A large marine eosauropterygian reptile with affinities to nothosauroid diapsids from the Early Triassic of British Columbia, Canada

TORSTEN M. SCHEYER, ANDREW G. NEUMAN, and DONALD B. BRINKMAN


Sauropterygia, one of the main clades of Mesozoic marine reptiles, diversified shortly after the Permo-Triassic biotic crisis and afterwards remained one of the major components of Early Triassic and later Mesozoic marine ecosystems. On the other hand, actual specimens of marine reptiles of Olenekian age are still rare in the fossil record, coming only from a few localities worldwide. Here we describe associated remains of a larger marine reptile of around 4 m body length, with nothosauroid affinities from the Sulphur Mountain Formation exposed at the L cirque locality of Wapiti Lake area in British Columbia. Although the specimen records only scattered parts of the posterior vertebral column, some gastral ribs and most notably, the proximal portion of one hind limb together with a fan-shaped ischium, it represents one of the oldest records of Sauropterygia and larger representatives of aff. Nothosauroidea specifically, as well as the northernmost occurrence of such animals in the Triassic. As such, the new specimen is important for understanding the biogeography and early evolution of the group and that of Sauropterygia, in general.

Key words: Reptilia, Eosauropterygia, paleobiogeography, biotic recovery, apex predator, Olenekian, British Columbia, Ganoid Ridge.

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Introduction

The Early and early Middle Triassic are key periods for understanding the recovery phase of global ecosystems following the largest mass extinction in Earth’s history, the End-Permian Extinction phase. The late Early Triassic records a turnover of ocean vertebrate communities, induced by the invasion and habitation of oceanic environments by several lineages of reptiles, including the Ichthyosauromorphs (the fish-shaped ichthyosaurs and hupehsuchians), the Thalattosauriformes and the Sauropterygia (Scheyer et al. 2014). Of those, Sauropterygia is the most long-lived, speciose, and perhaps morphologically most diverse clade (Bardet et al. 2014). Among sauropterygians, the different clades have specialized on a variety of feeding strategies, with Nothosauroidea including some of the largest predatory forms that roamed the Triassic oceans. Together with Pachypleurosauroidae and Pistosauroidae they form the clade Eosauropterygia, which is the sister taxon to Placodontiformes, the latter including the durophagous placodonts (Rieppel 2000; Neenan et al. 2013). Nothosauroidea ingroup relationships are still far from resolved, although there is indication that Simosaurus Meyer, 1842 is sister to all remaining nothosaurs, followed by Germanosaurus Nopcsa, 1928, and the remaining genera Nothosaurus Münster, 1834 and Lariosaurus Curioni, 1847 are sister taxa (e.g., Münster 1834; Meyer 1842; Curioni 1847; Nopcsa 1928; Neenan et al. 2013; Jiang et al. 2014; Li et al. 2014). In a recent analysis focusing on Nothosaurusia only, Liu et al. (2014) found a less clear separation of the latter two highly nested nothosaurs leading to a mixture between Nothosaurus and Lariosaurus species, because many new Chinese taxa were indicated to share morphological characters intermediate between the two genera. Other sauropterygian taxa such as Corosaurus Case, 1936 from the Spathian (late Early Triassic) Alcova Sandstone, Wyoming, USA, and Cymatosaurus Fritsch, 1894 from the Anisian (Middle Triassic) of Europe and ?Israel also constitute large marine predators (Fritsch 1894; Case 1936;
Biogeographically, nothosaurs are now well known both from the western (present-day Europe) and eastern Paleotethys (present-day China) with more than 20 described species in total (e.g., Rieppel and Wild 1996; Rieppel and Hagdorn 1997; Hagdorn and Rieppel 1998; Li et al. 2002; Li and Rieppel 2004; Jiang et al. 2006; Klein and Albers 2009; Liu et al. 2014). Other non-plesiosaur Triassic sauropterygians also show a Paleotethys-wide distribution, whereas, with the exception of the aforementioned Early Triassic Corosaurus and the Middle Triassic Augustasaurus from Nevada, USA (east Panthalassa, modern-day east Pacific), the record of Triassic Sauropterygia in western North America is extremely sparse (Neenan et al. 2013; Scheyer et al. 2014; Bardet et al. 2014; Kelley et al. 2014).

Here we report on fragmentary postcranial remains of a large reptile taxon with affinities to Nothosauroidea from the Triassic Sulphur Mountain Formation of the Wapiti Lake Area, British Columbia, Canada. Although the specimen was recovered as float, there are compelling indications for an Early Triassic age of the specimen. Irrespective of its geological age, this is the first recognition of Sauropterygia from the northern parts of the Panthalassa province and the northernmost occurrence of the group during the Early—Middle Triassic. We briefly discuss the paleobiogeography of the find and its implications for the timing of the recovery phase following the End-Permian mass extinction.

Institutional abbreviations.—PIMUZ, Palaeontological Institute and Museum, University of Zurich, Switzerland; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; SMF, Senckenberg Naturmuseum Frankfurt, Frankfurt am Main, Germany.

Material and methods

The specimen TMP 1995.116.0023 was found in the Sulphur Mountain Formation at Ganoid Ridge, Wapiti Lake area, British Columbia (Fig. 1) and is curated at the Royal Tyrrell Museum of Palaeontology. It was studied with a stereomicroscope and a 10 × hand lens. Images of the specimen were taken with a Nikon D90 SLR digital camera and processed using Adobe Creative Suite. Measurements were taken with steel calipers and, due to the weathered state of the bones, rounded to the nearest mm. All bone (or imprint) measurements are compiled in Table 1.

Geological setting

Many fishes and marine reptile specimens are recovered as float from the Sulphur Mountain Formation at Ganoid Ridge and thus lack good stratigraphic control. It is thus often difficult to elucidate if they are Early Triassic or Middle Triassic in age. In the case of TMP 1995.116.0023,
the position of the find at the L cirque locality (54°30′32″N; 120°41′24″W) of Ganoid Ridge, SSE of Wapiti Lake, is certain (Fig. 1; see Orchard and Zonneveld 2009 for an overview of the area and the lithology). In the unpublished field notes of one of us (AN), TMP 1995.116.0023 was recorded to have been found in a talus slope above the “marker bed” and below the Whistler Member (Middle Triassic) of the Sulphur Mountain Formation, together with other slabs containing bivalves (“Posidonia”, now referred to Peribositra; Orchard and Zonneveld 2009), fish remains, and ichthyosaur material assignable to Utatsusaurus. The majority of this talus slope appears to have derived from a big notch in the Vega-Phroso Member; the “marker bed” corresponding to the Meosin Mountain Member, which in certain outcrop areas in western Canada (including the Wapiti Lake area) separates the Phroso Member (Griesbachian to middle Spathian - see also Orchard and Zonneveld 2009). Other specimens recovered from other cirques at Ganoid ridge (e.g., Schaeffer and Mangus 1976; Neuman 1986; Mutter and Neuman 2008, 2009; Anderson and Woods 2013; see also Romano et al. 2016), especially from the upper part of the Phroso Member (Orchard and Zonneveld 2009). Other specimens recovered from the L cirque locality include for example the osteichthyans (Orchard and Zonneveld 2009). It is therefore likely that TMP 1995.116.0023 might represent a rare find of an Early Triassic marine reptile of Olenekian (Smithian or Spathian) age. Unfortunately, no conodonts could be recovered from the matrix slab that would further constrict the stratigraphic age of the find. In either case, the depositional environment of TMP 1995.116.0023 is similar for both, the Vega and Phroso members and the Whistler Member, as they comprise fine siliciclastic sediments (silts and shales) deposited below the storm wave base on the distal shelf during a first transgressive-regressive cycle (Edwards et al. 1994) that unconformably overlies the Permian Mowitch Formation (Orchard and Zonneveld 2009).

Abundant and well preserved fish faunas have been described from several layers in the Early Triassic succession from other cirques at Ganoid ridge (e.g., Schaeffer and Mangus 1976; Neuman 1986; Mutter 2004; Mutter and Neuman 2008, 2009; Anderson and Woods 2013; see also Romano et al. 2016), especially from the upper part of the Phroso Member (Orchard and Zonneveld 2009). The majority of this talus slope appears to have derived from a big notch in the Vega-Phroso Member; the “marker bed” corresponding to the Meosin Mountain Member, which in certain outcrop areas in western Canada (including the Wapiti Lake area) separates the Phroso Member (Griesbachian to middle Spathian) age. Unfortunately, no conodonts could be recovered from the matrix slab that would further constrict the stratigraphic age of the find. In either case, the depositional environment of TMP 1995.116.0023 is similar for both, the Vega and Phroso members and the Whistler Member, as they comprise fine siliciclastic sediments (silts and shales) deposited below the storm wave base on the distal shelf during a first transgressive-regressive cycle (Edwards et al. 1994) that unconformably overlies the Permian Mowitch Formation (Orchard and Zonneveld 2009).

### Systematic paleontology

*Sauropetrygia* Owen, 1860  
*Eusauropterygia* Tschanz, 1989  
*Nothosauroidea* Huene, 1956  
aff. *Nothosauroidea* gen. et sp. indet.

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**Table 1. Measurements (in mm) of TMP 1995.116.0023 tentatively identified as Nothosauroidea and PIMUZ T 4829 (= holotype of *Paranotothosaurus amsvieri* Peyer, 1939, 385 cm in total body length) of Nothosaurus giganteus for comparison based on measurements from Peyer (1939). For the ratios in the latter, the mean of left and right femur were taken.**

<table>
<thead>
<tr>
<th>Measurement</th>
<th>TMP 1995.116.0023 (left)</th>
<th>PIMUZ T 4829 (left / right)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Femur</td>
<td></td>
<td></td>
</tr>
<tr>
<td>maximum proximodistal length</td>
<td>238</td>
<td>260 / 260</td>
</tr>
<tr>
<td>proximal maximum expansion</td>
<td>72*</td>
<td>54 / 57</td>
</tr>
<tr>
<td>distal maximum expansion</td>
<td>95*</td>
<td>52 / 54</td>
</tr>
<tr>
<td>minimum shaft midline diameter</td>
<td>57*</td>
<td>29 / 29</td>
</tr>
<tr>
<td>ratio total length / prox. expansion</td>
<td>4.68</td>
<td></td>
</tr>
<tr>
<td>ratio total length / dist. expansion</td>
<td>4.91</td>
<td></td>
</tr>
<tr>
<td>Tibia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>maximum proximal expansion</td>
<td>61</td>
<td>41 / 37</td>
</tr>
<tr>
<td>Width of femoral articular surface</td>
<td>40</td>
<td>31 / 30</td>
</tr>
<tr>
<td>Fibula</td>
<td></td>
<td></td>
</tr>
<tr>
<td>proximal maximum expansion</td>
<td>56</td>
<td>34 / 30</td>
</tr>
<tr>
<td>Hemal arches (chevron bones) median</td>
<td>maximum height as preserved</td>
<td>82 – 91</td>
</tr>
<tr>
<td>maximum width as preserved</td>
<td>53</td>
<td></td>
</tr>
</tbody>
</table>
elements and that none of the non-axial elements appears twice, we assume that all pertain to a single large individual. The two larger slabs of siltstone matrix fit easily together, whereas the two smaller slabs did not show continuity with the larger slabs. The skeletal remains on the larger slabs include an isolated cluster of six lateral gastral elements (whether from the right or left side of the body cannot be elucidated), a few strongly weathered Y-shaped elements that most likely represent hemal arches or chevron bones, as well as few smaller (caudal?) vertebrae and neural arches, and most importantly, three hind limb bones (stylopod and zeugopod) and one ischium. On one of the smaller slabs, possibly one caudal transverse process is present.

The hind limb remains are represented by the clear impression of a left femur (whose preaxial border is partially not preserved proximally) and the proximal parts of a tibia and fibula in ventral view. The femur has a slightly sigmoidally curved shaft with a postaxial concave border and preaxial straight to slightly convex margin. It also has an overall massive appearance as indicated by its length and width measurements (Table 1). Because it is mostly preserved as imprint, there are only few additional anatomical features visible, such as the internal trochanter forming a prominent crista postaxially. The zeugopodial elements meet proximally and form a larger spatium interosseum, the dimensions of which cannot be measured. Proximally the tibia has an angled (somewhat rounded) facet, whereas the fibula shows a single straight facet for articulation with the femur. The well-developed distal facets of the femur left behind distinct imprints, forming a broad angle of 128°.

In addition, the partial impression of one large pelvic girdle element, identified herein as an ischium, is present. The bone impression as preserved shows a strong constriction with a steep angle between the proximal acetabular region and the flaring fan-shaped ventral blade.

The gastral rib elements all lie closely spaced to each other and resemble straight elongated and slightly conical bones, representing the lateral-most elements of six gas-
tralia. Unfortunately, none of them is complete enough to allow total length measurements, but the longest imprint of a single element extends over 148 mm.

Several Y-shaped bones, interpreted herein as hemal arches or chevron bones of proximal caudal vertebrae, lie scattered on the stone slabs in various states of preservation and orientation. All bones show different stages of breakage, with most consisting of a mixture of weathered bluish bone matrix flaking off to leave behind only imprints in the sediment matrix. Alas, the imprints are usually incomplete, which makes it difficult to trace their shape accurately. The length of the more complete bones ranges between 75 and 90 mm. These bones are not identified as neural arches and spines however, which in some nothosaurs such as *N. haasi* (Rieppel et al. 1999) can also be quite high, because of a complete lack of ventral structures that would articulate with the caudal centra forming the lateral walls of the neural canal. Instead the bones show laterally projected bases which would articulate with the ventral surface of the caudal centra.

Four bone imprints are tentatively identified as belonging to axial elements, including one isolated neural arch, which is embedded close to the gastralia elements and three vertebrae associated with remnants of neural arches. Other smaller incomplete imprints and patches of bone fragments are scattered among the Y-shaped hemal arches/chevron bones, but they are too poorly preserved to be positively identified.

The smaller slabs of rock also show bone impressions with little remains of bone tissue still attached. Most of the imprints cannot be associated with any recognizable bone, with the possible exception of one imprint. This imprint shows a weak striation of the bone surface and a slight constriction separable from an expanded area, thus resembling the distal part of a caudal transverse process (compare to Peyer 1939: pl. 70).

**Remarks.**—TMP 1995.116.0023 derives from a large Triassic marine reptile that has the following character combination: femur robust, with proximal head expanded and distal epiphysis distinctly expanded; distal condylar facets are well developed and defined, forming a broad angle; ischium hatchet-shaped with strong constriction between acetabular region and wide, fan-shaped ventral blade;ibia and fibula form distal spatium interosseum; tibia with angled proximal facet; fibula with straight proximal facet; both tibia and fibula proximally similarly expanded; lateral gastralia elements straight.

Given the enormous femoral size of more than 230 mm in length, there are only a few Triassic marine reptiles that reach similar dimensions, those being representatives of Ichthyopterygia among Ichthyosauromorphs, as well as Nothosaura and Pistasauroida among Sauropterygia. This would already preclude an assignment of the new form to small-sized sauropexyrian pachypleurosaurs or heavily armed forms such as placodonts or saurosphargids (e.g., *Sinosauroparghis*). However, size and age of the fossil alone are not deemed valid characters on their own to separate taxa. Although we identified TMP 1995.116.0023 as pertaining to Sauropexyra with affinities to Nothosauroida based on the above mentioned characteristics, we performed an osteological comparison (see Appendix 1) also with other marine reptiles from the Triassic, including (i) protorosaurs, (ii) saurosphargids, (iii) thalattosaurs, (iv) ichthyosauromorphs, (v) placodonts and *Helveticosaurus*.

Although TMP 1995.116.0023 does not show any of the synapomorphies of Nothosauroidea as noted by Sues (1987; three pertaining to the cranium; one to the humerus, and one to the intermediate in the forelimb), it nevertheless closely resembles the hind limb and ischium anatomy (and size) described for one of the largest species of *Nothosaurus*, *N. giganteus* (which includes the holotype PIMUZ T 4829 of the so far largest and most complete, articulated nothosaur “Paranothosaurus amsleri”, from the Besano Formation, Monte San Giorgio, Ticino, southern Switzerland; Peyer 1931; Rieppel 2000). The ratios of femoral epiphyseal expansion, however, differ between the new specimen and the Middle Triassic *N. giganteus*. The lateral gastralia elements and the axial elements preserved in TMP 1995.116.0023 are morphologically in accordance with those described for *Nothosaurus* (Peyer 1939; Rieppel and Wild 1996), with the former bones being densely packed and straight, rod-like elements tapering into a single tip laterally, and the latter bones having moderately elongated and not strongly anteposteriorly expanded neural arches and Y-shaped hemal arches.

Furthermore, larger specimens of *Ceratosaurus–Lariosaurus* (e.g., *C. calcagni* PIMUZ T 4836, *C. lanzi* PIMUZ T 2464; Hänni 2004; see also Rieppel 2000 and Liu et al. 2014 for discussion on the taxonomic status of *Ceratosaurus* and *Lariosaurus*) show also similar ischium, femur, tibia, and fibula shapes (SOM 2).

TMP 1995.116.0023 resembles to some degree also other sauropexyrians, but it also shows distinctive features. As such, the new specimen differs from the non-nothosauroid eosauropexyrian *Majiasanosaurus discocoracoidis* from the Olenekian (Spathian) of China in overall body size (the partial skeleton of the holotype of *M. discocoracoidis* is less than 50 cm long) and in the shape of the ischium and proximal hind limb shape (Jiang et al. 2014). The ischium of *M. discocoracoidis* is of overall plate-like shape with a weakly concave anterior margin; its femur impression indicates a straight bone, which was expanded proximally and distally, and straight tibia and fibula (Jiang et al. 2014).

TMP 1995.116.0023 differs from *Simosaurus gaillardoti* in that the femora of the latter are all proximally slightly more expanded than distally (Rieppel 1994), and Sues (1987) noted that the bones of *S. gaillardoti* are slender. The shapes of the articulation facets of the femur, tibia and fibula of *Simosaurus gaillardoti* do not match those of TMP 1995.116.0023, but the ischium does exhibit the strong constriction seen in the latter.

Furthermore, TMP 1995.116.0023 differs from *Corosaurus alcovenisis*, the so far oldest and only eosauropexyrian taxon from the Early Triassic of the North American continent described, in having a much more robust but less sigmoidally curved femur (although that could be assigned to taphonomic alteration of the bone), as well as a more
acute constriction in the ischium (Zangerl 1963; Storrs 1991; Rieppel 1998). Storrs (1991: 36–38) further noted that the “distal articular face of the femur is roughly semicircular [in which] the two equisized tibial condyles are reduced relative to the primitive condition but remain distinct. There is, however, no intercondylar fossa, although ventrally a shallowly depressed popliteal space exists. No clear fibular facet is present” in *Corosaurus*. The lack of a fibular facet is in clear contrast to the morphology of TMP 1995.116.0023.

The new specimen differs also from the non-plesiosaur pistosauroid eosauropterygians *Pistosaurus*, *Yunguisaurus*, and *Wangosaurus* in the general shape of the femur and the ischium (Geissler 1895; Sues 1987; Sato et al. 2014; Ma et al. 2015). For the *Pistosaurus* sp. femur (SMF R4041c), Sues (1987: 117) noted that the “proximal articular end is much more robust than the distal one”, whereas the ischium (SMF R76) was shown to be less constricted than in TMP 1995.116.0023. Theibia and fibula are only insufficiently known on block SMF R4041b of *Pistosaurus*, *Yunguisaurus liae* and *Wangosaurus brevirostris*, on the other hand, have similarly robust zeugopodial and stylopodial elements (Sato et al. 2010, 2014; Ma et al. 2015), and in *Yunguisaurus*, also a fan-shaped ischium is present (not known in *Wangosaurus*). The shaft of the ischium, however, is wide and the blade less flaring than in TMP 1995.116.0023. The distal articulation of the femora and the proximal articulation facets of the tibiae and fibulae in *Yunguisaurus* are distinctly different from those seen in TMP 1995.116.0023. The Canadian specimen lacks the proximal broadening of the tibia visible in *Yunguisaurus liae*, resembling more the condition seen in nothosaurs and in *Wangosaurus*. The femur of *Wangosaurus* is distinctly sigmoidally curved, with a slender shaft and it appears to be more expanded proximally than at the distal end (Ma et al. 2015; TMS personal observation), thus showing a different shape to TMP 1995.116.0023. Finally, in *Y. liae*, the left and right hemaphophyseal elements do not fuse to form Y-shaped chevron bones as are present in TMP 1995.116.0023 (Sato et al. 2014; the condition is not known in *Pistosaurus* and *Wangosaurus*).

The upper Anisanian *Augustasaurus* from Nevada, USA, does not have hind limbs or the posterior axial skeleton preserved (Sander et al. 1997). TMP 1995.116.0023 differs from *Bobosaurus forojuliensis*, potential sister taxon to all remaining plesiosaurs (Dalla Vecchia 2006; Fabбри et al. 2014), in having lower neural arches in the sacro-caudal region and a more constricted ischium; a femur is not present for comparison in *Bobosaurus*. TMP 1995.116.0023 further differs from the oldest known plesiosaur *Rhaeticosaurus mertensi* from the Late Triassic of Germany (Wintrich et al. 2017) and more highly nested plesiosauroids such as *Tetanectes laramiensis*, *Peloneustes philarchus*, and *Meyerasaurus victor* by having more and thinner gastralia, a slightly sigmoidal femur with both proximal and distal epiphyses being expanded (e.g., Smith and Vincent 2010; Ketchum and Benson 2011; O’Keefe et al. 2011). Plesiosaur femora are usually straight and the distal epiphyses much broader than the proximal articular heads, the latter often not being expanded at all. Furthermore, the zeugopodial elements in TMP 1995.116.0023 appear to be much longer and not indicative of a plesiosaur-type paddle.

**Discussion**

Based on the comparisons described above, all observable anatomical details of the bones of TMP 1995.116.0023 are conform with non-pistosauroid nothosaurian eosauropterygians; although some disparity in proportions and the ratios of femoral epiphyseal expansions are present due to the robustness of the new specimen. In contrast, similarities to only some bones of certain pistosauroid taxa do exist (as nothosaurs and pistosaurs share some characteristics in their postcrania), but disparity among these taxa and TMP 1995.116.0023 is larger in comparison to the nothosaurs. We therefore tentatively assign TMP 1995.116.0023 to Eosauropterygia aff. Nothosauroidae indet. We cannot completely rule out, however, the possibility that the Canadian taxon is a yet unknown form of non-nothosaurian eosauropterygian. In either case, the new taxon indicates that eosauropterygians were more widely spread in North America than previously known.

The femur of the specimen is slightly shorter than that of PIMUZ T 4829, one of the largest and almost complete specimens of *Nothosaurus giganteus* (see Table 1), a similar total body size of around 4 m, but much more robust body shape (based on the femoral proximal and distal expansion in comparison to the femur length) is proposed for the Canadian taxon. Assuming a predatory lifestyle as in all other known nothosaurians (e.g., Liu et al. 2014) it is reasonable to assume that the new Canadian taxon could have been an apex predator in the ancient ecosystem. A possible late Early Triassic age of the specimen TMP 1995.116.0023 would further indicate one of the oldest records of nothosaurian eosauropterygians, which was so far represented by material identifiable as *N. marchicus* from the early Anisanian Jena Formation of Winterswijk, The Netherlands and Rüdersdorf in Germany (Albers 2005; Voeten et al. 2015), as well as by indeterminate remains of *Nothosaurus* sp. from the Röt Formation, lowermost Anisan, of Central Europe (Hagdorn and Rieppel 1998; Rieppel et al. 1999).

Among the largest representatives of nothosaurians, *N. giganteus* ranges between the upper Anisan (Illyrian) and Carnian (Julian) (Dalla Vecchia 1994; Rieppel and Wild 1996; Vickers-Rich et al. 1999; Kear et al. 2008; Kelley et al. 2014), whereas the largest Chinese nothosaurian material, *Nothosaurus zhangi*, is from the middle Anisan (Pelsonian; Liu et al. 2014) and thus slightly older. Furthermore, the so far oldest described eosauropterygian, *Majiashanosaurus discocoracoidis*, together with some of the basal-most members of ichthyosauriforms (Motani et al. 2014a), was recovered from the Upper Member of the Nanlinghu Formation (Spithian, Early Triassic) of Majiashan, Chaohu
Large apex predators such as the macrophagous ichthyosaur *Thalattoarchon saurophagus* from Nevada, USA (Fröbisch et al. 2013) and the nothosaurid *Nothosaurus zhangi* from Luoping, southern China (Liu et al. 2014), have been used as indicators of recovery and ecosystem stabilization following the aftermath of the Permo-Triassic mass extinction event by the Anisian (Middle Triassic). A definition for gigantic apex predators was proposed by Liu et al. (2014), with the criterion being a minimum body length of 5 m. This categorization, which would include also very large individuals of *Nothosaurus giganteus* and *N. zhangi*, has merits as important indicators of ecosystem recovery and food web complexity on a global scale. Following a context-dependent approach similar to assessing missing megafaunal elements in Pleistocene-modern ecosystems (Hansen and Galetti 2009) on different-sized land masses, distinguishing between “normal-sized”, “large-sized”, and “gigantic” apex predators on local or regional scales might seem less important when analyzing global recovery dynamics. Accordingly, apex predators (also smaller ones with <5 m body length) were present in marine ecosystems throughout the Early Triassic, although with different faunal composition and community structures (Scheyer et al. 2014) and as such, the smaller sized eosauropterygian *Majiashanosaurus* might...
still have played the role of apex predator in its environment in which other faunal elements were also of smaller size.

Scheyer et al. (2014) indicated a transition from fish-amphibian to fish-reptile dominated faunas in marine ecosystems around the Smithian/Spathian boundary, about 2 Ma after the Permo-Triassic mass extinction. The appearance of a Canadian large reptile with nothosaurid affinities in the late Early Triassic thus adds another piece to the puzzle of the timing of the recovery phase following the extinction event. Similar to the case of Thalattoarchon saurophagus and *Nothosaurus zhangi*, TMP 1995.116.0023 could act as further indication for globally reestablishing complex marine ecosystems towards the end of the Early Triassic.

Rieppel (1999) noted that many of the smaller-sized Triassic sauropterygians probably lacked the capacity to cross open oceans; instead, dispersal occurred likely along the coastlines of Pangaea in these taxa. It is doubtful whether this would have been a hindrance for a larger animal of four or more meters in body length. However, as has been proposed for Early Triassic ichthyopterygians (Cuthbertson et al. 2013), pre-Olenekian intermittent shallow epi-continental seaways spanning Laurasia, thus connecting the western Paleothetics with the eastern Panthalassa faunal province, might have facilitated the dispersal of other marine reptile groups such as the nothosaurs as well.

Conclusions

The description of a new, large fossil with nothosaurid affinities from Canada adds data to our understanding of the early evolution of this important group of sauropterygian reptiles. It also serves as a reminder that the Early Triassic remains the key period to (i) understand the origins and paleogeography of Mesozoic marine reptiles (see also Jiayang et al. 2014) in general, and (ii) reconstruct the timing of the oceanic recovery phase following the largest mass extinction event in Earth history. As such, the Early Triassic sites at Ganoid Ridge in British Columbia, Canada, deserve renewed attention in future studies pertaining to these research areas.

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Appendix 1

Additional osteological comparison.

(i) TMP 1995.116.0023 differs from larger protorosaurs such as *Dinocephalosaurus orientalis* (Rieppel et al. 2008) in the absence of a strongly concave posterior margin of the femur and the equal robusticity and proximal expansion of the zeugopodial elements, and from *Tamystropheus longobardicus* (Wild 1973) in having a distinctly greater expansion and differently shaped femoral epiphyses. A large spatium interossium between the zeugopodial bones is shared with *D. orientalis* (Rieppel et al. 2008); whereas the ischial shape in TMP 1995.116.0023 resembles only weakly that of some earlier growth stages of *T. longobardicus* (see Wild 1973: fig. 92g). It further differs from the Chinese marine archosaur *Qianosuchus mixtus* (see Li et al. 2006) in having a fan-shaped ischiadic ventral blade, overall much more robust stylopod and zeugopodial elements, and a less sigmoidal shaped robust femur.

(ii) It differs from the Chinese saurosphargid *Largocephalosaurus qianensis* (Li et al. 2014) in the similarly broad expansions of the proximal and distal ends of the femur, the proximal shapes of the tibia and fibula, and the strong constriction of the ischium.

(iii) TMP 1995.116.0023 differs from large thalattosaurs such as *Askeptosaurus italicus*, *Anshunsaurus wushanensis*, *Concavispina biseridens*, and *Miodentosaurus brevis* (these are the largest thalattosaurs known) in femur shape. Thalattosaur femora lack clearly developed distal condyles of the femur for the articulation with the tibia and fibula. In addition, these femora usually reach only slightly more than half the size of TMP 1995.116.0023, except in *Miodentosaurus*, whose femur almost reaches the dimensions of the Canadian specimen (Müller 2005; Rieppel et al. 2006; Wu et al. 2009; Liu et al. 2013). Furthermore, thalattosaur taxa lack the strong constriction of the ischiadic shaft region and the broader ventral fan-shaped blade.

(iv) TMP 1995.116.0023 differs from ichthyosauromorphs, including the Chinese hupehsuchians *Parahupehsuchus longus* and *Hupehsuchus nanchangensis* (Chen et al. 2014), as well as ichthyosauriforms (e.g., the Triassic forms *Cartorhynchus lenticerpus*, *Chaohusaurus* spp., *Mixosaurus* spp., *Utatsusaurus hataii*, *Shastasaurus* spp.) in having a less broadened femur with a long diaphyseal shaft and widely expanded proximal and distal epiphyseal areas and there is further no indication for the formation of paddle-shaped hind limbs with reduced or plate-like/lunate-shaped ischia as are typical for ichthyopterygians (Callaway 1997; McGowan and Motani 2003; Motani et al. 2014a, b).

(v) TMP 1995.116.0023 shares with the enigmatic marine reptile *Helveticosaurus* from the Middle Triassic of Monte San Giorgio, Switzerland, the massive stylopod and zeugopod, a spatium interossium between tibia and fibula, as well as the similar proximal articulation facets in these elements (Rieppel 1989). However, TMP 1995.116.0023 differs in femoral shape and its distal articulation facets, as well as the distinctly different shape of the ischium. In addition, the new specimen differs also from larger placodonts including *Placodus gigas* and *Pararcarus diepenbroeki* (Drevermann 1933; Klein and Scheyer 2014) in possessing a constricted rather than plate like ischium.