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Author for correspondence:

Adiël A. Klompmaker,
Email: adielklompmaker@gmail.com

Adiël A. Klompmaker and Timo J.B. van Eldijk shared first authorship, and they contributed about equally to this work.

A non-marine horseshoe crab from the Middle Triassic (Anisian) of the Netherlands

Adiël A. Klompmaker¹ , Timo J.B. van Eldijk² , Herman Winkelhorst³ and Jelle W.F. Reumer^{4,5,6} 

¹Department of Museum Research and Collections & Alabama Museum of Natural History, University of Alabama, Tuscaloosa, Alabama, USA; ²Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands; ³Molenstraat 14, Aalten, The Netherlands; ⁴Faculty of Geosciences, Utrecht University, Utrecht, The Netherlands; ⁵Natural History Museum Rotterdam, Rotterdam, The Netherlands and ⁶Naturalis Biodiversity Center, Leiden, The Netherlands

Abstract

Horseshoe crabs (Xiphosura) have a long evolutionary history starting in the Ordovician, but they have rarely been reported from the Netherlands. We report on the first Triassic horseshoe crab from the Netherlands identifiable to the species level, a specimen of the limulid *Limulitella brononii*. We provide the first diagnosis for this species and refigure the holotype. The new specimen was found in the Middle Triassic (Anisian) Muschelkalk sediments of the Vossenveld Formation, in the Illyrian part of the stratigraphic profile of the Winterswijk quarry complex. The Winterswijk specimen represents the youngest occurrence of *L. brononii*. The inferred non-marine habitat of this horseshoe crab species elsewhere in conjunction with occurrences of plant and insect remains within the same layer at Winterswijk suggest the specimen herein most probably did not live in marine conditions either. This species has previously been found in non-marine sediments in France and Germany, expanding its geographic range northward. Several faunal elements from Winterswijk including *L. brononii* show resemblance to the roughly co-eval non-marine components of the Anisian Grès à Voltzia Formation in NE France, suggesting a paleobiogeographic connection between these regions in Western Europe.

Introduction

The four extant species of horseshoe crabs (Xiphosura) are often touted as an example of morphological conservatism. The fossil record of the horseshoe crabs stretches all the way back to the Ordovician and reveals a rather different picture (e.g., Rudkin et al., 2008; Van Roy et al., 2010; Lamsdell et al., 2022). This fossil record, which has seen a renewed interest in recent years (e.g., King et al., 2019; Tashman et al., 2019; Haug & Haug, 2020; Lamsdell, 2020; Bicknell et al., 2021, 2022; Lamsdell et al., 2021), displays a remarkable diversity, both in terms of morphological disparity and species richness (>80 extinct species) (Bicknell & Pates, 2020; Lamsdell, 2020). Furthermore, whereas modern-day horseshoe crabs are restricted to marine environments, multiple extinct species inhabited brackish and freshwater environments (Lamsdell, 2016, 2020). A phylogenetic analysis has shown that the transition from salt to freshwater environments occurred multiple times (Lamsdell, 2016).

One extinct species considered to have inhabited freshwater environments is *Limulitella brononii* (Schimper, 1853) from France (Lamsdell, 2016; Bicknell & Pates, 2020). Here, we present the first well-preserved horseshoe crab specimen from the Middle Triassic (Anisian) strata of the Winterswijk quarry complex in the eastern Netherlands, also attributable to *L. brononii*. We discuss the implications of this new find for our understanding of the paleoecology of the Winterswijk deposits.

Geological background

Whereas small exposures of Upper Triassic, Early Jurassic and Oligocene sediments have been reported from the Winterswijk quarry complex (51.967°, 6.781°) in the eastern Netherlands (Herengreen et al., 2005; Klompmaker & Van den Berkmortel, 2007; Klompmaker et al., 2010; Diependaal & Reumer, 2021), Middle Triassic (Anisian) carbonates dominate the exposures (Herengreen et al., 2005; Boekschoten & Van den Bosch, 2019; Van Hinsbergen et al., 2019). These Lower Muschelkalk deposits belong to the Vossenveld Formation and form an approximately 40 m thick outcrop (Hagdorn & Simon, 2010; During et al., 2019). These deposits consist of finely laminated micritic limestones interspersed with marly limestones, dolomite, clayey marls and dolomitic clay layers (Borkhataria et al., 2006; Klein et al., 2015; Maxwell et al., 2016; During et al., 2019). The sediments were deposited at the edge of the epicontinental Germanic-basin at a paleolatitude of $14 \pm 3^\circ\text{N}$, in paleogeographic conditions

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somewhat reminiscent of the Persian Gulf today (Van Hinsbergen *et al.*, 2019). They documented an environment that alternated between shallow marine and sabkha-like (hypersaline) intertidal mudflats (Oosterink & Winkelhorst, 2013; Klein *et al.*, 2015; During *et al.*, 2019). The intertidal nature of the deposits is emphasised by the preservation of algal laminates, polygonal mud cracks, burrowing traces, reptile trackways and reptile swimming traces (Knaust, 2013; Oosterink & Winkelhorst, 2013; Maxwell *et al.*, 2016; Schulp *et al.*, 2017; During *et al.*, 2019; Marchetti *et al.*, 2019). It should be noted that whereas saline conditions likely persisted throughout the entire stratigraphic profile, a hypersaline depositional environment has been suggested for the top section (top 10 m) of the stratigraphic profile in particular (During *et al.*, 2019).

The Anisian deposits at Winterswijk have yielded many different types of fossils. Reptiles, such as nothosaurs, pachypleurosaurs, placodonts and tanystropheids (Klein *et al.*, 2015; Heijne *et al.*, 2019; Spiekman *et al.*, 2019), range in preservation from isolated bones to almost complete skeletons (Heijne *et al.*, 2019). Furthermore, actinopterygian and chondrichthyan fish remains belonging to at least ten different genera have also been discovered (Haarhuis & Diependaal, 2019). An abundance of trace fossils has also been reported including invertebrate grazing traces, invertebrate burrowing traces, fish swimming traces, several different types of reptile trackways and reptile swimming traces (Knaust, 2013, 2015; Schulp *et al.*, 2017; Marchetti *et al.*, 2019). In addition, many different invertebrate fossils have also been described, including mollusks (18 bivalve species, 2 gastropods and 1 ammonite), brachiopods (2 species), possible jellyfish and representatives of several clades of arthropods (e.g., Oosterink, 1981; Akkerman & Mulder, 2012; Oosterink & Winkelhorst, 2013; Klompmaker, 2019; Van Eldijk *et al.*, 2019). Amongst these arthropod finds are the remains of three species of lobsters, *Clytiopsis argentoratensis* Bill, 1914, *Oosterinkia neerlandica* Klompmaker & Fraaije, 2011, and *Audogaster* cf. *P. spinosa* (Assmann, 1927), which constitute the oldest known lobsters from the Netherlands (Klompmaker & Fraaije, 2011). Furthermore, the isopod *Gelrincola winterswijkensis* Schädel *et al.*, 2020, and the cycloid *Halicyno oosterinkorum* Schweitzer *et al.*, 2019, are only known from Winterswijk and are both only known from single specimens (Schweitzer *et al.*, 2019; Schädel *et al.*, 2020). In addition, Winterswijk is the only Muschelkalk outcrop that has yielded a small assemblage of insect remains, including, amongst others, the elytron of a beetle (Coleoptera), a partial dragonfly wing (Odonata) and a complete forewing of a cockroach (Blattodea) (Van Eldijk *et al.*, 2017). In addition, a single, poorly preserved horseshoe crab has previously been described from Winterswijk by Hauschke *et al.* (2009). This specimen was tentatively assigned to the genus *Limulitella* (Hauschke *et al.*, 2009), which was subsequently confirmed by Zuber *et al.* (2017).

The occurrence of the bivalve *Myophoria vulgaris* (von Schlotheim, 1820), the occurrence of the ammonite *Beneckeia buchi* (von Alberti, 1834) and palynological evidence (Herngreen *et al.*, 2005) firmly date the outcrops at Winterswijk to the Anisian stage of the Triassic (247.2–242 million years ago) (Akkerman & Mulder, 2012; Cohen *et al.*, 2013). Originally, 39 stratigraphic horizons were identified in the outcrops at Winterswijk by Oosterink (1986). However, during expansion of the quarry complex, new layers were identified by the Working Group Muschelkalk Winterswijk, which were added to the profile and numbered according to the system established by Oosterink (1986) (see Van Eldijk *et al.*, 2017; During *et al.*,

2019). Amongst these newly added horizons is an approximately 1.20 m thick layer, known as layer 43, in which the specimen we describe here, RGM.1333509, was discovered by one of the authors (HW). Layer 43 has previously yielded exceptionally well-preserved fossil fishes (Maxwell *et al.*, 2016), insect remains (Van Eldijk *et al.*, 2017) and the only known specimen of the isopod *G. winterswijkensis* (Schädel *et al.*, 2020). Based on the occurrence of the bivalve *Neoschizodus orbicularis* (Bronn, 1837), the top section of the profile at Winterswijk, to which layer 43 belongs, has been tentatively dated to the youngest substage of the Anisian (Illyrian) (Hagdorn & Simon, 2010). Herngreen *et al.* (2005) suggested that part of the top section of the profile (up until approximately layer 37) belonged to the older Bithynian substage of the Anisian based on palynological data. A more recent work (During *et al.*, 2019) suggested that the exposed Muschelkalk layers span the Bithynian, Pelsonian and the earliest Illyrian, with layer 43 being ascribed to the earliest Illyrian.

Methods and materials

The specimen described here was found in August 2020 in the top section of the aforementioned layer 43 in the Winterswijk quarry (Fig. 1). The fossil specimen consists of a part and its counterpart. The specimen is housed in the collection of the Naturalis Biodiversity Center, Leiden, The Netherlands (RGM.1333509). Photographs were made using a Cannon Eos 77D camera, a Cannon EF 18–55 mm IS STM-lens and a Sigma 105 mm F2.8 EX DG OS HSM Macro lens. Scale bars were inserted, images were cropped and compound images were stitched together using Adobe Photoshop 2021. We used limulid xiphosuran terminology after Bicknell *et al.* (2021, fig. 1).

Systematic palaeontology

Subphylum Chelicerata Heymons, 1901.

Class Xiphosura Latreille, 1802.

Order Xiphosurida Latreille, 1802.

Suborder Limulina Richter & Richter, 1929.

Superfamily Limuloidea Zittel, 1885.

Family Limulidae Leach, 1819.

Genus *Limulitella* Størmer, 1952.

Type species

Limulites bronnii (Schimper, 1853).

Other species

Limulitella (?) *liasokeuperensis* (Braun, 1860); *L. tejraensis* Błażejowski *et al.*, 2017; *L. (?) volgensis* (Ponomarenko, 1985).

Limulitella bronnii (Schimper, 1853)

Figures 2, 3, and 4.

Limulites bronnii Schimper, pp. 6–7, pl. 3.

Limulites bronnii Schimper; Bill, 1914, pp. 327–330, pl. 15.8.

Limulus sandbergeri Kirchner, 1923, pp. 635–636, fig. on p. 635.

? *Limulus bronnii* (Schimper); Pfannenstiel, 1928, pp. 536–541, figs. 1 and 2.

Limulitella bronnii (Schimper); Størmer, 1952, fig. 1K.

Limulitella bronnii (Schimper); Gall, 1971, p. 35, pl. 7.1.

Limulitella bronnii (Schimper); Mader, 1984, fig. 5.

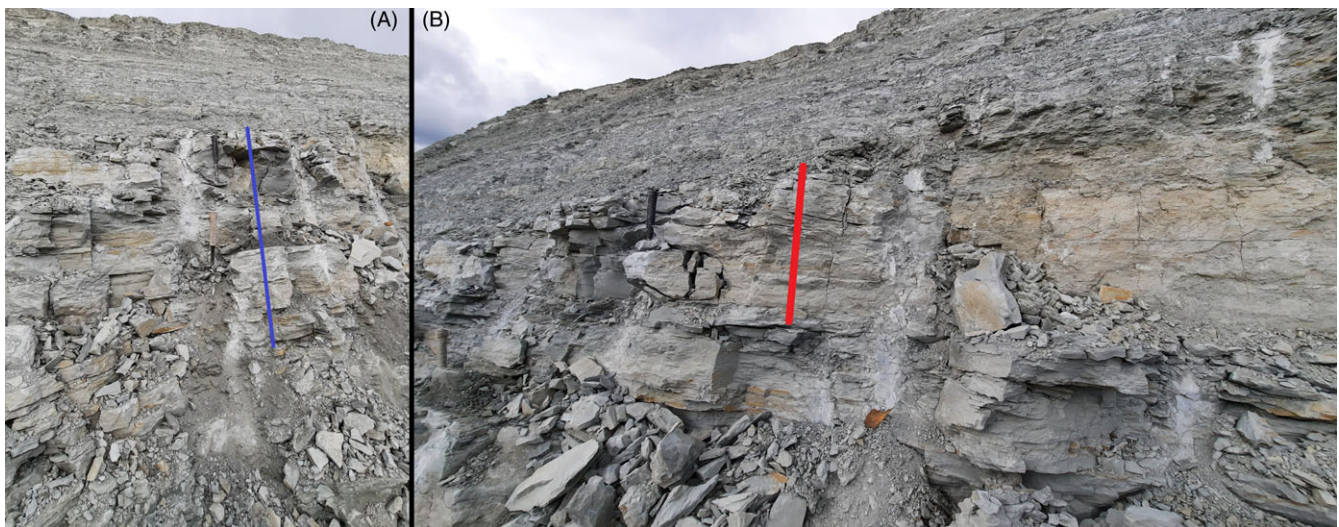


Fig. 1. Layer 43 of the Muschelkalk exposed in the Winterswijk quarry complex (~30 m away from the location where specimen RGM.1333509 was found), the eastern Netherlands. (A). Blue line indicates entire layer 43. Hammer is ~30 cm long. (B). Red line indicates the upper part of layer 43 in which the horseshoe crab was found. Pictures by Gerard Goris taken in April–May 2022.

Limulitella bronni (Schimper); Gall & Grauvogel-Stamm, 1999, fig. 8.

Limulitella bronni (Schimper); Weber & Lebrun, 2014, p. 11, figs. 3 and 4.

Limulitella bronni (Schimper); Röhling & Heunisch, 2010, fig. 5.

Limulitella bronni (Schimper); Bicknell & Pates, 2020, fig. 28A.

Limulitella bronni (Schimper); Bicknell et al., 2021, fig. 4C.

Diagnosis

Prosoma including genal spine wider than long (l/w ratio ~ 0.75). Prosomal length $\sim 30\%$ longer than thoracetrion, as measured along axis. Genal spines not clearly separated from occipital bands, making this part relatively wide. Posterior margins of genal spines straight or nearly so, at $\sim 140^\circ$ from posterior margin of central part of prosoma. Ophthalmic ridges somewhat sinuous. Cardiac margins straight, somewhat converging to anterior prosoma. Cardiac ridge present. Thoracetrion subtriangular, with 6–7 movable spines laterally and two fixed spines posteriorly adjacent to longitudinal axis. Apodemal grooves converging to posterior thoracetrion. Long medial ridge present. Flange with distinct groove, somewhat diverging from lateral margin of thoracetrion toward posterior thoracetrion. Telson nearly as long as combined length of prosoma and thoracetrion [based on specimens in Schimper (1853), Gall (1971), Bicknell & Pates (2020), and herein].

Studied material

RGM.1333509.

Type material

Holotype: UNISTRA.2015.0.50968 (collections de paléontologie, Jardin des sciences de l'Université de Strasbourg), figured in Weber & Lebrun (2014, p. 11, fig. 4) and herein (Fig. 4b).

Description

Prosoma including genal spine wider than long (l/w ratio ~ 0.75), with faint ridge along outer margin. Prosomal length $\sim 30\%$ longer

than thoracetrion, as measured along axis. Anterior portion prosoma not preserved. Genal spines not clearly separated from occipital bands, making this part relatively wide. Posterior margin of genal spine straight or nearly so, at $\sim 140^\circ$ from posterior margin of central part of prosoma. Ophthalmic ridges sinuous due to presence of eye, anterior portion not exposed. Eyes directed laterally, convex toward lateral side, ~ 4 times as long as wide and height comparable to width. Cardiac margins straight, converging to anterior prosoma. Cardiac ridge most prominent at base of axis, fainter more anteriorly. Ocelli not exposed. Thoracetrion subtriangular, with 6 partially preserved, non-decorated, flattened, posterolaterally directed spines on left lateral margin. Lateral margins of thoracetrion with small triangular extensions in between aforementioned spines and with faint, straight ridge slightly more inward. Apodemal grooves straight overall, may contain small beads, converging to posterior thoracetrion. Long medial ridge extending towards posteriormost preserved part, more prominent than cardiac ridge. Flange with distinct groove, initially diverging from lateral margin of thoracetrion toward posterior thoracetrion, then appears to split and reconnect more posteriorly, perhaps due to preservation. Telson and posteriormost part thoracetrion not preserved. (Description based on new specimen, RGM.1333509.)

Remarks

We assign the new specimen to *Limulitella bronni* because the specimen herein resembles the figured specimens of *L. bronni* in detail (e.g., Gall, 1971, pl. 7.1; Weber & Lebrun, 2014, p. 11, figs. 3 and 4; Bicknell & Pates, 2020, fig. 28A), including the holotype (Fig. 4) that is less well preserved than other specimens. The Winterswijk specimen also originates from the Anisian and is also from Western Europe. A diagnosis of *L. bronni* is provided for the first time herein.

The new specimen cannot be ascribed to *Limulitella* (?) *liaso-keuperensis* from the Early Jurassic of Germany because representatives of this species have narrower genal spines and proportionally smaller eyes (Braun, 1860, fig. 1; Hauschke & Wilde, 1984, figs. 1 and 3; Bicknell & Pates, 2020, fig. 30D). *Limulitella tejaensis* from the Middle Triassic (Anisian–early Ladinian) of Tunisia,



Fig. 2. Photo plate of specimen RGM.1333509 (part), *Limulitella bronniei* (Schimper, 1853) from the Anisian of Winterswijk. (A) shows a top view of the specimen. (B) A detail photograph of the compound eye and the ophthalmic ridge. (C) Detail of the opisthosoma. (D) (composite image) A photo taken from an angled perspective. (E) (composite image) Display of top view of the specimen but under oblique lighting. Scale bars: 10.0 mm.

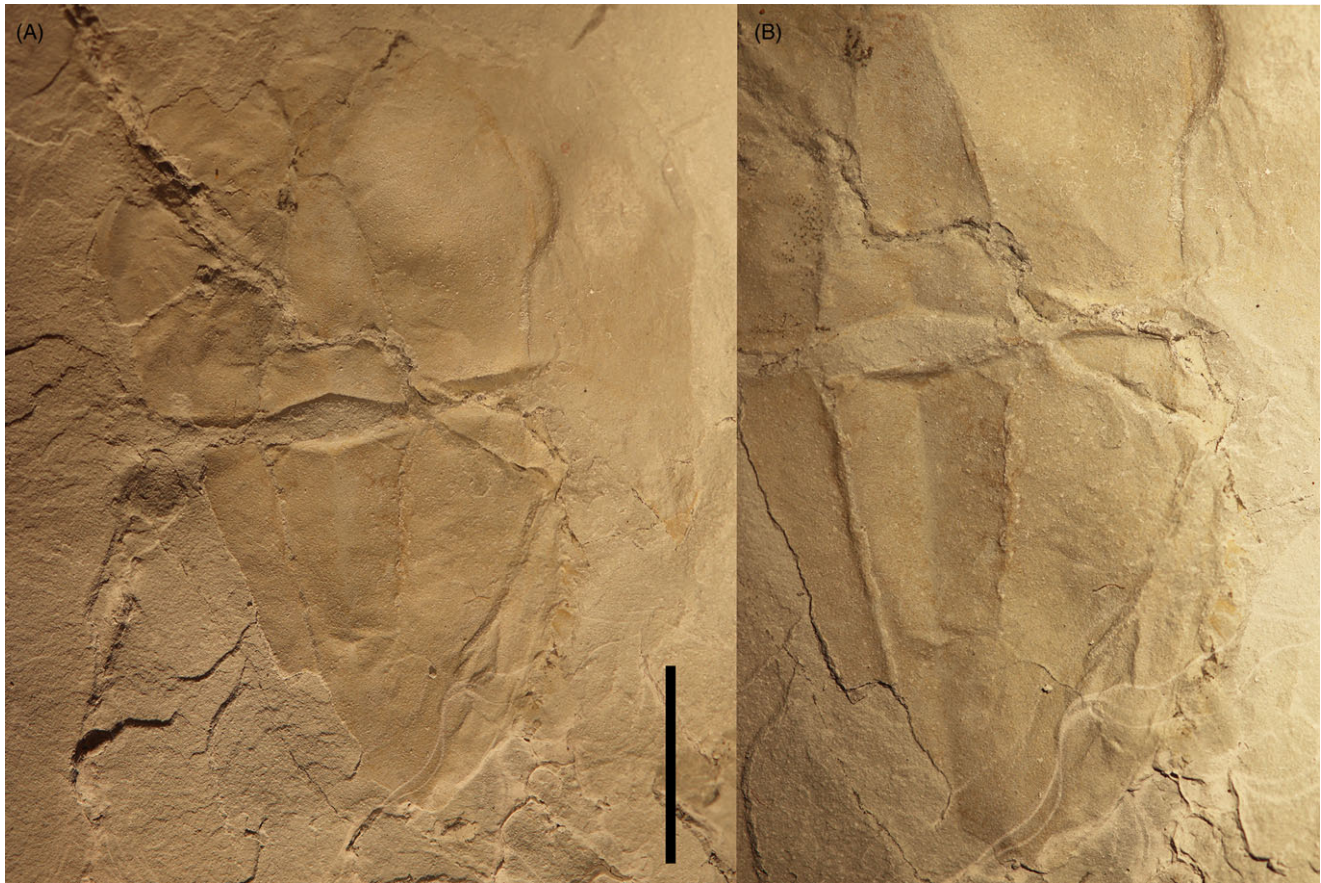


Fig. 3. Photo plate of specimen RGM.1333509 (counterpart), *Limulitella bronnii* from the Anisian of Winterswijk. (A) A top view of the complete specimen. (B) A more detailed photograph. Scale bar: 10.0 mm.

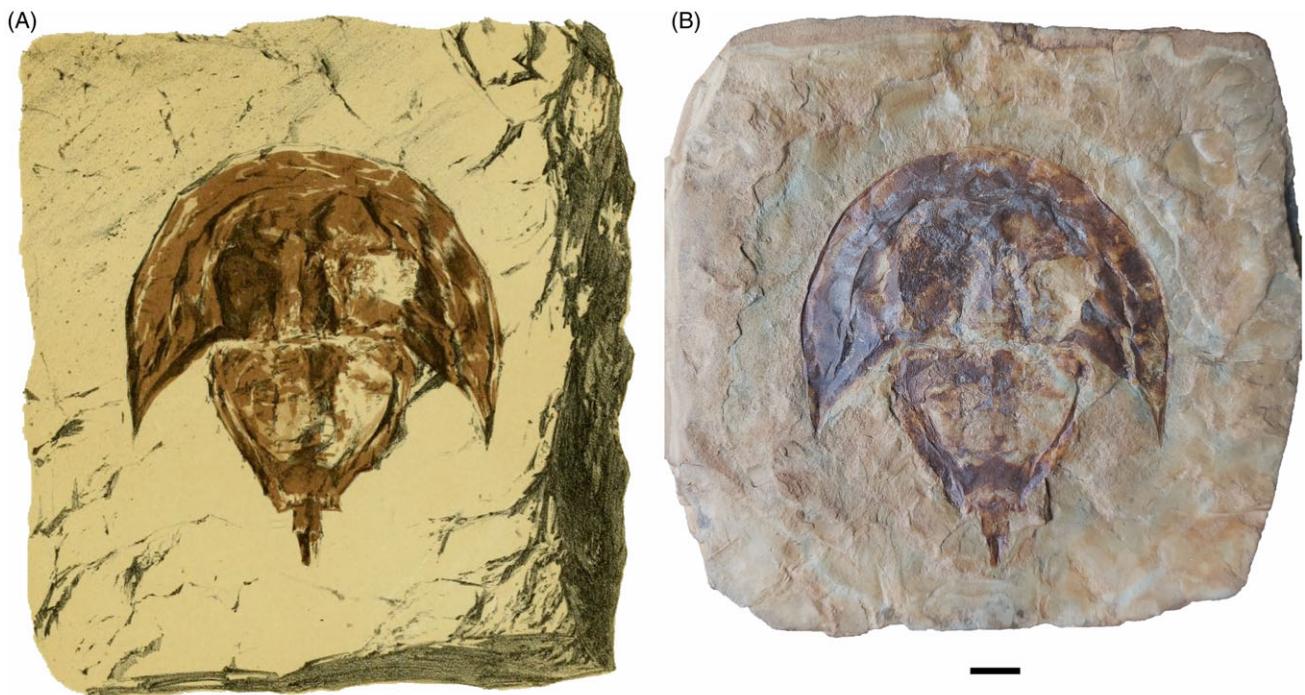


Fig. 4. Holotype of *Limulitella bronnii* (Schimper, 1853) from the Middle Triassic (lower Anisian) Grès à Voltzia Formation of the Upper Buntsandstein in NE France. (A). Drawing in Schimper (1853, pl. 3) interpreted to be inverted. (B). Photo of UNISTRA.2015.0.50968, courtesy of Lea Grauvogel-Stamm and used with permission. Scale bar: 10.0 mm.

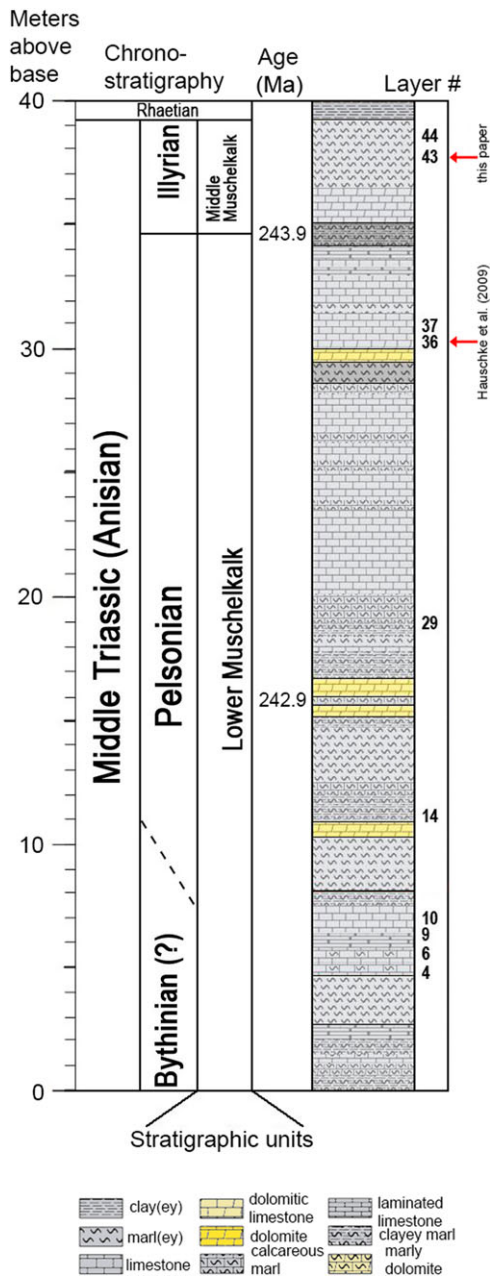


Fig. 5. Stratigraphy of the exposed Muschelkalk layers at the Winterswijk quarry complex in the eastern Netherlands with the horseshoe crab finds indicated. Modified from During *et al.* (2019, figs. 1 and 6), used with permission.

morphologically close to *L. bronniei*, appears to have an ophthalmic ridge that is more S-shaped overall and the interophthalmic ridge of *L. tejaensis* is more sinuous than the specimen herein (Błażejowski *et al.*, 2017, fig. 3). *Limulitella* (?) *volgensis* from the Early Triassic (Olenekian) of Russia exhibits a lower (inner) margin of the genal spine at a substantially lower angle relative to the axial posterior margin of the prosoma than in the specimen herein (compare Bicknell *et al.*, 2021, fig. 4F).

While Lamsdell (2020) put both *Limulitella henkeli* (von Fritsch, 1906) and *L. vicensis* (Bleicher, 1897) in different genera, Bicknell *et al.* (2021) did not. Therefore, we also compare *L. bronniei* to these species. The specimen herein does not compare favourably

with *L. henkeli* from the Middle Triassic (Anisian) of Germany because representatives of this German species have a clear angle on the posterior side of the genal spine (or the occipital band is absent) (Bicknell *et al.*, 2021, fig. 4E), which is not seen in the specimen herein. *Limulitella vicensis* from the Late Triassic (Carnian-Norian) of France (Lamsdell, 2020, fig. 6D; Bicknell *et al.*, 2021, fig. 4A) appears to have smaller eyes and the ophthalmic ridge is straighter.

Limulitella bronniei was first reported from a quarry with Buntsandstein deposits near Wasselonne in NE France (Schimper, 1853), ~500 km south of Winterswijk, from the Middle Triassic (lower Anisian) Grès à Voltzia Formation of the Upper Buntsandstein (Gall & Grauvogel-Stamm, 2005), and was considered to be part of the freshwater to brackish fauna of this formation. Schimper (1853, p. 7) reported that the specimen was found in 1851. Weber & Lebrun (2014, p. 11, fig. 4) figured a specimen reminiscent of the holotype, shown also herein (Fig. 4b). The locality information and date when the specimen was found provided by Weber & Lebrun (2014) (Soultz-les-Bains [~10 km south of Wasselonne], in the early part of the 19th century) do not fully match the information provided by Schimper (1853), but the features of the fossil and the size match the drawing and description by Schimper (1853, pl. 3), so we accept this specimen to represent the holotype. The drawing in Schimper (1853) may have been inverted due to the use of an engraving technique (e.g., Gould, 1995; Allmon, 2007; Hyžný, 2014) because the rock surrounding the fossil differs markedly in outline when comparing the drawing to the photographed specimen (Fig. 4), but the horseshoe crab is identical in the placement of many features (hole in between the cardiac margin and the ophthalmic ridge on the right side, details near telson, etc.). In that case, one would represent the part and the other the counterpart. Alternatively, Schimper (1853) did not depict the rock surrounding the specimen accurately.

Bill (1914) figured a different specimen from the same locality near Wasselonne. Gall (1971, p. 35) and Weber & Lebrun (2014) reported this species from the Grès à Voltzia Formation exposed at several localities in the same area in NE France the type specimen originated from. The species has also been reported from Germany. A small specimen ascribed to this species was reported from Villingen in Baden-Württemberg, SW Germany, from the fluvial Plattensandstein Formation (Pfannenstiel, 1928) of the Upper Buntsandstein, which is Middle Triassic (early Anisian (Aegean)) in age (Hagdorn & Nitsch, 2009; Hochuli *et al.*, 2020). Earlier, Kirchner (1923) described *Limulus sandbergeri* from the Plattensandstein of Bad Brückenau, Unterfranken, in southern Germany, a species subsequently synonymised with *L. bronniei* (e.g., Lamsdell, 2020).

A specimen provisionally (cf.) ascribed to this species from lowermost Jurassic marine deposits of Germany by Wincierz (1960) should not be considered conspecific because only the ventral side is preserved, implying that too few diagnostic characters of this species are available to assess this hypothesis. Moreover, the temporal gap of ~50 million years renders conspecificity highly unlikely.

The new specimen represents the third country from which this species is recorded. It is also the youngest representative of the species because the specimen originates from the late part of the Anisian (earliest Illyrian). The temporal range of this species within the Anisian is now a few million years.

Stratigraphic and geographic distribution

Winterswijk quarry complex (sector M18, at approximately 51.96750°N, 6.78172°E), The Netherlands. Vossenveld Formation, upper part Layer 43, uppermost substage of the Anisian (earliest Illyrian).

Discussion and conclusions

Horseshoe crabs from the Netherlands are rare. Other than the specimen herein and the one from the same locality reported previously (Hauschke et al., 2009; Zuber et al., 2017), we are only aware of various Late Carboniferous (Westphalian) horseshoe crabs from the mine area in the southern part of the Limburg province in the southeastern Netherlands (Van der Heide, 1951). Van der Heide (1951) reported on *Belinurus reginae* Baily, 1863, *Belinurus* sp., *Prestwichianella rotundata* (Prestwich, 1840), *Euproops cambrensis* Dix & Pringle, 1929, *E. danae* (Meek & Worthen, 1865), *E. communis* Van der Heide, 1951, *E. orbicularis* Van der Heide, 1951, and *Euproops* sp.

The first-reported horseshoe crab from Winterswijk identified as *Limulitella* sp. (Hauschke et al., 2009; Zuber et al., 2017) originated from layer 36, interpreted to be deposited during the Pelsonian substage (During et al., 2019). Thus, the specimen herein from the upper part of layer 43 is younger, perhaps a few hundreds of thousands of years (During et al., 2019, fig. 6) (Fig. 5). Diedrich (2011, fig. 5D) figured a horseshoe crab trackway (*Kouphichnium* Nopcsa, 1923) from Winterswijk, but the layer in which this specimen was found was not provided.

Little terrigenous influence was reported within layer 43 in During et al. (2019, fig. 1) based on a terrigenous weight percentage analysis (lithogenic wt% TGA). The observations of one of the authors (HW) indicate that the amount of marine versus terrestrial influence may vary both within the profile of 1.20-m-thick layer 43 as well as across the different places at which layer 43 has been sampled. Some parts appear fully marine given the presence of marine fish fossils (Wijngaarden et al., 2019), whereas other parts appear to have a terrestrial signal because of the presence of plant and insect fossils (e.g., Van Eldijk et al., 2017). Lobsters, fishes and insects found by one of us (HW) within layer 43 originate from horizons lower than the layer where the horseshoe crab originated from. Lobsters described previously, for which the exact stratigraphic layer is unknown, were interpreted to have inhabited a low energy, stressed environment with fluctuating salinity levels (Klompmaaker & Fraaije, 2011). The specific horizon in which the horseshoe crab was found does not contain many other body fossils (pers. obs. HW). Although more detailed analyses within layer 43 would be welcome, many of the other faunal elements present in layer 43 suggest the horseshoe crab is unlikely to be marine. This suggestion is further corroborated by the fact that previous records of *L. bronniei* in Germany and France are considered non-marine (see above).

In addition to the horseshoe crab species herein, another part of the Winterswijk fauna resembles that of the interpreted non-marine faunal elements of the Grès à Voltzia Formation (Middle Triassic, lower Anisian) in the Vosges mountains of NE France (see Gall & Grauvogel-Stamm, 2005, table 1). In terms of the brackish/freshwater elements, a lobster, a cyclidan crustacean and a bivalve overlap. The lobster *Clytiopsis argentoratensis* Bill, 1914, is found in both deposits, and this species is the most common

lobster at Winterswijk (Klompmaaker & Fraaije, 2011). Congenerics of the cyclidan *Halicynne* are also known from both faunas (Gall & Grauvogel-Stamm, 2005; Schweitzer et al., 2019). For bivalves, *Myophoria vulgaris* occurs in both faunas and is even dominant at Winterswijk (Van Eldijk et al., 2019). However, *M. vulgaris* occurs throughout the stratigraphic column at Winterswijk (Oosterink, 1981, 1986), and others have considered *M. vulgaris* to be also marine (Szulc et al., 2015). More terrestrial elements have been reported from both faunas such as plants and insects (e.g., Gall & Grauvogel-Stamm, 2005; Van Eldijk et al., 2017).

In summary, the specimen of *L. bronniei* presented here expands the temporal range of this species. Furthermore, as this species is most probably non-marine, it could indicate some freshwater/terrestrial influx in the top section of the Winterswijk quarry complex. Finally, this specimen highlights the overlap between the fauna from Winterswijk and the fauna of the Grès à Voltzia Formation in NE France.

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