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Nothosaurus edingerae SCHULTZE, 1970: Diagnosis of the Species and Comments on its Stratigraphical Occurrence

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With 5 Figures

Summary

A new specimen of *Nothosaurus edingerae* SCHULTZE, 1970, allows the diagnosis of the species on the basis of homology (synapomorphy) within the genus *Nothosaurus*, and therewith a first step in the taxonomic revision of this group of marine Triassic reptiles. The new specimen comes from the upper Gipskeuper and therewith represents the most completely preserved skull in the geologically youngest specimens of its genus.

Zusammenfassung

Ein Neufund von *Nothosaurus edingerae* SCHULTZE, 1970, erlaubt die Diagnose der Art auf der Basis von Homologie (Synapomorphie) innerhalb der Gattung *Nothosaurus*, und somit einen ersten Schritt in der taxonomischen Revision dieser triassischen Gruppe mariner Reptilien. Zugleich stellt das hier beschriebene Fossil aus dem oberen Gipskeuper den besterhaltenen Schädel unter den geologisch jüngsten Vertretern der Gattung dar.

1. Introduction

The systematics of sauropterygian reptiles (KUHN-SCHNYDER, 1967; CARROLL, 1981; SCHMIDT, 1987; SUES, 1987; RIEPPEL, 1989; TSCHANZ, 1989; STORRS, 1990) in general, and of the genus *Nothosaurus* in particular (KUHN-SCHNYDER, 1966; SCHULTZE, 1970), have remained a controversial issue to the present day. Part of the problem derives from the nature of the data and the methods used in their analysis (STORRS, 1990; RIEPPEL, 1993); another problem relates to the proper definition, or diagnosis, of the terminal taxa (species) and the genera which contain them, particularly with respect to the genus *Nothosaurus*. First erected by MÜNSTER (1834), the genus was originally based on remains of a postcranial skeleton named *Nothosaurus mirabilis* (MÜNSTER, 1834), associated only with the anterior part of a lower jaw exhibiting the characteristically striated surface of the curved teeth. As a consequence of the fragmentary material originally used to diagnose the genus and its type species,

the association of skull material to this species name (KUHN-SCHNYDER, 1966), as well as the diagnosis of the genus *Nothosaurus*, continue to be problematical. An inordinate number of species of *Nothosaurus* have been described (reviewed by EDINGER, 1921, and SCHULTZE, 1970), but the validity of these species and their generic association as judged by the relation of homology (synapomorphy) remains largely unknown (STORRS, 1990). TSCHANZ (1989) provided a first step towards a cladistic definition of the genus *Nothosaurus*, but his characters remain few and problematical: the relation of the jugal bone to the orbit remains unknown in a number of genera of nothosauriform (sensu STORRS, 1990) sauropterygians (e. g. *Lariosaurus*: O. RIEPPEL, pers. comm., contra TSCHANZ, 1989), and the posterior displacement of the pineal opening is variable among the species currently referred to *Nothosaurus* (see the description of *Nothosaurus edingerae* below), thus leaving the presence of two caniniform maxillary teeth as the only presently known diagnostic feature of the genus.

Further investigations are necessary in order to elucidate sauropterygian interrelationships. This paper is a first contribution towards an improved understanding of the terminal taxa (species) traditionally referred to the genus *Nothosaurus*, without which the diagnosis of this genus, and hence the understanding of its interrelationships to other sauropterygians, must remain obscure. Throughout the text we will use the taxon name *Nothosaurus* with the understanding that the genus is presently poorly defined, and that an improved understanding of terminal taxa may result in a revision of their generic interrelationships. We offer a diagnosis of one terminal taxon (species) of the genus *Nothosaurus, Nothosaurus edingerae* (SCHULTZE, 1970), based on monophyly (syn- or autapomorphy) in the description of a well preserved skull from the upper Gipskeuper (middle Upper Triassic). Nothosaur remains are fairly common in the Lower and Upper Muschelkalk (Middle Triassic), but very few specimens have become known from the Middle Keuper (Gipskeuper), among which the holotype of *Nothosaurus edingerae* (SCHULTZE, 1970), a poorly preserved nothosaur (SCHULTZE & WILCZEWSKI, 1970) as well as remains of *Simosaurus*, both from the lower Gipskeuper (HUENE, 1959). The specimen here described comes from the upper Gipskeuper and therefore is the geologically youngest representative of the specimens traditionally referred to the genus *Nothosaurus*.

2. Provenance, geology and stratigraphy of SMNS 59072

The skull was collected in ?1951 by G. BUCK, a private collector, from Affaltrach, community of Obersulm, during the recultivation of a vineyard on the western slopes of the Löwenstein Mountains. The specimen was presented to the late O. LINCK, Güglingen, who incorporated it in his collection. LINCK arranged for the preparation of the specimen by the late preparator J. AICHINGER at the Paläontological Institute of the University of Zürich, Switzerland. LINCK donated parts of his collection of fossil vertebrates from the Keuper to the Staatliches Museum für Naturkunde in Stuttgart in the years 1973 and 1980. The latter donation contained the skull here described (SMNS 59072).

The stratigraphic provenance of this specimen is indicated in the following table:

Keuper Group
Middle Keuper Subgroup
Gipskeuper Formation (Km1)
Estherienschichten Member
Anatinenbank Bed

The Anatinenbank of the upper Gipskeuper is a Steinmergelbank (LINCK, 1972), a dolomite layer of 20–30 cm thickness which contains a bivalve fauna of high abundance but poor taxonomic diversity (pers. comm. Dr. M. WARTH, Stuttgart, who is revising the mollusc fauna described by LINCK, 1972). Vertebrate remains are rare and consist mainly of isolated skeletal elements of chondrichthyans (mainly dorsal finspines), osteichthyans, metoposaurid amphibians and sauropterygians. The latter are represented by *Simosaurus* (probably *Simosaurus guilielmi* [cf. HUENE, 1959]), and a small species of *Nothosaurus*, represented by the skull here described and identified as *Nothosaurus edingerae*. It is interesting to note that the holotype of *Nothosaurus edingerae* SCHULTZE (1970) comes from a stratigraphic horizon in the Estherienschichten of the Bodenmühle near Bayreuth in Franconia (MÜLLER, 1974) which corresponds to the Anatinenbank in Suebia. *Nothosaurus edingerae* represents the geologically youngest occurrence of the genus *Nothosaurus* in the epicontinental Germanic Basin. Its occurrence documents marine influence in the Anatinenbank and the Estherienschichten.

3. Systematic Paleontology

Sauropterygia OWEN, 1860
Nothosauridae BAUR, 1899

Genus *Nothosaurus* MÜNSTER, 1834

Type species: *Nothosaurus mirabilis* MÜNSTER, 1834

Diagnosis. – At present, the genus remains poorly diagnosed (STORRS, 1990). The jugal bone is excluded from the posterior margin of the orbit; the pineal foramen is usually displaced posteriorly to a position close to the occipital crest of the parietal; the maxilla bears two caniniform teeth (TSCHANZ, 1989).

Fig. 1. The holotype of *Nothosaurus edingerae* SCHULTZE (SMF R-4035).

Nothosaurus edingerae SCHULTZE, 1970

Holotype: Senckenberg-Museum, Frankfurt a. M. (SMF R-4035; Fig. 1), originally described by EDINGER (1922) and re-described by SCHULTZE (1970); Middle Keuper, Bayreuth (associated with *Estheria* [now *Palaeoestheria*: WARTH, 1969] *laxitexta*: A. GROSSMANN, in lit. 10. 6. 1920).

Referred specimen: Staatliches Museum für Naturkunde in Stuttgart (SMNS 59072; Fig. 2); upper Gipskeuper (Estherienschichten, Anatinenbank), Affaltrach.

Diagnosis. – Small (adult) overall size, posterior (nasal) processes of the premaxillae reach to a level well behind the posterior margin of the external nares, upper temporal fossae 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.

Morphological Description of SMNS 59072

The specimen SMNS 59072 consists of a dorsoventrally compressed skull of 129 mm total length (as preserved), exposed in dorsal and ventral view (Fig. 2). The small size of the specimen matches *Nothosaurus juvenilis* (EDINGER, 1921) and *Nothosaurus edingerae* (SCHULTZE, 1970). Extensive co-ossification of cranial elements not only renders the morphological description of the specimen difficult, but also testifies to its status as an adult. The same observation holds for the holotype of *Nothosaurus edingerae*. Other characters separating the specimen from *Nothosaurus juvenilis* will be mentioned in the discussion following the morphological description.

Dorsal view (Fig. 3). – The tip of the snout is missing, but as preserved, the premaxillae are elongate as in *Nothosaurus*. However, relative rostrum length cannot be indicated for the species. There is no distinct constriction of the snout in front of the orbits, at the level of the anterior margins of the external nares, as is otherwise typical for representatives of the genus *Nothosaurus* (including *juvenilis* and *edingerae*: SCHULTZE, 1970: 213), but the absence of this feature appears to be correlated with the dorsoventral flattening of the skull.

The area between the external nares and the orbitae is very difficult to interprete because of extensive breakage as well as co-ossification of the elements, but a number of observations can be ascertained. The maxilla does not form the entire lateral margin of the external naris, but rather meets the premaxilla at the anterior 1/3 of the lateral margin. This is in contrast to other skulls of *Nothosaurus* (including *juvenilis*). In the holotype of *Nothosaurus edingerae*, the premaxilla meets the maxilla in the anterolateral edge of the external naris.

The premaxillae form an elongate and slender posterior (nasal) process, entering deeply between the nasal bones and extending to a level well beyond the posterior margin of the external nares. This character, otherwise unknown in skulls referred to the genus *Nothosaurus*, is also observed in the holotype of *Nothosaurus edingerae*. Due to breakage it remains unknown, however, whether the premaxillae meet the frontal bone in SMNS 59072, in which case they would completely separate the nasals from one another along the dorsal midline of the snout. In the holotype of *Nothosaurus edingerae*, the relations of the premaxillae to the nasal and frontal bones are again obscured by partial fusion of individual elements, but surface ornamentation of the bone indicates that the posterior processes of the maxillae may, indeed, separate the nasals from one another as they reach to frontal.

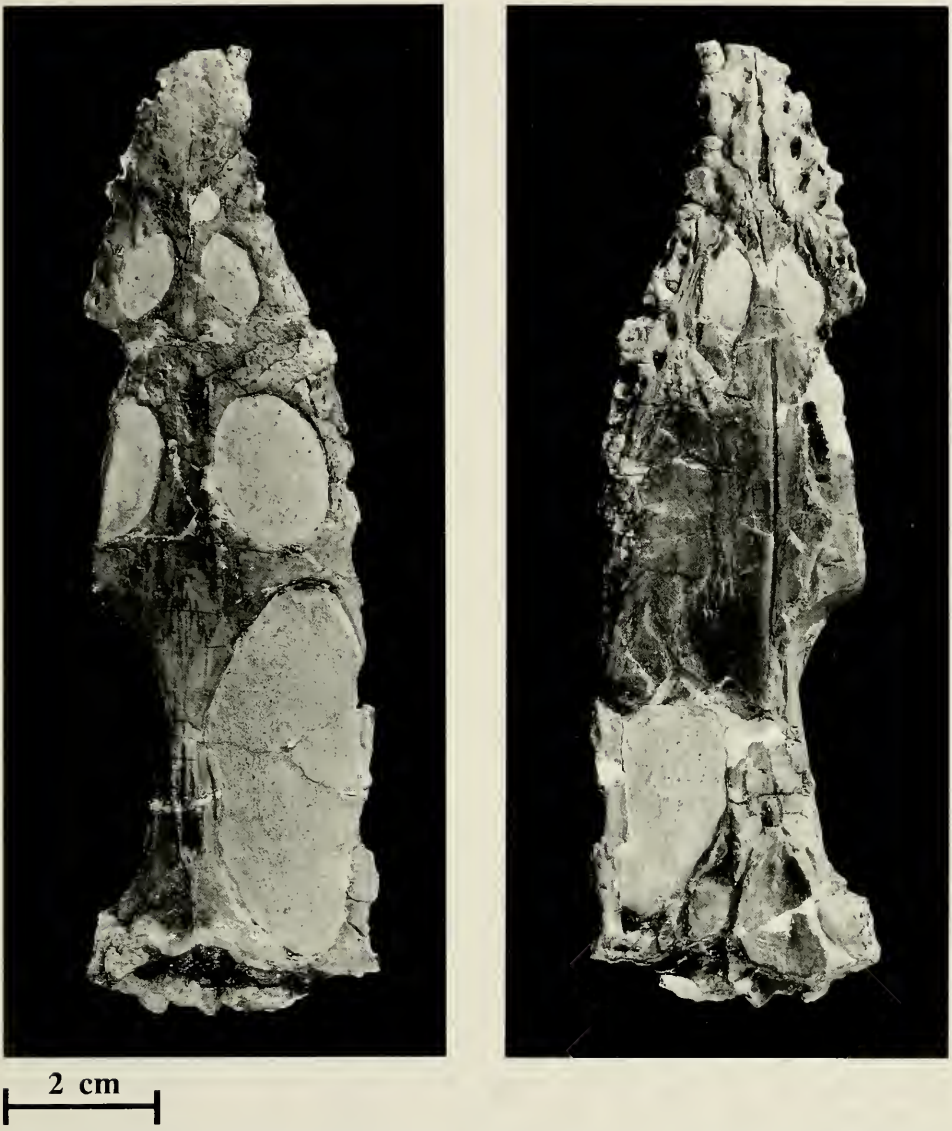

Fig. 2. The skull of *Nothosaurus edingerae* (SMNS 59072) in dorsal (left) and ventral (right) views.

The nasal bones form most of the medial margins of the external nares, although they do not reach up to the level of the latter's anterior margins. It seems that the nasal bones also form most of the posterior margins of the external nares, although breakage makes it difficult to ascertain whether the nasals are not restricted to the posteromedial margins of the external nares. The posterior relations of the nasal bones to the prefrontals and the frontal bone remain unknown due to breakage (as is also true of the holotype: SCHULTZE, 1970).

The prefrontals gain a substantial exposure on the dorsal aspect of the facial skull anterodorsomedial to the orbits, much as in representative of the genus *Nothosaurus*

from the Upper Muschelkalk and in *Nothosaurus juvenilis* (SCHULTZE, 1970). The character remains unknown in the holotype of *Nothosaurus edingerae* (SCHULTZE, 1970), and the anterior relations of the prefrontals remain obscure in SMNS 59072. However, considerable variation may affect the superficial exposure of the prefrontal (SCHULTZE, 1970, and O. RIEPPEL, personal observation).

The prefrontal and postfrontal bones remain widely separated along the dorsal margin of the orbit, most of which is formed by the frontal bone. The shape of the postfrontal seen in SMNS 59072 is very different from the broad and plate-like elements observed in *Nothosaurus juvenilis* (the postfrontal is poorly preserved in the type specimen of *Nothosaurus edingerae*: SCHULTZE, 1970). In SMNS 59072 the postfrontal broadly enters the posterodorsal margin of the orbit, but more posteriorly the bone is reduced to a narrow posterior process situated between the parietal and the postorbital and presumably entering the anteromedial margin of the upper temporal fossa. A participation of the postfrontal in the formation of the anteromedial margin of the upper temporal fossa can be ascertained on the left side of the skull of the holotype of *Nothosaurus edingerae* (SCHULTZE, 1970).

The relations of the postorbital in SMNS 59072 are somewhat obscured by breakage, but the bone appears to form most of the posterior and posteroventral margin of the orbit. The element defines the anterior part of the upper temporal fossa which appears rather smoothly curved (as in *Nothosaurus juvenilis*: SCHULTZE, 1970, Fig. 13), rather than angulated (as in the holotype of *Nothosaurus edingerae*: SCHULTZE, 1970, Fig. 14). The anterior corner of the upper temporal fossa is distinctly constricted in the Upper Muschelkalk species of *Nothosaurus* (SCHULTZE, 1970, Figs. 9–12), but not in the species from the Lower Muschelkalk (SCHULTZE, 1970, Figs. 6–8) nor in SMNS 59072.

The fronto-parietal suture is deeply interdigitating in SMNS 59072, indicating a broad overlap of the two bones. An important feature of this small skull is the relatively anterior position of the pineal foramen, and the development of a distinct sagittal crest behind it. The elongated pineal foramen (5.1 mm long) lies in a deep trough at approximately two thirds of the length of the parietal bone (the distance between the posterior margin of the pineal foramen and the occipital crest of the parietal is 13.5 mm). Behind the pineal foramen, the last third of the parietal bone is raised into a distinct sagittal crest which posteriorly merges into the transversely orientated occipital crest of the parietal. The presence of a sagittal crest behind the pineal foramen is a synapomorphy which SMNS 59072 shares with the holotype of *Nothosaurus edingerae* (SCHULTZE, 1970; longitudinal diameter of pineal foramen: 3.5 mm; distance between the posterior margin of the pineal foramen and the occipital crest of the parietal: 10.5 mm). In some specimens of *Nothosaurus* from the Lower Muschelkalk, the pineal foramen lies in a relatively more anterior position than in nothosaurs from the Upper Muschelkalk (*Nothosaurus mirabilis*), but none of these specimens have been reported to show a sagittal crest of the parietal (SCHRÖDER, 1914; SCHULTZE, 1970). *Micronothosaurus* (HAAS, 1963) shows a pineal foramen in a very forward position, but it lacks a sagittal crest and probably is referable to *Cymatosaurus* (SCHULTZE, 1970).

The (right) upper temporal arch is only partially preserved in SMNS 59072. The holotype of *Nothosaurus edingerae* shows a well preserved left upper temporal arch, with the postorbital and squamosal meeting in its middle portion. The posterior part of the squamosal is distinctly broadened, and carries a ventrally projecting longitu-

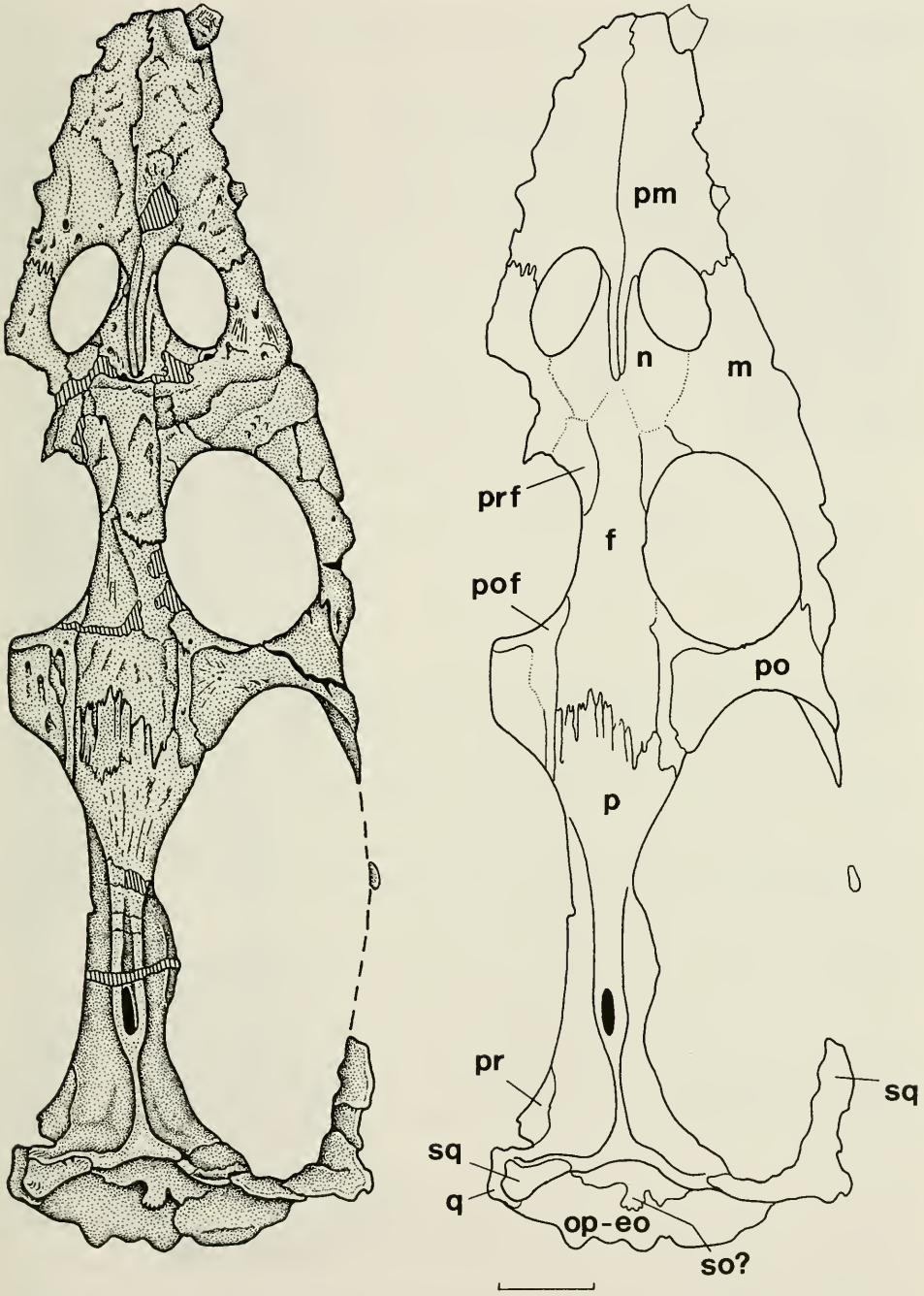

Fig. 3. The skull of *Nothosaurus edingerae* (SMNS 59072) in dorsal view. The scale bar equals 10 mm. Abbreviations: f = frontal; m = maxilla; n = nasal; op-eo = opisthotic-exoccipital; p = parietal; pm = premaxilla; po = postorbital; pof = postfrontal; pr – prootic; prf = prefrontal; q = quadrate; so = supraoccipital; sq = squamosal.

dinal crest for muscle attachment. A similar structure is observed on the lower surface of the posterior extremity of the right squamosal in SMNS 59072.

Occipital view. – The occiput is badly crushed and poorly exposed in SMNS 59072. The parietal shows an occipital flange which seems to be co-ossified with the supraoccipital. A small posttemporal fenestra can be identified on the left side of the occiput, situated between the parietal, supraoccipital and opisthotic-exoccipital. The occipital exposure of the squamosal cannot be delineated. SCHULTZE (1970) described the well preserved although dorsoventrally compressed occiput of the holotype of *Nothosaurus edingerae*. The most conspicuous feature is the large size of the basioccipital tubers, whose transverse diameter (7 mm) is slightly larger than the transverse diameter of the occipital condyle (6.7 mm). This is different from *Nothosaurus* cf. *N. mirabilis*, where the basioccipital tubers remain distinctly smaller than the occipital condyle (RIEPPEL, 1994). The basioccipital tubers are not sutured to the pterygoid in the holotype of *Nothosaurus edingerae*, although dorsoventral flattening of the skull obscures the size and shape of the eustachian fenestra.

Ventral view (Fig. 4). – The palate of SMNS 59072 is typically nothosaurian (sensu TSCHANZ, 1989). Four premaxillary tooth positions can be identified, with the anteriormost tooth located at the broken anterior tip of the premaxilla. A total of five premaxillary tooth positions may thus be inferred. The position of two enlarged (caniniform) fangs can be identified in the anterior portion of the maxilla. The premaxilla meets the maxilla at the level of the anterior margin of the internal naris, but as in other representatives of *Nothosaurus*, the premaxilla remains excluded from the anterior margin of the internal naris by a contact of the vomer with the maxilla.

The vomer extends posteriorly beyond the posterior margins of the internal nares, meeting the pterygoids posteriorly and the ectopterygoids posterolaterally. The palatines, located between the maxillae and the pterygoids, form the entire posterior margins of the internal nares and in SMNS 59072 are more or less co-ossified with the pterygoids. Breakage renders it difficult to analyze the anterior relationships of the pterygoids, but it seems that the pterygoids enter between the vomers, the latter thus separating the pterygoids from the palatines at the posteromedial corners of the internal nares. The relations of the bones in the anterior part of the palate of the holotype of *Nothosaurus edingerae* do not differ from SMNS 59072.

The pterygoids extend posteriorly, concealing the basicranium in ventral view, as is typical of sauropterygians in general. Extensive breakage renders a detailed analysis of the posterior exposure of the ventral view difficult, however. The holotype of *Nothosaurus edingerae* shows the extensive lateral flanges on the quadrate ramus of the pterygoid, as is typical for the genus *Nothosaurus* in general (RIEPPEL, 1994).

4. Discussion

Nothosaurus edingerae (SCHULTZE, 1970) and SMNS 59072 differ from other skulls traditionally referred to the genus *Nothosaurus* by the relatively anterior position of the pineal foramen, a character reminiscent of *Cymatosaurus*, another nothosauriform genus with an even further anteriorly placed pineal foramen (SCHULTZE, 1970). However, the prefrontal and postfrontal bones remain widely separated along the dorsal margin of the orbit in SMNS 59072, in contrast to *Cymatosaurus*, in which the prefrontal and postfrontal meet dorsal to the orbit; in addition, *Cymatosaurus*

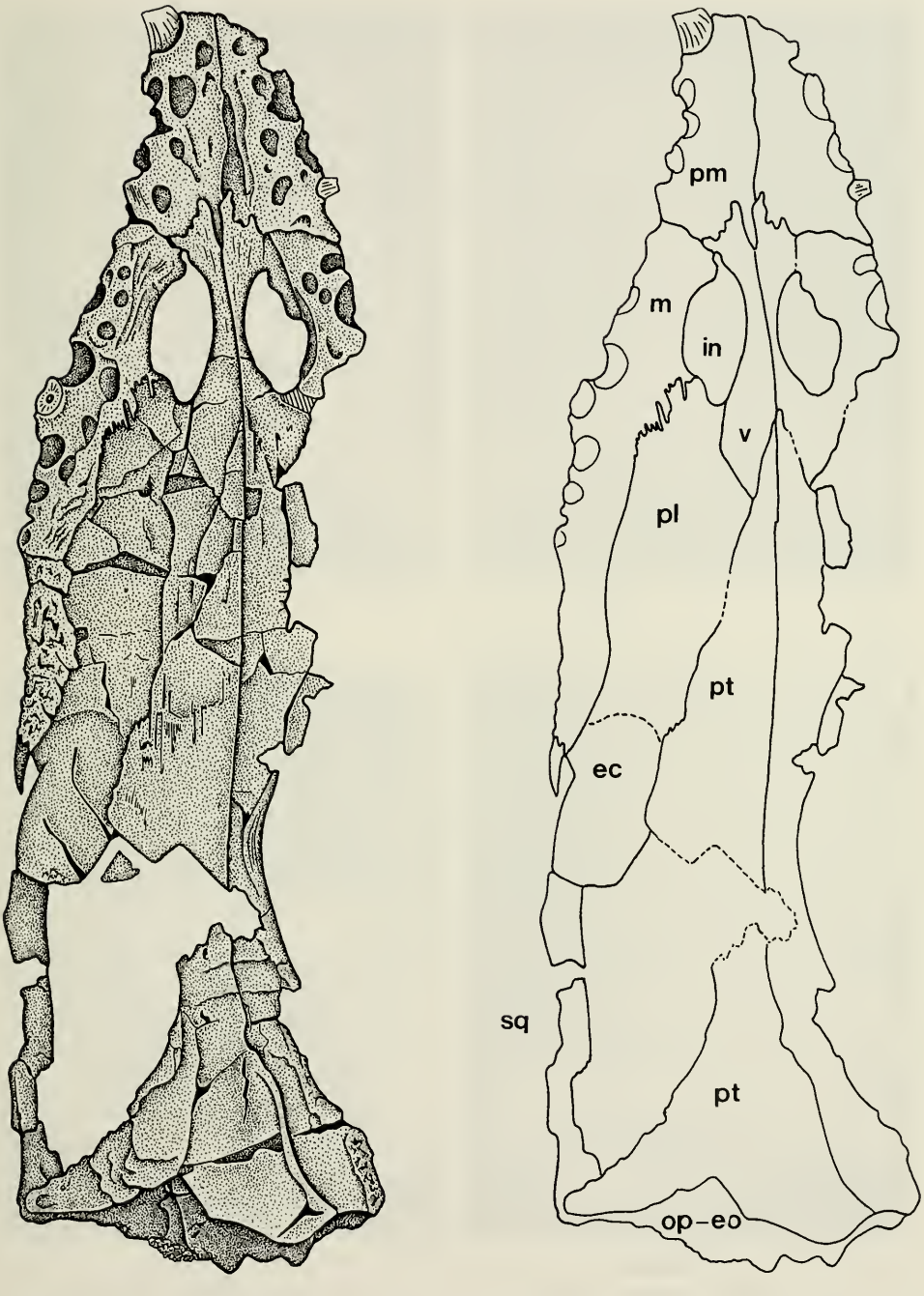

Fig. 4. The skull of *Nothosaurus edingerae* (SMNS 59072) in ventral view. The scale bar equals 10 mm. Abbreviations: ec = ectopterygoid; in = internal naris; m = maxilla; op-eo = opisthotic-exoccipital; pl = palatine; pt = pterygoid; sq = squamosal; v = vomer.

lacks a sagittal crest, and differs from *Nothosaurus edingerae* in overall size, a generally more robust skull and a suite of additional features (O. Rieppel, personal observation).

The fossil here described (SMNS 59072) differs from all other species currently referred to the genus *Nothosaurus* by a weak rostral constriction. The lack of a rostral constriction might be age-related (Tschanz, 1989), but co-ossification of cranial bones indicates adult age for SMNS 59072. Alternatively, the apparent lack of rostral constriction may be related to the extensive dorsoventral crushing of the skull.

SMNS 59072 shares with fossils from the Lower Muschelkalk currently referred to *Nothosaurus* the small overall adult size (SMNS 59072 being smallest), and the position of the pineal foramen at some distance from the occipital crest of the parietal. However, it differs from the Lower Muschelkalk nothosaurs by the broad superficial exposure of the prefrontals (admittedly a variable character) and by the relatively narrow postorbital arch. The distance orbit – external naris divided by the distance orbit – temporal fossa is 2.16 in SMNS 59072 (2.63 in the holotype of *Nothosaurus edingerae*: Schultze, 1970), but around 1.1 to 1.2 in the Lower Muschelkalk species (data taken from Schultze, 1970; see also Schröder, 1914).

SMNS 59072 differs from fossils from the Upper Muschelkalk currently referred to *Nothosaurus* by its small overall adult size, and by the broad and smoothly curved anterior corner of the upper temporal fossa.

Nothosaurus juvenilis was tentatively considered a juvenile specimen of one of the large species of *Nothosaurus* from the Upper Muschelkalk by Edinger (1921). The latter assumption was denied by Schultze (1970: 225). SMNS 59072 differs from *Nothosaurus juvenilis* by distinctly smaller orbits (correlated with co-ossification of cranial elements indicating adult status at a comparably small size), and by the narrow posterior processes of the postfrontals. The longitudinal diameter of the orbit divided by the longitudinal diameter of the external naris is 2.7 in *Nothosaurus juvenilis*, as compared to 1.8 in SMNS 59072 (approximately 1.7 in the type specimen of *Nothosaurus edingerae*: Schultze, 1970).

SMNS 59072 differs from the holotype of *Nothosaurus edingerae* (Schultze, 1970) by the shape of the postfrontal, by the relative width of the postorbital arch (see above) and by the smoothly curved anterior corner of the upper temporal fossa (angulated in the holotype of *Nothosaurus edingerae*). SMNS 59072 shares with the holotype of *Nothosaurus edingerae* (Schultze, 1970) the position of the pineal foramen in a deep trough (less elongated in the holotype of *Nothosaurus edingerae*), its position well in front of the occipital crest of the parietal, and the differentiation of a sagittal crest behind the pineal foramen (Fig. 5). A sagittal crest is unknown in pachypleurosauroids, *Simosaurus*, *Cymatosaurus*, or any other known representative of the Nothosauridae (sensu Rieppel, 1994), and hence is an autapomorphy diagnostic of *Nothosaurus edingerae*. Other derived characters shared by SMNS 59072 and the holotype of *Nothosaurus edingerae* are the extensive posterior (nasal) process of the premaxilla and, possibly, the broadened posterior end of the squamosal bearing a longitudinal ventral crest for the attachment of superficial jaw adductor muscle fibres. It is for these reasons that SMNS 59072 is referred to *Nothosaurus edingerae* (Schultze, 1970), a species diagnosed by additional autapomorphies not preserved in SMNS 59072 such as the large basioccipital tubers.

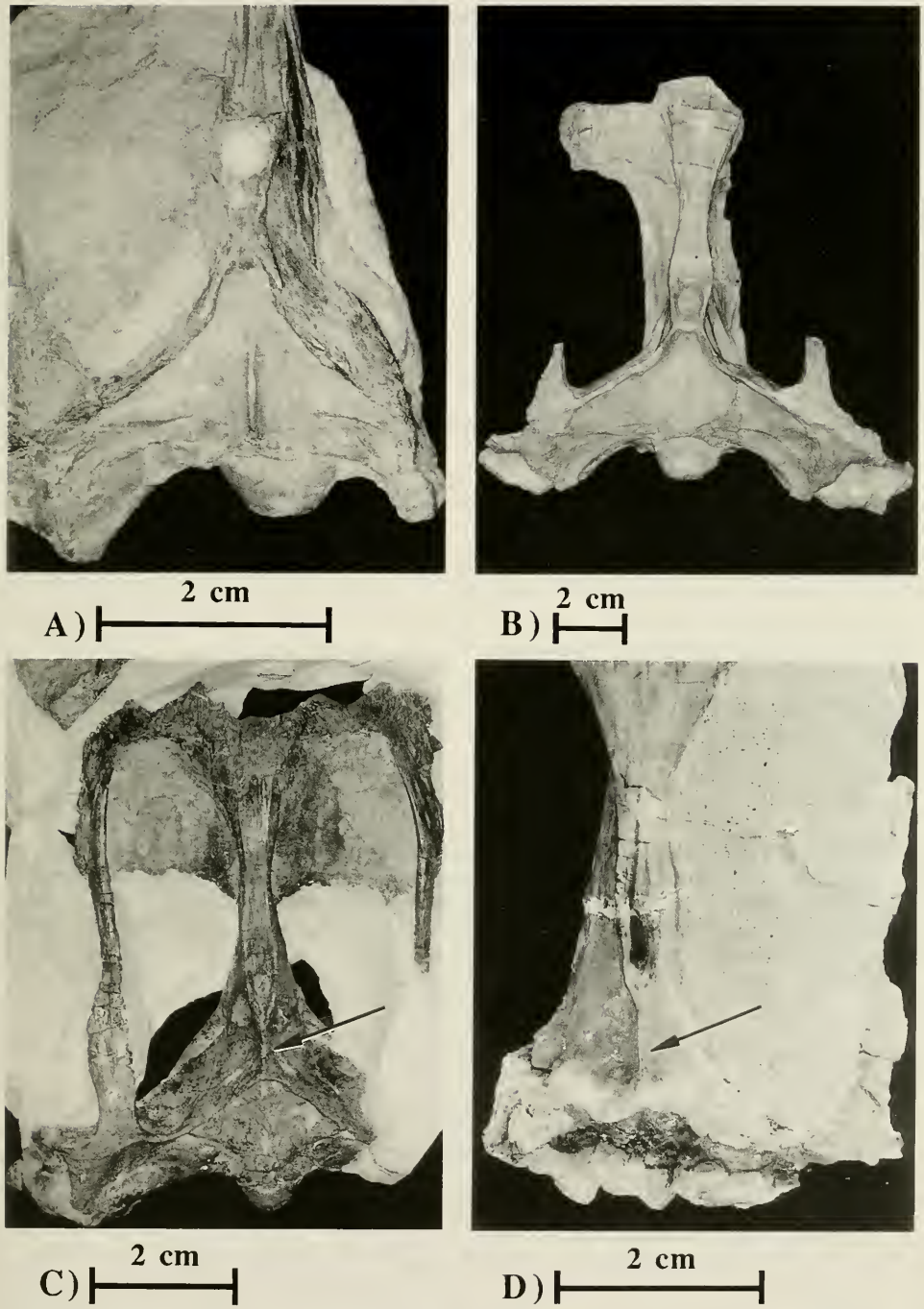

Fig. 5. The posterior skull table in nothosaurs. A) *Nothosaurus* cf. *N. venustus* (SMF R-4537b, Lower Muschelkalk, Oberdorla, Thüringen; B) *Nothosaurus mirabilis* (SMF R-641, Upper Muschelkalk, Bayreuth); C) *Nothosaurus edingerae*, holotype (SMF R-4035); D) *Nothosaurus edingerae* (SMNS 59072). Arrows point to the sagittal crest.

Tab. 1. Measurements of *Nothosaurus edingerae* SMNS 59072 (values for the holotype are those of SCHULTZE, 1970, confirmed by one of us [O. R.]). All measurements in mm (values in brackets are from left side of skull).

	SMNS 59072	Type specimen
Total length of skull (as preserved)	129	± 138
Distance: tip of snout to anterior margin of external naris	24	21 (20.2)
Longitudinal diameter of external naris	11.6 (11.6)	13 (13.3)
Transverse diameter of external naris	7.2 (6.3)	7.5 (7)
Longitudinal diameter of orbit	20.9	± 22.5
Transverse diameter of orbit	16	–
Longitudinal diameter of upper temporal fossa	50.8	(53.5)
Transverse diameter of upper temporal fossa	22	19.6 (17.7)
Distance: external naris (posterior margin) to orbit (anterior margin)	10.6	10
Distance: orbit (posterior margin) to upper temporal fossa (anterior margin)	4.9	4 (3.6)
Lengt of parietal bone	47.5	–
Distance: parietal foramen (posterior margin) to posterior margin of parietal	13.5	–
Relation: longitudinal diameter of external naris to longitudinal diameter of orbit	1:1.8	–
Relation: distance orbit-temporal fossa to distance orbit-external naris	1:2.16	1:2.8

Acknowledgements

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