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A new species of the sauropsid reptile *Nothosaurus* from the Lower Muschelkalk of the western Germanic Basin, Winterswijk, The Netherlands

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A nothosaur skull recently discovered from the Lower Muschelkalk (early Anisian) locality of Winterswijk, The Netherlands, represents at only 46 mm in length the smallest nothosaur skull known today. It resembles largely the skull morphology of *Nothosaurus marchicus*. Differences concern beside the size, the straight rectangular and relative broad parietals, the short posterior extent of the maxilla, the skull proportions, and the overall low number of maxillary teeth. In spite of its small size, the skull can not unequivocally be interpreted as juvenile. It shows fused premaxillae, nasals, frontals, and parietals, a nearly co-ossified jugal, and fully developed braincase elements, such as a basisphenoid and massive epipterygoids. Adding the specimen to an existing phylogenetic analysis shows that it should be assigned to a new species, *Nothosaurus winkelhorsti* sp. nov., at least until its juvenile status can be unequivocally verified. *Nothosaurus winkelhorsti* sp. nov. represents, together with *Nothosaurus juvenilis*, the most basal nothosaur, so far.

Key words: Sauropterygia, *Nothosaurus*, ontogeny, Anisian, The Netherlands.

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Introduction

The Lower Muschelkalk locality of Winterswijk has yielded a high number of predominantly marine reptiles (Hooijer 1959; Oosterink et al. 2003; Albers and Rieppel 2003; Albers 2005a, b; Bickelmann and Sander 2008; Klein 2009), consisting of mainly isolated bones. However, associated and at least partially articulated skeletons can be found as well. Most of the bones are found in the so-called layer 9 of the quarry (Oosterink 1986), which is part of the newly established Vossenveld Formation, and is of early Anisian age (Hans Hagdorn, personal communication 2008).

The most common reptile from Winterswijk is the pachypleurosaur *Anarosaurus heterodontus* Rieppel and Lin, 1995. It is known from numerous species and so far is the only pachypleurosaur described from this locality (Rieppel and Lin 1995; Klein 2009). The less common nothosaurs seem to be more diverse, with two species described: *Nothosaurus winterswijkensis* Albers and Rieppel, 2003 and *Nothosaurus marchicus* Koken, 1893 (see Albers 2005a). Similarities in skull morphology between *N. marchicus* and *N. winterswijkensis* suggest that they represent one evolutionary lineage (Albers 2005a) and are presumably closely related, if not the same taxon. Furthermore, humerus morphology of nothosaurs implies gener-

ally a more diverse nothosaur fauna than is yet described. Size differences also point to a larger taxonomic diversity of nothosaurs at Winterswijk (Voeten and Sander 2008).

Nothosaurus marchicus is very common in the entire Lower Muschelkalk of the Germanic Basin and has a large geographic distribution in the Anisian of Central Europe (Rieppel and Wild 1996; Rieppel 2000). It is well described from localities such as Rüdersdorf (near Berlin, Germany; Schröder 1914) and possibly from Esperstädt (summarized in Rieppel and Wild 1996). *N. winterswijkensis* is restricted to the locality of Winterswijk. From the slightly older lower Muschelkalk Beds of Gogolin, Poland, *Nothosaurus* sp. (Chrząstek and Niedźwiedzki 1998), and the eusauropterygian *Cymatosaurus* Fritsch, 1894 (see Gürich 1891), and *Germanosaurus* Nopsca, 1928 (see Arthaber 1924) have been described.

Although several skulls of eusauropterygians have been recovered from the Lower Muschelkalk of the Germanic Basin, very little is known about the origin and radiation of nothosaurs. Furthermore, their intraspecific variation, size range and ontogenetic diversity remain unknown (Rieppel 1994a; Rieppel and Wild 1996; Rieppel and Werneburg 1998). Knowledge of nothosaur ontogeny is hampered by the general lack of juveniles in the fossil record.

Recently, a small nothosaur skull was discovered in the locality of Winterswijk, which provides insights into the taxonomy as well as into the intraspecific and ontogenetic variation of basal nothosaurs. In the current study, we present a detailed description of its morphology, and discuss its ontogenetic stage as well as its phylogenetic position.

Institutional abbreviations.—IPB, Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Bonn, Germany; NME, Natuurmuseum Enschede, The Netherlands; NMNHL, National Museum for Natural History, Leiden (Naturalis), The Netherlands.

Systematic paleontology

Sauropterygia Owen, 1860
Eosauropterygia Rieppel, 1994b
Nothosauridae Baur, 1889
Genus *Nothosaurus* Münster, 1834
Type species: *Nothosaurus mirabilis* Münster, 1834.

Type locality: Oschenberg near Laineck (Lainecker Höhenzug) east of Bayreuth, Bavaria, Germany.

Type horizon: Trochitenkalk or lower Meißner Formation, Upper Muschelkalk, Anisian, Middle Triassic.

Included species.—*N. giganteus* Münster, 1834; *N. marchicus* Koken, 1893; *N. juvenilis* Edinger, 1921; *N. edingerae* Schultze, 1970; *N. tchernovi* Haas, 1980; *N. cymatosauroides* Sanz, 1983; *N. haasi* Rieppel, Mazin, and Tchernov, 1997; *N. jagisteus* Rieppel, 2001; *N. winterswijkensis* Albers and Rieppel, 2003; *N. youngi* Li and Rieppel, 2004; *N. rostellatus* Shang, 2006; *N. yangjuanensis* Jiang, Maisch, Hao, Sun, and Sun, 2006.

Nothosaurus winkelhorsti Klein and Albers sp. nov.
Figs. 1–6; Tables 1, 2.

Etymology: In honour of Herman Winkelhorst, a dedicated collector and member of the Muschelkalk workgroup of Winterswijk who found this specimen.

Holotype: NMNHL RGM 443825 almost complete skull.

Type locality: Winterswijk quarry, Winterswijk, The Netherlands.

Type horizon: Layer 9 (see Oosterink 1986), Vossenveld Formation, Lower Muschelkalk (early Anisian, lower Middle Triassic).

Table 1. Measurements of NMNHL RGM 443825 (*Nothosaurus winkelhorsti* sp. nov.) from the Lower Muschelkalk of Winterswijk.

Tip of the snout to occipital condyle		46.5	
Tip of the snout to posterior margin of supraoccipital		46.2	
Tip of the snout to posterior margin of parietal skull table	*	42.3	
Tip of the snout to anterior margin of upper temporal fossa		28.7	27.35
Tip of the snout to anterior margin of the orbit		15.5	14.3
Tip of the snout to anterior margin of the pineal foramen		34.1	
Tip of the snout to anterior margin of external naris		7.65	7.2
Tip of the snout to the anterior margin of internal naris		–	
Width of skull across postorbital arches	*	15	
Width of skull at anterior margin of orbits	*	10	
Width of skull at roots of maxillary fangs	*	9	
Width of skull at rostral constriction	*	6	
Maximum width of premaxillary rostrum	*	7	
Longitudinal diameter of external naris		3.4	2.9
Transverse diameter of external naris		2.0	1.4
Longitudinal diameter of orbit		9.0	9.45
Transverse diameter of orbit		5.2	–
Longitudinal diameter of upper temporal fossa		15.4	15.25
Transverse diameter of upper temporal fossa		–	
Longitudinal width of the pineal foramen		1.8	
Transverse width of the pineal foramen		0.65	
Longitudinal diameter of internal naris		–	
Transverse diameter of internal naris		–	
Distance from posterior margin of external naris to anterior margin of orbit		4.45	4.35
Distance from posterior margin of orbit to anterior margin of upper temporal fossa		3.75	3.65
Middorsal bridge between external nares		2.4	
Middorsal bridge between orbits (minimum width)		3.45	
Middorsal bridge between upper temporal fossae (behind the pineal foramen)		3.8	

* only estimation due to the lateral compression

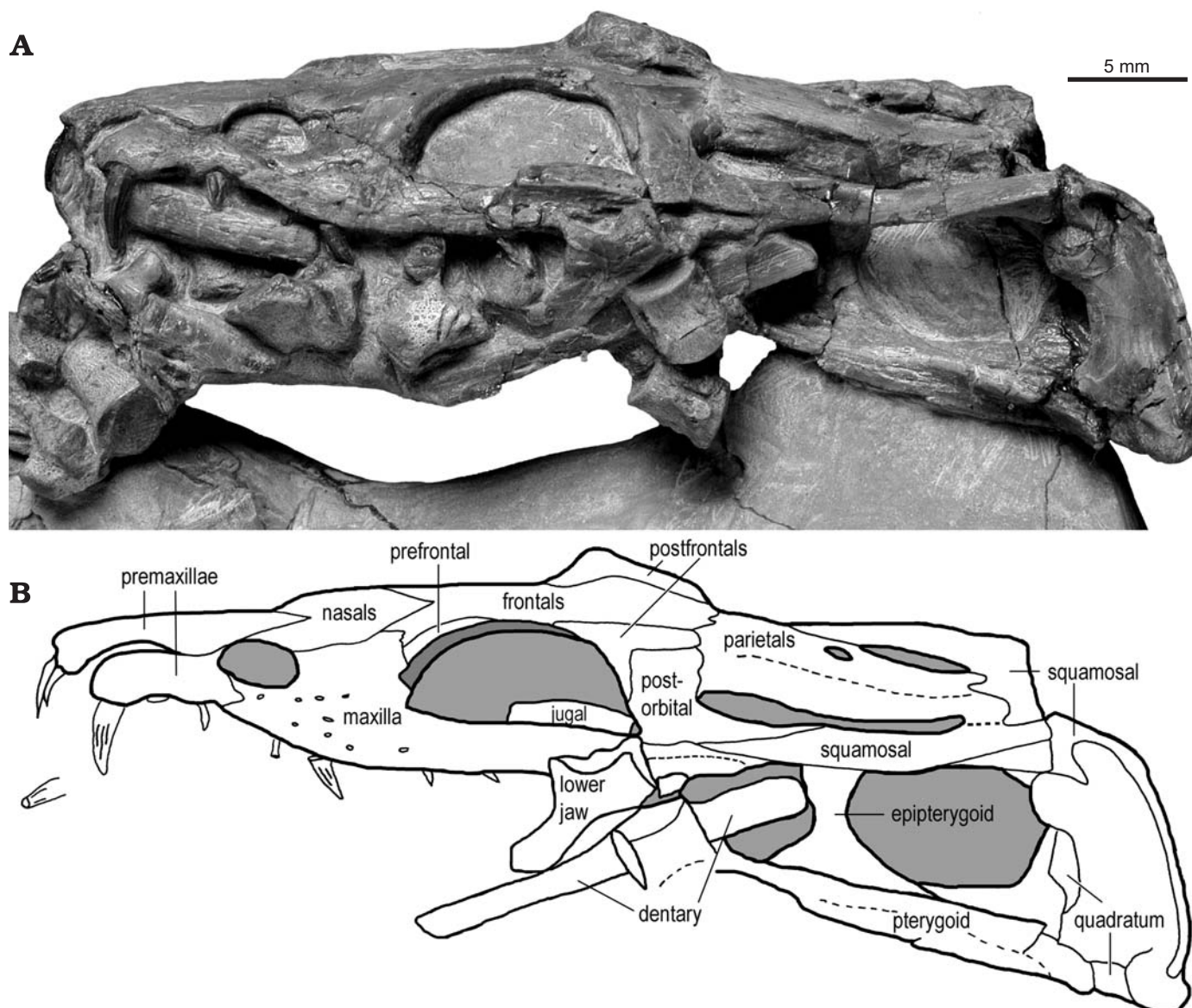


Fig. 1. Basal nothosaurid *Nothosaurus winkelhorsti* sp. nov., NMNHL RGM 443825 from the Lower Muschelkalk of Winterswijk, in left lateral view. A. Photograph. B. Explanatory drawing.

Diagnosis.—A small species of *Nothosaurus* with a skull-condylobasal length of 46 mm; skull length to ratio of skull length/upper temporal length distinctly different to *N. marchicus* and *N. winterswijkensis*; fused premaxillae and nasals; straight rectangular and broad parietals; short posterior extend of maxilla; fully developed massive braincase elements; an overall low number of maxillary teeth.

Material.—Holotype only.

Description.—The skull measures 46.5 mm from its snout to the occipital condyle (Table 1). The premaxillae, nasals, frontals and parietals are fused. Sutures are well ossified and are difficult to distinguish or have been obliterated completely. The skull has been laterally compressed postmortem. In general, a distinct sculpture comprising small pits covers the entire skull. However, some elements (e.g., the posterior

part of the premaxillae and the nasals show more pits and grooves than others. Several elements of the palate, the occipital region, and the left lower jaw are also preserved. However, their description is limited because these elements are distinctly compressed, broken or incomplete.

Premaxilla.—The premaxilla has a long, slender, tapering posterior process, which reaches far back along the skull midline, extending beyond the external naris. In dorsal view the anterior medial margin of the external naris is bordered by the premaxilla. The posterior medial margin of the naris, however, is separated from the premaxilla by an anterior lateral tapering process of the nasal. The premaxilla extends laterally to a level below the middle of the external naris. Its end is tapered and the tip is enclosed by the maxilla. The premaxillae are clearly divided into antero-lateral and postero-

Table 2. Comparison of skull proportions and dentition in *Nothosaurus* including *Nothosaurus winkelhorsti* sp. nov. (NMNHL RGM 443825). Abbreviation: Ø = diameter.

	<i>N. winkelhorsti</i>	<i>N. juvenilis</i> **	<i>N. yangiuanensis</i>	<i>N. youngi</i>	<i>N. winterswijkensis</i>	<i>N. marchicus</i>	<i>N. jagisteus</i>	<i>N. tchernovi</i>	<i>N. haasi</i>	<i>N. mirabilis</i>	<i>N. giganteus</i>	<i>N. edingeriae</i> **
snout-external naris/ rostral constriction	1.24	1.55**	1.20	1.4	1.04–1.15	1.1–1.4	1.98	2.0	2.62	1.5–2.5	1.2–1.6	1.3
snout-orbit/ snout-external naris	2.01	1.74	1.98	1.9	1.86–1.88	1.8–2.0	1.55	1.59	1.5	1.5–1.7	1.6–2.0	1.88
snout-upper temporal fossa/ snout-external naris	3.77	2.74	3.31	3.0	3.15*–3.19	2.9–3.4	2.41	2.45	2.04	2.2–2.7	2.6–3.4	2.88
longitudinal Ø external naris/ transverse Ø external naris	1.85	1.37	1.09	1.5	1.33*–1.40	1.0–1.4	1.79	1.56	2.59	1.6–2.2	Juv: 1.3–1.4 Ad: 1.7–1.85	1.85
premaxillary dentition	4+1	undetermined	4+1	5(4+1)?	4+1	5	5	5	5	5	4+1	undetermined
maxillary dentition	3+1(2?)+ (7–?)	undetermined	5+2+16	4+2+16	3+2+ (19–21)	5+2+23	4+2+20	4+2+~18	3+2+8	(3–4)+2+ (20–21)	4+2+21–?	undetermined

* estimated; ** missing tip of snout estimated

medial parts. The latter has a distinct form, which recalls a pumpkin seed, with a broad round anterior part. The posterior part ends in a tapering peak. Additionally, the bone surface is smoother. The round-oval shaped external nares measure only 40% of the longitudinal length (Table 2) of the orbits. The snout is constricted anterior to the external nares; however, the dimensions of the constriction are rather difficult to see because of the lateral distortion of the skull. Each premaxilla bears five fangs.

Maxilla.—The maxilla extends from below the middle of the external naris to about the level of the anterior margin of the upper temporal opening. It ascends between the external naris and the orbit. The maxilla contacts the nasal with a broad suture at the level of the dorsal margin of the external naris. The maxilla limits the anterior process of the frontal and the prefrontal. The anterior part of the maxilla forms the ventral and posterior margin of the external naris. The dorsal part of the maxilla borders the anterior and entire ventral margin of the orbit but is excluded from the entire posterior part of the orbit. Ventrally, a thin tapering process of the maxilla reaches below the jugal up to the anterior edge of the upper temporal opening. At this level, the maxilla shows a pointed contact with the dorsally ascending ectopterygoid. The suture with the palatine cannot be seen in detail.

The maxillary tooth row bears teeth that are distinctly smaller than the premaxillary fangs, except in positions four and maybe five, in which (as is common in *Nothosaurus*) they resemble larger fangs. None of the tooth rows is complete: on the right side 10 maxillary teeth are preserved, but on the left side only four.

Nasal.—Thin, tapering anterior processes of the nasals border the inner anterior-dorsal margin of the external naris, below the posterior processes of the premaxillae. Medially, the nasals broaden and their sutures to the maxillae are rounded. The posterior processes of the nasals taper again, and each nasal ends in a short pointed tip. The nasals are fused along the midline of the skull. The posterior processes of the nasals are broader and ex-

tend backward to a level between the anterior third of the orbits. Their suture with the frontal is interdigitated. Ventrally, the anterior part of the nasal broadly contacts the maxilla; posteriorly, it touches the anterior process of the frontal. The nasals are highly sculptured by longitudinal pits.

Prefrontal.—The left prefrontal is a rather short and slender element, lining the anterior third of the dorsal part of the orbit. On the right side it appears anteriorly broader and thicker, possibly due to the compression of the skull.

Jugal.—The massive and thick jugal is anteriorly and antero-ventrally bordered by the maxilla as well as dorsally by the postorbital. Posteriorly and postero-ventrally it contacts the squamosal and the ectopterygoid. The jugal is rectangular-shaped and deeply sculptured by grooves. It is located between the orbit and the lower temporal opening. It reaches anteriorly to the posterior margin of the orbit. Posteriorly, it meets the anterior part of the squamosal and ventrally the ectopterygoid, just in front of the anterior margin of the upper temporal opening. The jugal is separated from both openings by the postorbital. Only the anterior suture of the jugal is distinct whereas all the other sutures around the jugal are difficult to make out. The elements are nearly co-ossified in this area.

Frontal.—The tips of the antero-lateral processes of the fused frontals contact the tips of the dorsally ascending maxillae. Their medial margins meet the antero-lateral margin of the nasals, and their lateral margins run parallel to the prefrontal. The medial processes of the frontals meet the tip of the anterior nasals. The body of the fused frontals forms a relatively small interorbital bridge that separates the posterior part of the prefrontal from the anterior part of the postfrontal. The latero-posterior processes of the frontals are limited, laterally by the posterior part of the postfrontal, and dorsally by the parietals. The medial processes of the frontals are shorter than their lateral processes and contact the parietals. However, in this specimen the postero-lateral processes of the frontals are compressed together with the

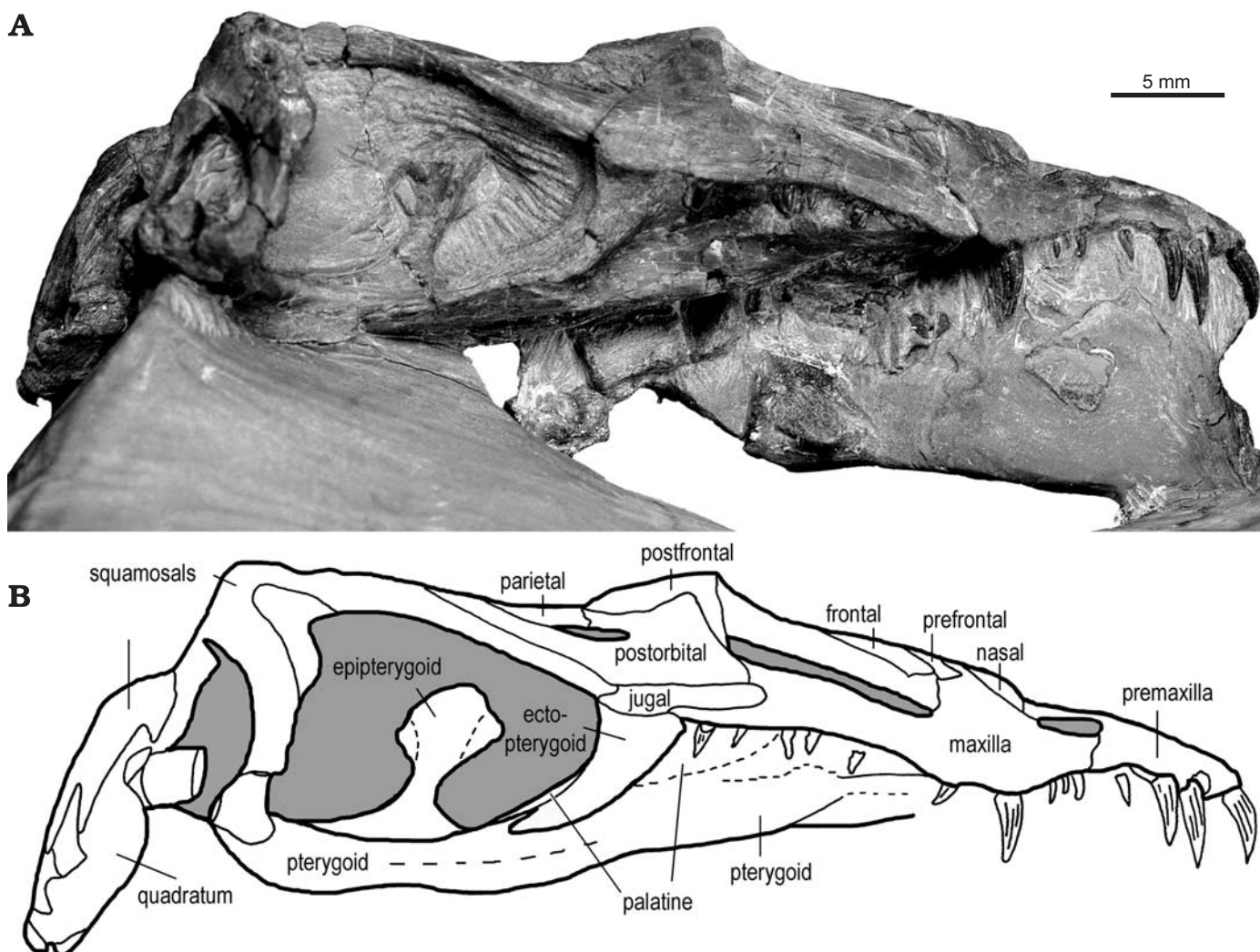


Fig. 2. Basal nothosaurid *Nothosaurus winkelhorsti* sp. nov., NMNHL RGM 443825 from the Lower Muschelkalk of Winterswijk, in right lateral view. A. Photograph. B. Explanatory drawing.

medial processes of the parietals and their sutures are only ill-defined.

Postfrontal.—The anterior part of the postfrontal bifurcates in a tapering dorsal and ventral part, which together form much of the posterior border of the orbit. The posterior process of the postfrontal is nearly rectangular in outline and is bound dorsally by the postero-lateral processes of the frontals and ventrally by the postorbital. The postfrontal does not enter into the margin of the upper temporal opening but meets the parietal dorsally at a level of the anterior third of the temporal opening.

Postorbital.—The postorbital is a massive bone that builds laterally nearly the entire postorbital arch. The postorbital ascends dorsally up to a level of the dorso-posterior orbit, where it deeply borders the postfrontal with a broad peak. It forms the anterior margin of the upper temporal opening before it meets the parietal posteriorly. The anterior postorbital limits the posterior edge of the orbit and slightly wedges be-

tween the maxilla and jugal. The tapering posterior part of the postorbital limits the anterior third of the ventral margin of the upper temporal opening and meet the squamosal at the temporal arch.

Parietal.—The fused parietals are more or less rectangular in outline and occupy the entire space between the upper temporal openings. The ventral part of the parietals broadens anteriorly so that a huge bulge is visible in dorsal view. Anteriorly, they have small medially running processes which interdigitate with the frontals and are coated by their postero-lateral processes. The postero-medial part of the parietals is deeply emarginated. Their dorso-lateral processes are longer and meet the squamosals at the posterior edge of the skull roof. Their ventro-lateral processes are very thin and elongated. They run postero-ventrally parallel to the squamosal, and extend up to the middle of the supraoccipital. The pineal foramen is located centrally between the upper temporal openings. It is not embedded in a distinct depression.

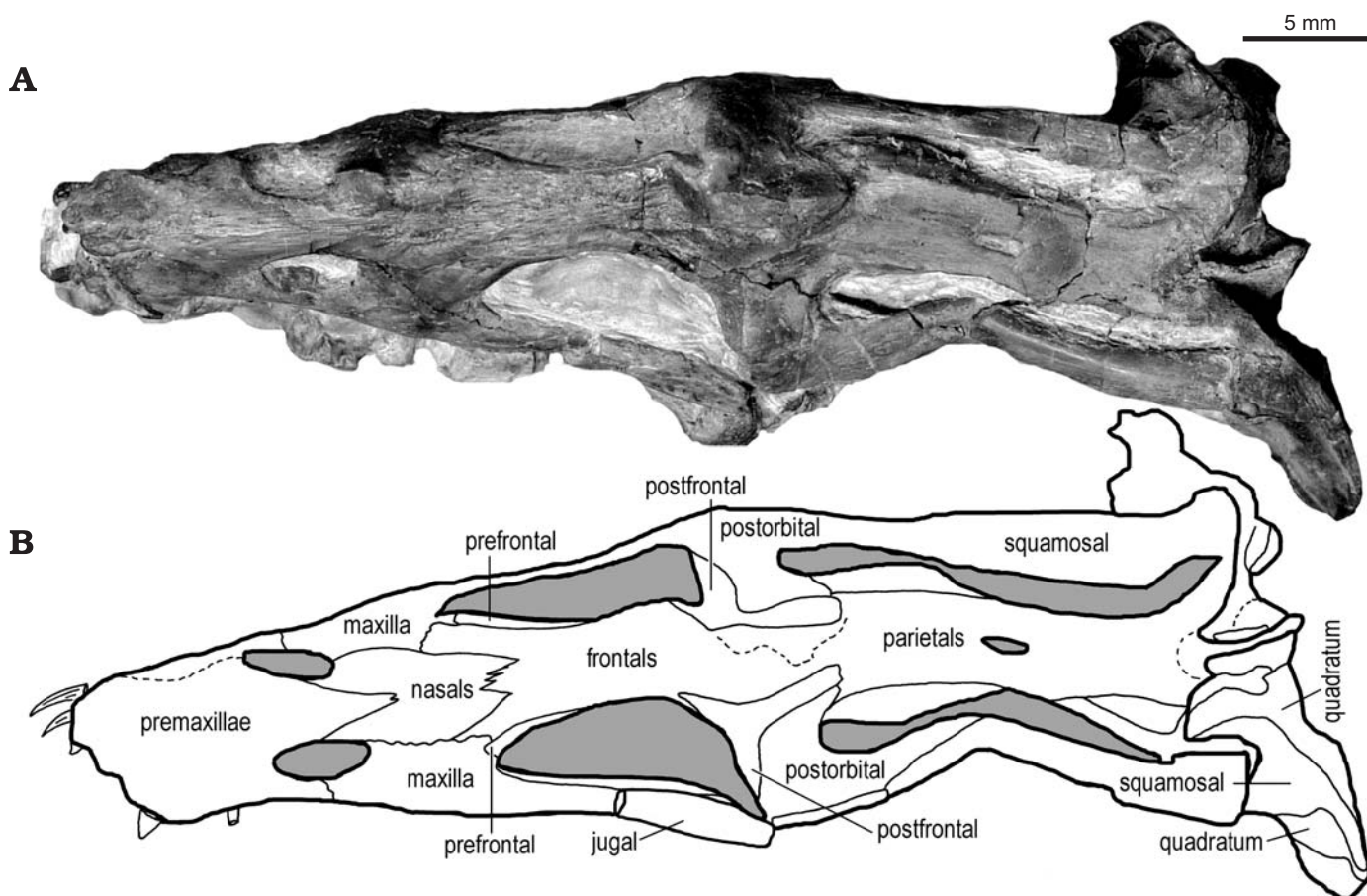


Fig. 3. Basal nothosaurid *Nothosaurus winkelhorsti* sp. nov., NMNHL RGM 443825 from the Lower Muschelkalk of Winterswijk, in dorsal view. A. Photograph. B. Explanatory drawing.

Squamosal.—The squamosal has a lateral process that is directed anteriorly at the skull roof and extends posteriorly in a large lobe down toward the jaw joint. The anterior part of this process is relatively thin and rectangular. Laterally, it forms the dorsal margin of the lower temporal arch. Dorsally it borders two thirds of the upper temporal opening and extends ventral to the postorbital to the anterior margin of the upper temporal opening. Its short medial process contacts the parietal. Posteriorly, the squamosal divides into a lateral process that reaches far down to the jaw joint, covering the postero-lateral edge of the quadrate. Medially is a postero-medial directed sheet, enclosing a third, short, and slender pointed process.

Quadrate.—The quadrate is a broad and massive element that forms the postero-ventral part of the skull. On its posterior side, it has two deep grooves and it ends in a prominent articular facet. The mandibular condyles are also prominent. The antero-lateral edge of the quadrate is covered by the postero-lateral processes of the squamosal. In lateral view, the quadrate defines the posterior margin of the lower temporal embayment. On the ventral inside of the lower temporal embayment the suture from the quadrate to the basisphenoid and the pterygoid are visible. No quadratojugal is present.

Pterygoid.—The posterior part of the pterygoid is divided by a distinct step into a medial part and a wing-shaped postero-lateral process. The postero-lateral process of the pterygoid contacts the quadrate underneath the posterior squamosal process, where the pterygoid supports the mandibular condyle. A prominent flange separates the medial and lateral regions of the pterygoid. This flange also forms the inner margin of the subtemporal embayment. In the anterior part of the subtemporal embayment the eipterygoid ascends dorsally from the pterygoid. The anterior pterygoids taper towards the skull midline, until they meet the vomers at a level of the anterior margin of the upper temporal openings. Laterally, the pterygoid runs parallel to the palatine.

Palatine.—The palatine is incompletely preserved and strongly compressed medio-laterally. The element appears thin and shiny compared to all the other skull elements. Sutures cannot be confidently assigned. It fills the area between maxilla, anterior pterygoid, and vomer.

Ectopterygoid.—The ectopterygoid ascends dorsally from the anterior half of the pterygoid. Dorsally it clearly broadens, and, together with the palatine, supports the postorbital region. It is directed anteriorly and dorsally supports the

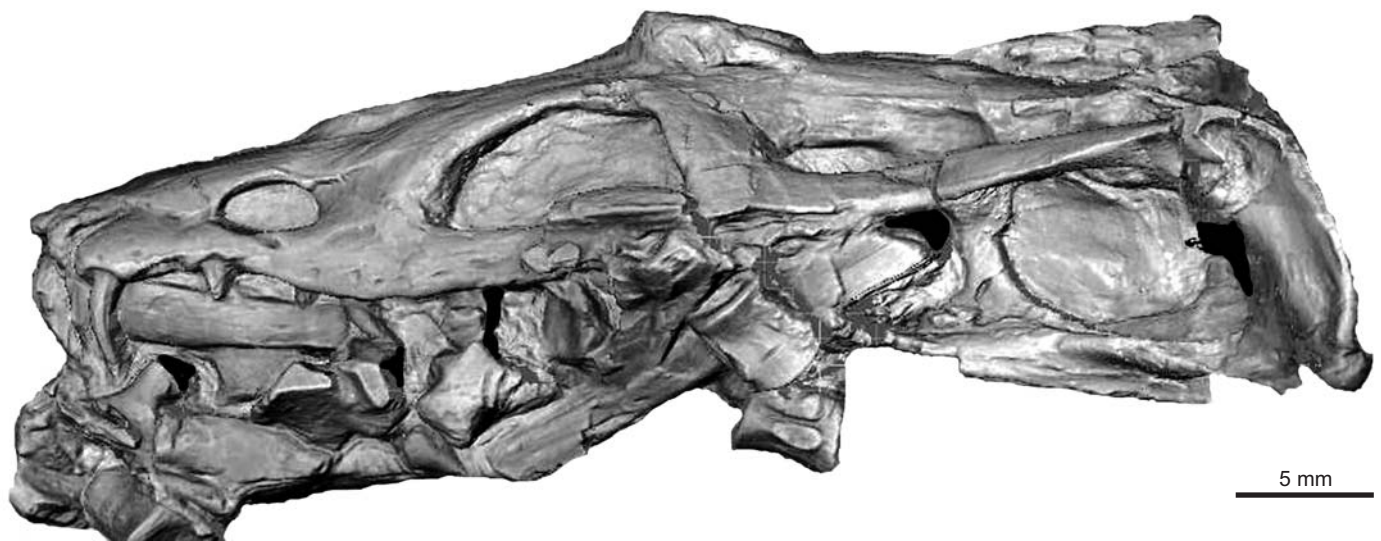


Fig. 4. Basal nothosaurid *Nothosaurus winkelhorsti* sp. nov., NMNHL RGM 443825 from the Lower Muschelkalk of Winterswijk, surface scan of the skull in left lateral view. Here, bone and sediment are well distinguished, which allows a better visualization of the skull openings. The picture is the sum of a computer calculation of all possible views of the skull. (surface scanner OptoTOP with the configurations HE 1289 and HE 1301, Firma Breuckmann).

jugal. Posteriorly, a tiny tip contacts the anterior squamosal process. Anteriorly, it also has a connection to the maxilla.

Supraoccipital.—The supraoccipital, the paired exoccipitals, and the basioccipital are still articulated but are displaced ventrally from their original positions. The supraoccipital is still attached to the parietals, as well as to the medial part of the squamosal. Originally, the supraoccipital was oriented horizontally, in alignment with the parietals and the skull roof. The supraoccipital carries a sagittal crest.

Exoccipital.—Due to distortion the exoccipitals are dorsally rather than horizontally oriented. Laterally, the jugular foramina are preserved with the foramen magnum located centrally between them. All preserved foramina are distinctly compressed mediolaterally. The foramen magnum is defined ventrally and laterally by the exoccipitals as well as dorsally by the supraoccipital.

Opisthotic.—The opisthotics are large and are located lateral to the exoccipitals. They are somewhat half-rounded and fill the space between the thin, long ventro-posterior directed processes of the parietals, the squamosal, and the quadrate. Their sutures cannot be confidently assigned. Again, due to the lateral compression of the skull, the opisthotic points backwards.

Basisphenoid.—The basisphenoid is visible within the left lower temporal embayment. It has been uplifted and shifted such that its dorsal surface now faces laterally. However, the basisphenoid is still articulated with the palate and functions as a strong supporting connection between the pterygoid and the basioccipital. Its posterior end bifurcates and covers the basioccipital.

Epipterygoid.—The left and right epipterygoids are visible in the subtemporal embayments. They are broad based and extend antero-dorsally. The epipterygoid is a massive ele-

ment, bracing the skull roof against the palatine. Its ventral part is expanded antero-posteriorly, forming a kind of massive foot. This “foot” joins a long suture with the posterior part of the pterygoid. The dorsal part of the epipterygoid is thick and rounded, with some thinner lateral expansions. It joins the parietals near a level adjacent to the middle of the upper temporal openings.

Dentition.—The dentition is heterodont, comprising large fangs with smaller teeth in between. The premaxilla carries five fangs, of which the fifth is distinctly the smallest. The maxillary tooth row has teeth that are noticeably smaller, except in positions four and (perhaps) five, which contain larger fangs. The teeth in positions two and three (anterior to the maxillary fangs) are clearly smaller than all other teeth. While only a few teeth are preserved on the maxillae (right side 10, left side four), the alveolar counts suggest at least 15 to 16 teeth positions, as can be determined from the right maxilla. The tooth row extends up to the anterior part of the upper temporal opening. The teeth seem to set in groups of two to three, presumably resulting from a pattern of tooth replacement in tooth rows (Edmund 1969).

The fangs are conical, pointed and recurved. The enamel surface of the fangs is covered with longitudinal striations. The “normal” teeth are also pointed but not re-curved, and their surface is smooth. The tooth implantation is thecodont. The largest fang has a crown height of 0.375 mm, the smallest hardly 0.05 mm.

Phylogenetic analysis

Skull characters of specimen NMNHL RGM 443825 were added to the existing phylogenetic analysis of Rieppel (2001)

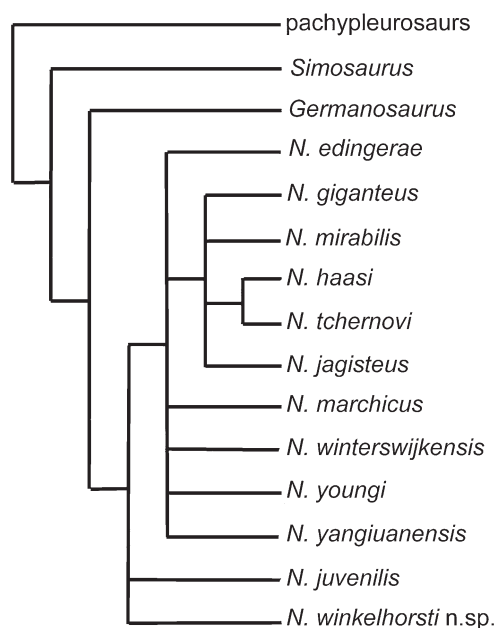


Fig. 5. Phylogenetic relationships of the genus *Nothosaurus*. The cladogram includes *Nothosaurus winkelhorsti* sp. nov. from the Lower Muschelkalk of Winterswijk. Note the basal position of the new species and its close relation to *N. juvenilis* from the Lower Hauptmuschelkalk (mo1).

supplemented with data from the nothosaurs of the eastern Tethys, *Nothosaurus youngi* (see Li and Rieppel 2004) and *N. yangiuanensis* (see Jiang et al. 2006). The phylogenetic analyses were performed using Paup 4.0b10 (Swofford 2002). All analyses ran through the branch-and-bound search. All characters were equally weighted and treated as unordered. The genus *Nothosaurus* was treated as the monophyletic in-group, which was rooted on pachypleurosaurs, *Simosaurus*, and *Germanosaurus*.

First, the analysis was run without *Nothosaurus winkelhorsti* sp. nov., to replicate the results of Jiang et al. (2006). The branch-and-bound search yielded the same nothosaur interrelationships as reported by Jiang et al. (2006). In a second analysis, specimen NMNHL RGM 443825 was added to the data matrix, with the characters coded [11011 ?0110 01110 10010 1101?]. The branch-and-bound search yielded 31 most parsimonious trees, each with a tree-length of 62 steps, a Consistency Index of 0.5862, and a Retention Index of 0.6522. The trees show an unresolved trichotomy for *Nothosaurus winkelhorsti* sp. nov., *N. juvenilis* and remaining species, which formed a monophyletic cluster (Fig. 5).

Discussion

Ontogenetic stage.—As far as we are aware, the smallest nothosaur skull that has been described to date measures 116 mm (Schröder 1914). Therefore, *Nothosaurus winkelhorsti* sp. nov., which measures only 46 mm, is exceptionally small. However, an early ontogenetic stage is doubtful because of the well ossified sutures of the skull, which are quite difficult

to recognize in places. The premaxillae, nasals, frontals, and parietals are completely fused and the jugal is partially co-ossified with the maxilla. In none of the other known *Nothosaurus* species are the premaxillae and nasals fused (Rieppel 2000, 2001; Jiang et al. 2006). Compared to juvenile pachypleurosaurs (Klein 2009), and in general all other amniotes, this high grade of ossification is not known for any juvenile vertebrate. However, theoretically, fusion of the cranial elements along the midline (nasal, frontal, parietal, vomer) need not completely exclude the possibility of the skull to grow.

The overall low number of maxillary teeth could be interpreted as juvenile character because the number of teeth can increase up to a certain growth stage in reptiles (Edmund 1969). However, the replacement pattern visible in the tooth row of NMNHL RGM 443825 is typical for nothosaurs (Edmund 1969, Rieppel 2001) and suggests not a juvenile set of teeth. Different skull proportions could also be related to shape changes during ontogeny. However, skull length plotted versus the ratio of skull length and upper temporal opening shows clearly that specimen NMNHL RGM 443825 is not a juvenile of *N. marchicus* or *N. winterswijkensis* (Fig. 6).

Rieppel and Werneburg (1998) excluded a juvenile status for the small basal pistosauroid *Cymatosaurus minor* Rieppel and Werneburg, 1998 because of the fused vomer and the fused posterior part of the parietals. Rieppel (1994a) also excluded an early ontogenetic stage for *N. juvenilis* Edinger, 1921 on the basis of the fused frontals. Furthermore, the fully developed and ossified bones of the braincase in NMNHL RGM 443825 (Figs. 1, 2, 4) are untypical in juvenile amniotes. As stated in Romer (1956: 64), the epipterygoid is slow to ossify and Rieppel (1994a), and Rieppel and Werneburg (1998) took the fusion of the dermatocranium as an adult character as well. In *Nothosaurus winkelhorsti* sp. nov., both epipterygoids are visible as broad based, massive and stable bones and the basisphenoid is fully developed as well (Figs. 1, 4).

Future research e.g., on bone histology will be needed to examine how the ontogenetic development of *Nothosaurus*

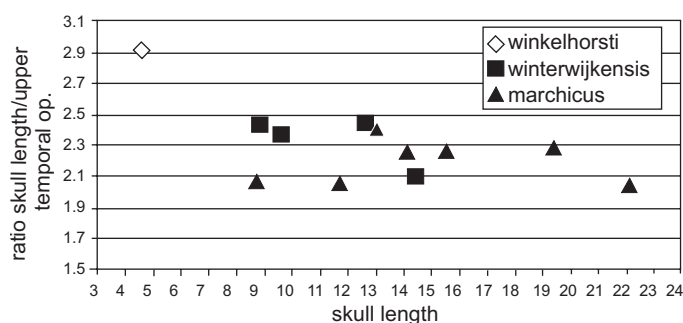


Fig. 6. Skull length plotted versus the ratio of the skull length and the maximal length of the upper temporal opening for NMNHL RGM 443825 and several species of *Nothosaurus marchicus* and *N. winterswijkensis* from the localities of Winterswijk and Rüdersdorf. Measurements of Winterswijk specimen were taken first hand in NME and NMNHL (Oosterink et al. 2003; Albers and Rieppel 2003), those of specimens from Rüdersdorf based on Schröder (1914).

can be ascertained. Acknowledging the problems mentioned above, based on evidence in hand we conclude that we are dealing with an adult specimen.

Taxonomic status.—Contrary to the close similarities in skull morphology, skull proportions differ clearly in NMNHL RGM 443825 and *N. marchicus* Koken, 1893 (Tables 1, 2, Fig. 6). Differences in skull proportions could be the result of ontogenetic variation but as discussed above, we assume that NMNHL RGM 443825 represents an adult. The smallest yet known skull of *N. marchicus* is nearly 2.5 times larger (Schröder 1914) than NMNHL RGM 443825. Such an adult size range is not likely for a biological species and not known for any other extinct or living species. The phylogenetic analysis has also shown that *N. marchicus* and NMNHL RGM 443825 do not represent closely related taxa. Therefore we decided to erect a new species for NMNHL RGM 443825, *Nothosaurus winkelhorsti*, sp. nov.

Pathology.—A third explanation for the unclear status of this atypical small nothosaur skull could be (pathological) dwarfing of this particular individual. However, this seems to be highly unlikely because the skull shows no abnormalities, aside from taphonomic distortion and compression.

Conclusion

The small size of NMNHL RGM 443825 combined with the assumption that it represents an adult, its skull proportions, and the results of the phylogenetic analyses, indicate that the specimen represents a distinct species, *Nothosaurus winkelhorsti* sp. nov.

The results of the preliminary phylogenetic analysis suggest a basal position of *N. winkelhorsti* sp. nov. in the cladogram; the unresolved trichotomy as well as a similarly basal position for *N. juvenilis*, are unexpected. Skull morphology of *N. juvenilis* (see Rieppel 1994a, 2000) differs clearly from that of *N. winkelhorsti* sp. nov.; the former is also geologically younger. The taxonomic status of *N. juvenilis* is also still arguable as is its basal phylogenetic position and its ontogenetic stage. It is conceivable that *N. juvenilis* and *N. winkelhorsti* sp. nov. do after all represent juveniles, in spite of their well-ossified skulls. This would at least give a more parsimonious explanation of their basal position in the analysis, which clearly resembles heterochrony effects, where juveniles recapitulate basal forms. However, to resolve this problem new fossil material and a more comprehensive data matrix for a new phylogenetic analysis are necessary.

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