk of Winterswijk (undescribed material in private collections). The left scapula is partially exposed, as are both coracoids, which lack their proximal heads. Nothing can therefore be said on the position of the coracoid foramen, which in other nothosaurs is located between the scapula and the coracoid.

The humerus is distinctly curved or "angulated" (Fig. 44A); it shows a well-differentiated deltopectoral crest, an ectepicondylar groove, and an entepicondylar foramen. The distal articulations for radius and ulna are not separated. The radius shows a straight preaxial and a weakly convex postaxial margin, with the proximal head slightly more expanded than the distal head. The ulna is broader than the radius and shows a rather straight postaxial and a deeply concave preaxial margin; this results in the formation of a distinct spatium interosseum between radius and ulna. The carpus comprises three ossifications: an intermedium located distal to the spatium interosseum, an ulnare located distal to the ulna, and a fourth distal carpal. The metacarpals and phalanges are all disarticulated. The exact phalangeal formula can therefore not be determined for the manus.

Both ilia are incompletely exposed. The (left) pubis shows a slitlike but proximally completely closed obturator foramen and a distinct concavity in its ventral (medial) edge (see also Rieppel, 1994a). The ischium shows a narrow proximal head and a wide distal expansion. A well-defined thyroid foramen separates pubis and ischium.

The femur (Fig. 44B) is relatively long and slender, with a weak sigmoidal curvature. The trochanter is only weakly developed. The tibia is a rather straight element and the fibula is more distinctly curved; this again creates a spatium interosseum between the two bones. The tarsus comprises three ossifications: the astragalus, located distal to the spatium interosseum, the calcaneum, located distal to the fibula, and a fourth distal tarsal. Three ossifications are also present in an isolated tarsus from the Schaumkalk of Oberdorla (SMF R-4546, perhaps from the *orbicularis* layers, lower middle Muschelkalk; see comments above). Within the metatarsal series, the third is the longest. The phalangeal count again remains incompletely known for the pes.

Discussion

Originally reported from the lower and basal middle Muschelkalk of Rüdersdorf near Berlin (Schröder, 1914), the occurrence of *Nothosaurus marchicus* in the upper Muschelkalk of Bad Sulza (mu_1 and/or mu_2) and Bayreuth (mu_1: Fig. 45) shows again that species of *Nothosaurus* bridge stratigraphic boundaries. Both at Bad Sulza and in Bayreuth, *Nothosaurus marchicus* coexisted with *Nothosaurus mirabilis.*

The holotype of the genotypical species *Nothosaurus mirabilis* shows a distinct (derived) vertebral structure with high neural spines in the anterior and middle dorsal region of the vertebral column. Comparable vertebrae have never been recorded from lower and middle Muschelkalk deposits, where isolated nothosaur neural arches of the dorsal region consistently show a low neural spine, domed pre- and postzygapophyses with almost horizontally oriented articular surfaces, well-developed accessory intervertebral (zygosphene–zygantrum) articulations, and short and stout transverse processes. Unfortunately, the structure of the neural arches in the holotype of *N. raabi* (MB R. 007.18) remains incompletely known, because the specimen is prepared in ventral view. An articulated but only partially preserved postcranial skeleton without the skull comes from the Schaumkalk (upper lower Muschelkalk; or *orbi-*

FIG. 44. *Nothosaurus raabi* Schröder (holotype; MB I. 007.18); lower middle Muschelkalk, Rüdersdorf. **A,** Left forelimb, ventral view; **B,** right hind limb, ventral view. Scale bar = 20 mm.

cularis layers, lower middle Muschelkalk: see comments above) of Oberdorla (MB R. 150) and was first described by Peyer (1939, Figs. 23, 24). It shows a string of 7 cervical and 17 dorsal vertebrae with the associated ribs in dorsal view, parts of the pectoral girdle, humerus, and fragments of gastral ribs in ventral view. As far as comparison is possible, the torso (MB R. 150) is identical to the holotype of *N. raabi* (MB R. 007.18), and it shows neural arches with the low neural spine typical for isolated vertebrae from the lower and middle Muschelkalk (e.g., MB R. 149, described by Peyer, 1939, Fig. 22). Similar isolated neural arches with a low neural spine have also been found in great numbers in the upper Muschelkalk of Bad Sulza, layers that have also produced—albeit fewer in number—the neural arches typical for *Nothosaurus mirabilis* (with a high neural spine). It is conceivable that relatively small dorsal vertebrae carrying a neural arch with a low neural spine should be referred to *Nothosaurus marchicus,* where they occur in deposits that have also yielded skulls of that species.

Peyer (1939) compared neural arches of dorsal vertebrae with a low neural spine from the lower Muschelkalk to those of "*Paranothosaurus amsleri*" from the Grenzbitumenzone (Anisian–Ladinian boundary) of Monte San Giorgio (Switzer-

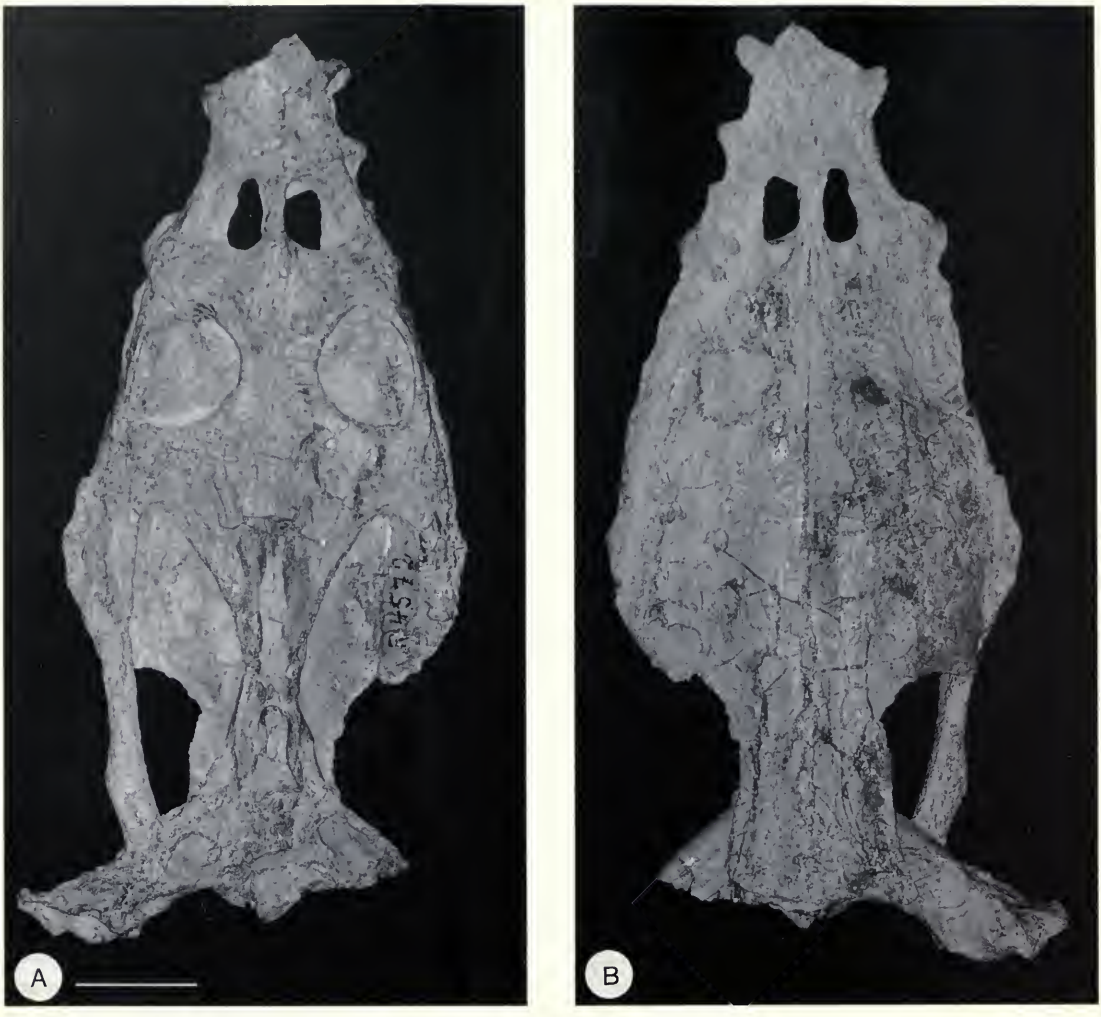


FIG. 45. *Nothosaurus marchicus* Koken (SMF R-4572; original of Edinger, 1921a: 37 ["*Nothosaurus*" sp.]); upper Muschelkalk, Bayreuth. **A,** The skull in dorsal view; **B,** the skull in ventral view. Scale bar = 20 mm.

land), corresponding in age to the boundary between the lower (mo_1) and middle (mo_2) upper Muschelkalk. Indeed, other than its large size, vertebral morphology has been cited as the only character differentiating "*Paranothosaurus*" and *Nothosaurus* (Peyer, 1939; Kuhn-Schnyder, 1966). Large isolated neural arches with a low dorsal spine are known from the upper Muschelkalk (mo_1 to mo_3, most abundantly in the mo_3) and may be associated with large skulls from the same deposits that represent *Nothosaurus giganteus* (Münster, 1834), a senior synonym of "*Paranothosaurus amsleri.*" The question thus arises as to whether the skulls referred to *Nothosaurus marchicus* may not, in fact, represent juvenile specimens of the latter taxon, because they occur in deposits that also yielded small dorsal vertebrae with a low neural spine.

The degree of ossification of the skulls referred to *Nothosaurus marchicus* does not suggest juvenile status for any of the material (except for the possibly paired frontals in one skull from Bad Sulza; see above), nor does the postcranial skeleton of the holotype of *Nothosaurus raabi* (MB R. 007.18), which shows a well-differentiated humerus, with the entepicondylar foramen distinctly set off from the distal end and complete closure of the obturator foramen in the pubis. The relatively short rostrum (as compared to *Nothosaurus mirabilis*) could be regarded as a juvenile feature,

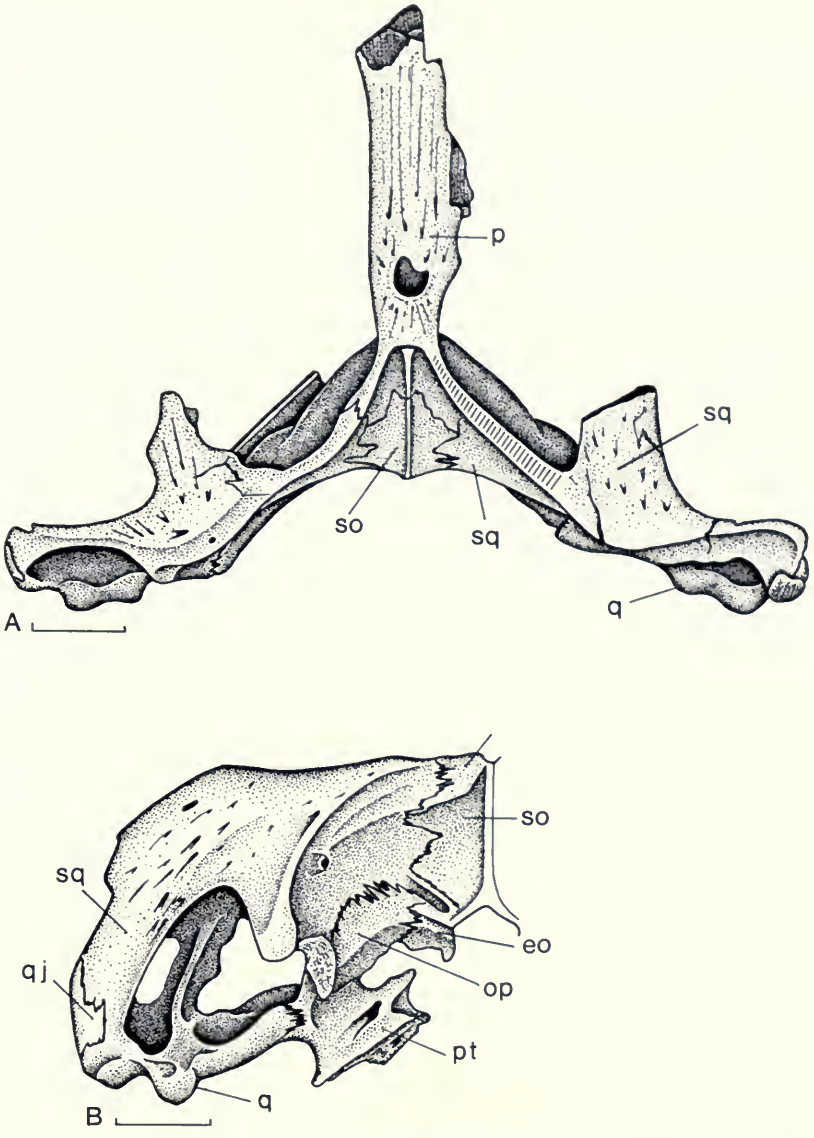


FIG. 46. *Nothosaurus* sp. (MB R. 1775); lower Muschelkalk, Freyburg/Unstrut. Skull fragment. **A,** Dorsal view; **B,** occipital view. Scale bar = 20 mm. Abbreviations: eo, exoccipital; op, opisthotic; p, parietal; pt, pterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal.

but the rostrum in the large skulls of *Nothosaurus giganteus* is again relatively shorter than that of *Nothosaurus mirabilis.* One of the geologically earliest and best-preserved/prepared skulls of *Nothosaurus giganteus* is the holotype of *Nothosaurus baruthicus* Geissler, 1895, from the upper Muschelkalk (mo_1) of Bayreuth. Division of the condylobasal length of the skull by the longitudinal diameter of the orbit yields a ratio of 6.8–8.0 for the skulls here referred to *Nothosaurus marchicus,* 6.4 for *N. muensteri* (treated as juvenile *Nothosaurus mirabilis* by Rieppel, 1994c), 7.9–10.9 for *Nothosaurus mirabilis,* and 8.9 for the holotype of *Nothosaurus baruthicus.* These values indicate that *N. marchicus* has slightly larger orbits than *Nothosaurus mirabilis* or *Nothosaurus giganteus,* but the difference is more likely related to phylogenetic size increase in *Nothosaurus gi-*

ganteus than to a juvenile status of specimens referred to *Nothosaurus marchicus*. Finally, skulls that correspond to *Nothosaurus giganteus* in absolute size differ morphologically from those referred to *Nothosaurus marchicus* in the slender nasals, the (variable) contact of the premaxilla with the frontal, the (variable) contact of the frontal with the maxilla, the maxillary tooth count (four rather than five teeth preceding the maxillary fangs), the posterior location of the frontoparietal suture, and the lesser anterior extension of the ectopterygoid.

Nothosaurus remains distinctly larger than the material referred to *Nothosaurus marchicus* are exceedingly rare in the lower and middle Muschelkalk. Neural arches of the size characteristic of adult *Nothosaurus giganteus* have never been found in the lower or middle Muschelkalk. Relatively large but very incomplete cranial and postcranial remains (Ha, uncatalogued) indicate the occurrence, in the Schaumkalk of Freyburg/Unstrut, of a nothosaur taxon of larger size than is typical for *Nothosaurus marchicus*; two mandibular fragments of large size from the same locality (Got, uncatalogued; P.99) show a symphysis with a length-to-width ratio of 1.05 and 1.1, respectively. A partial skull (MB R. 1775; Fig. 46), again from the same deposit, comprises most of the occiput and is again distinctly larger than *Nothosaurus marchicus,* from which it differs by the presence of a quadratojugal. Due to their incomplete nature, the status of these specimens with respect to any of the species of *Nothosaurus* described to date remains problematical.

Nothosaurus mirabilis Münster, 1834

1834 *Nothosaurus mirabilis,* Münster, p. 525.
1837 *Nothosaurus mirabilis* (partim), Bronn, p. 189.
1838 *Nothosaurus münsteri,* Meyer, p. 559.
1840 *Nothosaurus mirabilis,* Braun, p. 80, Pl. 2, Pl. 7, Fig. 7.
1840 *Nothosaurus münsteri,* Braun, p. 80, Pl. 4, Fig. 1.
1847 *Nothosaurus mirabilis* Giebel, p. 159.
1847 *Nothosaurus münsteri,* Giebel, p. 160.
1847 *Dracosaurus bronnii,* Giebel, p. 162.
1847–55 *Dracosaurus bronni,* Meyer, p. 4.
1847–55 *Nothosaurus bergeri,* Meyer, p. 150, Pl. 67, Figs. 4–5.
1847–55 *Nothosaurus mirabilis,* Meyer, pp. 15–19, Pl. 1, Figs. 1–4; Pl. 2, Figs. 1–2, Pl. 3, Figs. 1–2; Pl. 4, Figs. 1–4; Pl. 5, Figs. 1–3; Pl. 6, Fig. 1; Pl. 7, Figs. 1–7; Pl. 13, Figs. 1–5.
1847–55 *Nothosaurus münsteri,* Meyer, pp. 20–21, 61, Pl. 9, Figs. 1–7; Pl. 19, Fig. 3.
1859 *Dracosaurus bronni,* Gervais, p. 477, Pl. 55, Fig. 7.
1864 *Nothosaurus bergeri,* Alberti, p. 223.
1864 *Nothosaurus mirabilis,* Alberti, p. 220.
1864 *Nothosaurus münsteri,* Alberti, p. 222.
1889 *Dracosaurus bronni,* Lydekker, p. 288.
1889 *Nothosaurus bergeri,* Lydekker, p. 299.
1889 *Nothosaurus mirabilis,* Lydekker, p. 288.
1889 *Nothosaurus münsteri,* Lydekker, p. 299.
1893 *Nothosaurus mirabilis,* Seeley, p. 157, Fig. 6.
1895 *Nothosaurus mirabilis,* Geissler, p. 334 *ff.*
1896 *Nothosaurus mirabilis,* Fraas, p. 11.
1896 *Nothosaurus münsteri,* Fraas, p. 11.
1899 *Nothosaurus münsteri,* Schrammen, Pl. 24, Fig. 4b.
1899 *Nothosaurus mirabilis,* Schrammen, Pl. 24, Fig. 4f.
1914 *Nothosaurus mirabilis,* Schröder, pp. 81, 85, Figs. 19, 24.
1914 *Nothosaurus münsteri,* Schröder, p. 85, Fig. 26.
1914 *Nothosaurus mirabilis,* Williston, Fig. 46.
1921c *Nothosaurus mirabilis,* Edinger, p. 122, Fig. 1.
1924 *Nothosaurus mirabilis,* Arthaber, Fig. 3.
1928 *Nothosaurus mirabilis,* Corroy, p. 37, Pl. 3, Fig. 1, 42; Pl. 4, Figs. 1–4.
1928 *Nothosaurus münsteri,* Corroy, p. 39, Fig. 1112.
1928 *Nothosaurus mirabilis,* Schmidt, p. 397, Fig. 1112.
1928 *Nothosaurus münsteri,* Schmidt, p. 397, Fig. 1113.
1929 *Nothosaurus mirabilis,* Edinger, p. 120, Fig. 82.
1931 *Nothosaurus mirabilis,* Peyer, p. 58.
1934 *Nothosaurus mirabilis,* Kuhn, pp. 28–30.
1934 *Nothosaurus münsteri,* Kuhn, pp. 33.
1935 *Nothosaurus mirabilis,* Edinger, pp. 330, 337, Figs. 6a, 8a.
1937 *Nothosaurus mirabilis,* Boni, p. 82.

1939 *Nothosaurus mirabilis,* Peyer, p. 8 *ff.*
1952 *Nothosaurus mirabilis,* Huene, pp. 176, 178, Figs. 68, 72, 73, 76, 77.
1956 *Nothosaurus mirabilis,* Huene, p. 338.
1956 *Nothosaurus münsteri,* Huene, p. 338.
1964 *Nothosaurus mirabilis,* Kuhn, p. 7.
1964 *Nothosaurus münsteri,* Kuhn, p. 8.
1966 *Dracosaurus bronnii,* Kuhn-Schnyder, p. 534.
1966 *Nothosaurus mirabilis,* Kuhn-Schnyder, p. 534 *f.*
1966 *Nothosaurus münsteri,* Kuhn-Schnyder, p. 534.
1966 *Nothosaurus bergeri,* Kuhn-Schndyer, p. 534.
1970 *Nothosaurus mirabilis,* Schultze, p. 221, Fig. 9.
1974 *Nothosaurus mirabilis,* Kuhn-Schnyder, p. 61.
1979 *Nothosaurus mirabilis,* Kruckow, p. 55.
1979 *Nothosaurus münsteri,* Kruckow, p. 55.
1992 *Nothosaurus mirabilis,* Alafont, p. 54, Fig. 3.8.
1993b *Nothosaurus mirabilis,* Rieppel, p. 972, text fig. 4.
1994c *Nothosaurus mirabilis,* Rieppel, p. 733 *ff.*, Fig. 7c.
1994 *Nothosaurus mirabilis,* Rieppel and Wild, Fig. 5B.

HOLOTYPE—Partial postcranial skeleton (BT, uncatalogued); original of Meyer, 1847–1855, Pl. 23.

PARATYPES—BT, uncatalogued, originals of Meyer, 1847–1855, Pl. 2, Figs. 1–2 and Pl. 3, Fig. 1; Pl. 3, Fig. 2 and Pl. 4, Figs. 1–3 (Figs. 47–50 in this paper).

LOCUS TYPICUS—Upper Muschelkalk (mo_1), Oschenberg near Laineck (also referred to as Lainecker Berg), east of Bayreuth, Bavaria, Germany.

DIAGNOSIS—A species of *Nothosaurus* of intermediate size with an adult condylobasal skull length of up to 460 mm; rostrum long and slender with parallel lateral edges; length-to-width ratio of mandibular symphysis 1.5–1.7; five fangs on each premaxilla; four small maxillary teeth preceding the paired maxillary fangs; rostral constriction weakly expressed; external nares long and slender; upper temporal fenestra elongate, with a constricted anterior corner and with the maxillary tooth row extending to a level below its midpoint; high neural spines on dorsal vertebrae.

DISTRIBUTION—Upper Muschelkalk and lower Keuper, Germanic Triassic, central and western Europe; perhaps also Ladinian, southern Alps. (For a discussion of possible occurrences in the lower Muschelkalk of Europe and Israel, see below.)

REFERRED MATERIAL—BMNH R-42829 (skull, upper Muschelkalk, probably Bayreuth, original of Lydekker, 1889: 288). BSP 1935 I. 16 (skull, upper Muschelkalk, Bayreuth); BSP 1952 XV 108 (lower jaw, lower Keuper, Hoheneck near Ludwigsburg). BT, uncatalogued; skulls, originals of Meyer, 1847–1855, Pl. 2, Figs. 1–2 and Pl. 3, Fig. 1; Pl. 3, Fig. 2 and Pl. 4, Figs. 1–3; Pl. 6, Figs. 2–3 and Pl. 7, Fig. 1; a skull not figured or described by Meyer, 1847–1855; lower jaw, original of Meyer, 1847–1855, Pl. 13, Figs. 2–4; syntypes of *N. muensteri,* originals of Meyer, 1847–1855, Pl. 9, Figs. 1–3; Pl. 9, Fig. 4; Pl. 9, Figs. 6–7. Gö 756-1, holotype of *N. bergeri,* lower Keuper, Molsdorf. SMF R-472 (skull, upper Muschelkalk, Bayreuth, original of Edinger, 1921a: 29–33); SMF R-473 (skull, upper Muschelkalk, Bayreuth, original of Edinger, 1921a: 27–29); SMF R-474 (mandibular symphysis, upper Muschelkalk, Bayreuth); SMF R-641 (skull, upper Muschelkalk, Bindlach near Bayreuth, original of Edinger, 1921a: 20–27, and Schultze, 1970: 221–222, Pl. 2, Fig. 2). SMNS 13155 (skull, upper Muschelkalk, Crailsheim); SMNS 15174 (skull, upper Muschelkalk [*spinosus* biozone], Weissach); SMNS 16247 (skull, upper Muschelkalk, Bayreuth); SMNS 16433 (skull, upper Muschelkalk, Crailsheim); SMNS 17877b (skull, upper Muschelkalk, [*Discoceratites* layers], Heldenmühle near Crailsheim); SMNS 56286 (skull, upper Muschelkalk [*nodosus* biozone], Berlichingen); SMNS 56587 (skull, upper Muschelkalk, Crailsheim); SMNS 59074 (skull, upper Muschelkalk [*spinosus* biozone], Hegnabrunn near Kulmbach); SMNS 59360 (lower jaw, upper Muschelkalk, Berlichingen); SMNS 59817 (mandibular symphysis, upper Muschelkalk [*enodis–nodosus* biozone], Hegnabrunn near Kulmbach); SMNS, uncatalogued, coll. M. Wild no. 2074 (lower jaw, upper Muschelkalk, Hegnabrunn near Kulmbach); SMNS, uncatalogued, coll. M. Wild no. 564 (lower jaw, upper Muschelkalk, Hegnabrunn near Kulmbach).

POSTCRANIUM—Disarticulated postcranial elements of *Nothosaurus mirabilis* abound in public repositories (Rieppel, 1994a). Articulated skeletons include the holotype (BT, uncatalogued) and an as yet undescribed specimen, perhaps referable to *N. mirabilis* (SMNS 56618, from the upper Muschelkalk, upper *nodosus* biozone, Berlichingen).

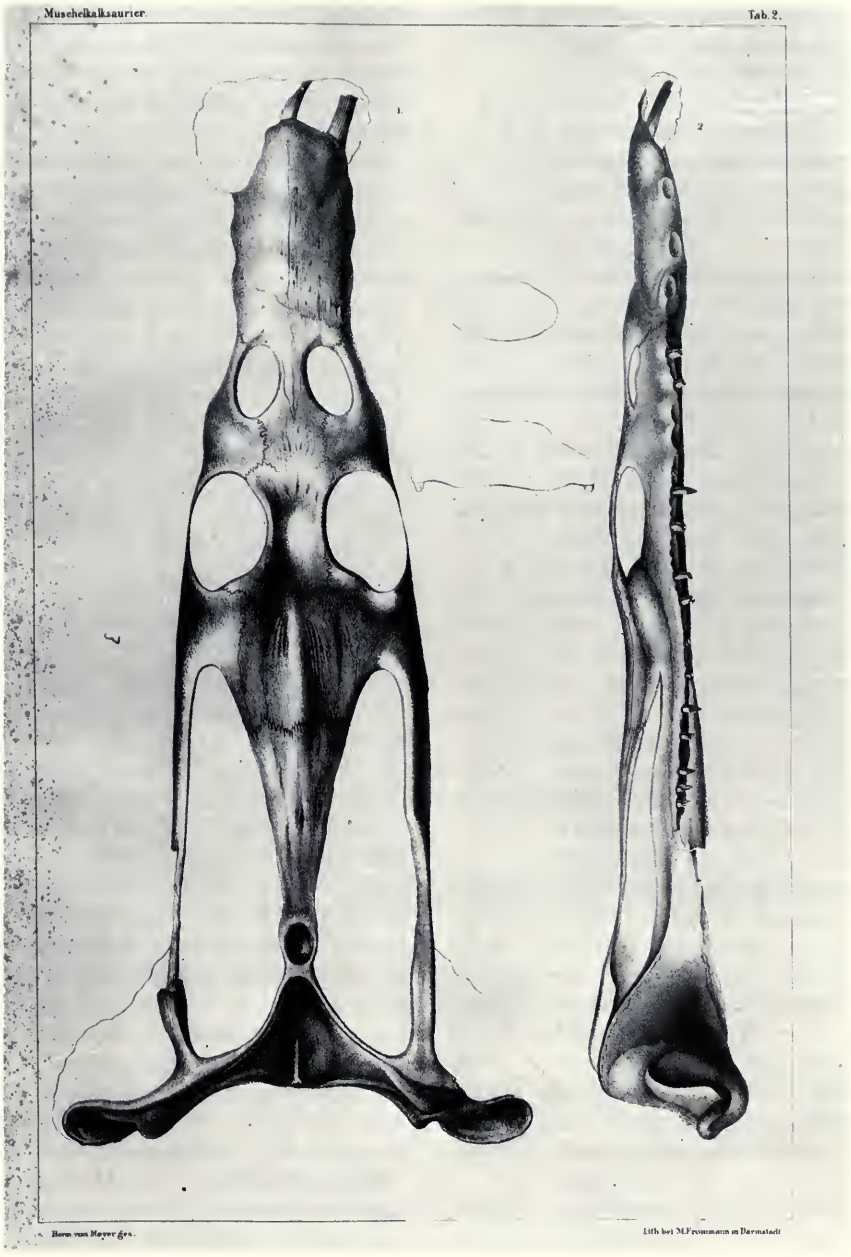


FIG. 47. *Nothosaurus mirabilis* Münster, paratype. Upper Muschelkalk, Bayreuth. Plate 2 of Meyer, 1847–1855 (SMNS negative no. 9170).

COMMENTS—Following his description of *Nothosaurus mirabilis,* Münster (1834: 526 *f.*) mentioned further material from the upper Muschelkalk of Bayreuth that he referred to as *Dracosaurus* (no species name given). This specimen was referred to as *Dracosaurus bronni* by Meyer (1847–1855: 4; *Dracosaurus bronnii* in Giebel, 1847: 162). A cast figured by Gervais (1859, Pl. 55, Fig. 7; MHNP AC.9559) was designated as *Dracosaurus bronnii* on the original label; the cast corresponds to the skull referred by Meyer (1847–1855: 165, Pl. 5, Figs. 1–3) to *Nothosaurus mirabilis.* Dividing the longitudinal diameter of the upper temporal fenestra by the longitudinal

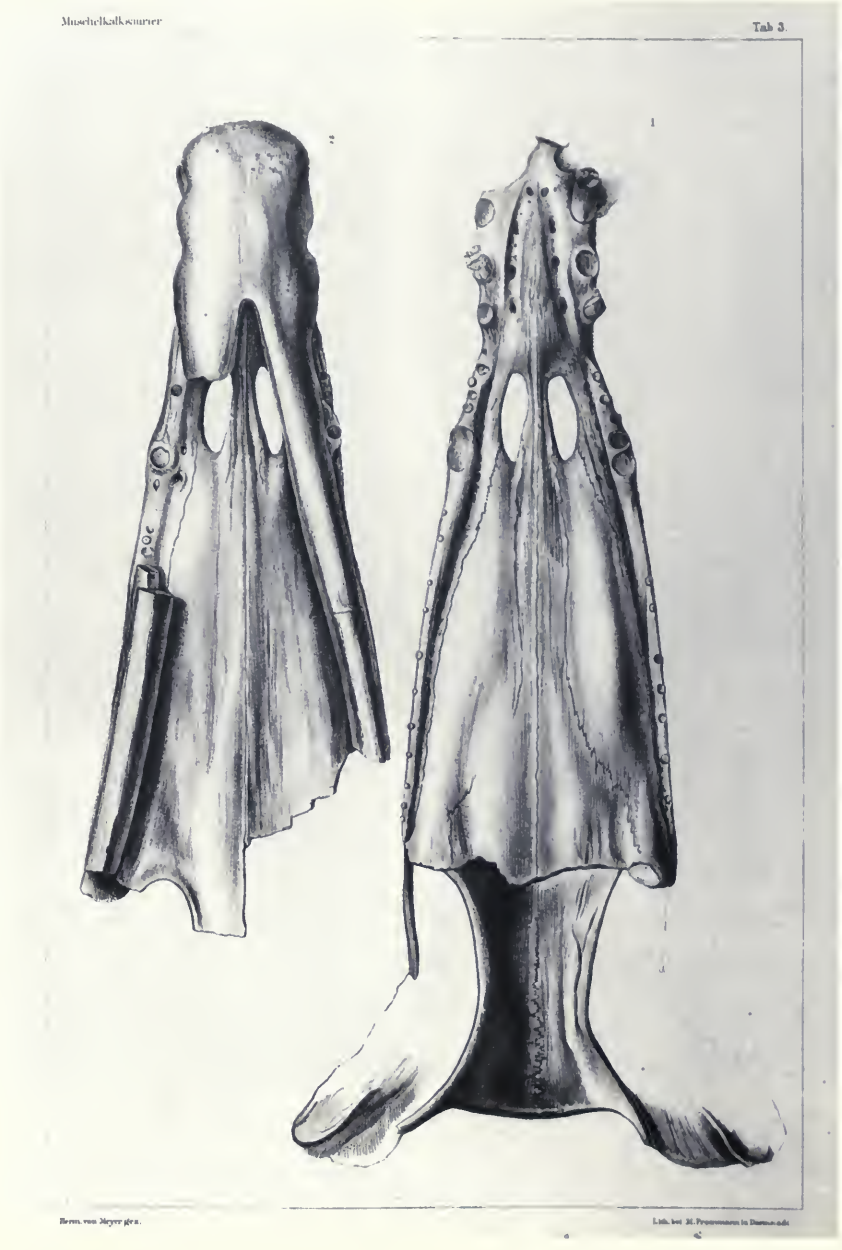


FIG. 48. *Nothosaurus mirabilis* Münster, paratype. Upper Muschelkalk, Bayreuth. Plate 3 of Meyer, 1847–1855 (SMNS negative no. 9172).

diameter of the orbit yields a value of approximately 3.7 (MHNP AC.9559), which falls into the range of variation of *Nothosaurus mirabilis*.

In the same paper, Münster (1834: 526 *f.*) refers to further fossil bones from the upper Muschelkalk of Bayreuth under the names *Plesiosaurus speciosus* and *Metriorhynchus priscus*. Both species names are nomina nuda, but they were listed as junior synonyms of *Nothosaurus mirabilis* by Kuhn (1934).

Simosaurus mougeoti, based on a mandibular symphysis, was formally described by Meyer in 1842. The same specimen was later figured by Meyer (1847–1855: Pl. 15, Fig. 3), but designated

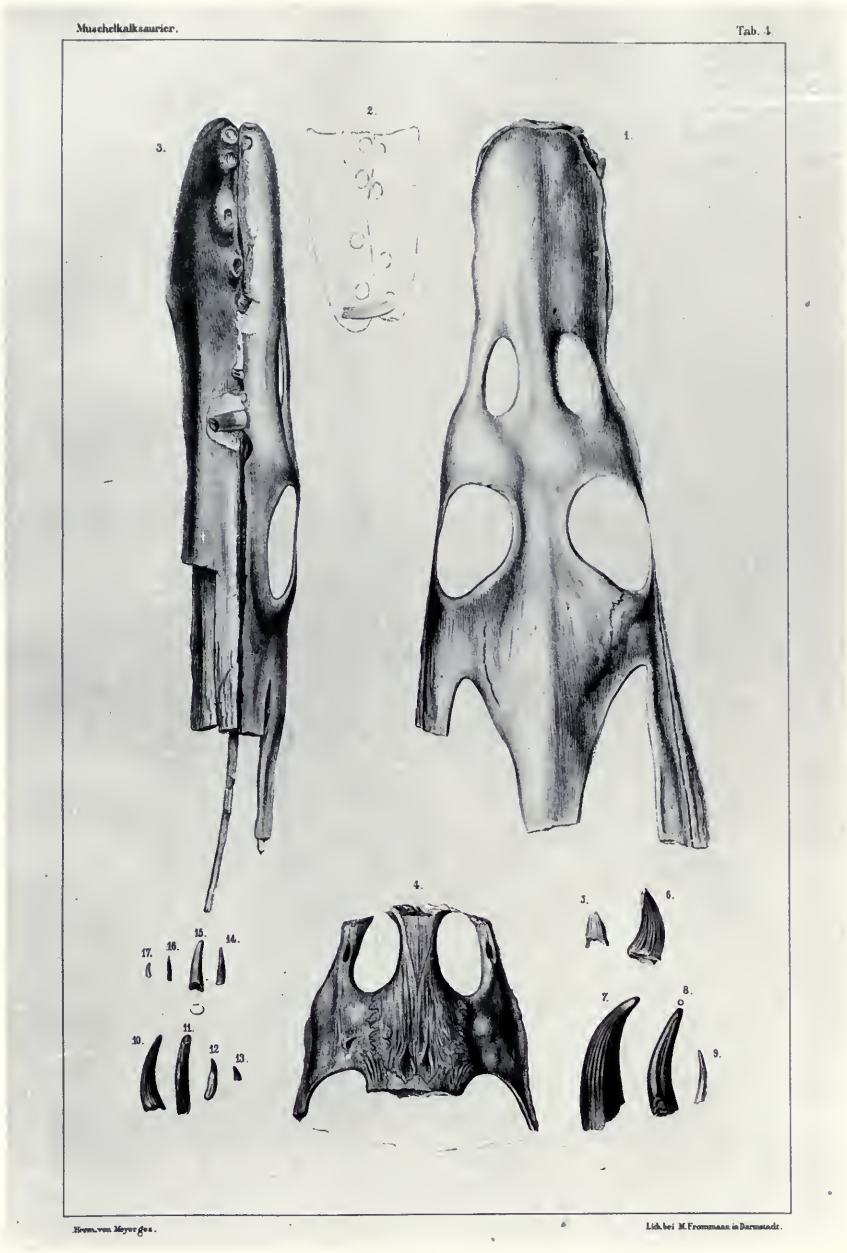


FIG. 49. *Nothosaurus mirabilis* Münster, paratype. Upper Muschelkalk, Bayreuth. Plate 4 of Meyer, 1847–1855 (SMNS negative no. 9171).

as *Nothosaurus mougeoti* in the figure caption (p. 165). In the text, Meyer (1847–1855: 19) referred to the specimen as "the first fragment of the lower jaw of *Nothosaurus* ever found." Indeed, the characteristic elongation of the symphyseal area of the lower jaw, with, in its posterior part, large alveoli for fangs opposing the paired maxillary fangs, is diagnostic for the genus *Nothosaurus*. The specimen is too incomplete, however, to allow specific identification. The holotype of *Simosaurus mougeoti* can no longer be located today, and the species name *mougeoti* (*mougeotii* in Alberti, 1864: 224) must be considered a nomen dubium.

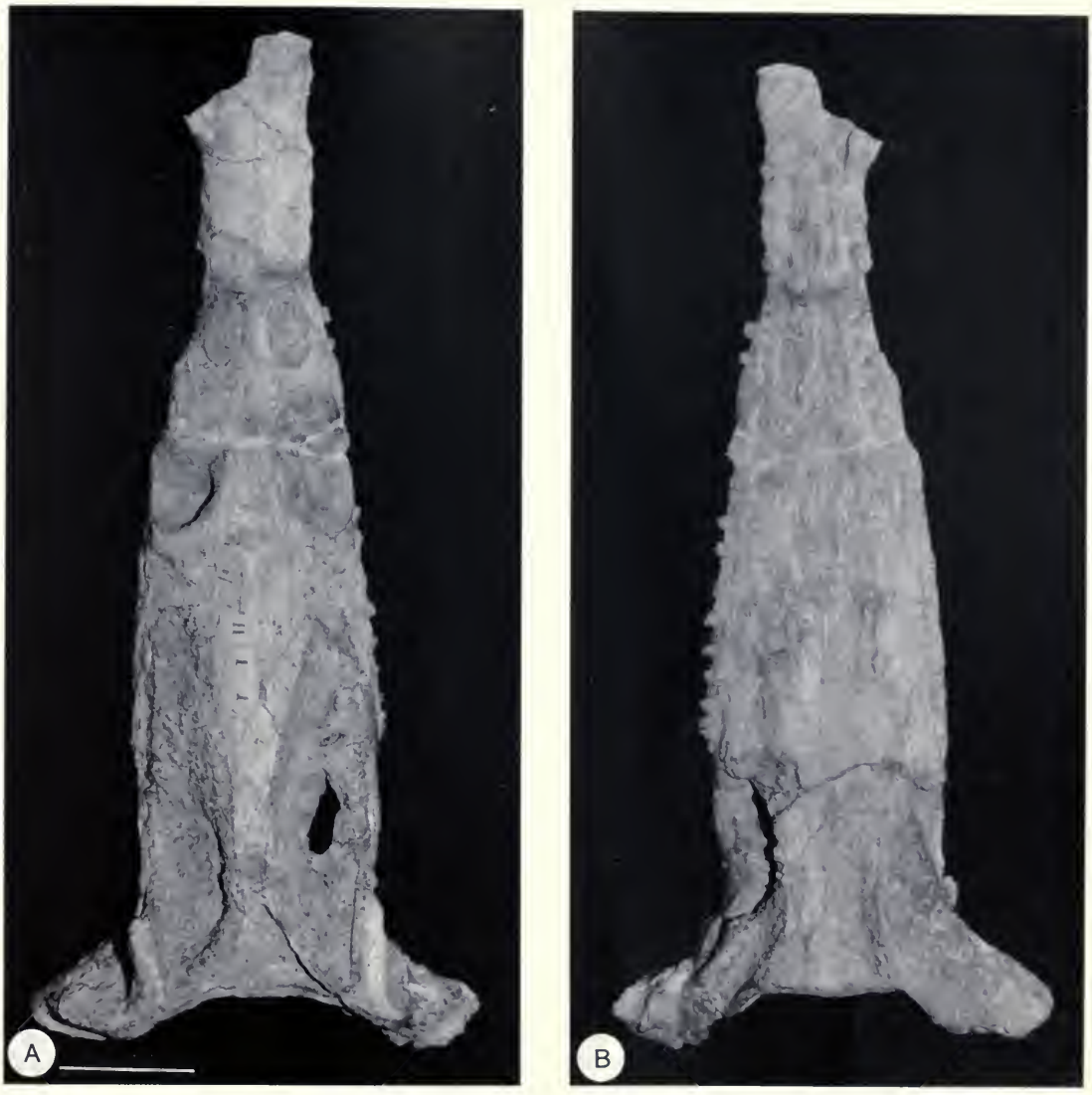


FIG. 50. *Nothosaurus mirabilis* Münster (BT, uncatalogued; original of Meyer, 1847–1855, Pl. 2, Figs. 1–2, Pl. 3, Fig. 1); upper Muschelkalk, Bayreuth. **A,** The skull in dorsal view; **B** the skull in ventral view. Scale bar = 20 mm.

Elmosaurus lelmensis Huene, 1957, was based on a very fragmentary skull from the upper Muschelkalk (*Ceratites* layers) of Lelm near Braunschweig. Redescription of the specimen (Rieppel, 1993b) showed it to be a partial skull of *Nothosaurus* that may be referred to *Nothosaurus mirabilis*. Owing to its incomplete nature, the specimen lacks diagnostic characters, and the species name must therefore be considered a nomen dubium.

Fraas (1896: 11, Fig. 4) first described *Nothosaurus blezingeri* on the basis of six isolated teeth from the Grenzbonebed (between Muschelkalk and Keuper) of Crailsheim. Edinger (1921a) and Kruckow (1979: 55) treated *Nothosaurus blezingeri* as a junior synonym of *Nothosaurus mirabilis*. In fact, the teeth described by Fraas (1896) are those of *Tanystropheus*.

Chop (1857) described isolated teeth from the lower Keuper of Schlotheim as *Nothosaurus picardi*. Edinger (1921a) questioned the generic identity of these teeth (see also Schmidt, 1928: 397), and *Nothosaurus picardi* is here considered a nomen dubium.

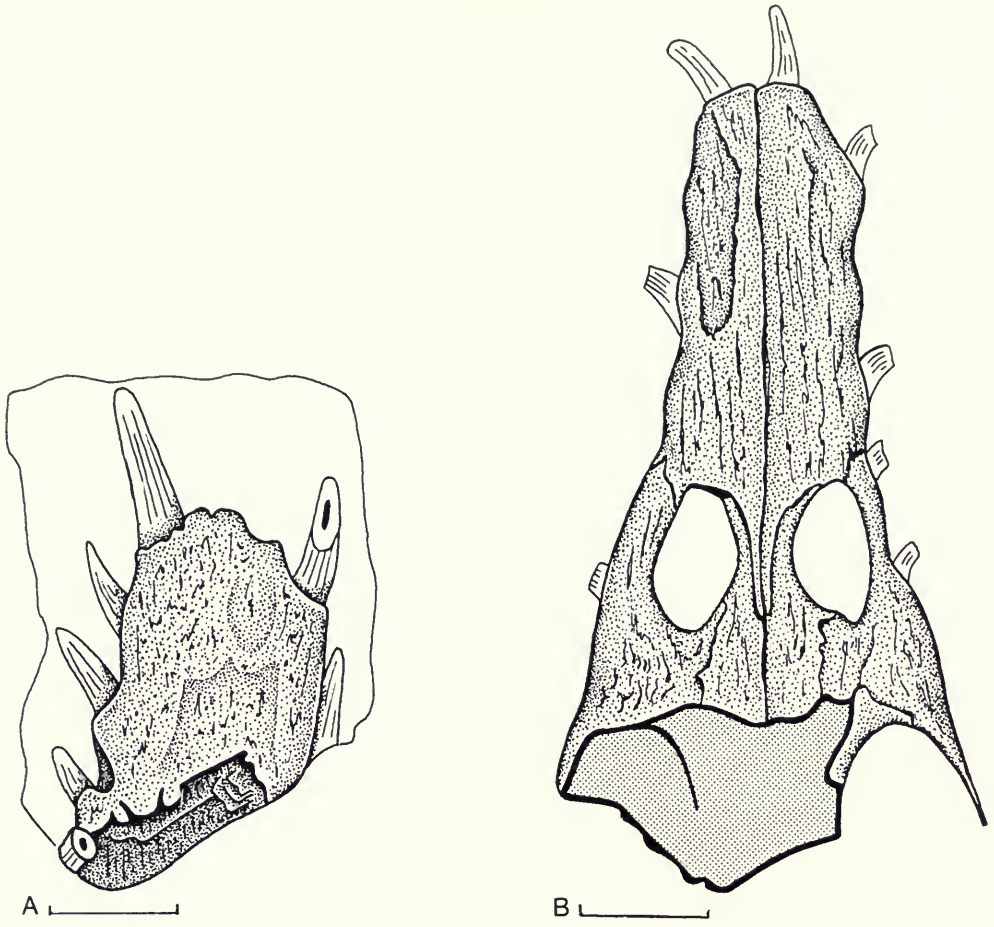


FIG. 51. *Nothosaurus cuvieri* Quenstedt; lower Keuper, Hoheneck near Ludwigsburg. Partial skulls. **A,** SMNS, uncatalogued (original of Fraas [1896: 12], and Schmidt [1928, Fig. 1114]); **B,** SMNS 17291 (undescribed specimen). Scale bar = 20 mm.

Quenstedt (1885: 215, Pl. 16, Figs. 2–6, 12–15) referred isolated nothosaur teeth from the lower Keuper to a new species, *Nothosaurus cuvieri.* Isolated nothosaur teeth are not diagnostic, and the naming of a new species probably was based on stratigraphic considerations. *Nothosaurus cuvieri* therefore is a nomen dubium. Fraas (1896: 12) referred a snout fragment (SMNS, uncatalogued; Fig. 51A) from the lower Keuper of Hoheneck to *Nothosaurus cuvieri*; the specimen was later figured by Schmidt (1928, Fig. 1114). Fraas's (1896) tooth count is erroneous, as is Schmidt's (1928) figure; five premaxillary fangs are preserved on the left side. This as well as the narrow and parallel-sided shape of the fragment indicates that it represents *Nothosaurus mirabilis.* Another as yet undescribed snout fragment from the lower Keuper of Hoheneck (SMNS 17291; Fig. 51B) is more complete and shows the elongate and slender rostrum characteristic of *Nothosaurus mirabilis.* Dividing the distance from the tip of the snout to the anterior margin of the external naris by the width of the skull at the rostral constriction yields a value of 1.9. Dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris results in an index of 1.57. Finally, dividing the longitudinal diameter of the external naris by its transverse diameter yields a value of 1.73. All of these values fall squarely into the range of variation of *Nothosaurus mirabilis.* The specimen therefore is unequivocal evidence of the extension of *Nothosaurus mirabilis* beyond the Muschelkalk into the lower Keuper. The same is indicated by the elongated lower jaw symphysis from the lower Keuper

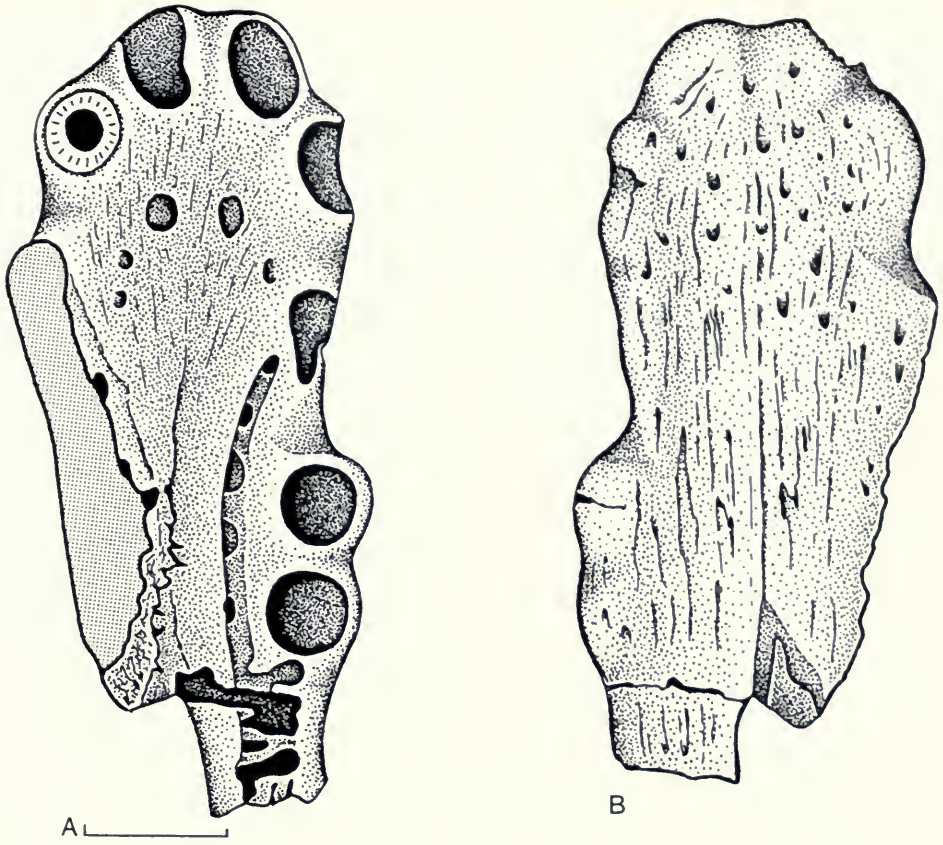


FIG. 52. *Nothosaurus bergeri* Meyer (holotype; Gö 756-1); lower Keuper, Moldsdorf. Mandibular symphysis. **A**, Dorsal view; **B**, ventral view. Scale bar = 20 mm.

of Molsdorf (Gö 756-1), described as *Nothosaurus bergeri* (Fig. 52) by Meyer (1847–1855: 150, Pl. 67, Figs. 4–5; length/width ratio of the mandibular symphysis is approximately 1.75).

Nothosaurus muensteri (Meyer, 1839: 559; 1847–1855) is based on three specimens (Fig. 53A–C) from the Muschelkalk (mo_1) of Bayreuth (Meyer, 1847–1855, Pl. 9, Figs. 1–3; Pl. 9, Fig. 4; Pl. 9, Figs. 6–7; BT, uncatalogued). All three syntypes are poorly preserved and prepared, with severe damage to the bone surface. *Nothosaurus muensteri* has been treated as juvenile *Nothosaurus mirabilis* by Edinger (1921a), Schultze (1970), Kruckow (1979), and Rieppel (1994c). As far as can be established, *Nothosaurus muensteri* indeed closely resembles *Nothosaurus mirabilis* except for one specimen (Meyer 1847–1855, Pl. 9, Fig. 4), which shows broadly exposed prefrontals establishing a broad contact with the nasals, and with a relatively short vomer (cf. Meyer, 1847–1855, Pl. 9, Fig. 2). Unfortunately, relative rostrum length remains unknown for *Nothosaurus muensteri* due to incomplete preservation. Condylobasal length divided by the longitudinal diameter of the orbit yields a ratio of 6.4 for *Nothosaurus muensteri* (for the specimen figured by Meyer, 1847–1855, Pl. 9, Figs. 1–3), whereas the corresponding ratio ranges from 7.9 (a relatively small individual, SMNS 13155) to 10.9 in *Nothosaurus mirabilis*. These values indicate negative allometric growth of the orbit and support the conclusion that *Nothosaurus muensteri* represents juvenile *Nothosaurus mirabilis*. It should be noted, however, that because of their incomplete nature and poor preparation, the specimens of *Nothosaurus muensteri* are hardly diagnostic, and the name might just as well be treated as a nomen dubium.

A skull from the upper Muschelkalk of Crailsheim (SMNS 16433), first mentioned by Berckhemer (1930: xxi), was listed as *Nothosaurus* nov. spec. by Kuhn (1934: 36). In fact, this skull (Fig.

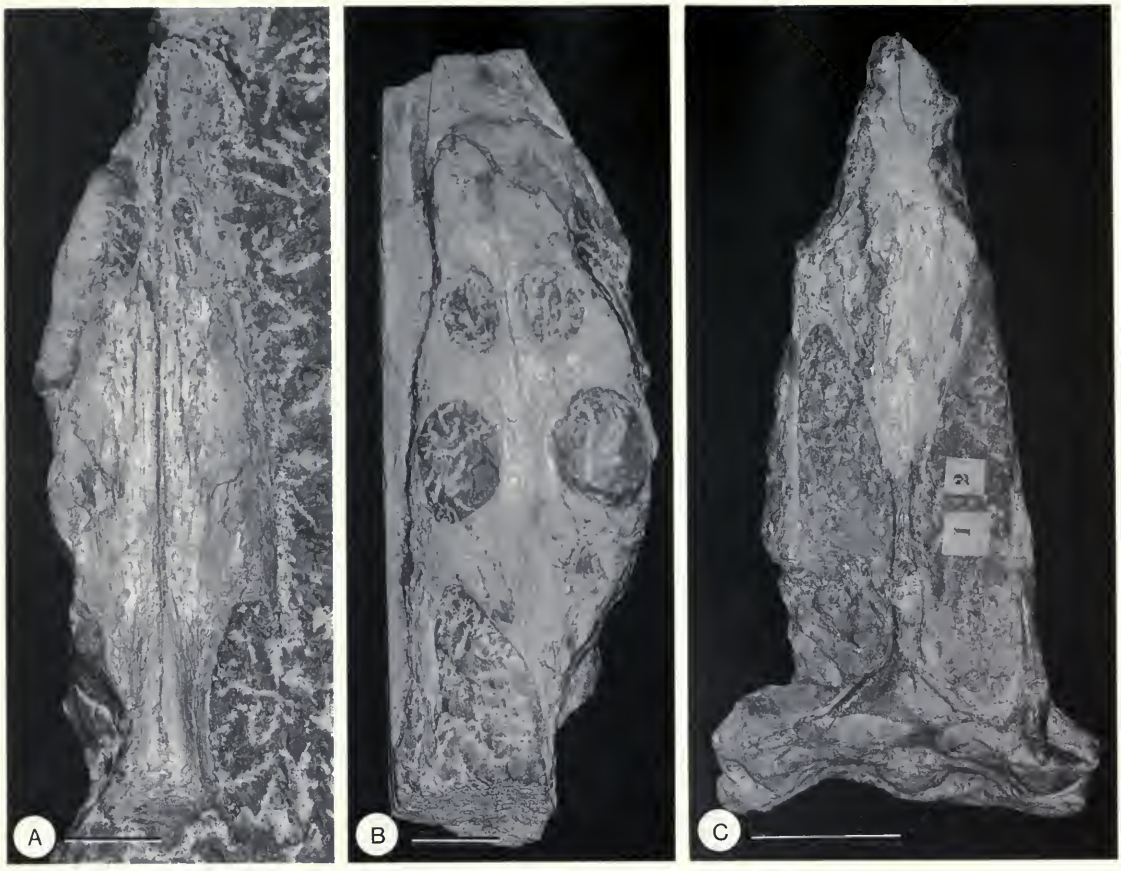


FIG. 53. *Nothosaurus muensteri* Meyer (BT, uncatalogued); upper Muschelkalk, Bayreuth. **A,** Original of Meyer, 1847–1855, Pl. 9, Figs. 1–3; **B,** original of Meyer, 1847–1855, Pl. 9, Fig. 4; **C,** original of Meyer, 1847–1855, Pl. 9, Figs. 6–7). Scale bar = 20 mm.

54) cannot be distinguished from other *Nothosaurus mirabilis.*

Huene (1902: 41, Fig. 44) figured sacral (Fig. 55) vertebrae that he referred to *Nothosaurus mirabilis.* This identification is questionable, and the specimens most probably belong to *Nothosaurus giganteus.*

Of particular interest is a specimen (MB I. 007.16) from the lower middle Muschelkalk of Oberdorla (Fig. 56) that closely corresponds to *Nothosaurus mirabilis.* The skull (condylobasal length: 393 mm) is characterized by a relatively long and slender rostrum, a weak rostral constriction, and a location of the pineal foramen close to the posterior margin of the parietal skull table. Dividing the distance from the tip of the snout to the anterior margin of the external naris by the width of the skull at the rostral constriction yields a value of approximately 2.1; dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris results in an index of 1.68; dividing the distance from the tip of the snout to the anterior margin of the upper temporal fenestra by the distance from the tip of the snout to the anterior margin of the external naris yields a ratio of 2.42; and finally, dividing the longitudinal diameter of the external naris by its transverse diameter yields a value of 2.17. All of these ratios are closely comparable to those of *Nothosaurus mirabilis* (see discussion above) and distinctly different from those of *Nothosaurus marchicus.* In fact, nothing contradicts identification of that specimen as *Nothosaurus mirabilis,* and the fossil may thus represent the earliest record of that

FIG. 54. *Nothosaurus mirabilis* Münster (SMNS 16433; original of Berckhemer, 1930: xxi); upper Muschelkalk, Crailsheim. Skull. Scale bar = 50 mm.

species. Such a conclusion raises the question, however, of why neural arches with high neural spines, diagnostic of *Nothosaurus mirabilis*, have so far never been found in the lower or middle Muschelkalk. Nothosaur remains have also been reported from the lower Muschelkalk of Israel (Brotzen, 1955, 1957), and some of these have been compared to *Nothosaurus mirabilis* (Swinton, 1952; Peyer, 1955). The material is too incomplete, however, to be diagnostic (the vertebra described by Swinton [1952] is a caudal centrum with no neural arch).

The specimen previously identified as the earliest record for *Nothosaurus mirabilis* is the ho-

FIG. 55. *Nothosaurus giganteus* Münster (SMF R-276); upper Muschelkalk, Bayreuth. Sacral vertebra (original of Huene, 1902: 41, Fig. 44; Schmidt, 1928, Fig. 1112d). Scale bar = 20 mm.

lotype of *Nothosaurus schimperi* (Meyer, 1847–1855, Pl. 10, Fig. 19), synonymized with *Nothosaurus mirabilis* by Quenstedt (1852: 134). The specimen came from the upper Buntsandstein and is now lost. Meyer's (1847–1855, Pl. 10, Fig. 19) figure shows a relatively shorter mandibular symphysis, and the fifth fang is located behind the symphysis, indicating that the treatment of *Nothosaurus schimperi* as junior synonym of *Nothosaurus mirabilis* may be erroneous. *Nothosaurus schimperi* should be considered a nomen dubium.

Morphological Description

THE SKULL—The skull of *Nothosaurus mirabilis* (Figs. 50–59) is of a highly characteristic elongate and slender shape. The rostrum is relatively longer, its lateral edges are almost parallel, and consequently the constriction of the snout is less distinct than in all other species of the genus. The external naris is elongate and slender. Dividing the distance from the tip of the snout to the anterior margin of the external naris by the width of the skull at the rostral constriction yields a value of 1.5–2.5 for *N. mirabilis*. Dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris results in an index of 1.5–1.7. Dividing the distance from the tip of the snout to the anterior margin of the upper temporal fenestra by the distance from the tip of the snout to the anterior margin of the external naris yields a ratio of 2.2–2.7. Finally,

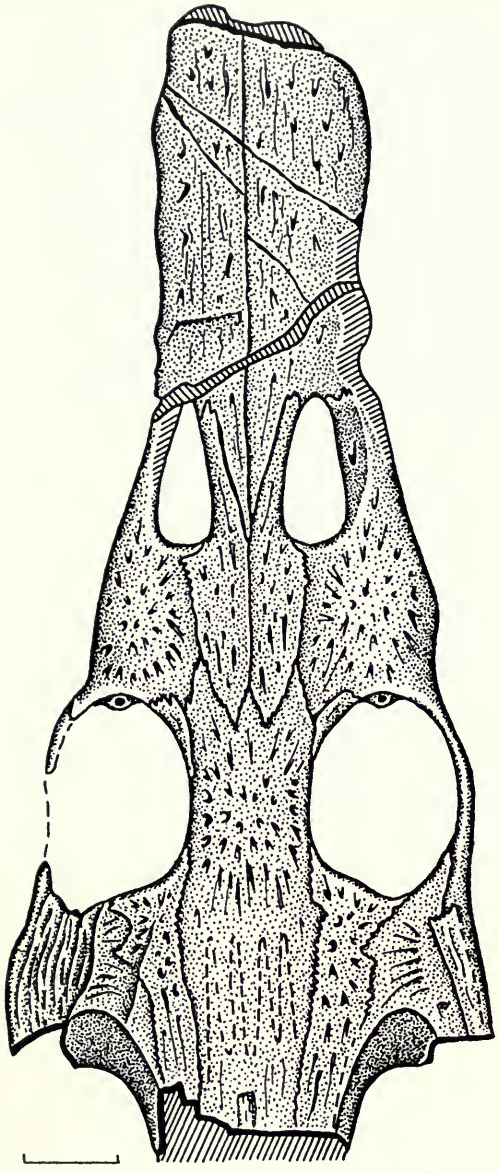


FIG. 56. *Nothosaurus* cf. *N. mirabilis* Münster (MB I. 007/16); lower Muschelkalk or lower middle Muschelkalk, Oberdorla. Scale bar = 20 mm.

dividing the longitudinal diameter of the external naris by its transverse diameter yields a ratio of 1.6–2.2.

The rostrum is formed by the premaxillae, which carry posterior nasal processes entering between the external nares, commonly reaching up to the level of the posterior margin of the latter. The nasals are relatively slender bones with straight lateral edges, defining the posterior margin of the external naris anteriorly, tapering to a blunt tip posteriorly, and embracing a short anteromedial process of the frontal in between them. In one specimen (SMNS 13155; Fig. 60A), the nasals remain separated from one another along the dorsal midline of the skull, exposing a long anteromedial process of the frontal, which reaches anteriorly to a level well in front of the posterior margins of the external nares, entering in between the posterior nasal processes of the premaxillae. The maxilla meets the premaxilla in the anterolateral edge of the external naris. Lateral to the external naris, the maxilla usually shows a marked medial depression with a distinct foramen of unknown function at its bottom. Between the external nares and the orbit, the maxilla bulges laterally to accommodate the roots of the maxillary fangs. The prefrontal lies at the anterodorsal margin of the orbit and has only a limited dorsal exposure. A lacrimal is absent, and the lacrimal foramen is located entirely within the maxilla. The frontal generally carries distinct anterolateral processes, which in most well-preserved specimens contact the maxilla and thus separate the prefrontal from the nasal (in contrast to Meyer's [1847–1855] composite reconstruction on Pl. 1, Fig. 1). The character is variable, however, because one specimen (SMNS 59077) shows a frontal–maxilla contact on the right side and a nasal–prefrontal contact on the left (Rieppel, 1993b). The frontal is unpaired in all available specimens.

The upper temporal fenestra is relatively longer in *N. mirabilis* than in *N. marchicus*; dividing the condylobasal skull length by the longitudinal diameter of the upper temporal fenestra yields a ratio of 2.3–2.5 for the former and 2.6–3.0 for the latter species. As compared to *N. marchicus,* the anterior corner of the upper temporal fenestra is distinctly constricted by the laterally convex anterior margin of the parietal. The maxillary tooth row extends to about the midpoint of the upper temporal arch in *N. mirabilis.* The jugal is a thin and splintlike bone wedged in between the maxilla and the postorbital. It usually remains excluded from the posterior margin of the orbit, except in one fragmentary skull (SMNS 56838) that shows the jugal entering the posteroventral corner of the orbit (Fig. 60B). Unfortunately, this specimen lacks the rostrum and hence is not diagnostic. It is referred to *N. mirabilis* on the basis of its size and the constricted anterior corner of the upper temporal fenestra. Because of their fragile nature, the upper temporal arches are commonly poorly preserved. The exact relations of the squamosal

FIG. 57. *Nothosaurus mirabilis* Münster (BMNH R-42829; original of Lydekker, 1889: 288, Fig. 83); upper Muschelkalk, Bayreuth. **A,** The skull in dorsal view; **B,** the skull in ventral view. Scale bar = 50 mm.

to the jugal could therefore not be established in any specimen.

Prefrontal and postfrontal remain separate along the dorsal margin of the orbit, which is formed by the frontal bone. The deeply interdigitating fronto-parietal suture is located at a level distinctly behind the anterior margin of the upper temporal fenestra. The postorbital defines the posteroventral margin of the orbit as well as the anterior circumference of the upper temporal fenestra. The postfrontal forms the posterodorsal margin of the orbit, from where it extends backward

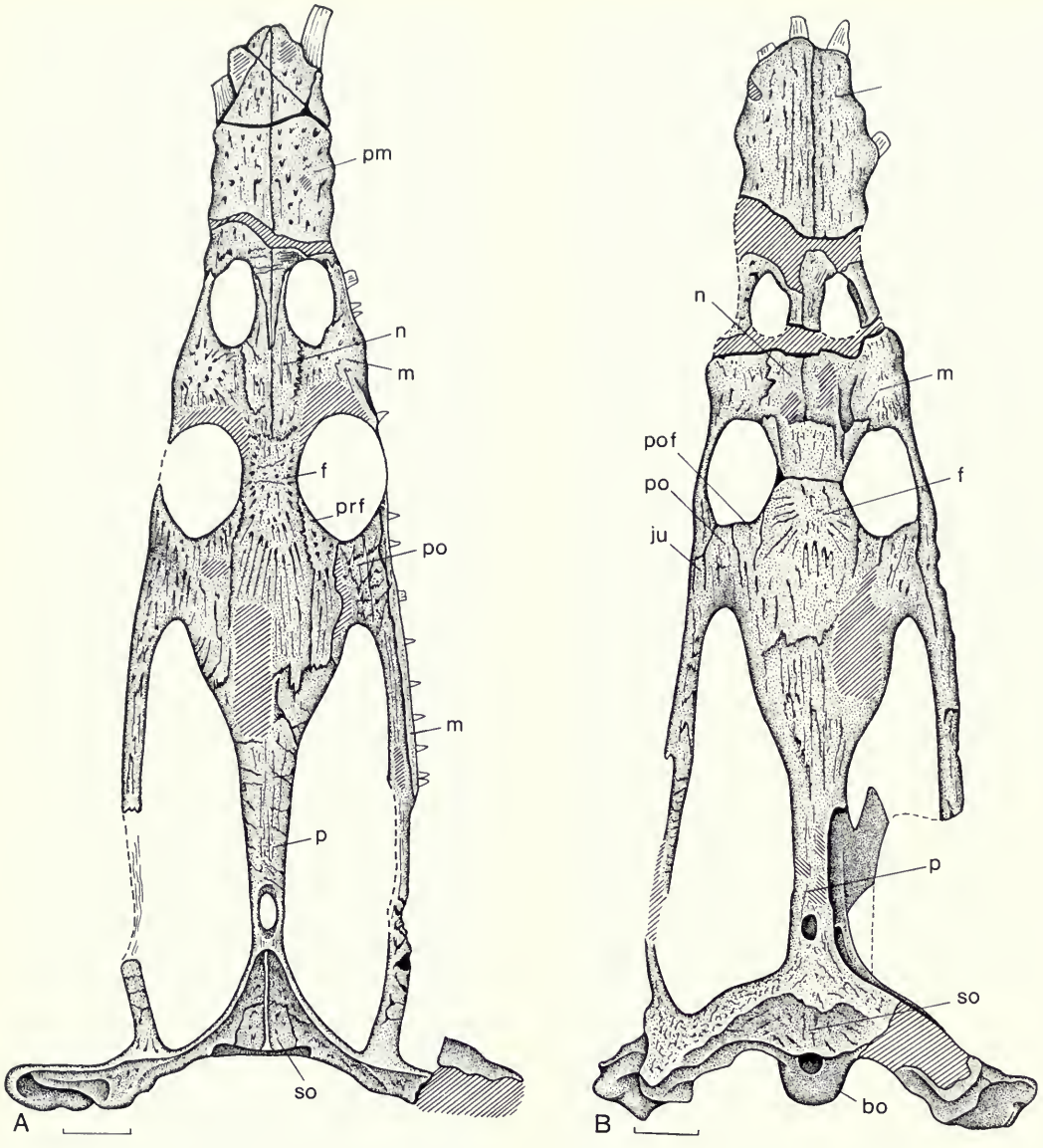


FIG. 58. *Nothosaurus mirabilis* Münster; upper Muschelkalk, Bayreuth. The skull in dorsal view. **A,** BT uncatalogued, original of Meyer, 1847–1855, Pl. 2, Fig. 1; **B,** BMNH, R-42829; original of Lydekker, 1889: 288, Fig. 83. Scale bar = 20 mm. Abbreviations: bo, basioccipital; f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; so, supraoccipital.

to the level of the frontoparietal suture. It is a relatively more elongate and slender element than in *N. marchicus,* with a less distinctly developed postorbital constriction. The postfrontal is not tapered posteriorly (as in *N. marchicus*), and it forms an interdigitating suture with the parietal. It usually remains excluded from the upper temporal fenestra, but it may narrowly enter the lateral edge of the fenestra with its posterolateral tip. The pineal foramen is dislocated posteriorly to a position close to the posterior margin of the narrow parietal skull table.

The occiput and braincase were described in detail by Rieppel (1994b) on the basis of two incomplete skulls that, by their size and stratigraphic origin, can be referred to *N. mirabilis.* A qua-

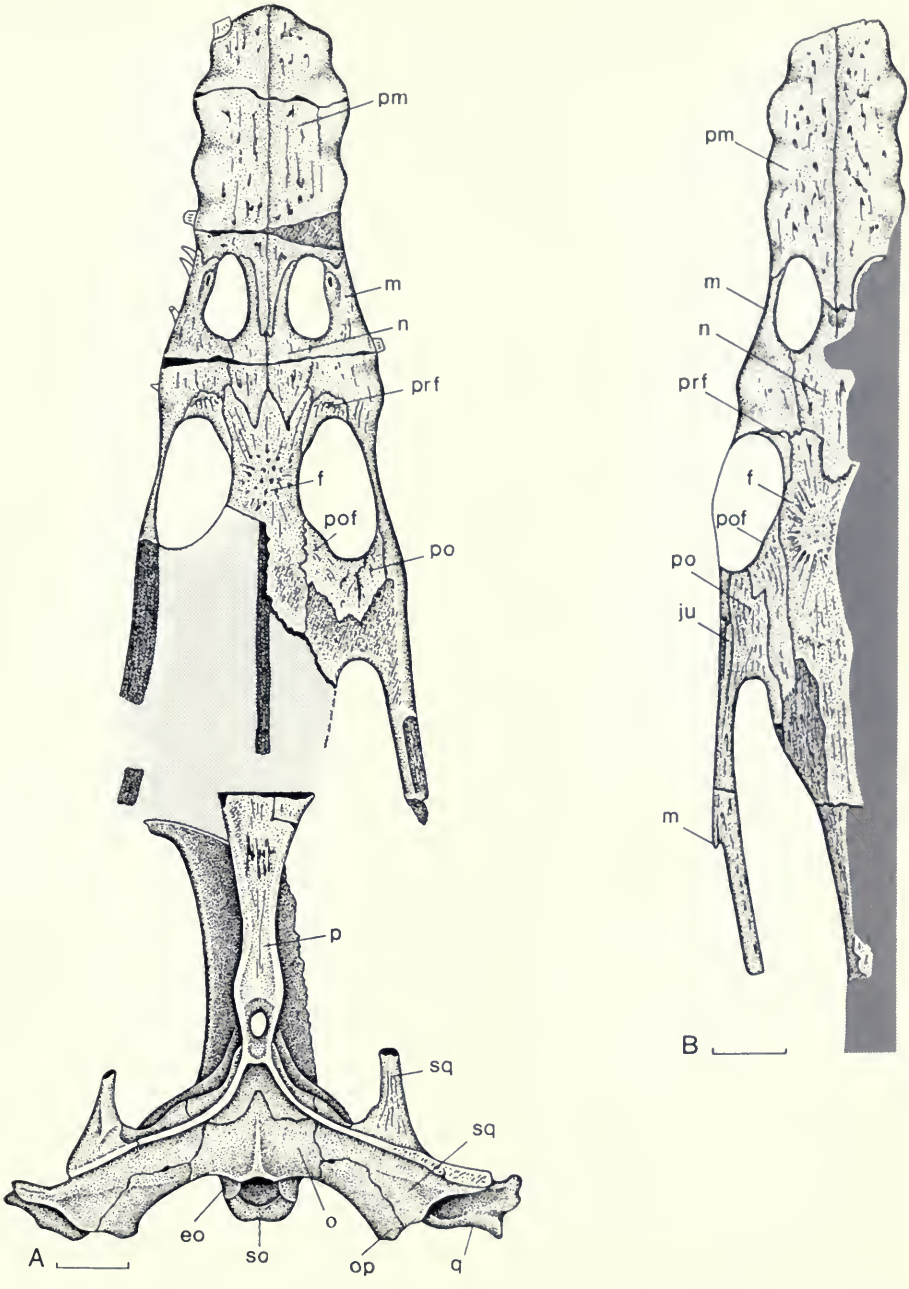


FIG. 59. *Nothosaurus mirabilis* Münster; upper Muschelkalk, Bayreuth. The skull in dorsal view. **A,** SMF R-641; **B,** SMF R-473. Scale bar = 20 mm. Abbreviations: bo, basioccipital; eo, exoccipital; f, frontal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; q, quadrate; so, supraoccipital; sq, squamosal.

dratojugal is present along the lateral edge of the quadrate, below the laterally descending process of the squamosal.

In palatal view (Figs. 61, 62) the positions of five premaxillary fangs are exposed; the fifth may be slightly smaller than the preceding teeth. Three or four (rather than five as in *N. marchicus*) maxillary teeth preceded the paired maxillary fangs.

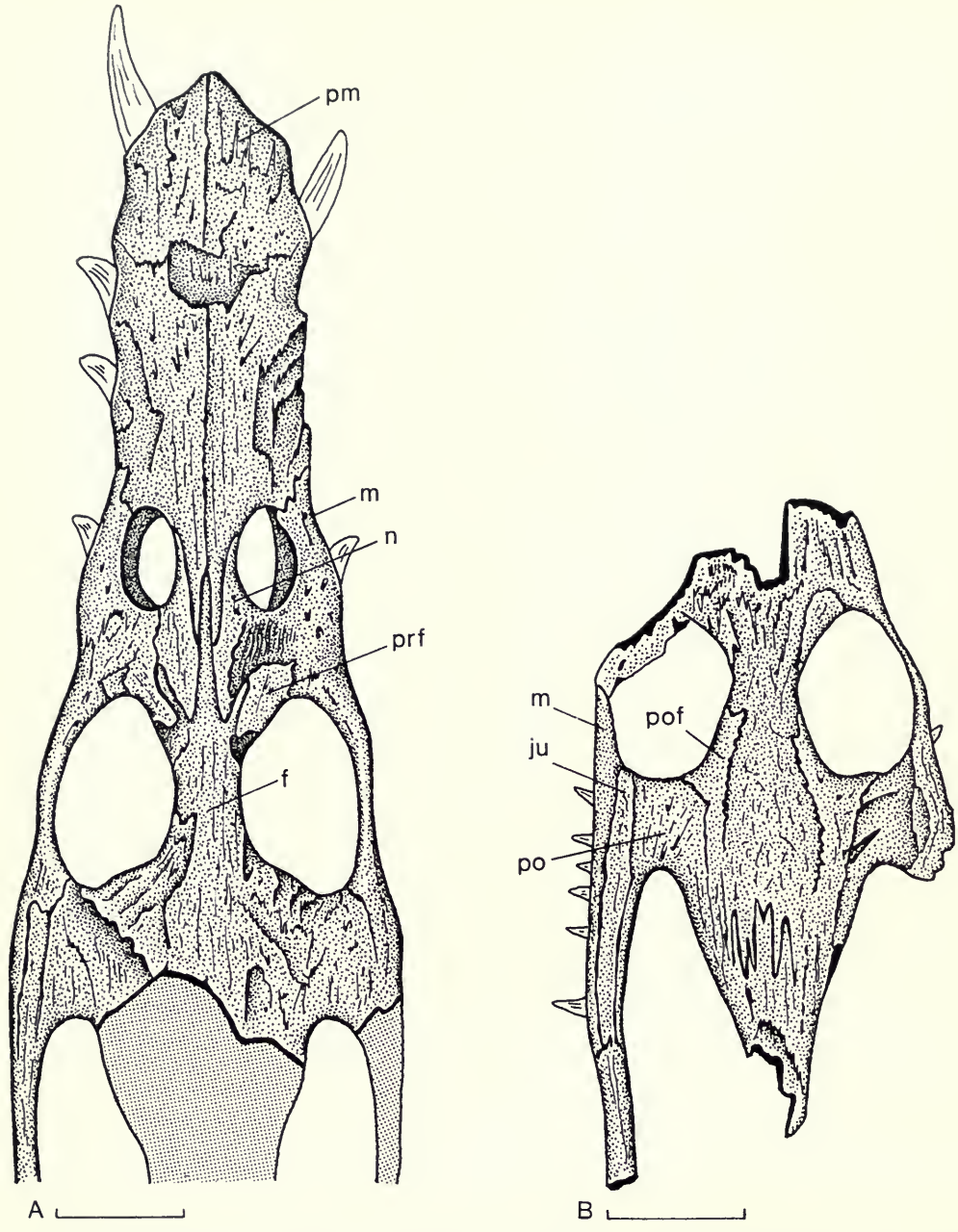


FIG. 60. *Nothosaurus mirabilis* Münster. Partial skulls, dorsal view. **A,** SMNS 13155, upper Muschelkalk, Crailsheim; **B,** SMNS 56838, upper Muschelkalk, Berlichingen. Scale bar = 20 mm. Abbreviations: f, frontal; ju, jugal; m, maxilla; n, nasal; po, postorbital; pof, postfrontal; prf, prefrontal.

The complete maxillary tooth count is 26 in SMNS 59074 (left maxilla, 20 postcanine maxillary tooth positions); BMNH R-42829 shows 21 postcanine tooth positions (right maxilla), raising the total number of maxillary teeth to 27 (assuming four precanine teeth).

The internal naris is enclosed between the vomer (medially), palatine (posteriorly), and maxilla (laterally). A contact of vomer and maxilla excludes the premaxilla from the anterior margin of the internal naris. A fontanelle (incisive foramen) may persist between the vomers and the premax-

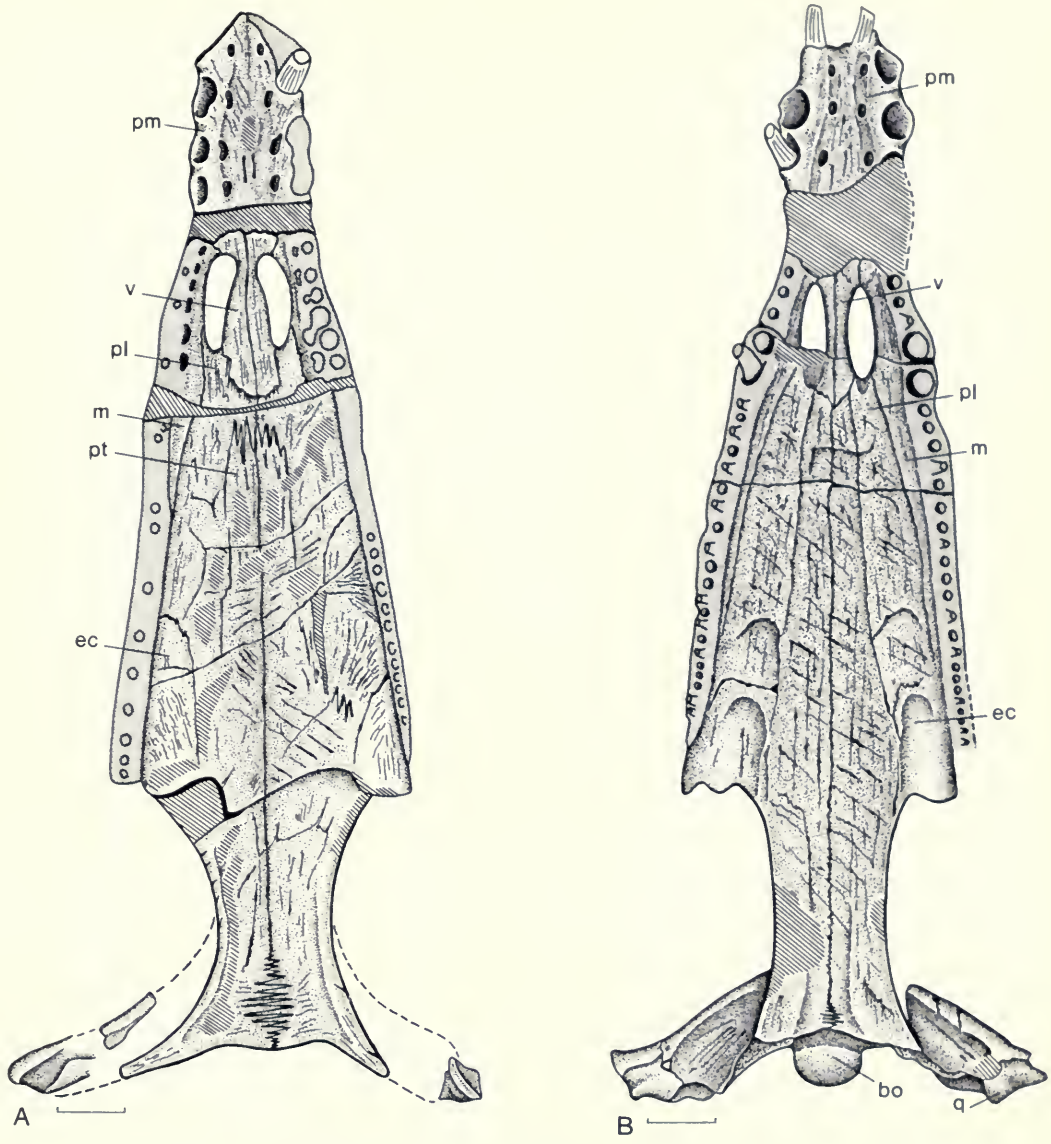


FIG. 61. *Nothosaurus mirabilis* Münster; upper Muschelkalk, Bayreuth. The skull in ventral view. **A,** BT, uncatalogued, original of Meyer, 1847–1855, Pl. 3, Fig. 1; **B,** BMNH R-42829; original of Lydekker, 1889: 288, Fig. 83. Scale bar = 20 mm. Abbreviations: bo, basioccipital; ec, ectopterygoid; m, maxilla; pl, palatine; pm, premaxilla; pt, pterygoid; q, quadrate; v, vomer.

illae. As in all specimens of *Nothosaurus,* the replacement pits for the premaxillary fangs are located in a shallow groove posteromedial to the functional teeth. The maxilla is broadest at the level of the maxillary fangs lateral to the internal nares, from where it tapers to a blunt tip posteriorly. The alveoli for the functional teeth, as well as the replacment pits medial to these, are located on a slightly elevated ridge lining the lateral edge of the maxilla. The ectopterygoid is relatively short and broad anteriorly, and it does not extend anteriorly between palatine and maxilla as far as the anteriorly tapering ectopterygoid of *N. marchicus.* Behind the palatine, and medial to the ectopterygoid, the pterygoid forms a transverse process that is distinctly less well developed than in

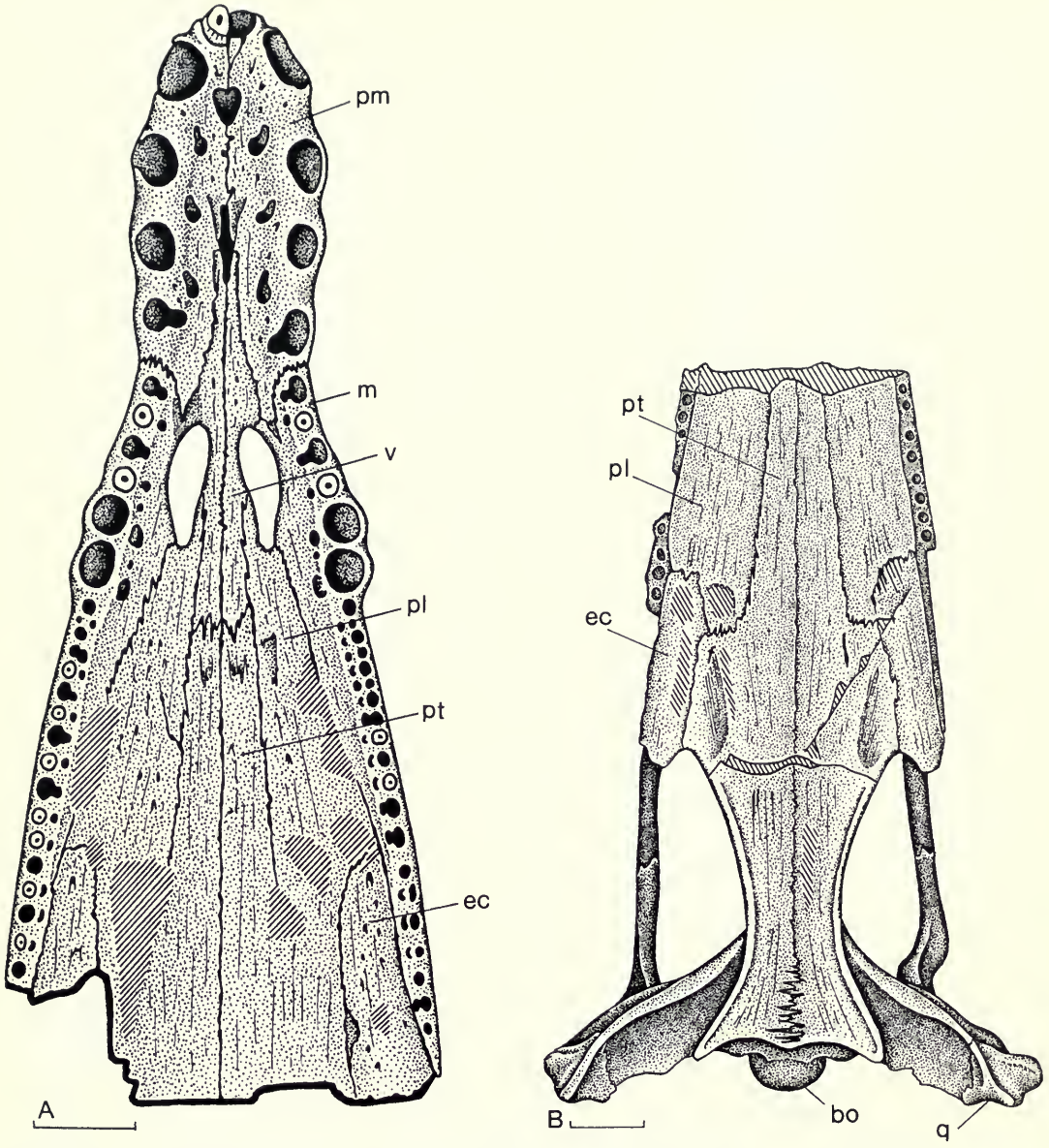


FIG. 62. *Nothosaurus mirabilis* Münster. Partial skulls, ventral view. **A,** SMNS 59074, upper Muschelkalk, Hegnabrunn near Kulmbach; **B,** SMF R-472, upper Muschelkalk, Bayreuth. Scale bar = 20 mm. Abbreviations: bo, basioccipital; ec, ectopterygoid; m, maxilla; pl, palatine; pm, premaxilla; pt, pterygoid; q, quadrate; v, vomer.

N. marchicus (SMF R-427) or may even be absent (BMNH R-42829). The anterior margin of the subtemporal fossa, bordered by pterygoid and ectopterygoid, is vaulted, but no distinct pterygoid flange is developed.

LOWER JAW—The mandibular symphysis mirrors the rostrum in being no less than 1.5 times as long as its maximal width (at the level of the fourth fang). It carries a total of five fangs, the posteriormost one located entirely or at least partially within the symphysis (Figs. 63, 64). The original of Meyer (1847–1855, Pl. 13, Figs. 2–4; BT, uncatalogued) shows the usual five fangs on the left side, but there are six fangs on the right side of the mandibular symphysis (Figs. 63A,B). The replacement pits are again located in a groove

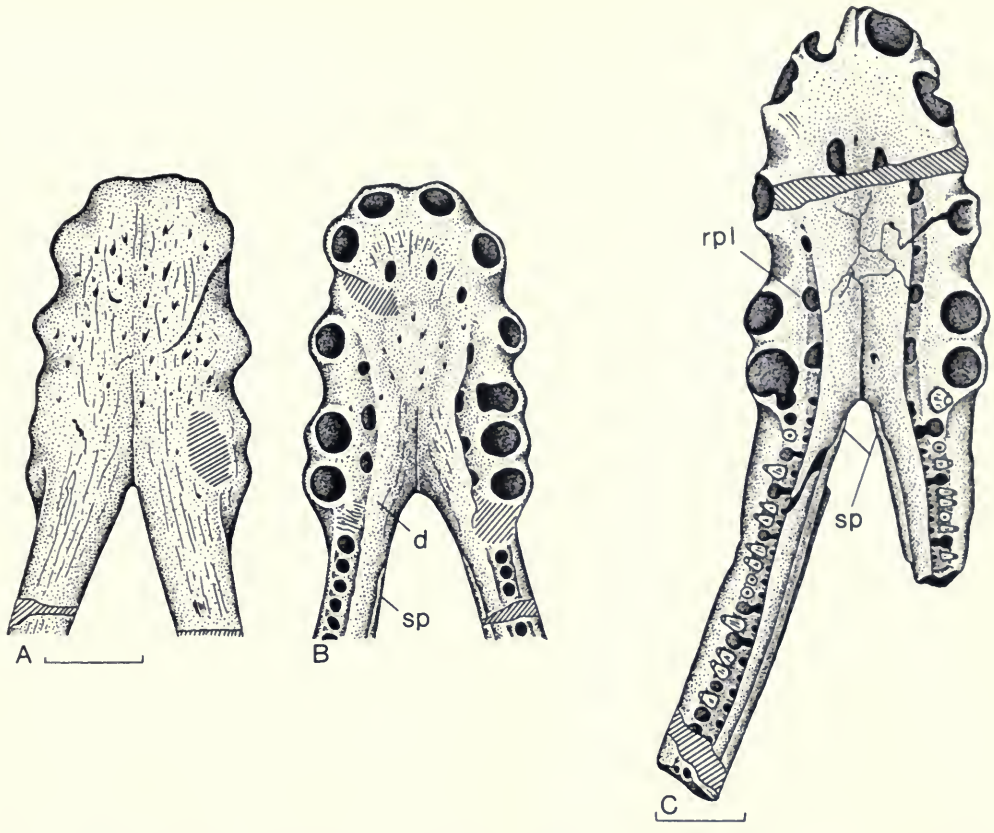


FIG. 63. *Nothosaurus mirabilis* Münster. **A,** Upper Muschelkalk, Bayreuth (BT, uncatalogued; original of Meyer, 1847–1855, Pl. 13. Fig. 2–4); mandibular symphysis in ventral view. **B,** Upper Muschelkalk, Bayreuth (BT, uncatalogued; original of Meyer, 1847–1855, Pl. 13, Figs. 2–4); mandibular symphysis in dorsal view. **C,** Upper Muschelkalk, Hegnabrunn (SMNS 59817), mandibular symphysis in dorsal view. Scale bar = 20 mm. Abbreviations: d, dentary; rpl, replacement pits; sp, splenial.

and posteromedial to the functional teeth. The splenial does not enter the mandibular symphysis.

The total number of dentary teeth could not be established in any of the specimens. The alveoli, as well as the replacement pits medial to these, are located on a slightly elevated ridge forming the dorsal margin of the dentary. As in *N. marchicus*, the splenial defines the anterior margin of the adductor fossa and closes the Meckelian groove medially, but it does not gain a ventral exposure on the lower jaw ramus. A well-preserved specimen (BSP 1952 XV. 108; Fig. 64) shows the tapering angular to extend far forward, beyond the midpoint of the mandibular ramus, and forming an overlapping suture with the splenial along the medioventral edge of the lower jaw. The angular is broadest at the level of the mandibular joint, where it covers most of the medially expanded ventral aspect of the lower jaw. It continues posteriorly into the retroarticular process, where it meets the surangular in a ventromedial suture.

The surangular covers the lateral surface of the retroarticular process and of the mandibular ramus lateral to the adductor fossa. It participates in the formation of the lateral part of the saddle-shaped articular surface (SMNS 59818: Rieppel, 1994a, Fig. 12). In front of the mandibular joint it forms a distinct "shoulder" for the insertion of superficial fibers of the jaw adductor muscle. A coronoid process is absent in *Nothosaurus*; the coronoid bone is restricted to the medial aspect of the lower jaw and located at the anterodorsal margin of the adductor fossa.

POSTCRANIAL SKELETON—The holotype of *N. mirabilis* (Oberfränkisches Erdgeschichtliches Museum, Bayreuth, BT, uncatalogued) has been packed for storage for decades and has not been available for study. The illustration given by Mey-

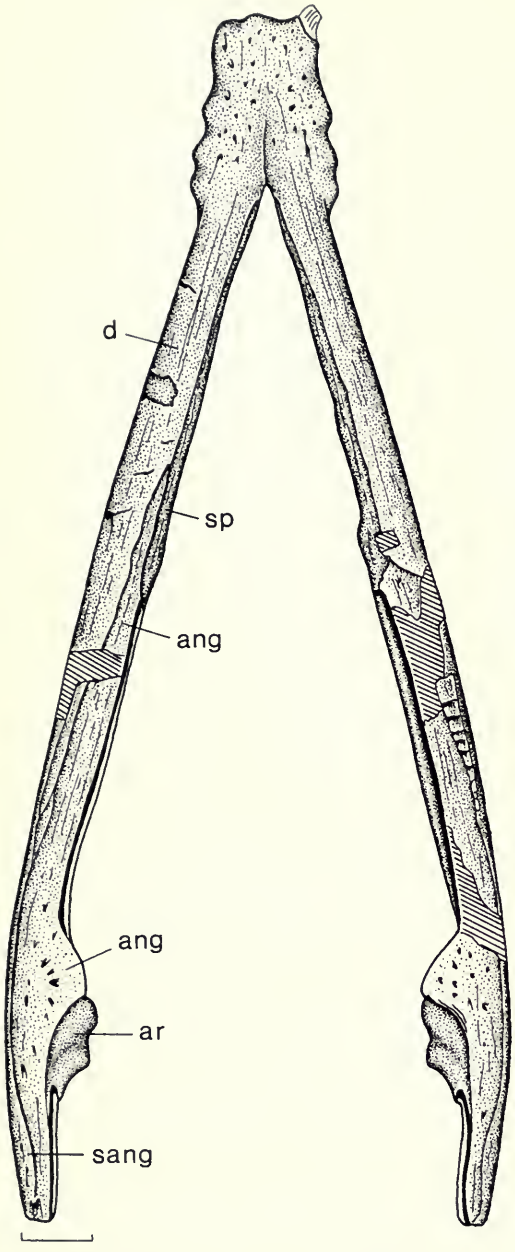


FIG. 64. *Nothosaurus mirabilis* Münster (BSP 1952 XV 108); Lettenkohle, Hoheneck near Ludwigsburg. Lower jaw in ventral view. Scale bar = 20 mm. Abbreviations: ang, angular; ar, articular; d, dentary; sang, surangular; sp, splenial.

er (1847–1855, Pl. 23) shows the high neural spines on the dorsal vertebrae diagnostic for the species. Meyer (1847–1855: 29) comments on the mistaken orientation of the specimen in Münster's (1834) original description.

A large number of dissociated postcranial elements of *Nothosaurus,* most probably referable to *N. mirabilis,* were figured and discussed in detail by Rieppel (1994a).

Discussion

A comparison of *Nothosaurus mirabilis* with *Nothosaurus marchicus* and the undescribed nothosaur material from Winterswijk (Oosterink, 1986; Oosterink & Diepenbroek, 1990) shows an interesting trend in the modification of a number of characters. The rostrum is relatively short and rounded in *Nothosaurus marchicus* and the Winterswijk material, but it is slender and elongate in *Nothosaurus mirabilis.* The mandibular symphysis mirrors these proportions: its length/width ratio varies between 0.7 and 1.0 in *Nothosaurus marchicus* and in the Winterswijk material, and between 1.5 and 1.6 in *Nothosaurus mirabilis.* The postorbital region of the skull is relatively longer in *Nothosaurus mirabilis.* The maxillary tooth row progressively extends posteriorly below the upper temporal fenestra, starting with the Winterswijk nothosaurs, continuing with *Nothosaurus marchicus,* and culminating in *Nothosaurus mirabilis.* The same taxonomic sequence demonstrates a progressive posterior displacement of the pineal foramen toward the posterior margin of the upper temporal fenestra and a posterior displacement of the fronto-parietal suture relative to the anterior margin of the upper temporal fenestra.

The trendlike development of these characteristics is, to some degree, mirrored by the stratigraphic distribution of the taxa in question. The Winterswijk material is from the lowermost Muschelkalk; *Nothosaurus marchicus* is known from the upper lower (mu_2), middle, and lower upper (mo_1) Muschelkalk; and *Nothosaurus mirabilis* occurs in the upper Muschelkalk (mo_1 to mo_3) and in the lower Keuper. To view this pattern of character variation as evidence for an ancestor-descendant lineage requires the analysis of sister-group relationships among the species of *Nothosaurus* as well as a detailed consideration of their stratigraphic occurrence.

Unfortunately, the *Nothosaurus* material from the Gogolin layers of Upper Silesia (now Poland) is very fragmentary and does not allow meaningful comparison with the (slightly younger) Winterswijk material. Its taxonomic status remains unknown. Further, relatively large but disarticulated and fragmentary remains from the Schaumkalk of

Freyburg/Unstrut are evidence of the presence of a large nothosaur with a relatively short symphysis (i.e., different from *Nothosaurus mirabilis*) in the upper lower Muschelkalk (mu_2) (see discussion of *Nothosaurus marchicus* above). The taxonomic status of this material again remains unknown.

The presence of a relatively large nothosaur, different from *Nothosaurus marchicus* as well as from *Nothosaurus mirabilis*, is also known for the Krähenhütte Quarry in Bad Sulza from the presence of a relatively large premaxilla (Er 78/507) and a coracoid of unusual shape (MB R. 491; referred to *Ceresiosaurus* by Schmidt, 1986). The precise stratigraphic provenience of the Bad Sulza material remains somewhat problematic. The quarry exposes the middle Muschelkalk, as well as mo_1 and mo_2 of the upper Muschelkalk (Seidel, 1972). Most of the specimens are labeled as coming from mo_2, but to judge from lithological clues it is more probable that they come from mo_1 (H. Hagdorn, in lit. 7 Dec. 1994). At any rate, the occurrence of neural arches with high neural spines diagnostic for *Nothosaurus mirabilis* indicates a stratigraphic overlap of this species and *Nothosaurus marchicus* in Bad Sulza. The presence of *Nothosaurus mirabilis* in Bad Sulza is also evidenced by a skull described by Langenhan (1915) as *Nothosaurus* (*Cymatosaurus*) *mirabilis* var. *wagneri* (the specimen can no longer be located). The two species also overlap in the mo_1 of Bayreuth, and with the provisions detailed above, one skull (MB I. 007.16) may indicate that the stratigraphic distribution of *Nothosaurus mirabilis* could reach back to the upper lower Muschelkalk (mu_2).

Taxonomic Conclusions

The systematic review recognizes the following species names as nomina dubia: *Conchiosaurus clavatus* Meyer, 1834; *Elmosaurus lelmensis* Huene, 1957; *Hemilopas mentzeli*, Meyer, 1847; *Kolposaurus dichthadius* Skuphos, 1893; *Nothosaurus cuvieri* Quenstedt, 1885; *Nothosaurus* (*Oligolycus*) *hecki* Fritsch, 1894; *Nothosaurus mougeoti* Meyer, 1842; *Nothosaurus picardi* Chop, 1857; *Nothosaurus schimperi* Meyer, 1847–1855; and *Nothosaurus venustus* Münster, 1834. Two species are recognized as nomina nuda: *Plesiosaurus speciosus* Münster, 1834; and *Metriorhynchus priscus* Münster, 1834. The generic name *Hemilopas* Meyer, 1847, is a nomen dubium. A petition to the ICZN declaring the genus name *Conchiosaurus* a nomen oblitum has been submitted.

The nothosaur species from the upper lower (mu_2) and lower middle Muschelkalk of Rüdersdorf, described by Schröder (1914: *crassus, oldenburgi, procerus, procerus* var. *parva, raabi*), as well as *Nothosaurus schroederi* E.v. Huene, 1944, are all recognized as junior synonyms of *Nothosaurus marchicus* Koken, 1893. Diagnostic material confirms the stratigraphic occurrence of that species in the upper lower Muschelkalk (Schaumkalk) and lower middle Muschelkalk (*orbicularis* beds) of Rüdersdorf and Oberdorla, in the lower middle Muschelkalk (Saurierkalk) of Esperstädt, and in the lower upper Muschelkalk (mo_1) of Bad Sulza and Bayreuth. At this time it remains unclear whether the species extends back to the lowermost lower Muschelkalk (mu_1), or whether it persists into the mo_2 of the upper Muschelkalk.

The relatively large nothosaur species from the upper Muschelkalk and lower Keuper, such as *Nothosaurus andriani* Meyer, 1839, *Nothosaurus angustifrons* Meyer and Plieninger, 1844, *Nothosaurus aduncidens* Meyer, 1847–1855, *Nothosaurus baruthicus* Geissler, 1895, and *Nothosaurus chelydrops* Fraas, 1896, are all recognized as junior synonyms of *Nothosaurus giganteus* Münster, 1834. On the basis of its large size, *Opeosaurus suevicus* Meyer, 1847–1855, is likewise treated as a junior synonym of *Nothosaurus giganteus* Münster, 1834. Synonymy of *Paranothosaurus amsleri* Peyer, 1939, with *Nothosaurus giganteus* Münster, 1834, indicates that the species had invaded the southern Alpine intraplatform basin facies by the Anisian–Ladinian boundary (equivalent to the transition between mu_1 and mu_2 in the Germanic Triassic).

Dracosaurus bronni Meyer, 1847–1855, *Nothosaurus bergeri* Meyer, 1847–1855, and *Nothosaurus muensteri* Meyer, 1838, are recognized as junior synonyms of *Nothosaurus mirabilis* Münster, 1834. Diagnostic material confirms the stratigraphic occurrence of that species in the upper Muschelkalk (mo_1 and mo_2) and lower Keuper. At this time it remains uncertain whether the species extends back to the lower Muschelkalk.

Perhaps the most salient result of this review of the genus *Nothosaurus* is the reduction of a total of some 22–25 published species of *Nothosaurus* (Kuhn lists 23 possible species in 1934 and 25 possible species in 1964) to five valid taxa. Edinger (1921a) had already taken the first step

in this direction, which was carried further by Schultze (1970), who recognized eight species. This is not to say that only five species of *Nothosaurus* ever existed in the Muschelkalk Basin. For example, a medium-sized to large nothosaur existed in the lower Muschelkalk, but the remains from that taxon are too fragmentary to permit the diagnosis of a separate species.

Other than a dramatic reduction of valid species names, this revision of the genus *Nothosaurus* also indicates that the chronological distribution of species bridges stratigraphic boundaries both within the Muschelkalk and between the Muschelkalk and the Keuper. This contrasts with the earlier literature, which tended to relate species nominations to stratigraphic boundaries.

The Phylogeny and Paleobiology of the Genus *Nothosaurus*

A total of five valid species are currently recognized in the genus *Nothosaurus,* some of which demonstrate a trendlike development of cranial characteristics as discussed above in the comparison of *Nothosaurus marchicus* and *N. mirabilis.* The notion of an ancestor-descendant relationship between the latter two species not only hinges on the completeness of the fossil record and the biostratigraphic control over the fossils, but also on a critical evalution of sister-group relationships between the different species. *Nothosaurus* is a morphologically rather uniform taxon, but the critical revision of its species allows the definition of at least a few characters potentially useful for cladistic analysis. Initial character polarization is based on outgroup comparison based on the sauropterygian phylogeny proposed by Rieppel (1994a,b), using *Cymatosaurus, Simosaurus,* and pachypleurosaurs as successive outgroups of the Nothosauridae.

1. Rostrum relatively short and broad (0) or long and slender (1).
2. Length-to-width ratio of the mandibular symphysis 0.7–1 (0), 1–1.3 (1), or 1.5–1.7 (2) (coded as unordered).
3. Four (0) or five (1) distinctly enlarged fangs in premaxilla. (The genotypical species *Cymatosaurus fridericianus* Fritsch, 1894, shows four premaxillary fangs; *Simosaurus* shows four teeth plus one minute tooth on each premaxilla [Rieppel, 1994a]).
4. Nasals broad and leaf-shaped (0), or narrow with nearly parallel lateral edges (1).
5. Postfrontal tapering posteriorly (0), or broad posteriorly and interdigitating with parietal (1).
6. Postfrontal enters the anteromedial margin of the upper temporal fenestra (0), or remains excluded therefrom (1). Because of continuous variation in this character, *Nothosaurus marchicus* is coded polymorphic for that character.
7. Postorbital forming part (0) or all (1) of the anterior margin of the upper temporal fenestra. Because of continuous variation in this character, *Nothosaurus marchicus* is coded polymorphic for that character.
8. Anterior corner of upper temporal fenestra broad (0), or constricted by a distinct lateral convexity of the parietal (1).
9. Longitudinal diameter of upper temporal fenestra 2–3 (0) or 3–4 (1) times the longitudinal diameter of orbit.
10. Frontoparietal suture at level of anterior margin of upper temporal fenestra (0), or shifted to a distinctly more posterior postion (1).
11. Pineal foramen at some distance from the posterior margin of skull table (0), or shifted to a position immediately in front of the posterior margin of parietal skull table (1) (see Rieppel & Wild, 1994, Figs. 5A,B).
12. Maxillary tooth row extending to a level between first and second third of the upper temporal fenestra (0), or extending to a level below the midpoint of the upper temporal fenestra (1).

A phylogenetic analysis using parsimony (PAUP, version 3.1.1: Swofford & Begle, 1993) shows characters 2 and 12 to be uninformative among the five species under analysis. The degree of posterior extension of the maxillary tooth row is autapomorphic for *Nothosaurus mirabilis,* and the length-to-width ratio of the mandibular symphysis remains uninformative because the lower jaw is not known in *Nothosaurus edingerae* and *Nothosaurus juvenilis.* Using the remaining characters in an exhaustive search rooted on an all-0-ancestor generated a single most parsimonious tree (Fig. 65), with a tree length of 15 steps, a consistency index of 0.867, and a rescaled consistency index of 0.674.

Nothosaurus marchicus is shown to be the sister-taxon of all other nothosaur species, which all share the relatively narrow nasals with nearly

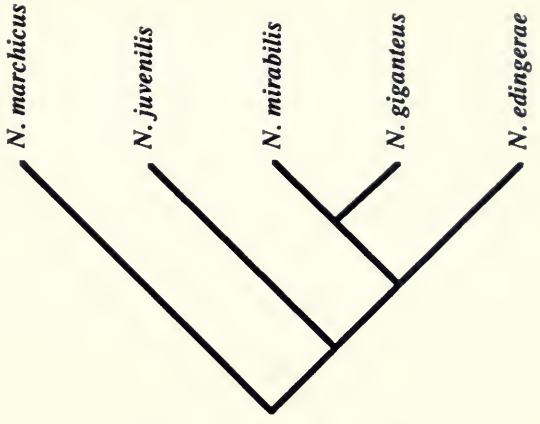


FIG. 65. Phylogenetic relationships of the species of *Nothosaurus*, based on 10 informative characters. Tree length = 15, consistency index = 0.867, rescaled consistency index = 0.674. See text for further discussion.

parallel lateral margins (4). *Nothosaurus juvenilis* is the sister-taxon of *Nothosaurus edingerae, giganteus,* and *mirabilis,* in all of which the postorbital forms the entire anterior margin of the upper temporal fenestra (7). *Nothosaurus edingerae* finally is the sister-taxon to *Nothosaurus mirabilis* and *giganteus.* The latter two species are united by a postfrontal that is broad posteriorly and interdigitates with the parietal (5), constriction of the anterior corner of the upper temporal fenestra (8), the relative size of the upper temporal fenestra (9), the posterior shift of the fronto-parietal suture (10), and the posterior shift of the pineal foramen (11) (DELTRAN character optimization).

There is an interesting correlation of the cladogram with the stratigraphic distribution of the species of *Nothosaurus* (Fig. 66). *Nothosaurus marchicus,* which is at the base of the cladogram, is also the first diagnostic species of *Nothosaurus* occurring in the Germanic Triassic (upper lower Muschelkalk of the eastern Germanic Basin). This is not taking into account the fragmentary material from the lowermost Muschelkalk of Gogolin, Upper Silesia, that may be referable to *Nothosaurus marchicus*; nor is the undescribed material from the lowermost Muschelkalk of Winterswijk (Oosterink, 1986; Oosterink and Diepenbroek, 1990), which may well represent a different taxon, included in this analysis. *Nothosaurus juvenilis* is the sister-taxon of all remaining species of *Nothosaurus,* and its first (and only known) occurrence is in the lower upper Muschelkalk (mo_1, Anisian) of Wiesloch near Heidelberg. The lower upper Muschelkalk (mo_1) is also the time of the first occurrence of the two sister-species *Nothosaurus giganteus* and *Nothosaurus mirabilis,* while *Nothosaurus marchicus* disappears (unless the species persists into mo_2 at Bad Sulza, a question that can only be answered by a better stratigraphic control over the occurrence of *Nothosaurus* at this locality). *Nothosaurus edingerae* is the sister-taxon of *Nothosaurus giganteus* plus *Nothosaurus mirabilis,* and it occurs in the middle Keuper (Gipskeuper), i.e., after all other nothosaurs have already disappeared from the Germanic Triassic. In fact, it represents the geologically youngest nothosaur species known (Rieppel & Wild, 1994).

The systematic revision of the genus *Nothosaurus* indicates an interesting differentiation of the five recognized species in terms of overall size. The relatively small *Nothosaurus marchicus* seems to have coexisted with a larger species of as yet unknown affinities in the upper lower and lower middle Muschelkalk (perhaps *Nothosaurus mirabilis*?), but it was replaced during the lower upper Muschelkalk (mo_1) by three species of different absolute size: *Nothosaurus juvenilis* (smaller than *Nothosaurus marchicus*), *Nothosaurus mirabilis* (of intermediate size), and *Nothosaurus giganteus* (of large size). Segregation of coexisting species into different size classes (presumably with different prey preferences) is a common phenomenon (see Rieppel, 1990, for a review) and has previously been noted for actinopterygian fishes of the genus *Saurichthys* in the Grenzbitumenzone of Monte San Giorgio (Rieppel, 1992). Testing the biological significance of trophic segregation of coexisting *Nothosaurus* species would require a quantitative analysis of the occurrence of the different species. This may be complicated by taphonomic bias. The great bulk of nothosaur material consists of isolated postcranial remains, which are hard to identify except for the diagnostic dorsal vertebrae of *Nothosaurus mirabilis,* and very large specimens referable to *Nothosaurus giganteus.* Increasing size likewise enhances the chances of fossilization. *Nothosaurus juvenilis* is known from a single skull, and the equally small *Nothosaurus edingerae* is known from a total of two skulls. A total of 21 skulls or skull fragments of *Nothosaurus mirabilis* have been identified in public repositories (with an additional 2 or more in private collections), as compared to 17 skulls or skull fragments of *Nothosaurus giganteus.* As would have to be predicted on theoretical

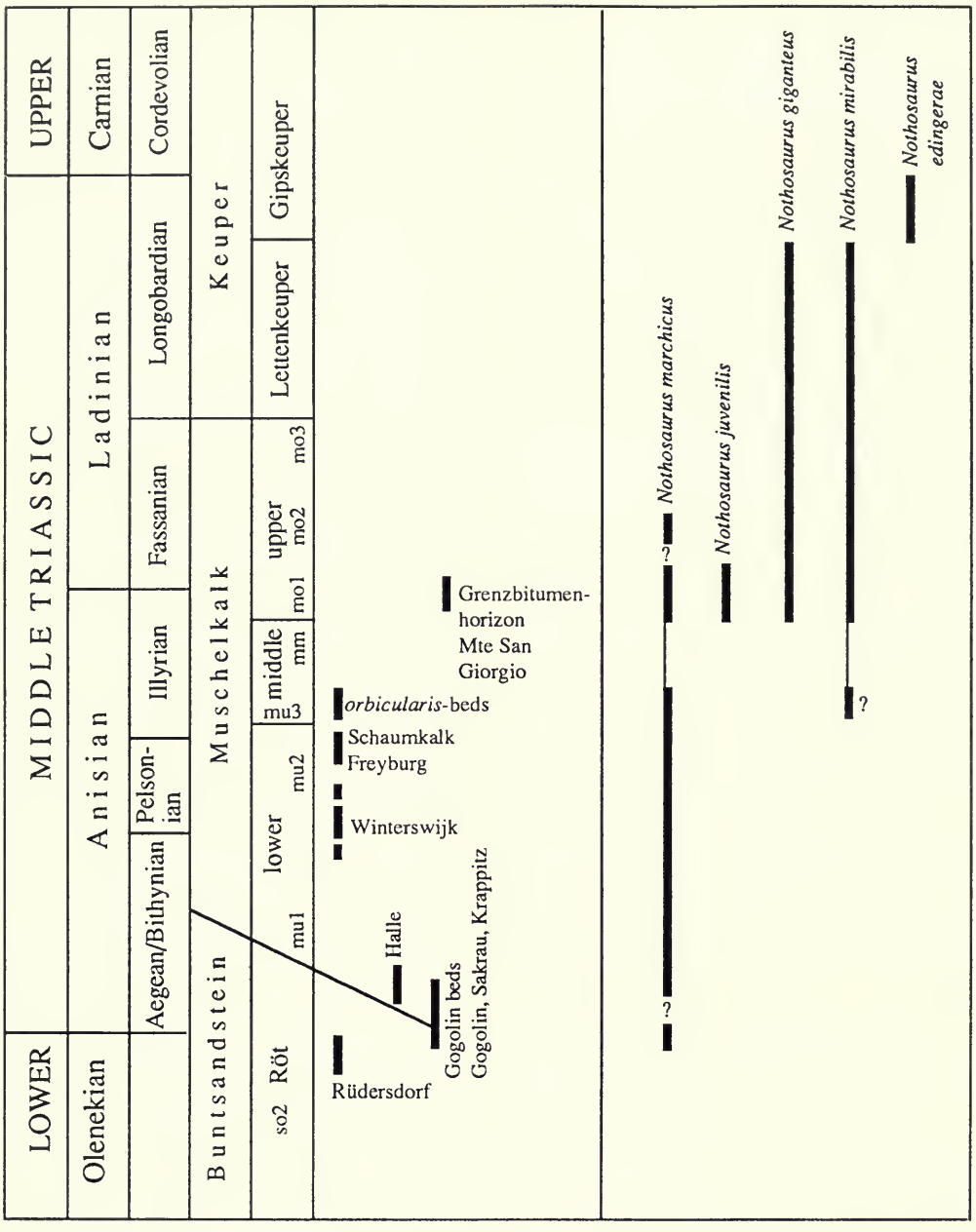


FIG. 66. Stratigraphy of the Middle Triassic in the Germanic basin and the temporal distribution of the species of *Nothosaurus*.

grounds, this indicates that the intermediate species *Nothosaurus mirabilis* is more frequent than the large species *Nothosaurus giganteus* (a conclusion supported by a cursory survey of postcranial remains deposited in public repositories). Yet as the top marine carnivore tetrapod of its time, *Nothosaurus giganteus* is still surprisingly frequent. The apparent abundance of the latter species as compared to *Nothosaurus mirabilis* may be a taphonomic artifact, enhanced by its larger size and hence greater potential for fossilization. In this context it is also interesting to

note an apparent restriction of *Nothosaurus giganteus* to a few fossil sites, most notably the areas around Bayreuth and Crailsheim, as compared to the wider distribution of *Nothosaurus mirabilis* across sites throughout the Muschelkalk Basin. Clearly, the paleobiology of the genus *Nothosaurus* warrants a more detailed numerical analysis of the distribution of the different species throughout the Muschelkalk and their relation to as yet undescribed nothosaur remains from the Alpine Triassic (Bürgin et al., 1991; Furrer et al., 1992).

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