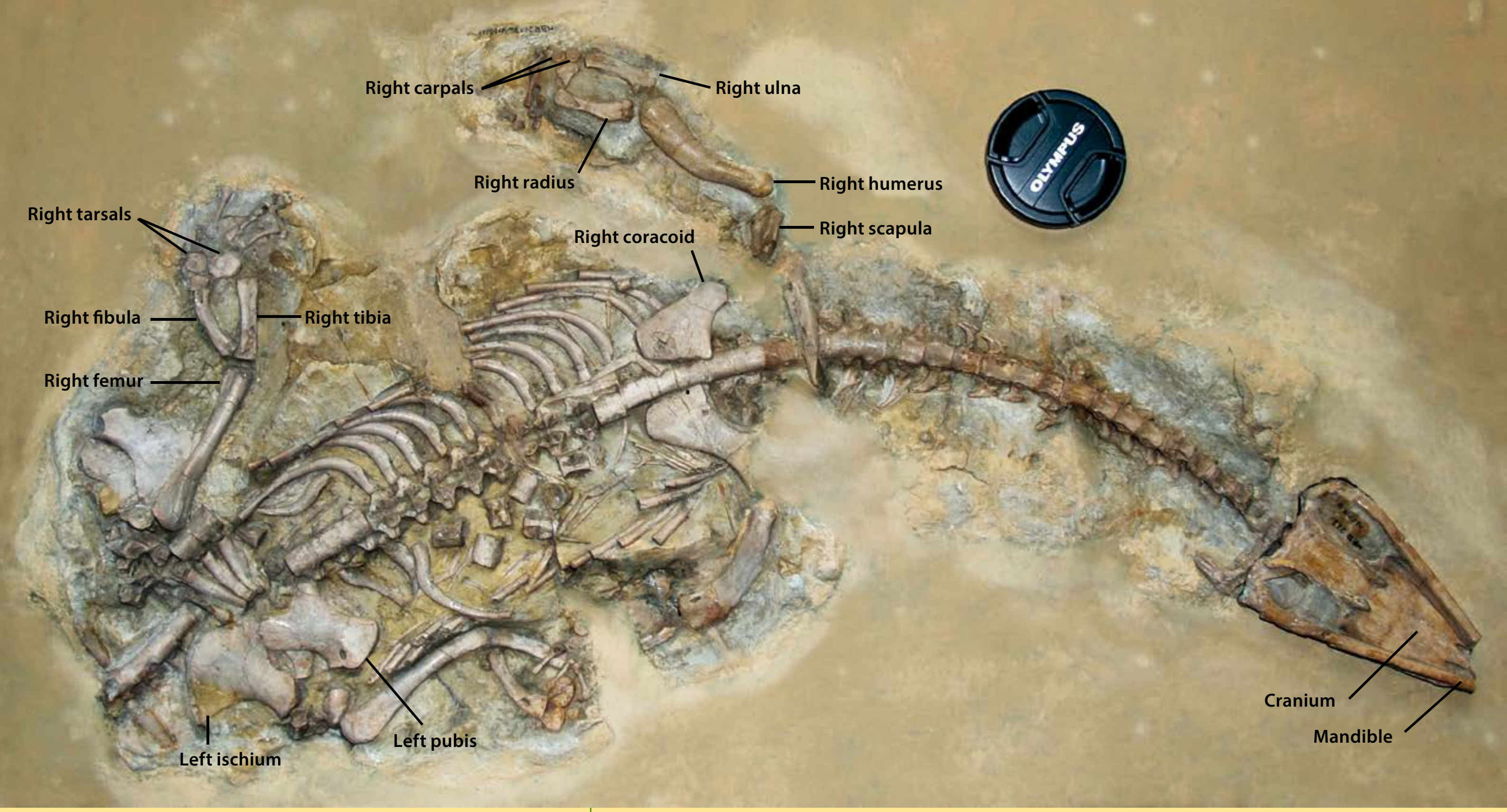

FIGURE 5. | *Articulated partial skeleton of* Nothosaurus marchicus *(MB.R.27) from Rüdersdorf (Germany) seen from below with selected elements indicated.*

Nothosauroidea from the Vossenveld Formation and their relatives

U vindt een samenvatting aan het eind van de tekst / You will find an abstract at the end of the text.

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Research into Sauropterygia in general and nothosaurs in particular has seen a long history (consider e.g. Conybeare (1821) and Münster (1834), respectively) that intimately ties in with the early development of vertebrate palaeontology as we know it today. Several species in the sauropterygian clade Nothosauroidea, colloquially referred to as nothosaurs, are presently recognised within the diverse vertebrate assemblage of the Anisian Vossenveld Formation. Here, we will introduce the phylogenetic, morphological, and ecological diversity of Middle Triassic nothosaurs in general, and those present in or contemporaneous with the Vossenveld Formation in particular.

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Systematic Palaeontology and Institutional Abbreviations

SAUROPTERYGIA Owen, 1860
EUSAUROPTERYGIA Tschanz, 1989
NOTHOSAUROIDEA Baur, 1889

MB: Museum für Naturkunde, Berlin, Germany
NMNHL: National Museum for Natural History Naturalis, Leiden, the Netherlands
TWE: De Museumfabriek (previous Museum TwentseWelle), Enschede, the Netherlands

Phylogeny and Distributions of Nothosauroidea

Nothosauroidea (Baur, 1889) includes the superfamilies Simosauridae (Huene, 1948), represented by *Simosaurus gaillardoti* and *Paludidraco multidentatus*, and Nothosauria, which includes the family Germanosauridae (with *Germanosaurus schafferi* as the only verifiable species; Rieppel, 2000), the family Nothosauridae, and likely also the newly described species *Hispaniasaurus cranioelongatus*. The family Nothosauridae contains the relatively species-rich genera *Nothosaurus* and *Lariosaurus*. A schematic overview of nothosauroid interrelations is presented in Figure 1.

Skeletal material assignable to *Simosaurus* has thus far been unambiguously recognised in Middle and Late Triassic outcrops in Austria, France, Germany, Israel, Italy, Saudi Arabia, and Spain (De Miguel Chaves *et al.*, 2018a and references therein). A peculiar simosaur, *Paludidraco multidentatus*, was recently described from the Carnian-Norian of Central Spain (De Miguel Chaves *et al.*, 2018b). In addition, the dubious sauropterygian species *Lamprosauroides / Lamprosaurus goepperti* from the Anisian of Poland has been proposed to be a simosaur as well (Rieppel, 1994; 2000).

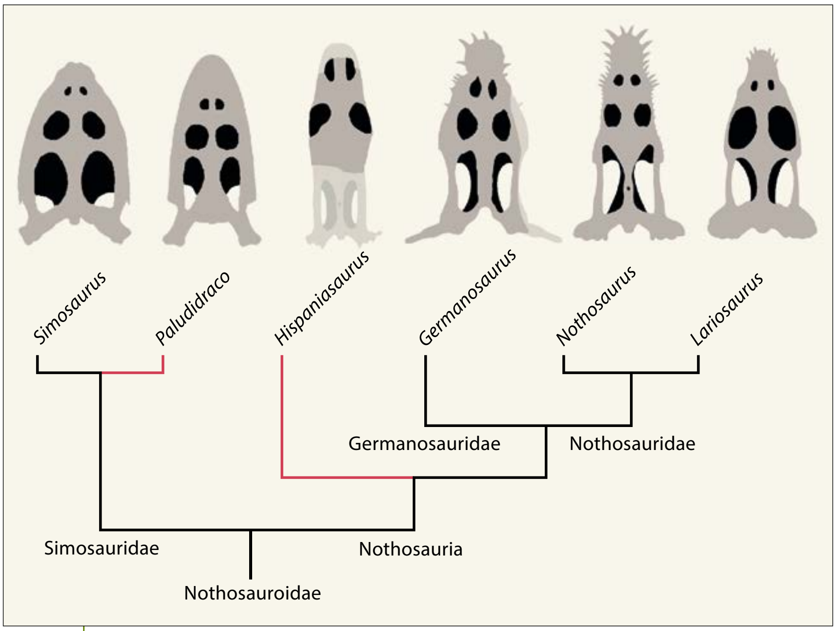

Figure 1. | *Phylogenetic solution for Nothosauroidea at genus level. Relations adopted from Rieppel (2000) supplemented with recently described Spanish nothosaurs (Marquez-Aliaga* et al.*, 2019; De Miguel Chaves* et al.*, 2018) as red branches. Cranial silhouettes not to scale.*

Germanosaurus is a fragmentarily known nothosaurid genus with a limited distribution in time and space that is exclusively known from the lower Anisian Gogolin Formation of southern Poland (Rieppel, 2000). *Germanosaurus schafferi* is the only species in its family and genus for which characteristic (diagnostic) cranial material is presently available (Rieppel, 1997). Type material of *'Cymatosaurus' latissimus* recovered from the Gogolin Formation in the nineteenth century (Gürich, 1891) has been lost from public collections but has been reassigned to *Germanosaurus* through literature (Rieppel, 1997). Nevertheless, because the lack of representative type material prevents evaluation of morphological characters beyond those provided in literature, the species *Germanosaurus latissimus* remains a *nomen dubium* (i.e. doubtful scientific name). The absence of information on the skeleton beyond the skull characters complicates reconstruction of the relations of *Germanosaurus* within Nothosauroidae (e.g. Klein *et al.*, 2016a).

Hispaniasaurus cranioelongatus was recently described as a member of Nothosauria from the Ladinian of Eastern Central Spain (Marquez-Aliaga *et al.*, 2019) based on an incomplete cranium. Although the limited availability of diagnostic characters prevented conclusive interpretation of its evolutionary position, a test of available characters strongly suggests that its lineage branched off before the evolutionary split between *Nothosaurus* and *Lariosaurus* (Marquez-Aliaga *et al.*, 2019).

Nothosaurus presently includes ten recognised species (*N. marchicus, N. zhangi, N. yangjuanensis, N. haasi, N. mirabilis, N. tchernovi, N. giganteus, N. cristatus, N. edingerae* and *N. jagisteus*; Hinz *et al.*, 2019). Although *Conchiosaurus* is a senior synonym of *Nothosaurus* (i.e. the first name given, which conventionally takes priority), the generic name *Nothosaurus* was conserved (Rieppel, 2000). *Nothosaurus* fossils have been found in lower

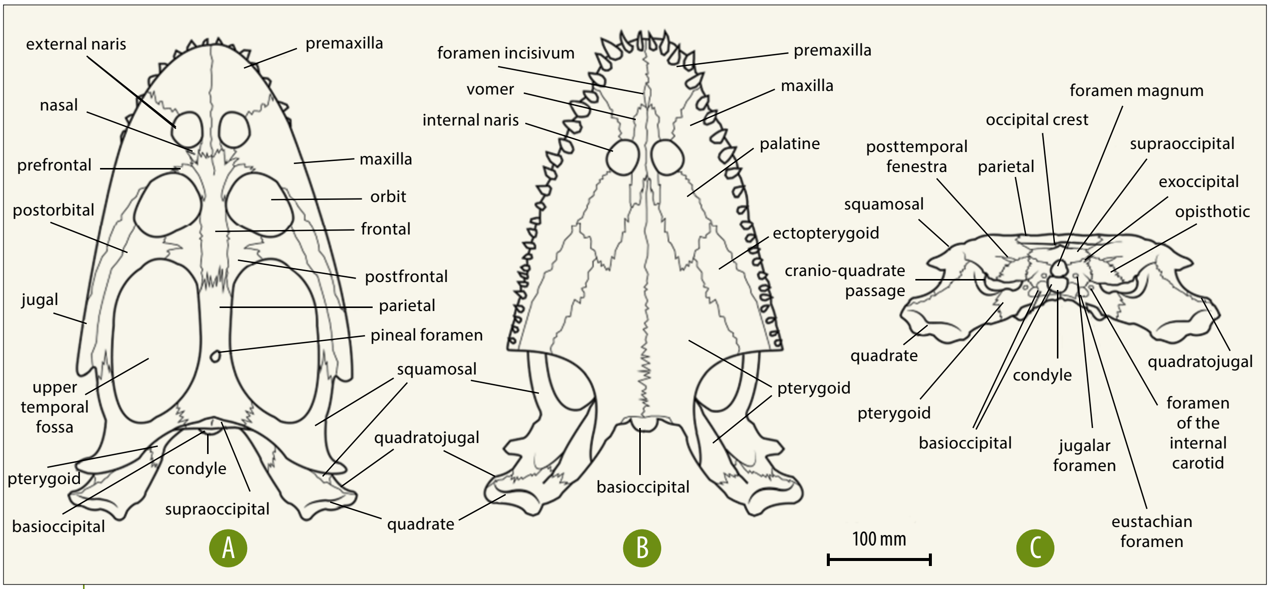

FIGURE 2. | *Idealised skull topology of* Simosaurus gaillardotti *in dorsal (A), ventral (B), and occipital (C) view. Adopted from De Miguel Chaves* et al. *(2018a) under CC BY 4.0.*

Anisian to lower Carnian marine deposits in Europe, northern Africa, and southern China (Liu *et al.*, 2014). Notably, during the earliest evolutionary chapter of the genus in Aegean and Bythinian times (i.e. between circa 247 and 245 million years ago), *Nothosaurus marchicus* is the only presently recognised representative of the genus (Liu *et al.*, 2014). Nevertheless, future research may reveal the presence of additional early *Nothosaurus* species in particularly Polish and eastern German deposits.

Our understanding of the evolutionary relations within Nothosauridae traditionally suffers from the incompleteness of the material and limited availability of morphological characters (Rieppel, 2000; Lin *et al.*, 2017). For example, *'N. juvenilis', 'N. youngi'*, and *'N. winkelhorsti'* were consistently recovered within the subfamily Lariosaurinae (e.g. Klein *et al.*, 2016a), which rendered the genera *Nothosaurus* and *Lariosaurus* polyphyletic (i.e. the phylogenetic tree of *Lariosaurus* illogically included members of *Nothosaurus*; Liu *et al.*, 2014). Recent revision (Lin *et al.*, 2017) reassigned these taxa to *Lariosaurus*, which presently includes eleven undisputed species (*L. hongguoensis, L. xingyiensis, L. vosseveldensis, L. buzzi, L. stensioei, L. valceresii, L. balsami, L. curionii, L. winkelhorsti, L. juvenilis, and L. youngi*). The genus is known from early Anisian to lower Carnian remains from central and southern Europe, the Middle East, and southern China (Klein *et al.*, 2016a, Lin *et al.*, 2017). Lariosaurinae furthermore includes the controversial genus *Ceresiosaurus*, which was deemed a valid genus with the species *C. calcagnii* and *C. lanzi* by Hänni (2004) but considered only weakly supported and therefore virtually synonymous with *Lariosaurus* by Rieppel (2000; 2007), as were *Silvestrosaurus* and *Micronothosaurus* (now designated as *L. buzzi* and *L. stensioei*, respectively).

Provenance and Morphology

Articulated and associated nothosaur remains have been recovered from relatively low-energy deposits (e.g. the Anisian Guanling Formation in China (Hu *et al.*, 2010) and the Ladinian carbonate–black shale successions of Monte San Giorgio in Switzerland (Stockar, 2010)). The higher-energy coastal and marine deposits of the European Muschelkalk (Anisian to Carnian) often show good bone preservation but only sparsely yield associated or articulated skeletons (Rieppel, 2000). Although the general skeletal morphology of nothosaurs is relatively well understood, several key species are presently only known from very limited or fragmented material (Rieppel, 2000; Lin *et al.*, 2017). This hampers reliable reconstruction of their complete morphology and anatomy and, in turn, complicates interpretations of their evolutionary placement, palaeobiology, and palaeoecology. Because *Simosaurus* and *Nothosaurus* illustrate the morphological range of nothosaurian skulls, their cranial morphologies are depicted in Figures 2 and 3.

Simosauridae

Cranium – The flat cranium of *Simosaurus gaillardoti* exhibits a unique shape among nothosauroids (see Figure 2). In dorsal view, the skull of *Simosaurus* is characterised by a rounded, subtriangular outline that anteriorly forms a short and broad (i.e. brevirostrine) snout (Rieppel, 1994a; De Miguel Chaves *et al.*, 2018a). The anterior half of the skull accommodates the circular to slightly kidney-shaped external nares and the round orbits, whereas the posterior half of the skull is dominated by the large, ovaloid upper temporal fenestrae that measure 1.5 to 2.5 times the size of the orbits (Rieppel, 1994a). *Simosaurus* lacks the pronounced fangs in the premaxillary and maxillary bones of more derived nothosaurs. A general topology of cranial elements in *Simosaurus* is presented in Figure 2. The cranium of *Paludidraco* superficially resembles that of *Simosaurus*, although it is substantially narrower throughout. This grants the temporal fenestrae a more constricted appearance, with their posteriormost aspects terminating in a pinched rather than a smooth and rounded margin. The dentition of *Paludidraco* is unique among nothosaurs in that it is composed of a multitude of small, recurved teeth that attach to the linguodorsal (i.e. upper interior) surface of the jaw bones (the so-called pleurodont condition) rather than being set in discrete (thecodont) sockets (De Miguel Chaves *et al*., 2018b). The mandible of *Paludidraco* is unusually slender, with the bowed mandibular rami meeting in a particularly short symphysis at the tip of the snout. The front part of the mandible (i.e. the symphysis) in *Nothosaurus* and *Lariosaurus* is 'spoon-shaped' and carries mostly large, recurved and striated fangs. In more basal taxa, the mandibular rami meet in a short symphysis that posteriorly opens up at a relatively large angle (the plesiomorphic or 'primitive' condition). In more derived forms with elongated skulls, the mandibular rami connect in a long symphysis and posteriorly diverge at a smaller angle (the apomorphic or 'derived' condition). Articular elements on the mandible project rearwards beyond the robust jaw joint and the connection of the skull with the neck (i.e. the cranial occiput). Through space and time, *Nothosaurus* crania exhibit a substantial morphological and size diversity (Fig. 4).

Postcranium –The skeleton of *Simosaurus* can be completely reconstructed by combining bones found in isolation. However, only a single partial skeleton of *Paludidraco* is known (Rieppel, 2000; De Miguel Chaves *et al*., 2018b). The type of vertebral articulation and strong development of the pectoral girdle and anterior limb relative to the posterior limb in *Simosaurus* might document an early shift from anguilliform (i.e. undulatory swimming, like crocodilians) to paraxial (i.e. flipper paddling, like sea turtles) locomotion, although this remains incompletely understood. *Simosaurus* was nevertheless capable of sustained active swimming (Rieppel, 1994a), although not as efficiently as other contemporaneous nothosaurs (Klein & Griebeler, 2016). *Paludidraco* preserves an axial skeleton and ribcage that are highly pachyostotic (i.e. exhibiting larger bone volume and density than related forms, which counteracts buoyancy; De Miguel Chaves *et al*., 2018b).
Ecology – *Simosaurus* likely foraged in shallow open water at moderate speeds, where its feeding apparatus would have enabled predation on (shelled) mollusks, such as ammonoids, and fish (Rieppel, 2000). The gracile feeding apparatus of *Paludidraco*, paired with a robust, pachyostotic postcranial skeleton, is most consistent with slow-speed bottom foraging on soft floral matter or faunal prey through some form of filter feeding (De Miguel Chaves *et al*., 2018b).

Germanosauridae

Cranium – The genus *Germanosaurus* and, by extension, the family Germanosauridae are only known from an isolated skull bone and a single skull of large size relative to those of contemporaneous (early Anisian) nothosaurs (Rieppel, 1997; 2000). The comparatively broad and somewhat triangular cranium features a short rostrum (i.e. snout) that is distinctly set off from the rest of the skull by a pronounced rostral constriction right in front of the ovaloid nares and rounded eye sockets (orbits). The top of the skull, at the level of the brain, features a pineal foramen that is positioned quite far backwards relative to the elongated upper temporal fenestrae (Rieppel, 1997). The skull of *Germanosaurus* is relatively robust, with the bones to the side to the orbit appearing quite massive compared to those in other nothosaurs.

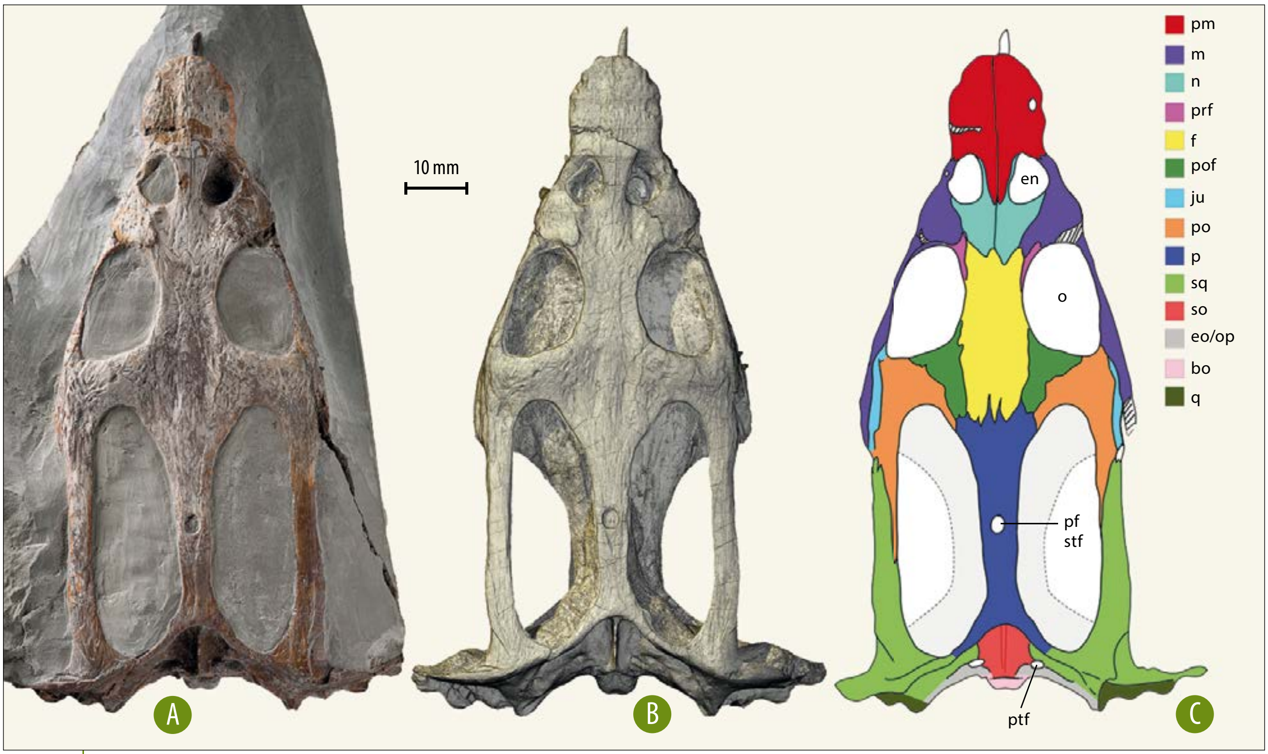

Figure 3. | *Cranium of* Nothosaurus marchicus *(TW480000375) from the Lower Muschelkalk of Winterswijk, the Netherlands, in dorsal view. A. Original cranium in matrix. B. Digital surface rendering. C. Interpretative line drawing with visible cranial bones colour coded. Note that the outlines of the ventrally situated pterygoids have been indicated in light grey, bordered by a stippled line. Abbreviations: bo, basioccipital; en, external naris; eo/op, exoccipital/opisthotic; f, frontal; ju, jugal; m, maxilla; n, nasal; o, orbit; p, parietal; pf, pineal foramen; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; ptf, posttemporal foramen; q, quadrate; so, supraoccipital; sq, squamosal; stf, supratemporal fenestra. Adapted from Voeten* et al. *(2018) under CC BY 4.0.*

Its skull bones are arranged in a pattern that shares certain conditions with *Nothosaurus*, with *Cymatosaurus*, or with both. Nevertheless, the cranial organisation of *Germanosaurus* is not 'intermediate' between those of *Nothosaurus* and *Cymatosaurus* from an evolutionary viewpoint (Rieppel, 2000). The premaxilla carries four or five fangs on each side that are distinctly larger than the teeth in the maxilla while maxillary fangs appear absent altogether (Rieppel, 2000).

Ecology –The cranium of *Germanosaurus* suggests a broadly piscivorous (i.e. fish-eating) to possibly herpetophagous (i.e. reptile-eating) diet. The unknown postcranium of *Germanosaurus* prevents further ecological interpretations but may be expected to be generally similar to that of *Nothosaurus*, including adaptations associated with early paraxial locomotion with a dominant role of the anterior limb that would have enabled successful predatory foraging in shallow marine environments.

Nothosauridae

Cranium – Despite lacking the snout and rear skull, the only known cranium of *Hispaniasaurus cranioelongatus* clearly exhibits a conspicuously tube-like shape that features relatively laterally placed orbits (Marquez-Aliaga *et al*., 2019). This partial skull furthermore demonstrates that the large temporal fenestrae characterising

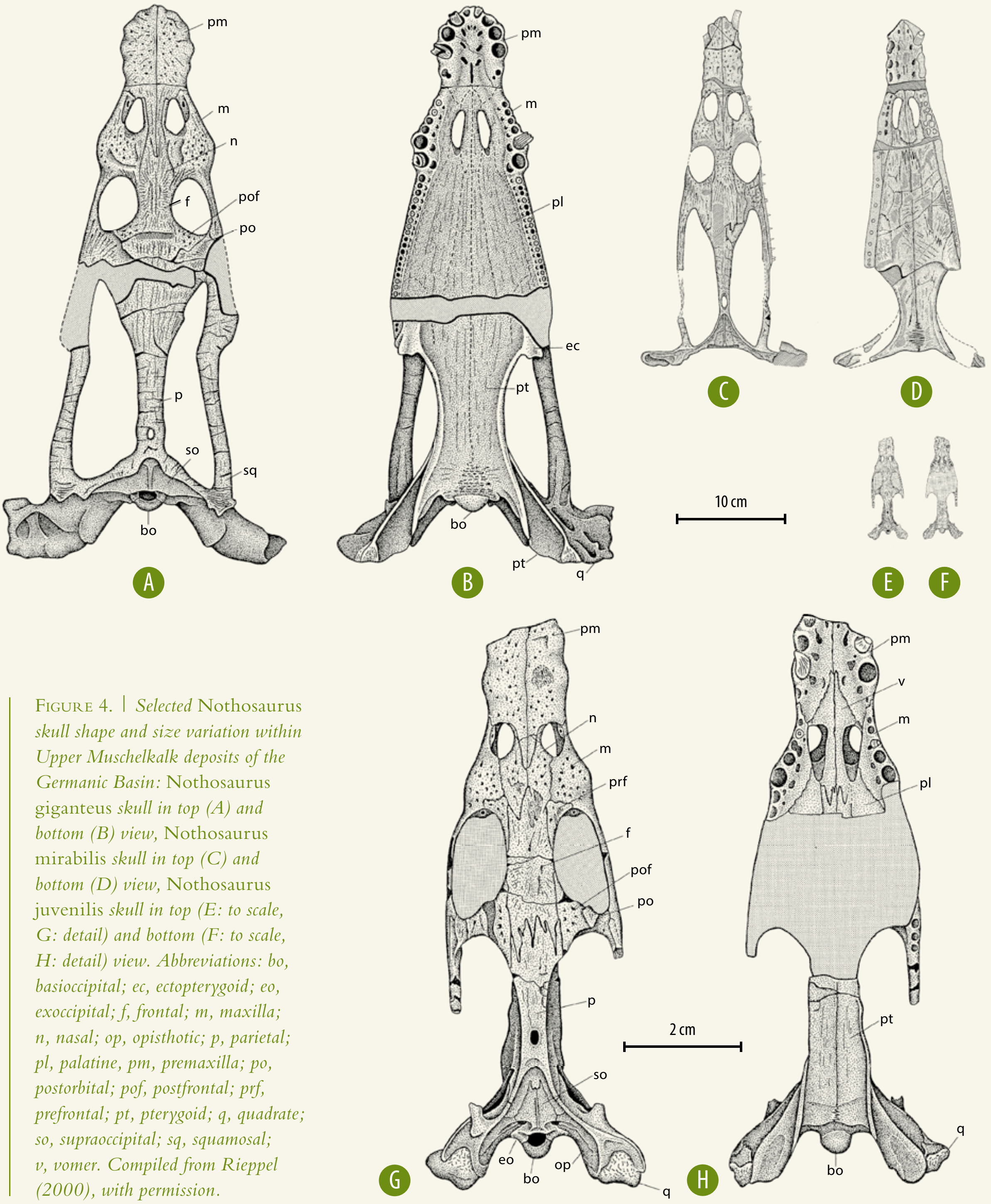

FIGURE 4. | *Selected* Nothosaurus *skull shape and size variation within Upper Muschelkalk deposits of the Germanic Basin:* Nothosaurus giganteus *skull in top (A) and bottom (B) view,* Nothosaurus mirabilis *skull in top (C) and bottom (D) view,* Nothosaurus juvenilis *skull in top (E: to scale, G: detail) and bottom (F: to scale, H: detail) view. Abbreviations: bo, basioccipital; ec, ectopterygoid; eo, exoccipital; f, frontal; 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. Compiled from Rieppel (2000), with permission.*

the crania of all other known nothosaurids are either displaced posteriorly (and possibly reduced), or secondarily closed in this taxon (Marquez-Aliaga *et al.*, 2019). Although teeth are missing in the *Hispaniasaurus* holotype skull, the preserved tooth sockets indicate a thecodont dentition with large teeth that are round to oval at their base.

Nothosaurus and *Lariosaurus* share a flat and elongated skull shape (see Figure 3) with the external nares and orbits placed on top, and upper temporal fenestrae that are usually longer than the orbits (two to four times the orbital length in *Nothosaurus*; Rieppel, 2000). The premaxillary rostrum houses four or five recurved, striated fangs on each side, and may support additional smaller conical teeth. The maxillae contain paired fangs at a level between the external nares and the orbits, and furthermore support a long row of small conical teeth extending to alongside the upper temporal fenestrae (Rieppel, 2000). The cranium has a roughly triangular outline in which the parietal bone, forming the braincase roof and carrying the pineal foramen, appears 'pinched' between the temporal fenestrae that accommodated the powerful jaw musculature during life.

Postcranium – *Nothosaurus* and *Lariosaurus* share vertebrae with a hollow articular surface in front and a flat articular facet on the back (i.e. platycoelous vertebrae). In *Nothosaurus*, the neural arches that supported the spinal cord carry either low or high (plesiomorphic respectively apomorphic) neural spines whereas the neural arch of *Lariosaurus* is always low and exhibits pachyostosis (Rieppel, 2000).

The trunk ribs of *Nothosaurus* also exhibit some degree of pachyostosis, although less so than those of *Lariosaurus*. *Nothosaurus* and *Lariosaurus* both feature a well-developed gastral rib basket in which each 'gastralium' (i.e. 'abdominal' or 'belly' rib) is composed of a median, bifurcated element that is laterally flanked by two pairs of slightly curved, overlapping osseous rods. In Lower Muschelkalk *Nothosaurus*, including those from the Vossenveld Formation, the development of an extra prong, resulting in a trifurcate rather than a bifurcate median gastralium, is relatively common (Oosterink *et al.*, 2003).

The pectoral (shoulder) and pelvic (hip) girdles consist of robust, interlocking elements that provide rigid anchor points for the limb articulation and musculature. The pectoral girdle is composed of a centrally positioned, somewhat 'T'-shaped interclavicle that connects to the transverse (and longest) bar of 'L'-shaped clavicle on each side. The shorter and rearwards projecting clavicular bar connects to the expanded body of the scapula that continues further rearwards into a distinct scapular process under which the scapular portion to the glenoid (i.e. shoulder joint) resides. Furthest down, the paired coracoids close the pectoral 'ring' by completing the glenoid most sideways and sharing a broad articular contact along the body midline. In the (somewhat less rigid) pelvic girdle, three paired pelvic elements all contribute to the acetabulum (i.e. hip joint) that articulates with the femoral head. Towards the torso, the flattened pubes contact one another along the midline of the body. To the side and slightly further back,

FIGURE 6. | *Partial postcranium of* Nothosaurus marchicus *(NMNHL St 87289) from the Vossenveld Formation of Winterswijk seen from below. This specimen was first depicted by Hooijer (1959) but was prepared further and described in great detail by Bickelmann & Sander (2008). Photo credit: Georg Oleschinski, Institut für Geowissenschaften, Universität Bonn.*

they articulate with small ilia that exhibit a relatively equidimensional but complex shape. Where the pubis reaches furthest rearwards, it carries a slit-like obturator foramen that may be either fully enclosed or opens up towards its articulation with the ischium. The 'stem' of the ischium projecting forward forms the rear of the acetabulum and its flared 'fan' projects towards the midline of the body where it connects to the corresponding portion of the mirrored ischium.

The humerus of *Nothosaurus* exhibits a complex and flattened morphology with a triangular cross section (Bickelmann & Sander, 2008) that is reminiscent of a hydrofoil (Krahl *et al.*, 2013). When extended sideways from the body, the preaxial margin of the humerus (pointing towards the head) includes a straight edge whereas the postaxial margin (pointing to the tail) is curved. Three distinct humeral shapes (i.e. morphotypes) are encountered in Winterswijk (Bickelmann & Sander, 2008, see also Voeten *et al.,* on eusauropterygian humeri on page 266 in this volume) while only one *Nothosaurus* species is presently recognised (Albers, 2011; Lin *et al.*, 2017). Since recent study was unable to link this humeral classification to different species (Klein *et al.*, 2016b), the significance of these shape groups remains unclear (but also consider the attempt of Voeten *et al.*, in this volume page 266). The ulna and radius are somewhat flattened and exhibit flared heads (Bickelmann & Sander, 2008, although ulna and radius are reversely labeled in their Figure 1).

The femur of *Nothosaurus* is relatively long, slender, slightly curved, and shows a (sub)circular cross section. It articulates with a relatively straight and massive tibia and a more curved slender fibula (Rieppel, 2000). Each wrist (carpus) and ankle (tarsus) consists of three bones. The manus (hand) and pes (foot) of *Nothosaurus* bear five digits of variable length (Rieppel, 2000; Bickelmann & Sander, 2008). A generalised overview of the nothosaurian skeleton seen from below is provided by Oosterink *et al.* (2003 – Figure 42), although the scapulae

Figure 7. | *Skull (right) with mandible (left) of* Nothosaurus marchicus *(TWE480000474) from the Vossenveld Formation of Winterswijk seen from the top. Photo credit: Georg Oleschinski, Institut für Geowissenschaften, Universität Bonn.*

are depicted in top view and the pubes and ischia would have shared a median contact or articulation rather than have slightly overlapped. A partial skeleton of *Nothosaurus marchicus* is depicted in Figure 5 (see title image).

Despite large variation within the genus (e.g. compare Renesto, 1993 - Figure 2; Rieppel, 1994b - Figure 2; Rieppel, 2000 - Figure 68, and Jiang *et al.*, 2006 - Figure 5), the humerus of *Lariosaurus* is generally less morphologically differentiated than that of *Nothosaurus*, is distinctly curved, and gradually widens towards the lower arm (Rieppel, 2000). The ulna is characteristically broadened and the radius is shorter and much more slender (Rieppel, 2000). The wrist of *Lariosaurus* comprises more elements than that of *Nothosaurus* (with some specimens exhibiting the highest number of carpal ossifications among Triassic Sauropterygia; Rieppel, 2000). The rear limb skeleton largely resembles that of *Nothosaurus*, although the ankle may accommodate up to four bones. The hand of *Lariosaurus* exhibits hyperphalangy (i.e. the condition in which more digital bones are present), as does the foot in specifically *Lariosaurus/Ceresiosaurus calcagnii* (Rieppel, 2000).
Ecology – *Lariosaurus* is generally associated with open water conditions whereas the Anisian *Nothosaurus* species *N. marchicus* has been interpreted as a principally shallow marine (Klein *et al.*, 2016a; Klein *et al.*, 2016b) piscivorous ambush predator that foraged near the sea floor (Voeten *et al.*, 2018 and references therein). The morphology and overall proportions of the front limb skeleton in both genera indicate aquatic paraxial locomotion with a propulsive bias on the front limb (Krahl *et al.*, 2013). This interpretation is supported by the long central articular surface shared by the coracoids that reinforces the pectoral girdle relative to the more poorly developed articular surfaces shared by the paired pubes and ischia in the pelvic girdle. This differs from the condition in contemporaneous pistosauroids that exhibit more asymmetrical ischia (Sander *et al.*, 2014; Voeten *et al.*, 2015), which accommodate a longer contact surface between the paired ischia and thereby support a more rigid pelvic girdle. Such an arrangement prefaces the capacity of 'four-flipper propulsion' in the iconic plesiosaurs (Muscutt *et al.*, 2017) that arose within Pistosauroidea.

The diversity of Nothosauroidea in the Vossenveld Formation with consideration of ontogenetic and heterochronic effects on cranial morphology

Vossenveld nothosaurs are typically represented by isolated elements that are common in the skeleton but have limited diagnostic value (i.e. teeth, vertebrae, ribs, and gastralia; Klein *et al.*, 2015; Heijne *et al.*, 2019). Because species description and identification of nothosaurs is largely achieved through skull morphology (Rieppel, 2000; Klein *et al.*, 2015), conclusive identification of Vossenveld nothosaurian diversity is notoriously problematic. Furthermore, the long history of research into this group has seen the creation of a rich but at times contradictory body of literature.

The first report of nothosaurians from the Vossenveld Formation presented mandibular and postcranial elements (Hooijer, 1959; see also Figure 6) that were likely recovered from horizons in the upper half of the present stratigraphic range of the Winterswijk quarry outcrops. Hooijer (1959) correctly recognised this material as *Nothosaurus* cf. *raabi* through comparison with finds from Rüdersdorf (Germany), notwithstanding that *Nothosaurus raabi* is nowadays considered synonymous with *Nothosaurus marchicus* (e.g. Rieppel, 2000 and references therein). However, the referred mandible (NMNHL St 445913) specifically assigned to *Nothosaurus raabi* (i.e. *marchicus*), as well as few isolated postcranial elements, may represent a larger, yet unnamed species (Bickelmann & Sander, 2008; Voeten *et al.*, 2015). *Nothosaurus venustus* was mentioned in several contributions referring to *Nothosaurus* in the Vossenveld Formation (e.g. Wild & Oosterink, 1984; Oosterink & Diepenbroek, 1990), but this taxon was demonstrated to be synonymous with *Nothosaurus marchicus* as well (Rieppel & Wild, 1996).

FIGURE 8. | *Holotype skull of* Lariosaurus winkelhorsti *(NMNHL RGM 443825) from the Vossenveld Formation of Winterswijk seen from the left. Photo credit: Georg Oleschinski, Institut für Geowissenschaften, Universität Bonn.*

FIGURE 9. | *Holotype skull of* Lariosaurus vosseveldensis *(TWE 480000504) from the Vossenveld Formation of Winterswijk seen from the top. Photo credit: Georg Oleschinski, Institut für Geowissenschaften, Universität Bonn.*

Within the body size range of *Nothosaurus marchicus*, the most abundant nothosauroid species recognised in the Vossenveld Formation (Fig. 7), substantial morphological variability is observed (e.g. Oosterink *et al.*, 2003; Albers & Rieppel, 2003; Albers, 2005; Bickelmann & Sander, 2008; Albers, 2011; Klein *et al.*, 2015, Voeten *et al.*, 2015) that likely involves the effects of ontogeny and sexual dimorphism. Large morphological variation in particularly the skull, with some crania notably exhibiting different conditions in their left and right side, casted doubt on the validity of certain features towards reliably discerning species.

In recognition of this uncertainty regarding diagnostically informative characters, the diagnosis of *Nothosaurus marchicus* was expanded (Albers, 2011, and references therein) to allow for inclusion of the earlier endemic taxon *Nothosaurus 'winterswijkensis'* (Albers & Rieppel, 2003; Albers, 2005). Furthermore, although *Nothosaurus marchicus* presently accounts for the oldest identifiable member of the genus (Liu *et al.*, 2014), its early occurrence is not reflected in an accordingly basal position in the present nothosaurian evolutionary tree (Lin *et al.*, 2017). This all may be partially explained by the suite of plesiomorphic characters (e.g. Voeten *et al.*, 2018) and broad diagnosis for the species (Rieppel, 2000; Albers, 2011). As a consequence, *Nothosaurus marchicus* presently spans an unusually large body size range, morphological diversity, and temporal and spatial distribution (e.g. Rieppel, 2000; Liu *et al.*, 2014, Lin *et al.*, 2017) that may conceivably involve more than one taxonomic entity, a complex ontogenetic diversity, or a combination of both. Nevertheless, this conundrum is unlikely to be resolved until a thorough revision of Nothosauridae involving broadly sampled and sufficiently available cranial and postcranial material is undertaken (Klein *et al.*, 2015 and 2016; Lin *et al.*, 2017). Improved insight into the morphological diversity of early Sauropterygia may also help to resolve the identity of the wealth of older but often isolated and non-diagnostic material from eastern Germany and Poland that, in turn, would help to clarify the earliest chapter of nothosaurian evolution.

Lariosaurus winkelhorsti is only known from a single and unusually small cranium (NMNHL RGM 443825; Figure 8) recovered from the Vossenveld Formation of Winterswijk (Klein & Albers, 2009). It exhibits a unique combination of cranial characters that inspired the erection of the designated species *'Nothosaurus' winkelhorsti* (recently reassigned to *Lariosaurus*; Lin *et al.*, 2017). Central to this motivation was the assumption that the apparently well-ossified skull roof is a robust hallmark of somatic maturity (Klein & Albers, 2009). The cranium of *Nothosaurus marchicus* was recently demonstrated to experience a mosaic heterochronic development involving distinctly paedomorphic (i.e. retention of 'juvenile' traits) and peromorphic (i.e. the accelerated establishment of 'adult' features) skull regions (Voeten *et al.*, 2018). Although the specimen studied by Voeten *et al.* (2018; TW480000375) exhibits well-ossified external cranial sutures, poor ossification (i.e. bone formation) of the prootic bone in the braincase conclusively revealed that somatic maturity had not yet been reached upon death. Despite NMNHL RGM 443825 featuring numerous well-developed braincase elements, the prootic bone remains obscured and can therefore not be evaluated. NMNHL RGM 443825 represents the smallest nothosaurid cranium described to date and *Lariosaurus* is furthermore known to harbour significant unexplained morphological variability (e.g. Lin *et al.*, 2017). Although nothosaurid embryos are incidentally reported (e.g. Renesto *et al.*, 2003), the cranial morphology of juvenile *Nothosaurus* in the size range of NMNHL RGM 443825 remains conspicuously unknown, even from Chinese localities that produced pregnant pachypleurosaurs (Cheng *et al.*, 2004) and isolated embryos (Klein pers. obs. 2006 in the Yichang collection).

Advanced external cranial ossification also prompted the 1921 erection of the small and aptly named *'Nothosaurus' juvenilis* (now *Lariosaurus*; Lin *et al.*, 2017) from the upper Anisian of southern Germany (Edinger, 1921; Haas, 1963; Rieppel, 1994b; Rieppel, 2000; Klein & Albers, 2009). After nearly 100 years following its original description, this taxon also remains represented by a single skull (Lin *et al.*, 2017). Relative to sympatric and quite common *Nothosaurus mirabilis* crania, the *Lariosaurus juvenilis* holotype exhibits similarly reduced upper temporal fenestrae, enlarged orbits, and a comparably more anteriorly positioned pineal foramen as *Lariosaurus winkelhorsti* relative to *Nothosaurus marchicus*. Edinger (1921) herself was not fully convinced that *'Nothosaurus' juvenilis* would persist as a valid species. The unlikely basal phylogenetic placement within *Nothosaurus*, which may reflect an influence of paedomorphosis, was also a concern to Rieppel (2000). Although this particular inconsistency was resolved by the work of Lin *et al.* (2017), their updated phylogeny remains inconsistent regarding overall phylogenetic ancestry and relative timing.

Lariosaurus vosseveldensis is thus far represented by a cranium associated with few postcranial elements (TWE 480000504; Figure 9) and an isolated parietal skull bone (TWE 480000505). Isolated occurrence of a skull bone indicates limited ossification of the original skull, thereby conclusively rendering TWE 480000505 subadult (Klein *et al.*, 2016a). Although TWE 480000504 preserves a substantially larger parietal and exhibits advanced cranial ossification and well-developed cranial ornamentation (Klein *et al.*, 2016a), profound cranial heterochrony in the sister genus *Nothosaurus* and in placodonts does call for caution when assessing maturity through cranial ossification (Neenan *et al.*, 2015; Voeten *et al.*, 2018). TWE 480000504 exhibits characters seen in both *Nothosaurus* and *Lariosaurus*, with its infracranial proportions presented in dominant support of a lariosaurian over a nothosaurian affinity (Klein *et al.*, 2016a). Because ontogeny may be expected to influence cranial proportions, infracranial ratios and the position of the pineal foramen (Lin *et al.*, 2017) only offer robust diagnostic characters when adulthood can be conclusively established.

The co-occurrence of two similar lariosaurian species in the same beds of the Vossenveld Formation is notable, since this would disagree with the general ecological principle of competitive exclusion proposing that two species competing for exactly the same resources cannot stably coexist. This effect has been proposed to explain the limited co-occurrence of *Nothosaurus* and *Cymatosaurus* (Rieppel & Werneburg, 1998), although vagrancy (i.e. movement outside normal ranges) or a taphonomic death assemblage (i.e. thanatocoenosis) may preserve taxa side by side that did not coexist during life (e.g. Voeten *et al.*, 2015).

These considerations all warrant a thorough reevaluation of the relation between morphological conditions and evolutionary relations in nothosaurs, as traditional approaches may fail to capture the underlying phylogenetic history of the clade. The well-preserved fossil assemblage preserved in the Vossenveld Formation has already importantly added to our knowledge of early sauropterygian evolution and may be expected to serve future discoveries for decades to come.

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Abstract

Nothosaurs (Nothosauroidea) represent an extinct order of reptiles that inhabited shallow seas during the Middle Triassic. They are part of the successful clade Sauropterygia and encompass the genus *Nothosaurus* as well as a rich diversity of related genera that evolved a broad variety of lifestyles and associated anatomical adaptations. In order to place the nothosaurs of the Vossenveld Formation in a larger context, we here offer a brief overview of the morphological diversity and evolutionary relations of Nothosauroidea.

Samenvatting

Nothosauriërs (Nothosauroidea) vormen een uitgestorven orde van reptielen. Ze bevolkten ondiepe zeeën tijdens het Midden-Trias. Nothosauriërs behoren tot de succesvolle groep der Sauropterygia en omvatten naast de soorten van het genus *Nothosaurus* een rijke diversiteit aan verwante genera die een grote variatie aan levensstijlen en bijbehorende anatomische aanpassingen ontwikkelde. Om de nothosauriërs uit de Vossenveld Formatie in een bredere context te plaatsen bieden we hier een beknopt overzicht van de morfologische diversiteit van en evolutionaire relaties binnen de Nothosauroidea.

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