

A new specimen of *Nothosaurus marchicus* with features that relate the taxon to *Nothosaurus winterswijkensis*

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2 tables, 2 figures

Abstract

A new incomplete skull of *Nothosaurus marchicus* was found in the Lower Muschelkalk of Winterswijk below the layers in which *Nothosaurus winterswijkensis* specimens are normally found. Although this skull resembles *N. marchicus* more closely than it does *N. winterswijkensis* it has several features which suggest an intermediate position. The specimen shares with *N. marchicus*, apart from general size, five teeth preceding the maxillary fangs, the body of the vomer not extending backwards for a greater distance than the longitudinal diameter of the internal naris and the absence of an anteromedial process of the prefrontal. It shares with *N. winterswijkensis* however that the prefrontal excludes contact between the maxilla and the frontal, the fifth premaxillary fang being distinctly smaller and the jugal entering (or at least almost entering) the orbit. As all other specimens of *N. marchicus* originate from localities further to the east and the presumed transgression of the Anisian Muschelkalk is from east to west, it is assumed that *N. marchicus* is an older species than *N. winterswijkensis*. Phylogenetic interrelationships however have put *N. winterswijkensis* at a more basal position than *N. marchicus*, which has now definitively been proven wrong by the stratigraphy of the Winterswijk finds.

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Abbreviations

ec	ectopterygoid	po	postorbital
f	frontal	pof	postfrontal
ju	jugal	prf	prefrontal
m	maxilla	pt	pterygoid
n	nasal	sq	squamosal
pl	palatine	v	vomer
pm	premaxilla		

NMNHL National Museum for Natural History, Leiden (Naturalis)

1. Introduction

An outcrop of the Lower Muschelkalk in Winterswijk (lower Anisian, lower Middle Triassic) has over the years yielded fossil marine reptiles of a particularly good three-dimensional quality. The fauna is known to include species such as *Placodus*, *Anarosaurus*, *Nothosaurus*, and *Tanystropheus* (see e.g. Oosterink *et al.*, 2003, and references in Albers & Rieppel, 2003). Most of this material remains in private collections.

In march of 2003 Erwin Donkers found a partial *Nothosaurus* skull in a layer that, until then, had not drawn any interest of the collectors, being considered 'to deep for the good stuff'. He immediately recognised the possible scientific importance of his find and subsequently donated it to the collection of the National Museum of Natural History (Naturalis) in Leiden, The Netherlands, where it remains under number: NMNHL St 449995.

The skull was found 0.6–0.7 metre above what was until recently assumed to be the top of the upper Bunter (Harsveldt, 1973) in what is also known as layer 4 (Oosterink, 1986). A recent gamma-ray stratigraphy compared with drilling results from the proximity of the quarry however has shown that the top of the upper Bunter must be at least 10–20 metres lower which is under the current floor of the quarry (Borkhataria, in press). These results also estimate this particular skull to be about 100 000 years earlier than the holotype of *Nothosaurus winterswijkensis* Albers & Rieppel, 2003, (NMNHL St 445530) which was found in layer 9 (Oosterink, 1986), the layer that has produced by far most of the material known from Winterswijk. This being the case, it is not remarkable that the *N. winterswijkensis* specimens known, also from private collections, several of which have been published or publicly exhibited (e.g. Oosterink, 1986; Oosterink & Diepenbroek, 1990; Oosterink *et al.*, 2003) are very alike and show little or no variation.

As already stated in the formal description of the holotype of *Nothosaurus winterswijkensis* it is possible that temporal distributions of *Nothosaurus marchicus* Koken, 1893 and *N. winterswijkensis* are close or even overlapping (Albers & Rieppel, 2003). As the 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, from which the known *N. marchicus* specimens originate, the expectation has to be derived that *N. marchicus* is most likely the older of the two taxa. Nevertheless analysis of the phylogenetic interrelationships has consequently put *N. winterswijkensis* below *N. marchicus* in the cladogram (Rieppel *et al.*, 1999; Rieppel, 2001). The support for these cladograms is however very poor and is not expected to reflect stratigraphical distribution of this genus (Rieppel, 2001).

2. Systematic palaeontology

Order Sauropterygia Owen, 1860
Suborder Eosauropterygia Rieppel, 1994
Family Nothosauridae Baur, 1889
Genus *Nothosaurus* Münster, 1834
Species *Nothosaurus marchicus* Koken, 1893

Type species and specimen as stated in the revision of Rieppel & Wild (1996: 34):

"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). [...]"

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."

3. Description

Specimen NMNHL St 449995 consists of the left half of a skull split more or less along the medial axis (figure 1). The left side of the frontal and the postorbital region are crushed. The parietal and occipital region are missing. Part of the squamosal is present defining the posterior margin of the upper temporal fossa. The left upper temporal arch is partly crushed, as is a small part of the region where the jugal meets the orbit. An additional break between the external naris and the orbit extends below the orbit backward exposing a part of the

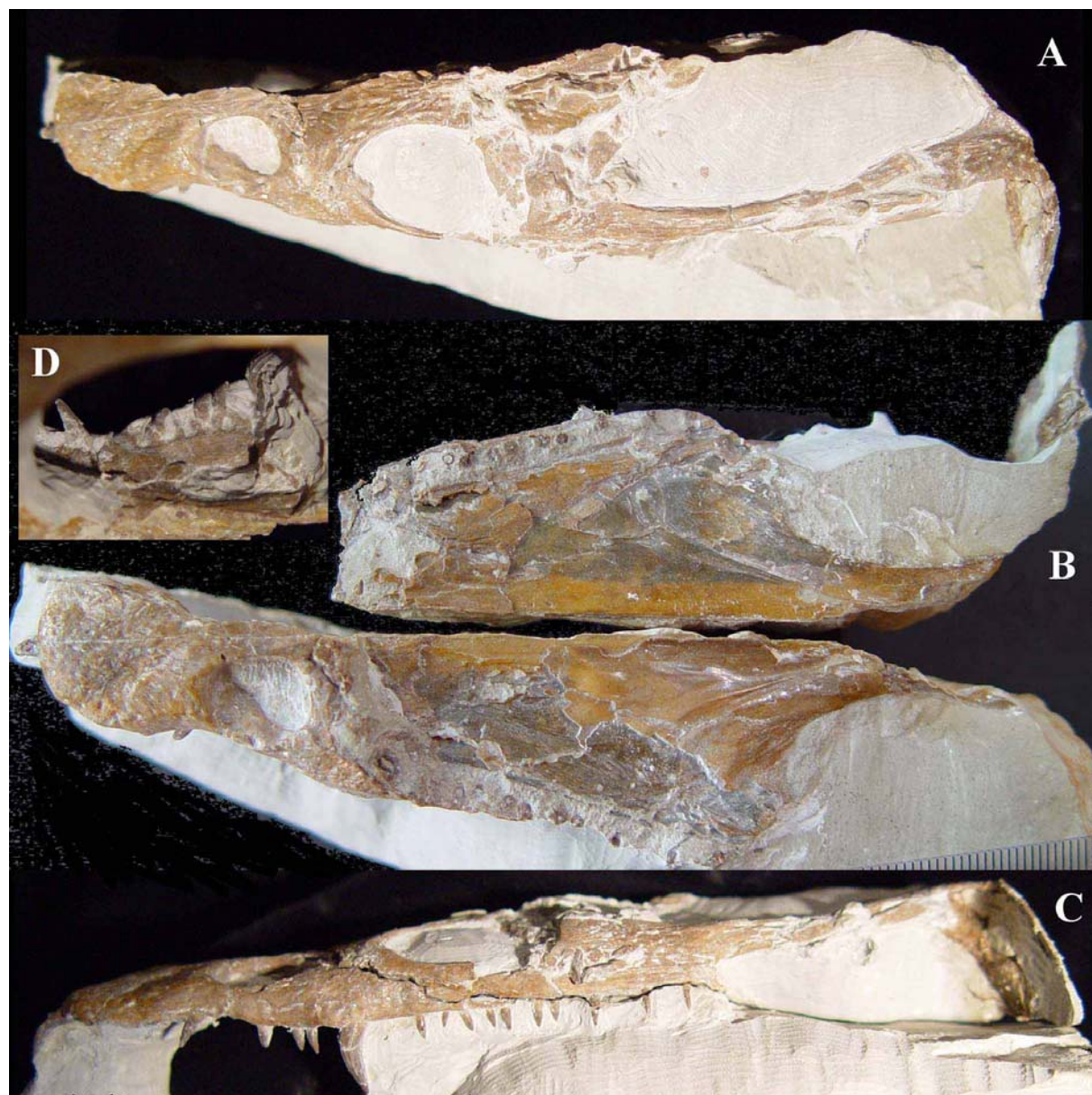


Figure 1. NMNHL St 449995. Skull in dorsal view (A); ventral view: showing both sides along a break at the level of the palate (B); lateral view (C) and detail of the ventral view around internal naris (D). Photograph by the author.

ventral side of skull, partly from the inside. Only part of the ventral side could be prepared, exposing most of the left internal naris and the tooth row. Measurements are given in table 1.

3.1. Dorsal view of the skull (figure 2A)

The measurements of the skull yield proportional ratios that are within or close to the range of variability of both *Nothosaurus marchicus* and *Nothosaurus winterswijkensis* (see table 2). The rostrum is relatively short and blunt, with rounded lateral edges. It is formed by the paired premaxillae, which do not seem to carry posterior processes that extend between the nasals, as is known from both *N. marchicus* and *N. winterswijkensis*, but only carry small posterior processes that just reach up to the level of the anterior margin of the external naris. The external naris is round but anterior and lateral of very shallow depth. If the margin of the naris is not considered to be at the edge but a little deeper one would conclude it is kidney-shaped. The nasal lines the entire medial margin of the external naris and a small part of both the anterior and the posterior margin. The surface of the nasal carries a radiating ornamentation. Posteriorly, the nasal contacts both the frontal and the prefrontal at the level of the anterior margin of the orbit. The rest of the anterior margin of the external naris and a small part

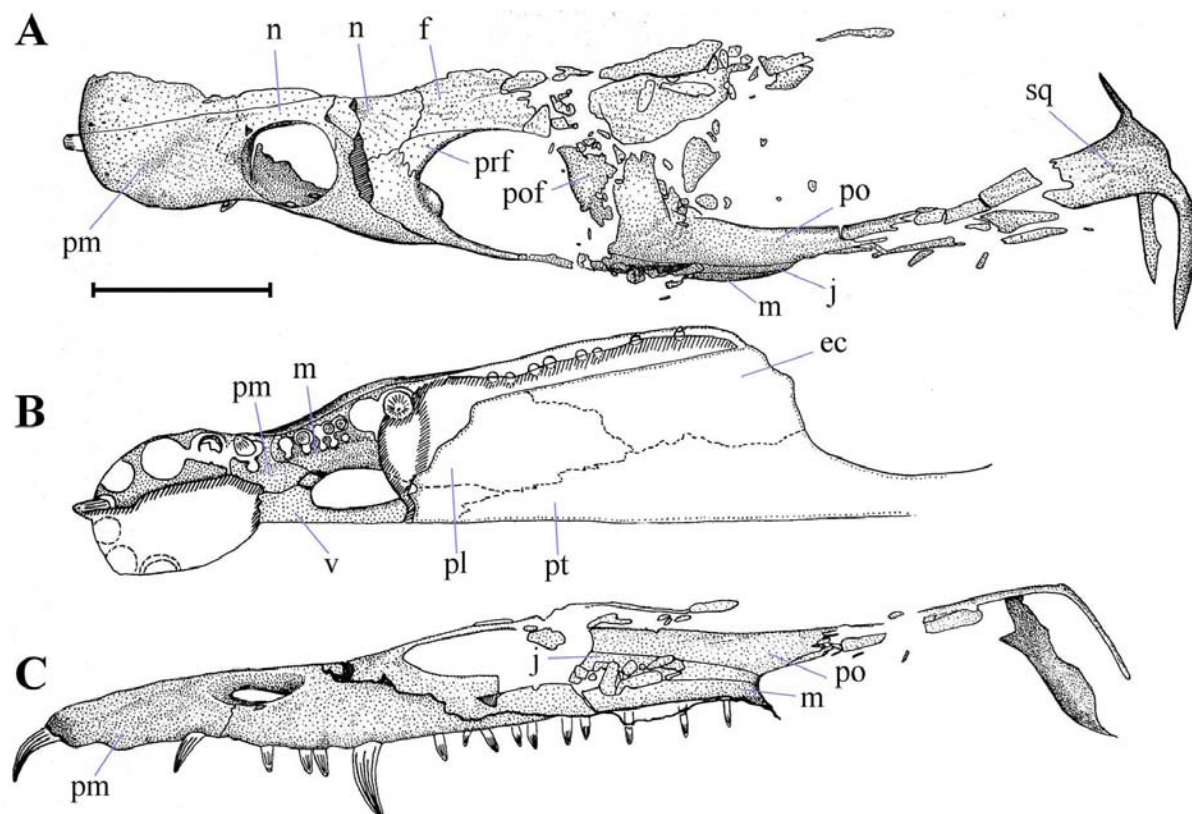


Figure 2. NMNHL St 449995. Skull in dorsal (A); ventral (B) and lateral view (C). Scale bar = 20 mm. Drawing by the author.

of its lateral margin consist of the premaxilla; most of the lateral and the rest of the posterior margin are formed by the maxilla. Two clear foramina are present in the maxillary part of the lateral edge of the external naris, the larger and most lateral of which probably serves the exit of the lateral branch of the superior alveolar nerve, as is described for most species of *Nothosaurus* (Rieppel & Wild, 1996).

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. Laterally, the maxilla shows a slight 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 the prefrontal, which fans out sufficiently in an anteromedial direction to separate the maxilla from the frontal. Lateral and ventral to the prefrontal, the maxilla defines the anterior margin of the orbit. The lacrimal is absent and no lacrimal foramen is exposed in the current preparation, which might be the result of the foramen having an atypical location similar to that of *Nothosaurus winterswijkensis* in which we also could not locate this foramen (Albers & Rieppel, 2003). Below and behind the orbit, the maxilla gradually tapers to a slender bone, carrying the maxillary tooth row backward about a fifth of the length of the upper temporal fenestra. Dorsolaterally the maxilla meets the jugal, which seems to enter the orbit. Damage, possibly by scavenging, makes it impossible to say with absolute certainty whether or not the jugal reaches the orbit, but at the least it is very close to it, reaching further forward than the level of the posterior margin of the orbit. It is thereby atypical for *Nothosaurus marchicus*, where the jugal mostly does not extend farther forward than the level halfway between the posterior margin of the orbit and the anterior margin of the upper temporal fenestra (Rieppel & Wild, 1996; and references therein).

It cannot be ascertained whether or not the frontal is unpaired (fused), although it can safely be assumed to have been as it is in all *Nothosaurus* (Rieppel, 2001). The frontal does not have an anterolateral process that protrudes farther than the level of the anterior margin of the orbit. On the surface radiating ornamentation can be seen. Most of the frontal however is crushed, possibly due to scavenging, and no information can be presented further backwards.

The parietal is missing; the postfrontal is thus crushed that no conclusions about its shape can be ascertained. The borders of medial side of the postorbital can also not be ascertained; laterally there is a clear suture with the jugal. The upper temporal arch is present but crushed midway thus that the suture between the

postorbital and squamosal is hidden. The posterior side of the squamosal is partly present just defining the posterior margin of the upper temporal fenestra, part of the upper temporal arch, and ventrally towards the quadrate of which a tiny part is just or just not present (the specimen does not allow further preparation without damaging it). The most lateral part of the squamosal is missing, leaving the status of the quadratojugal undecided. The whole occipital region is missing.

Description	Measurements [mm]
Tip of the snout to occipital condyle	130*
Tip of the snout to posterior margin of parietal skull table	116*
Tip of the snout to anterior margin of upper temporal fossa	67.2*
Tip of the snout to anterior margin of the orbit	41.3
Tip of the snout to anterior margin of external naris	20.9
Tip of the snout to the anterior margin of internal naris	26.7
Width of skull across postorbital arches	46.0**
Width of skull at anterior margin of orbits	36.2**
Width of skull at roots of maxillary fangs	32.1**
Width of skull at rostral constriction	19.3**
Maximum width of premaxillary rostrum	20.7**
Longitudinal diameter of external naris	10.4
Transverse diameter of external naris	9.7
Longitudinal diameter of orbit	21.2*
Transverse diameter of orbit	13.2
Longitudinal diameter of upper temporal fossa	48.0*
Transverse diameter of upper temporal fossa	17.0*
Longitudinal diameter of internal naris	11.7
Transverse diameter of internal naris	4.5*
Distance from posterior margin of external naris to anterior margin of orbit	10.0
Distance from posterior margin of orbit to anterior margin of upper temporal fossa	8.0
Middorsal bridge between external nares	3.9**
Middorsal bridge between orbits (minimum width)	13.0**

Table 1. Measurements. Values are restricted to the left side of the skull. * = estimation; ** = estimation by doubling the distance to the middorsal suture or an extrapolation of that suture.

	<i>Nothosaurus</i>		
	<i>marchicus</i>	NMNH St 49995	<i>winterswijkensis</i>
<u>snout – external naris</u> rostral constriction	1.1–1.4	1.08	1.04–1.15
<u>snout – orbit</u> snout – external naris	1.8–2.0	1.98	1.86–1.88
<u>snout – upper temporal fossa</u> snout – external naris	2.9–3.4	3.25	3.15–3.19
<u>longitudinal Ø external naris</u> transverse Ø external naris	1.0–1.4	1.07	1.33–1.40
premaxillary dentition	5	?(5)/4 + 1	4 + 1
maxillary dentition	5 + 2 + 23	5 + 2 + (21–?)	3 + 2 + (19–21)

Table 2. Skull proportion and dentition (for data on both taxa see Albers & Rieppel, 2003 and references therein).

3.2. Ventral view of the skull (figure 2B)

Ventral exposure is complicated by a break (which caused the skull to be found in the first place) going right through the skull between the external naris and the orbit and extends further caudally along the level of the palate (see figure 2C). The surface of the break gives information about shapes and sutures but these are partly impressions cast by the bone into the matrix, partly a view from inside the skull looking ‘out’ into the mouth, partly looking at the dorsal side of the pterygoid, and only a small part really looking ventrally on the bone. For most parts further preparation was not possible or prudent risking more damage.

The premaxilla carries five tooth positions, comprising four premaxillary fangs, followed by a distinctly smaller one, which is maybe too large to be called a tooth but too small to be called a fang. Also, it intermediates a position between *Nothosaurus marchicus*, which has five fangs (of which the fifth sometimes is a bit smaller), and *Nothosaurus winterswijkensis*, whereby the fifth tooth-position is filled by a premaxillary tooth. Three fangs are preserved in the left premaxilla, one of which is broken off (probably during life) close to the root. The edge of the specimen shows at least one more fang to have been preserved in the right premaxilla. A break, most likely caused by compression, clouds the unequivocal ascertainment of whether or not the premaxilla is excluded from the internal naris by a contact between the vomer and the maxilla. In both *N. marchicus* and *N. winterswijkensis* the premaxilla is excluded from the elongated oval internal naris.

The suture between the maxilla and the premaxilla defines that there are five tooth positions preceding the paired maxillary fangs similar to *Nothosaurus marchicus* and differing from *Nothosaurus winterswijkensis* which has only three tooth positions preceding the maxillary fangs. Behind the single maxillary fang that is present *in situ* there are 10 maxillary teeth preserved, but I estimate at least 21 tooth positions based on the space available (see table 2 for a comparison of the dentition of the specimen and both *N. marchicus* and *N. winterswijkensis*).

The anterior tip of the vomer is covered with matrix and the posterior end falls into the zone where establishing of sutures is based on impressions cast by the bone into the matrix and a view from within the skull. As a result of that, further description of the ventral side is limited and under the restriction of this possibly clouded view. Behind the internal naris the vomer extends backwards for a distance not exceeding the transverse diameter of the internal naris where it forms an interdigitating suture with the pterygoid. The suture between the palatine and the vomer starts at the posterior margin of the internal naris and continues backwards into the suture between the palatine and the pterygoid, which seems to interdigitate more than the suture with the vomer. The suture between palatine and maxilla is hidden, as is the suture between ectopterygoid and maxilla. The ectopterygoid forms a broad surface and reached to about the level of the midpoint of the palatine. The posterior part of the pterygoid is largely missing thus concluding the description of the ventral view.

4. Discussion

The description of the genus *Nothosaurus* is with a few exceptions entirely based on the description of skulls. In particular the Muschelkalk basin in northwest Europe has yielded hardly any complete skeletons of this genus. New finds of Triassic marine reptiles from southern China are however starting to shed a new light on this genus. In particular the description of *Lariosaurus xingyiensis* [Rieppel, Jinling & Jun, 2003](#) is suggesting ties between the genus *Lariosaurus* and *Nothosaurus* based also on postcranial evidence. The support for the cladograms describing the phylogenetic interrelationships within the genus *Nothosaurus* so far has always been very poor (Rieppel, 2001) and a revision seems eminent.

The currently described skull has a somewhat problematic position that can be dealt with in three ways. Either the diagnosis of *Nothosaurus marchicus* is stretched a little to include this skull, it is described as a new species, or the diagnosis of *N. marchicus* is stretched even more to also include both this skull and *Nothosaurus winterswijkensis*. All possibilities seem equally viable although the differences with *N. marchicus* seem relatively small.

The first of these three possibilities is taken here as it is the most conservative approach but it is also the most challenging to the recent cladograms. The stratigraphic position of NMNHL St 449995 below the known finds on *Nothosaurus winterswijkensis* underline that *Nothosaurus marchicus* should have a more basal position than *N. winterswijkensis* as would also be deduced from geological clues as mentioned in the introduction. One possibility would be to treat the reduction of teeth between the premaxillary and maxillary fangs as an ordered character; the fewer the more recent. However, given the current status of the genus *Nothosaurus/Lariosaurus* it does not seem useful to burden the future revision with too many speculations.

5. Acknowledgements

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