J. Paleont., 77(4), 2003, pp. 738–744

0022-3360/03/0077-738$03.00

A NEW SPECIES OF THE SAUROPTERYGIAN GENUS *NOTHOSAURUS* FROM THE LOWER MUSCHELKALK OF WINTERSWIJK, THE NETHERLANDS

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ABSTRACT—A new species of the genus *Nothosaurus* from the Lower Muschelkalk of Winterswijk, The Netherlands, shows relatively plesiomorphic features such as a relatively forward position of the pineal foramen. The jugal enters into the ventral margin of the orbit, which would also be regarded as plesiomorphic, were it not that this feature optimizes unequivocally as a reversal and, hence, as a diagnostic (derived) character of the new taxon. The new taxon does not, however, increase the fit of the cladogram for the phylogenetic relationships within *Nothosaurus* to the stratigraphic record of the genus. The basal position of *Nothosaurus juvenilis* remains problematic.

INTRODUCTION

FOSSIL MARINE reptiles have been reported from the Lower Muschelkalk of Winterswijk (lower Anisian, lowermost Middle Triassic) by Hooijer (1959). Additional reptile material was reported by Oosterink (1986), Oosterink and Diepenbroek (1990), Rieppel (1995), and Rieppel and Lin (1995). The fauna is known to include *Placodus* (Oosterink, 1986; Oosterink and Diepenbroek, 1990; Rieppel, 1995), *Anarosaurus* (Hooijer, 1959; Oosterink, 1986; Rieppel and Lin, 1995), *Nothosaurus* (Oosterink, 1986; Oosterink and Diepenbroek, 1990), and *Tanystropheus* (Oosterink, 1986), but almost all of this material remains in private collections. Here we present the formal description of a new species of *Nothosaurus* based on a skull, a partial lower jaw, and a possible hyobranchial element from Winterswijk recently accessioned into the collection of the National Museum of Natural History (Naturalis) in Leiden, The Netherlands (NMNHL St 445530). The only other *Nothosaurus* from Winterswijk deposited in a public repository is a very incompletely preserved skull (NME 480000126) of unknown stratigraphic provenance.

Near the town of Winterswijk, in the mid-eastern part of The Netherlands, the Muschelkalk is exposed in a relatively small area where Triassic limestone has been commercially exploited since 1935. The present skull was found in what is described as layer 9 by Oosterink (1986), which relates to what Harsveldt (1973) described as lower Wellenkalk, located 0.70–0.95 m below a distinct chocolate brown calcareous marl layer and 0.74–0.99 m above Dolomitic Limestone VI (Harsveldt, 1973). This is 2.31–2.56 m above the assumed top of the upper Bunter (Harsveldt, 1973). The location of the top of the upper Bunter has been questioned by Diedrich and Oosterink (2000, see also Diedrich, 2001), who placed the boundary between the Röt and the Muschelkalk 3 m above the conventional placement. In Germany, the boundary between the Röt and the Muschelkalk is placed at the base of the 'Grenzgelbkalk,' which itself is not expressed at the Winterswijk outcrops. The placement of the boundary between the Röt and the Muschelkalk by Diederich and Oosterink (2000) therefore solely depends on facies expression, and is not accepted here because laminated limestone that produces marine fossils would be placed in the Upper Bunter (H. Hagdorn, personal commun., 2001).

Transgression of the Early Muschelkalk sea proceeded from east to west such that the Lower Muschelkalk at Winterswijk is somewhat younger than the localities in the eastern part of the Muschelkalk Basin such as Halle/Saale and Gogolin (Hagdorn, 1991). As such, the new taxon from Winterswijk may more closely approach the temporal distribution of *Nothosaurus marchicus* (Rieppel and Wild, 1996).

Institutional abbreviations.—NMNHL—National Museum for Natural History, Leiden (Naturalis) and NME—Natuur Museum Enschede.

SYSTEMATIC PALAEONTOLOGY

Order SAUROPTERYGIA Owen, 1860
Suborder EOSAUROPTERYGIA Rieppel, 1994a
Family NOTHOSAURIDAE Baur, 1889
Genus NOTHOSAURUS Münster, 1834
NOTHOSAURUS WINTERSWIJKENSIS new species
Figures 1–4

Diagnosis.—A relative small species of *Nothosaurus* (condylobasal length of the skull 126.7 mm) with the fifth premaxillary tooth distinctly smaller than the preceding premaxillary fangs; three small maxillary teeth preceding the paired maxillary fangs; jugal broadly entering the posteroventral margin of the orbit; body of vomer extending backwards for a greater distance than the longitudinal diameter of the internal naris; pineal foramen located in a distinct depression (trough).

Etymology.—Named after the town nearest to the quarry.

Type.—The holotype is NMNHL St 445530: skull (Figs. 1, 3.1) with partial lower jaw (Fig 3.2) and possible hyobranchial element (Fig. 3.3). Its *stratum typicum* is the Lower Wellenkalk layer 9 (Oosterink 1986), (lower Anisian, lowermost Middle Triassic). The skull was found at the 'Winterswijkse Steen- en Kalkgroeve, Winterswijk, Netherlands'; see also the tectonic map and geological profiles of Harsveldt (1973). Gauss-Krüger coordinates: R 2252,6/H 5758,6.

Referred material.—An additional incomplete lower jaw (NMNHL St 445913) described by Hooijer (1959), an almost complete lower jaw (NMNHL St 447170) and an incomplete skull with partial lower jaw (NME 480000126) collected by Henk Kolstee. Additional *Nothosaurus* skulls are known from private collections (Oosterink and Diepenbroek 1990).

Description.—*Nothosaurus winterswijkensis* is represented by a skull of relatively small size, with a short, blunt snout (NMNHL St 445530). The right squamosal, pterygoid and quadrate, as well as a small part of the left squamosal halfway along the temporal fenestra, are largely missing. This results in incomplete upper temporal arches. The following description is based mainly on this skull NMNHL St 445530 as the only other skull in a public collection (NME 480000126) is very incomplete and lacks most of the diagnostic characters except for the three maxillary teeth preceeding the maxillary fangs. Due to its incompleteness we do not illustrate specimen NME 480000126 here. Measurements of both specimens are given in Table 1, however.

Dorsal view of skull (Fig. 2.1).—In general, the skull of *Nothosaurus winterswijkensis* is similar to *Nothosaurus marchicus* and measurements of the skull yield proportional ratios that are

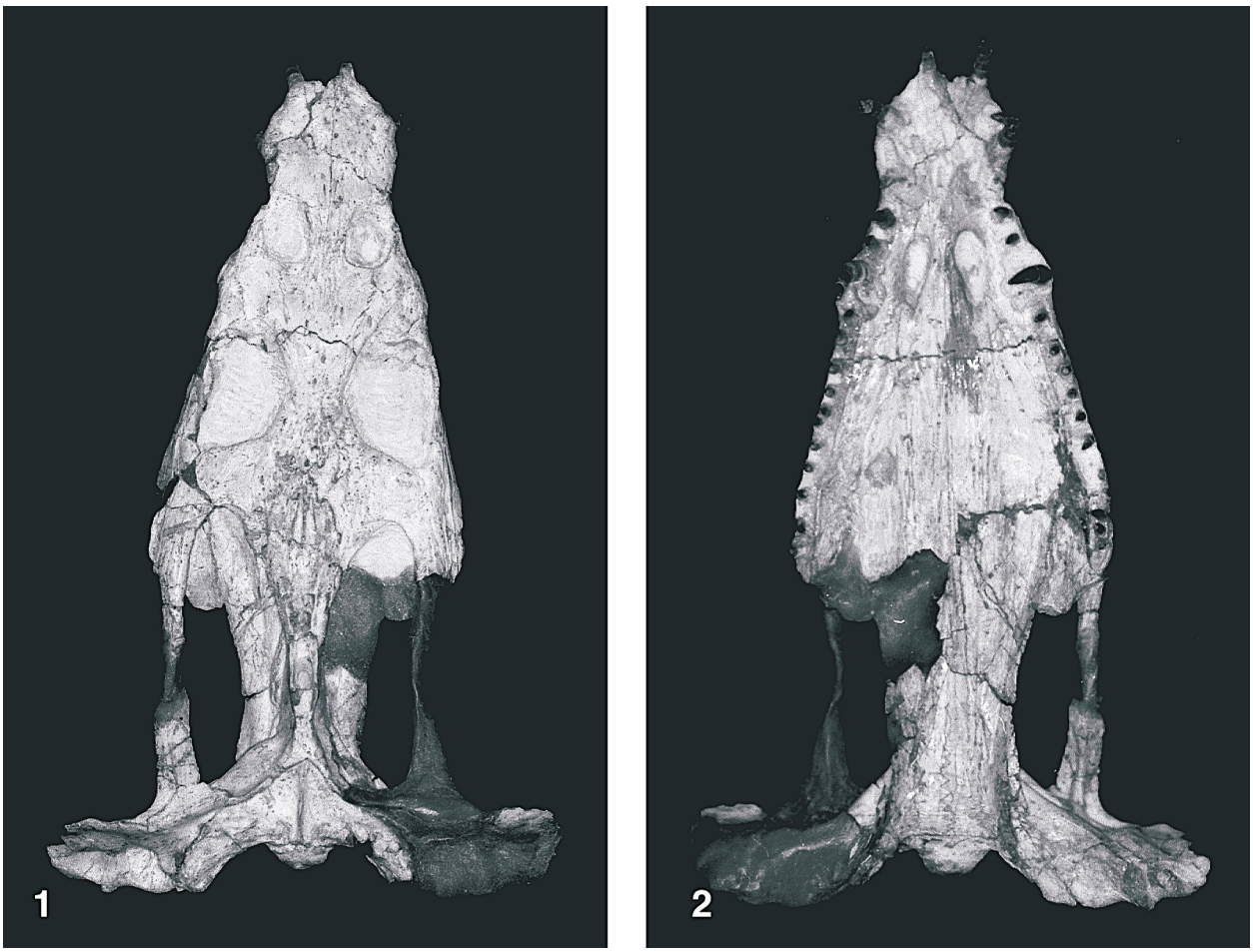

FIGURE *1—Nothosaurus winterswijkensis* n. sp.; holotype, NMNHL-St 445530; skull in *1,* dorsal; and *2,* ventral views. (Both ×0.73).

within the range of variability of *Nothosaurus marchicus* (see Table 2). The rostrum is relatively short and blunt, with rounded lateral edges. It is formed by the paired premaxillae, carrying posterior processes, which extend between the nasals up to a level slightly behind the posterior margin of the external nares. The external nares are kidney-shaped. The nasals form most of the posterior margin of the external nares and carry slender anteromedial processes which line the entire medial margin of the external nares. Posteriorly, the nasals contact both the frontal and the prefrontals at the level of the anterior margin of the orbit.

The suture between premaxilla and maxilla extends from a point located slightly posterior to the anteroventral corner of the external naris in an anterolateral direction, curving around the alveolus of the anteriormost maxillary tooth. The maxilla has a depression with a foramen at its bottom along the lateral margin of the external naris, serving as the exit of a lateral branch of the superior alveolar nerve; a similar foramen is present in most species of *Nothosaurus* (Rieppel and Wild, 1996). Laterally, the maxilla shows a slight but distinct bulge just behind the level of the posterior margin of the external naris, accommodating the roots of the maxillary fangs, located at the level between the external naris and the orbit. Behind the external naris, the maxilla meets the lateral margin of the nasal in a posteromedially trending suture. At the anterior margin of the orbit, the maxilla meets an anteromedial process of the prefrontal, which separates the frontal from the maxilla. Lateral and ventral to the prefrontal, the maxilla defines the anterior margin of the orbit. As in all sauropterygians the lacrimal is absent. In typical *Nothosaurus* the lacrimal foramen is fully enclosed by the maxilla, but the foramen is covered by matrix in the skull from Winterswijk. Below and behind the orbit, the maxilla gradually tapers to a slender bone, carrying the maxillary tooth-row backward a fifth of the length of the longitudinal diameter of the upper temporal fenestra. Dorsolaterally the maxilla meets the jugal, which broadly enters the posterolateral margin of the orbit and thus separates the maxilla from the postorbital.

In *Nothosaurus*, the prefrontal is usually a small element located at the anteromedial corner of the orbit. In the holotype of *Nothosaurus winterswijkensis*, the prefrontal carries a distinct anteromedial process sufficiently large to separate the maxilla from the frontal. A similar anteromedial process of the prefrontal is consistently absent in *Nothosaurus marchicus*, but may occur in *Nothosaurus mirabilis* (Rieppel and Wild, 1996). The frontal itself does not have anterolateral processes that protrude farther rostral than the level of the anterior margin of the orbit. The frontal is unpaired (fused) and enters the dorsal margin of the orbit between prefrontal and postfrontal. The deeply interdigitating fronto-parietal suture bridges the level of the anterior margin of the upper temporal fossa. The relative size of the upper temporal fossa is most closely comparable to that of *Nothosaurus marchicus*: dividing the condylobasal skull length by the longitudinal diameter of the upper temporal fossa yields a ratio of 2.74 for *Nothosaurus winterswijkensis*, and 2.6–3.0 for *Nothosaurus marchicus*.

The postfrontal defines the posteromedial margin of the orbit.

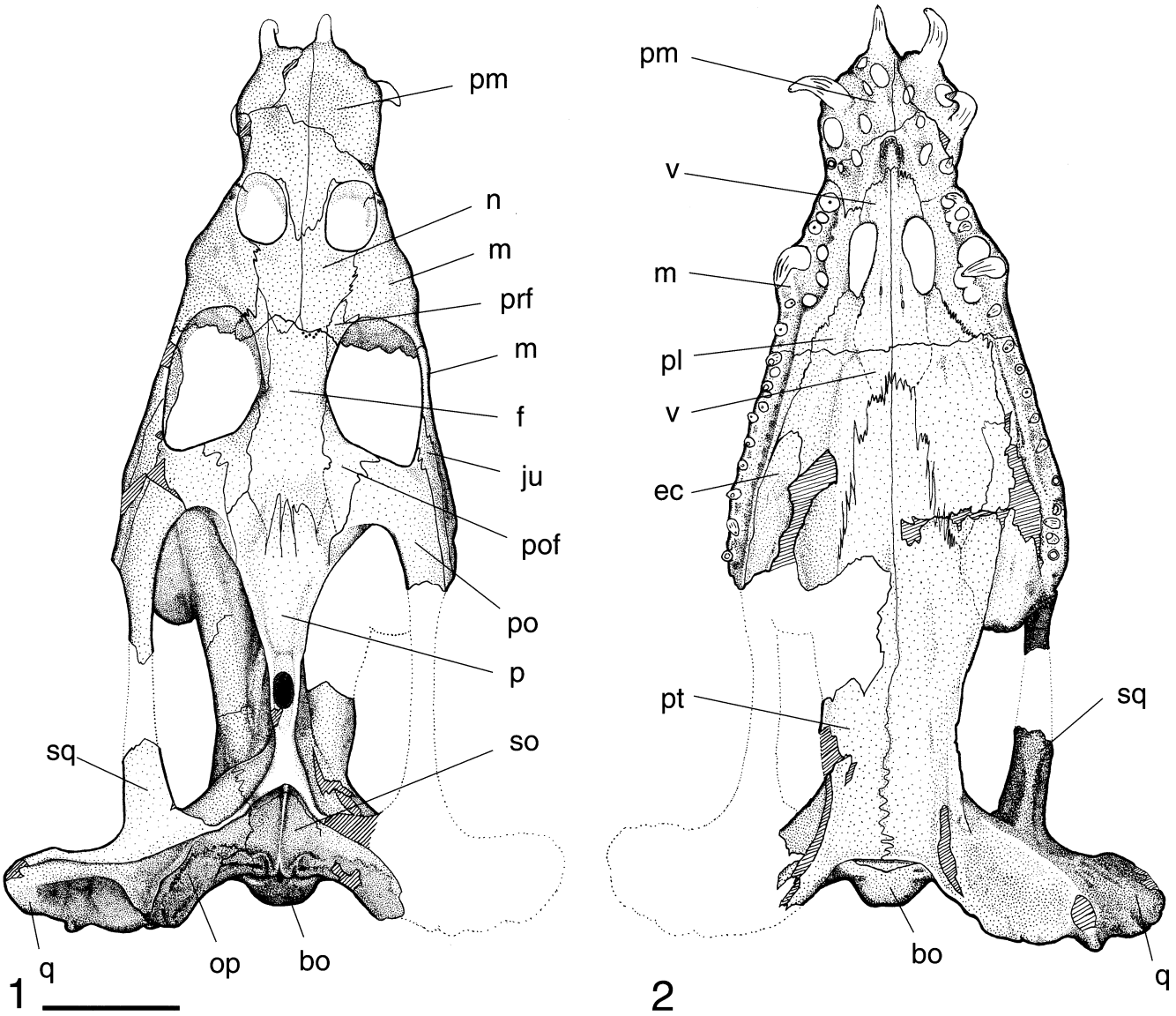

FIGURE 2—The skull of *Nothosaurus winterswijkensis* in *1*, dorsal; and *2*, ventral views. Scale bar represents 20 mm. Abbreviations: bo, basioccipital; ec, ectopterygoid; f, frontal; ju, jugal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, squamosal; v, vomer.

The tapering posterior tip of the postfrontal is excluded from the anteromedial margin of the upper temporal fossa by a relatively broad contact between postorbital and parietal. The left postfrontal shows an angulation of its left margin reminiscent of the distinct V-shaped indentation seen in several skulls of *Nothosaurus marchicus* (Rieppel and Wild, 1996, figs. 32, 36, 39), though not in all (see Rieppel and Wild, 1996, fig. 41). The right postfrontal, however, shows no constriction worth mentioning. The postorbital has a broad medial process that forms almost the entire postorbital arch and thus defines the anterior margin of the upper temporal fossa as well as the posterolateral margin of the orbit. Anteriorly, the postorbital contacts the jugal, and posteriorly the postorbital enters the upper temporal arch. Due to breakage, the relation of the anterior end of the squamosal to the jugal cannot be unequivocally assessed.

The parietal is unpaired (fused). The parietal diverges posteriorly to meet the squamosal at the posterior margin of the upper temporal fossa. Occipital exposure of the parietal is limited, as it meets the anterior margin of the supraoccipital in an interdigitating suture participating in the formation of the anterior part of the occipital crest of the occiput. The squamosal defines most of the posterior margin of the upper temporal fossa. Its anterior extent within the upper temporal arch cannot be unequivocally determined because of breakage. The posterior end of the left upper temporal arch is well preserved, however, and it shows a distinct ventrally projecting ridge formed by the squamosal. Posteriorly, the squamosal gains a broad occipital exposure. It is sutured to the parietal and supraoccipital medially and to the opisthotic posteriorly. Laterally, the squamosal reaches far down along the lateral aspect of the quadrate. At the ventral tip of the squamosal, where the quadratojugal might be expected, a chip of bone is missing, leaving the status of the quadratojugal unknown. However, just below the break, a small piece of bone appears to be enveloped by the squamosal that might represent part of the quadratojugal.

Ventral view of skull (Fig. 2.2).—Each premaxilla carries five

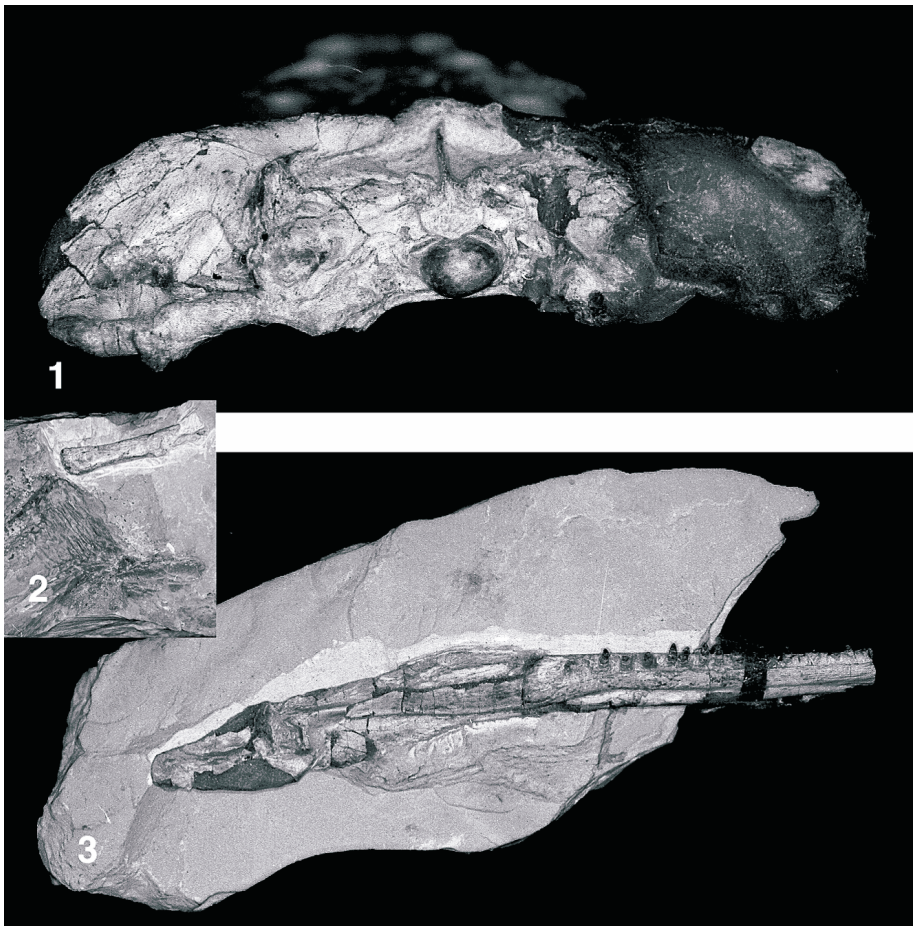

FIGURE 3—*Nothosaurus winterswijkensis* n. sp., holotype, NMNHL-St 445530. *1,* Skull in posterior view (×1.1); *2,* hyobranchial element (×0.75), below the ossification the imprint of the palate of the skull is visible; *3,* partial lower jaw (×0.75).

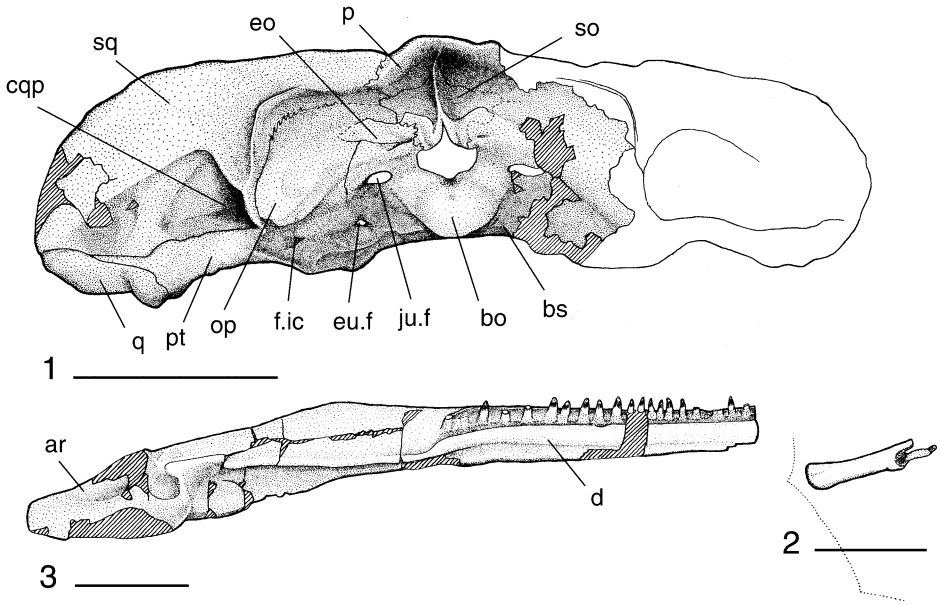

FIGURE 4—*Nothosaurus winterswijkensis* n. sp. *1,* Skull in posterior view; *2,* hyobranchial element, below the ossification the location of the imprint of the skull is marked with a dotted line; *3,* partial lower jaw. Scale bars represent 20 mm. Abbreviations: ar, articular; bo, basoccipital; bs, basisphenoid; cqp, cranio-quadrate passage; d, dentary; eo, exoccipital; eu.f, Eustachian foramen; f.ic, foramen for the internal carotid; ju.f, jugular foramen; op, opisthotic; p, parietal; pt, pterygoid; q, quadrate; so, supraoccipital; sq, squamosal.

TABLE *1*—Measurements for *Nothosaurus winterswijkensis* n.sp.; holotype, NMNHL St 445530 (and, if obtainable, for specimen NME 480000126 in italics, * estimated); all measurements are in mm; values in parentheses are for the right side of the skull.

Tip of the snout to occipital condyle	126.7	
Tip of the snout to posterior margin of supraoccipital	122.8	
Tip of the snout to posterior margin of parietal skull table	113.3	
Tip of the snout to anterior margin of upper temporal fossa	71.8 *73.0**	
Tip of the snout to anterior margin of the orbit	41.8 *43.7*	
Tip of the snout to anterior margin of the pineal foramen	94.8	
Tip of the snout to anterior margin of external naris	22.5 *23.2*	
Tip of the snout to the anterior margin of internal naris	26.3	
Width of skull across postorbital arches	49.2	
Width of skull at anterior margin of orbits	35.0	
Width of skull at roots of maxillary fangs	33.9 *37.0**	
Width of skull at rostral constriction	19.6 *22.4*	
Maximum width of premaxillary rostrum	22.5 *23.2*	
Longitudinal diameter of external naris	10.5 *12.3**	(10.4 *12.8*)
Transverse diameter of external naris	7.4	(7.5 *9.4*)
Longitudinal diameter of orbit	22.8 *21.9**	(22.8 *23.3**)
Transverse diameter of orbit	14.3 *13.7**	(14.7 *14.6**)
Longitudinal diameter of upper temporal fossa	46.3	(−)
Transverse diameter of upper temporal fossa	16.0	(−)
Longitudinal width of the pineal foramen	4.6	
Transverse width of the pineal foramen	2.9	
Longitudinal diameter of internal naris	11.4	(10.8)
Transverse diameter of internal naris	4.4	(4.1)
Distance from posterior margin of external naris to anterior margin of orbit	10.2	(10.3)
Distance from posterior margin of orbit to anterior margin of upper temporal fossa	9.1	(8.8)
Middorsal bridge between external nares	6.2	
Middorsa1 bridge between orbits (minimum width)	8.1 *10.0**	
Middorsal bridge between upper temporal fossae (behind the pineal foramen)	2.9	

tooth positions, comprising four premaxillary fangs, followed by a distinctly smaller premaxillary tooth. Of these, two fangs are preserved in each premaxilla; the left posterior premaxillary tooth is at an early stage of eruption, and the right premaxillary tooth has been broken off. The anteromedial fang in the right premaxilla is the smallest in size, but may not be fully erupted. The other fangs present are about equal in size, and are located in positions right 3, left 2, and left 4. The premaxilla remains excluded from the internal naris by a contact of the maxilla with the vomer at the anterior margin of the latter. The maxilla forms the lateral margin of the internal naris and extends backward lateral to the palatine and ectopterygoid. The suture between the maxilla and the premaxilla is clearly identifiable on the right side of the skull, and indicates that three tooth positions (two teeth preserved in situ) precede the paired maxillary fangs. One fang each is preserved in situ on each maxilla, but the presence of paired enlarged alveoli, as well as the corresponding replacement pits, unequivocally indicate the presence of paired maxillary fangs. Behind the paired maxillary fangs, the maxillary teeth are slightly smaller in size than those in front of the maxillary fangs. The count of preserved maxillary teeth behind the fangs is 11 on both sides, but we estimate the presence of between 19 and 21 tooth positions based on the number of exposed alveoli. This brings the total maxillary tooth count to 3+2+(19–21) (see Table 3 for a comparison with other species of *Nothosaurus*).

The paired vomers are elongate elements, which separate the internal nares from one another. The contours of the internal nares are elongated ovals. The tapering anterior end of the vomer enters between the premaxillae, forming a loose contact that results in slit-like fontanelles on either side. Behind the internal nares, the broad body of the vomer extends between the pterygoids for a distance that exceeds the longitudinal diameter of the internal nares. The suture between the posterior part of the vomer and the palatine is somewhat indistinct, but the deeply interdigitating suture between the broad posterior end of the vomer and the anterior end of the pterygoid is clearly identifiable.

The palatine forms the posterior margin of the internal naris with a shallow choanal groove that is not, however, as distinct as the one observed in *Nothosaurus juvenilis* (Rieppel, 1994b). Posteriorly the palatine is embraced by the maxilla, ectopterygoid, and pterygoid. The anterior end of the ectopterygoid is clearly identifiable on the left side of the skull and indicates that the ectopterygoid extends anteriorly along half the length of the palatine. The suture between the pterygoid and ectopterygoid is difficult to ascertain because of breakage. The pterygoid seems to form a weakly developed transverse process that, together with

TABLE *2*—Skull proportion in *Nothosaurus*.

	Nothosaurus								
	giganteus	*juvenilis***	*marchicus*	*winterswijkensis* n.sp.	*mirabilis*	*jagisteus*	*haasi*	*tchernovi*	*edingerae***
snout-external naris / rostral constriction	1.2–1.6	1.55	1.1–1.4	*1.04*–1.15	1.5–2.5	1.98	2.62	2.0	1.3
snout-orbit / snout-external naris	1.6–2.0	1.74	1.8–2.0	1.86–*1.88*	1.5–1.7	1.55	1.5	1.59	1.88
snout-upper temporal fossa / snout-external naris	2.6–3.4	2.74	2.9–3.4	*3.15**–3.19	2.2–2.7	2.41	2.04	2.45	2.88
longitudinal Ø external naris / transverse Ø external naris	juv: 1.3–1.4 ad: 1.7–1.85	1.37	1.0–1.4	*1.33**–1.40	1.6–2.2	1.79	2.59	1.56	1.85

For *N. winterswijkensis* the roman numerals represent specimen NMNHL St 445530, the italics represent specimen NME 480000126, * = estimated, ** = missing tip of snout estimated.

TABLE *3*—Dentition formula in *Nothosaurus*.

	premaxilla	maxilla	
N. winterswijkensis n.sp.	4 + 1	3 + 2	+(19–21)
N. marchicus	5	5 + 2	+23
N. giganteus	4 + 1	4 + 2	+
N. mirabilis	5	(3–4) + 2	+(20–21)
N. haasi	5	3 + 2	+8
N. tchernovi	5	4 + 2	+∼18
N. jagisteus	5	4 + 2	+∼20

Currently known fossils have not enabled determination of the dentition formulae of *N. juvenilis* and *N. edingerae*.

the ectopterygoid, forms a ventrally projecting (ecto)pterygoid flange. The shape of the pterygoid itself corresponds to the characteristic nothosaurian pattern (Riepel and Wild, 1996). At their posterior extremity the pterygoids meet in an interdigitating suture common to all *Nothosaurus* species.

Posterior view of the skull (Fig. 4.1).—The supraoccipital is a more or less horizontally oriented and relatively broad element that is intercalated between parietal and squamosals. A very distinct sagittal crest is born by the supraoccipital and completed anteriorly by the occipital exposure of the parietal. Towards its posterior margin, the supraoccipital carries a distinct lobe-shaped crest, concave posteriorly, which must have served as the insertion of epaxial neck musculature. Posterolaterally, the supraoccipital defines the medial margin of the rudimentary posttemporal fossa, and meets the exoccipital in the dorsolateral corner of the foramen magnum. The posttemporal fenestra is very much reduced on the left side and closed on the right side of the skull. The pedicels of the exoccipitals rest on the dorsolateral aspect of the occipital condyle (basioccipital), but remain separated from one another. The exoccipital defines the lateral margin of the foramen magnum, and in its dorsal part expands laterally, forming the ventral margin of the rudimentary posttemporal fossa (left side of skull). Lateral to the pedicel of the exoccipital and below its dorsolateral expansion is located the large metotic (jugular) foramen. The margins of the opisthotics remain largely indistinct, except for the left side of the skull where the distal contact of the opisthotic with the squamosal is clearly delineated. Lateral to this sutural contact the squamosal carries a distinct, curved (ventromedially concave) crest, which expands dorsomedially from the posterior opening of the cranio-quadrate passage. Just medial to the posterior opening of the cranio-quadrate passage, and below its dorsal sutural contact with the squamosal, the distal end of the opisthotic forms an overhanging lateroventral rim, which medially merges into a somewhat less prominently overhanging ridge that connects to the dorsal margin of the metotic (jugular) foramen. It is conceivable that this overhanging ridge corresponds to the ventral margin of the opisthotic laterally, and is formed by the exoccipital medially.

The distal end of the pterygoid contacts the squamosal dorsally and the quadrate medially. The posterior opening of the cranioquadrate passage is bordered by the squamosal, pterygoid, and quadrate. The left quadrate is well exposed with small parts missing because of breakage. It is unclear how far down the squamosal extends along the lateral and posterior aspects of the quadrate because the sutures remain indistinct (see also the discussion of the quadratojugal above). The 'Eustachian foramen' is open and located ventral to the jugular foramen at the height of the ventral margin of the basioccipital condyle. It delineates the basioccipital tuber, the transverse diameter of which (4.2 mm on the left side) is about half the transverse diameter of the occipital condyle (7.9 mm). The internal carotid foramen is located on the pterygoid lateral to the Eustachian foramen, below the overhanging most distal extension of the opisthotic.

The lateral wall of the braincase is not fully preserved on the left side of the skull, and missing on the right side. A part of the epipterygoid appears to be present on the left side, while the prootics cannot be identified on either side. Preservation is not good enough to allow for the description of structural detail.

Hyobranchial element (Fig. 4.2).—An elongate ossification 23 mm long and 3.5 mm wide at its midpoint was preserved immediately behind the palate. Both ends of the ossification are very slightly expanded, which is most parsimoniously interpreted as an ossified element of the hyobranchial skeleton.

Lower jaw (Fig. 4.3).—A partial left mandibular ramus is associated with the skull. The mandibular symphysis is missing but three other lower jaws from Winterswijk shows the short mandibular symphysis that represents the plesiomorphic condition within *Nothosaurus* [specimen NMNHL St 445913 described in Hooijer, (1959), specimen NMNHL St 447170 and specimen NME 480000126]. Specimen St 445530 allows the identification of approximately 28 post-symphysial tooth positions. (Specimen St 447170 has 30 post-symphysial teeth in situ on the right side and two to five empty tooth positions.) A prominent lateral flange of the surangular served as the site of insertion for the superficial jaw-abductor muscle fibres. The articular surface of the mandibular joint is not well preserved but must have been saddle-shaped to match the biconvex articular surface of the quadrate. The retroarticular process is slender and elongate.

Discussion.—The new species of *Nothosaurus* from Winterswijk may be expected to be of a rather plesiomorphic structure given its provenance from the Lower Muschelkalk. *Nothosaurus* material from the lowermost Muschelkalk at two localities in the eastern part of the Germanic Basin (Gogolin-Beds, Upper Silesia; Schaumkalk Halle/Saale) is unfortunately not diagnostic (Koken, 1893). However, both localities have yielded lower jaws with plesiomorphic proportions of the mandibular symphysis (Rieppel and Wild, 1996), and similar lower jaws are known from Winterswijk (see e.g., Hooijer, 1959, and specimens NMNHL St 447170 and NME 480000126).

The holotype of *Nothosaurus winterswijkensis* (NMNHL St 445530) shows a suite of relatively plesiomorphic characters, such as the relatively short, broad, and rounded rostrum; broad and kidney-shaped external nares; broad and leaf-shaped nasals; proportions of the upper temporal fenestrae relative to the orbits; relatively short posterior extension of the maxillary tooth-row; and pineal foramen in a relatively far forward position. In all of these characters, the skull from Winterswijk most closely resembles *Nothosaurus marchicus* Koken, 1893 from the basal Middle Muschelkalk of central Europe, but in addition to the characters mentioned in the *Diagnosis*, it differs from *Nothosaurus marchicus* by 1) the frontal being separated from the maxilla; 2) the presence of an anteromedial process of the prefrontal; 3) a somewhat more forward position of the pineal foramen (distance from the posterior margin of the pineal foramen to the posterior margin of the parietal skull table larger than two times the longitudinal diameter of the pineal foramen); and 4) the fifth premaxillary tooth being distinctly smaller than the preceding four premaxillary fangs.

Given that the early Anisian Muschelkalk transgression proceeded from east to west, the Lower Muschelkalk in the western part of the basin is relatively younger than the Lower Muschelkalk in the eastern part. This may bring the species from Winterswijk in rather close temporal proximity to *Nothosaurus marchicus*, with which the Winterswijk species shares additional characters such as overall size, a posteriorly tapering postfrontal, the ectopterygoid reaching to about one-half the length of the palatine, and the sometimes incompletely closed contact between the anteriorly tapering vomer and the premaxilla.

However, the *Nothosaurus* material from Winterswijk can be

diagnosed as a separate species on the basis of three maxillary teeth preceding the maxillary fangs instead of five as in *Nothosaurus marchicus* (three maxillary teeth precede the fangs in some *Nothosaurus mirabilis* (Rieppel and Wild, 1996), and in *Nothosaurus haasi* (Rieppel et al., 1999), both species of otherwise distinctly different morphology). The jugal always remains excluded from the orbit in *Nothosaurus marchicus* and all other nothosaurs, with a single exception known from an incomplete skull referred to *Nothosaurus mirabilis* (Rieppel and Wild, 1996). The entry of the jugal into the orbit in the Winterswijk species might be considered a plesiomorphic and, hence, non-diagnostic character. However, recent analyses of the phylogenetic interrelationships among the species of *Nothosaurus* included *Nothosaurus winterswijkensis* as an unnamed taxon, coded for a jugal entering the orbit (Rieppel et al., 1999; Rieppel, 2001). In those analyses, the entry of the jugal into the orbit in *Nothosaurus winterswijkensis* optimized unequivocably as a reversal, and hence as a diagnostic apomorphy for that species (for further details see Rieppel et al., 1999; Rieppel, 2001). A posterior extent of the vomers comparable to that seen in *Nothosaurus winterswijkensis* is not known in any other *Nothosaurus* species.

In addition, *Nothosaurus winterswijkensis* differs from *Nothosaurus marchicus* (and other species of *Nothosaurus*) in several other characters. The posteriormost (fifth) premaxillary tooth may be slightly smaller than the preceding four fangs in *Nothosaurus marchicus*, whereas the fifth premaxillary tooth is distinctly smaller in both skulls of *Nothosaurus winterswijkensis*, a condition otherwise known only in *Nothosaurus giganteus*. In *Nothosaurus winterswijkensis* the prefrontal carries a distinct anteromedial process separating the frontal from the maxilla. A comparable prefrontal process is consistently absent in *Nothosaurus marchicus*, but may variably be present in *Nothosaurus mirabilis* (Rieppel and Wild, 1996). Only *Nothosaurus marchicus* shows a similarly anterior position of the pineal foramen, but this character is variable in the latter species, and the distance between the posterior margin of the pineal foramen and the posterior margin of the skull table never exceeds twice the longitudinal diameter of the pineal foramen as it does in *Nothosaurus winterswijkensis*. Furthermore, the pineal foramen is located in a distinct trough in the parietal in the latter species, which is not observed in *Nothosaurus marchicus*, but which does occur, albeit in a modified condition, in *Nothosaurus edingerae*.

The addition of the new species from Winterswijk to an analysis of the phylogenetic interrelationships within the genus *Nothosaurus* did not increase the continuously weak support for the cladogram, nor did it remove *Nothosaurus juvenilis* (from the basal Upper Muschelkalk) from its position at the base of the tree (for details, see Rieppel et al., 1999; Rieppel, 2001). This continues to create a poor fit of the cladogam depicting phylogenetic interrelationships with the stratigraphic distribution of the species of *Nothosaurus*. Character optimization indicates that *Nothosaurus juvenilis* holds its basal position because of characters related to the relatively large size of the orbits, except for the proportions of the nasals (Rieppel et al., 1999; Rieppel, 2001: nasal relatively long and narrow; postfrontal enters the anterior margin of the upper temporal fossa; postorbital arch relatively narrow; temporal fossae relatively short). This raises the question again as to whether *Nothosaurus juvenilis* is, indeed, an adult specimen (Rieppel, 1994b). Unfortunately, this question will remain unanswered until new material becomes available that would allow a thorough analysis of ontogenetic variation in *Nothosaurus*.

ACKNOWLEDGMENTS

We thank H. Hagdorn, who shared his expertise on Muschelkalk stratigraphy. The management of the Winterswijk quarry is gratefully acknowledged for allowing access to the premises. We thank G. Storrs and M. Sander for useful comments. This research was supported, in part, by NSF grant DEB-9815235 (to OR).

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ACCEPTED 5 AUGUST 2002