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Bedding plane with several Lingularia zenkeri *specimens (H. Winkelhorst collection, no. CHW518, photograph by R. Heerschop).*

Non-arthropod invertebrates from the Middle Triassic of Winterswijk

U vindt een samenvatting aan het eind van de tekst.

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Abstract | **This article covers all macroinvertebrates not ascribed to the Arthropoda found in the Muschelkalk (Middle Triassic, Anisian) of Winterswijk. The Muschelkalk contains 18 bivalve species, two gastropod species, two brachiopod species, one ammonite species, and a putative jellyfish taxon. Five bivalve species not previously photographed from Winterswijk are figured herein. Briefly, we present the invertebrates known from the Upper Triassic shales and Lower Jurassic clays of Winterswijk. The invertebrates from the Muschelkalk suggest deposition in a hypersaline and stressed environment.**

Invertebrate taxa dominate the fossil record in terms of both diversity and abundance, and they have been used extensively to interpret paleoenvironmental conditions and for relative dating. We describe the non-arthropod macroinvertebrate body fossils found within the Middle Triassic (Anisian) Muschelkalk strata in the Winterswijk quarries, the eastern Netherlands. Many groups have received little attention over the last decades since the work of Oosterink (1986), particularly the bivalves, gastropods, and brachiopods. The goal of this paper is threefold: to (1) discuss the bivalves, gastropods, cephalopods, brachiopods, and possible jellyfish fossils from the Muschelkalk; (2) highlight the use of these invertebrates for the paleoenvironmental interpretation and dating; and (3) briefly highlight the invertebrate fossils found in the uppermost Triassic and lowermost Jurassic deposits of Winterswijk.

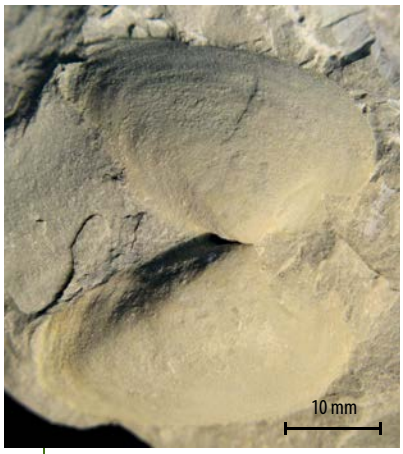

FIGURE 1. | Myophoria vulgaris, *A. Haarhuis collection (no. AHWW 0251), photograph by R. Heerschop.*

Mollusca

Bivalvia

Eighteen bivalve species are known from Winterswijk thus far (Table 1). Bivalves constitute the most diverse invertebrate clade at Winterswijk, but they have not been studied since Oosterink (1986). Consequently, the true number of bivalve species is subject to change. Furthermore, the stratigraphic distribution of taxa has not been examined in detail (Dertien & Dertien-te Voortwis, 1975; Oosterink, 1981; Hagdorn & Simon, 2010; Oosterink & Winkelhorst, 2013). The identification of many bivalves is compounded by post-depositional dissolution, so that they are only preserved as internal molds (steinkerns) and external moulds, as is common in the Muschelkalk (Oosterink, 1981; Klug *et al*., 2005). In some cases, recrystallization has occurred between the internal and the external molds due to the infiltration of carbonate-rich pore waters (see for example Figure 2D) (Oosterink, 1981; Hautmann & Hagdorn, 2013). Thus, a more extensive scientific study of the bivalves from Winterswijk is warranted. Here, we provide an overview of the existing literature and provide images of five species from Winterswijk that have not been photographed previously.

The most common bivalve species in the Muschelkalk are *Myophoria vulgaris* and *Myophoria* cf. *M. germanica* (Dertien & Dertien-te Voortwis, 1975; Oosterink, 1981, 1986, 2008, 2012). These species are found throughout the stratigraphic column, constitute more than 96% of all bivalve specimens, and their abundance can be as high as 99% at certain levels (Oosterink, 1981, 1986). These species are distinguished mainly by the presence or absence of ribs on their shell: *M. vulgaris* (Fig. 1) bears one pronounced rib and two weak ribs, whereas *Myophoria* cf. *M. germanica* has one blunt and one or two weak ribs (Dertien & Dertien-te Voortwis, 1975; Oosterink, 1981, 1986). There is some debate as to which of these species is the most abundant. Dertien & Dertien-te Voortwis (1975) claimed that the majority of bivalves actually represented *Neoschizodus orbicularis* (formerly *Myophoria orbicularis*). However, Oosterink (1981) mentioned that *Myophoria* cf. *M. germanica* was the most common bivalve, but Oosterink (2008, 2012) and Oosterink & Winkelhorst (2013) subsequently stated that the majority of bivalves belonged to *M. vulgaris*. These different opinions were probably somewhat exacerbated by the often poor, moldic preservation of the bivalves and the fact that not all taxa are equally abundant throughout the strata exposed in the quarries. For example, Hagdorn & Simon (2010) found that *N. orbicularis* only occurs within the top 3 m of the Winterswijk Muschelkalk outcrops. The latest assessment, indicating that *M. vulgaris* is the most common species, is in agreement with faunal abundances at other Muschelkalk localities in west-central Europe (Szulc, 2000).

In his descriptions of the bivalve fauna, Oosterink (1981, 1986) stated that *Neoschizodus orbicularis, Modiolus triquetra,* and *Pleuromya elongata* (Fig. 2B) are fairly common. Less common are *Gervillia modiolaeformis* (Fig. 2A), *Hoernesia socialis* (Fig. 2D), *Pleuromya brevis*, and *Homomya althausi* (Fig. 2E). Rare species include *Gervillia jenensis, Entolium discites, Entolium morrisi* (Fig. 2C), *Pseudomyoconcha goldfussi, Myoconcha gastrochaena, Pleuromya pulchra,* and *Homomya albertii* (Fig. 2F). In their description of the Vossenveld Formation, to which the strata outcropping at Winterswijk belong, Hagdorn & Simon (2010) mentioned two additional species of unknown abundance: *Bakevillia costata* (Fig. 2G) and *Arcomya fassaensis*. To our knowledge, specimens of *E. morrisi, G. modiolaeformis, Hom. albertii, Hom. althausi,* and *B. costata* have not been photographed previously from Winterswijk (compare Oosterink, 2012).

Gastropoda

Two species of gastropods (snails) are known from Winterswijk: *Loxonema obsoleta* (Fig. 3B) and *Naticopsis* sp. (Oosterink, 1986, 2012). Gastropods are relatively rare and, similar to the bivalve shells, occur only as molds as a result of early diagenetic dissolution. It has been suggested that *L. obsoleta* is the producer of the enigmatic trace fossil *Kimberichnus teruzzii*, which has also been found in Winterswijk (Knaust, 2015). These traces are thought to have been produced by the scraping action of the gastropod radula on matgrounds (Knaust, 2015).

Cephalopoda

Cephalopods are also rare in the Winterswijk quarries and only a single species

BIVALVES (18 SPECIES)	
Arcomya fassaensis (Salomon, 1895)	*Modiolus triquetra* von Seebach, 1862
Bakevillia costata (von Schlotheim, 1820)	*Myoconcha gastrochaena* Giebel, 1856
Entolium discites (von Schlotheim, 1820)	*Myophoria* cf. *M. germanica* Hohenstein, 1913
Entolium morrisi (Giebel, 1856)	*Myophoria vulgaris* (von Schlotheim, 1820)
Gervillia jenensis Passarge, 1891	*Neoschizodus orbicularis* (Bronn, 1837)
Gervillia modiolaeformis Giebel, 1856	*Pseudomyoconcha goldfussi* (Dunker, 1849)
Hoernesia socialis (von Schlotheim, 1823)	*Pleuromya brevis* Assmann, 1915
Homomya albertii (Goldfuss, 1841)	*Pleuromya elongata* (von Schlotheim, 1823)
Homomya althausi (von Alberti, 1864)	*Pleuromya pulchra* Assmann, 1915
GASTROPODS (2 SPECIES)	**BRACHIOPODS (2 SPECIES)**
Loxonema obsoleta (Sowerby & Murchison 1839)	*Coenothyris* cf. *C. ecki* (von Schlotheim, 1820)
Naticopsis sp.	*Lingularia zenkeri* (von Alberti, 1864)
AMMONITES (1 SPECIES)	**MEDUSOZOA? (1 SPECIES?)**
Beneckeia buchi (von Alberti, 1834)	Putative jellyfish

Table 1. | *Overview of all the marine non-arthropod invertebrates known from the Middle Triassic (Anisian) Muschelkalk of Winterswijk (data from Oosterink, 1981, 1986, 2010, 2012; Hagdorn & Simon, 2010; Oosterink & Winkelhorst, 2013). Oosterink (1981, 1986) also listed* Myophoria *sp.,* Gervillia *sp.,* Homomya *sp., and* Pleuromya *sp., which were often represented by poorly preserved specimens. These taxa could be conspecific to species from the same genus listed in the table, so they have not been included.*

of ammonite has been recorded: *Beneckeia buchi* (Fig. 3C) (Boekschoten, 1972; Dertien, 1972; Tjalkens, 1975). On the basis of its sutures, *B. buchi* is considered to have been an inhabitant of shallow waters (Akkerman & Mulder, 2012).

Brachiopoda

Although brachiopod shells superficially resemble those of bivalves, this similarity is due to convergence, as these two taxa are only distantly related. For example, within the shell, brachiopods have a specialized filter feeding organ known as the lophophore (Moore, 2001), which molluscs lack. In Winterswijk, brachiopods are represented only by two species: the inarticulate brachiopod *Lingularia zenkeri*, which is relatively common (Fig. 3A), and the articulate brachiopod *Coenothyris* cf. *C. ecki*, of which only a single specimen has been reported (Oosterink, 1986, 2010). Some have argued that *Lingularia zenkeri* is possibly synonymous with *Lingularia tenuissima* (Sykora *et al*., 2011), a taxon also mentioned by Oosterink (1986). Unlike molluscan shells, the shells of *L. zenkeri* did not undergo dissolution because they mostly consist of organophosphate, which is more resistant to dissolution than the calcium carbonate of which most molluscan shells are made (Moore, 2001).

Medusozoa?

One of the most enigmatic finds from Winterswijk concerns circular structures on the bedding plane interpreted as remains of jellyfish (Medusozoa) see Figure 3D (Oosterink & Winkelhorst, 2013). However, assigning such structures to jellyfish can be rather tricky because cnidarians are composed entirely of soft tissue, only leaving behind imprints if any. Consequently, Cadée (2013) was not convinced by the interpretation of these structures as jellyfish, instead ascribing some of these structures to scratch circles. Scratch circles are circular sedimentary structures formed when a tethered organism passively rotates, scratching into the surrounding sediment (Jensen *et al.,* 2018). Furthermore, if one strictly adheres to the criteria set by Young & Hagadorn (2010: p. 217), these structures cannot be ascribed to jellyfish because 'clear evidence of preburial transport, deformation, tearing, and/or desiccation' is lacking. Moreover, the central part of the structure does not show clear evidence of a gonad morphology, which would have allowed for unequivocal assignment to jellyfish.

However, several features of these circular structures do support a jellyfish interpretation. First of all, the thickened circular edge and the presence of some unclear structure in the center are consistent with the morphology of some jellyfish fossils. Furthermore, it seems probable that the exceptional preservational conditions at Winterswijk, as evidenced by the well-preserved wave ripples that occur within the same layer as these circular structures (Young & Hagadorn, 2010; Oosterink & Winkelhorst, 2013), would allow for the preservation of jellyfish. The possible interpretation of these structures as gas bubbles is inconsistent with the fact that microscopic analyses have revealed no clear disturbance of the lamination within the structures (Oosterink & Winkelhorst, 2013). Scratch circles could explain some of the structures, such as Figure 12 in Oosterink & Winkelhorst (2013). However, almost all of these structures lack numerous concentric circles and have a clear thickened edge, which makes an interpretation of all structures as scratch circles unlikely. Considering all of the above, we consider these structures putative jellyfish fossils for now.

Relevance

What is the relevance of these non-arthropod invertebrates for the general interpretation of the Muschelkalk deposits at Winterswijk? First of all, these taxa are important for the relative dating of the deposits at Winterswijk. The presence of *Beneckeia buchi* and *Myophora vulgaris* indicates that the majority of these strata belong to the Bithynian substage of the Anisian stage (Rieppel, 1995; Renesto *et al*., 2014). Additionally, the occurrence of *Neoschizodus orbicularis* in the uppermost part of the section suggest that a correlation with the Illyrian substage of the Anisian is possible (Hagdorn & Simon, 2010), but this inference is inconsistent with the palynological data obtained by Herngreen (2005a, 2005b) (see also Van Eldijk *et al*., 2017).

Furthermore, these non-arthropod invertebrates are also informative for reconstructing the paleoenvironment. The size of the bivalves (including *M. vulgaris*), ammonites, and gastropods found at Winterswijk appears small compared to their conspecifics from other localities (Faber, 1966; Oosterink, 1981). In addition, the lobsters, the fishes, and reptiles from Winterswijk were also mentioned to be relatively small (Oosterink, 1981;

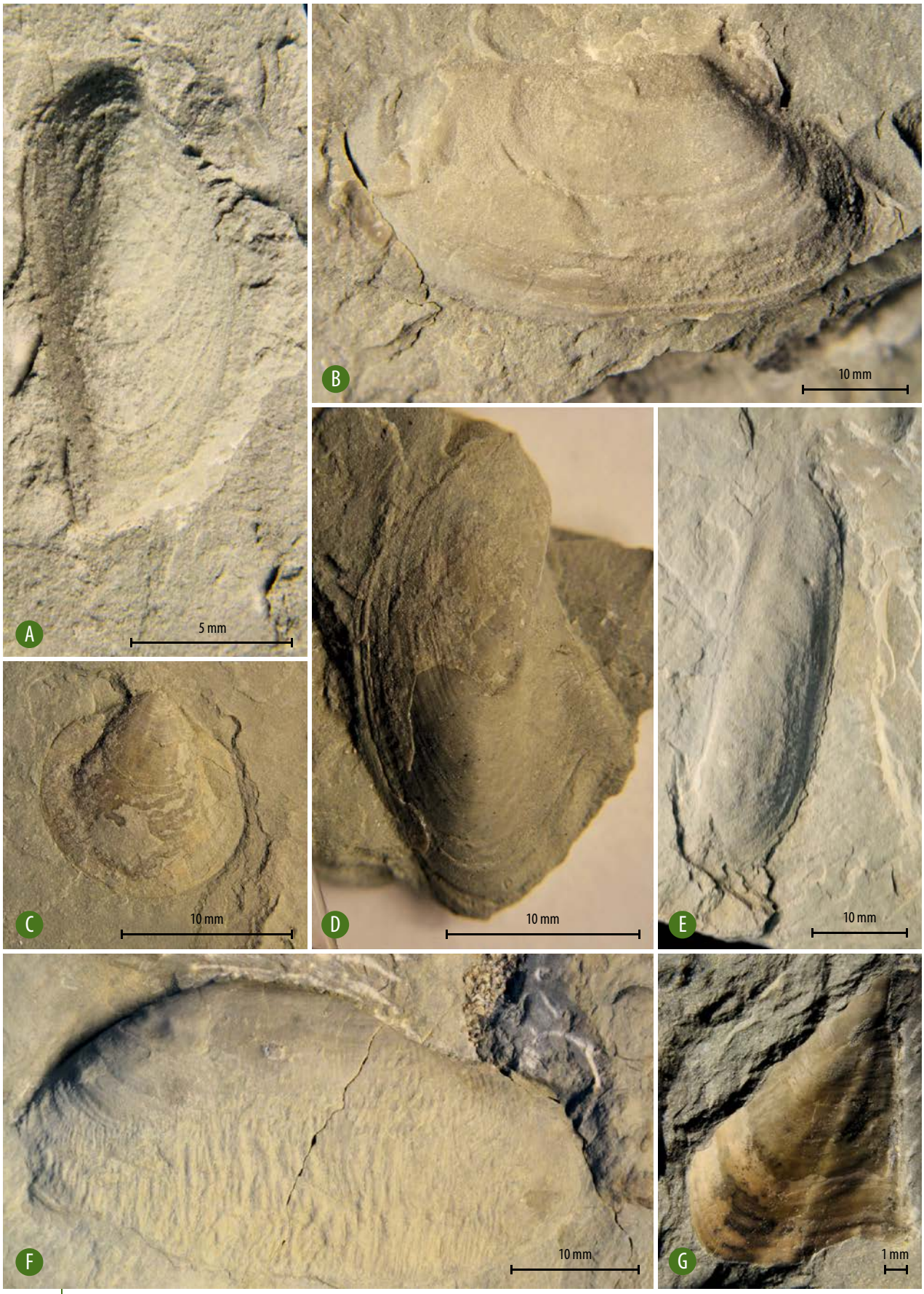

FIGURE 2. | *Selected taxa to illustrate the bivalve diversity in the Middle Triassic Muschelkalk of Winterswijk (all specimens: A. Haarhuis collection; all photographs by R. Heerschop). A:* Gervillia modiolaeformis *(no. AHWW 0203). B:* Pleuromya elongata *(no. AHWW 0230). C:* Entolium morrisi *(no. AHWW 0202). D:* Hoernesia socialis *(no. AHWW 0174). E:* Homomya althausi *(no. AHWW 0410). F:* Homomya albertii *(no. AHWW 0201). G:* incomplete specimen *of* Bakevellia costata *(no. AHWW 0275).*

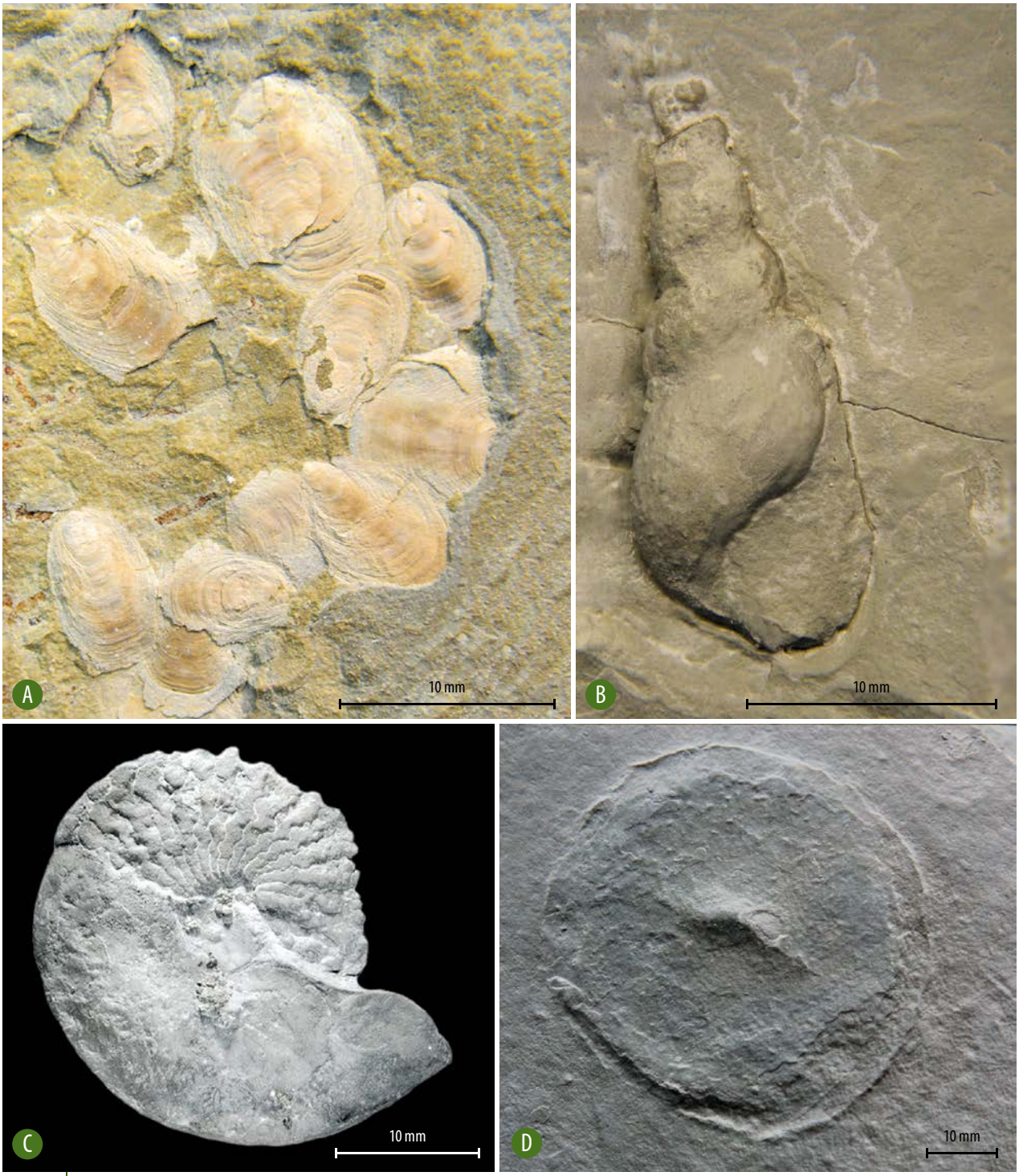

FIGURE 3. | *Selected non-bivalve taxa from the Middle Triassic Muschelkalk of Winterswijk. A: Bedding plane with several* Lingularia zenkeri *specimens (H. Winkelhorst collection, no. CHW518, photograph by R. Heerschop). B:* Loxonema obsoleta *(A. Haarhuis collection, no. AHWW 0204, photograph by R. Heerschop). C:* Beneckeia buchi *(adapted from Akkerman & Mulder, 2012: plate 9D) (W. Berkelder collection no. 032). D: Putative imprint of a jellyfish (from Oosterink & Winkelhorst, 2013: fig. 9) (collection of the former museum Freriks Winterswijk, no. MFW 21367).*

Klompmaker & Fraaije, 2011), but quantitative size comparisons are lacking for most groups. Regardless, the fauna at Winterswijk has been interpreted as stressed, most likely due to hypersaline conditions (Oosterink, 1981; Klompmaker & Fraaije, 2011; Heijne *et al.*, 2019). The absence of crinoids and other echinoderms, as well as sponges, corals (which are generally considered stenohaline), and the extremely low ammonite diversity further support the interpretation of a hypersaline, harsh habitat (Rieppel, 1995; Hagdorn, 1985; Klompmaker & Fraaije, 2011).

Late Triassic and Early Jurassic macroinvertebrates

Invertebrates are not restricted to the Muschelkalk, but have been found in uppermost Triassic (Rhaetian) shales, exposed in a subrosion pipe or sinkhole in the past and currently still present in the northern part of the

active quarry at Winterswijk. Fossils includ seven bivalve species: *Isocyprina* sp., *Tutcheria cloacina* (Quenstedt, 1856), *Rhaetavicula contorta* (Portlock, 1843) (Fig. 4), *Pteromya* sp., *Protocardia rhaetica* (Mérian in Escher, 1853), *Modiolus* sp., and *Lyriomyophoria postera* (Quenstedt, 1856) (see Klompmaker *et al*., 2010). This low-diverse assemblage also comprises a single species of brittle star, *Aplocoma agassizi* (von Münster, 1839) (see Thuy *et al*., 2012), which is the oldest reported record of a fossil ophiuroid from the Netherlands thus far. A trace fossil representing a burrow is further evidence of invertebrate life (Estes-Smargiassi & Klompmaker, 2015). The sinkhole also contained clays in which molds of three genera of ammonites were found, which allowed to date the clays to the earliest Jurassic (Hettangian) (Klompmaker & Van den Berkmortel, 2007).

FIGURE 4. | *The common Rhaetian bivalve* Rhaetavicula contorta *(Naturalis Biodiversity Center collection, RGM 550317, from Klompmaker* et al.*, 2010: fig. 4C).*

Acknowledgments

We thank John Jagt for a very helpful review of this manuscript.

Samenvatting

Dit artikel behandelt alle macroinvertebraten die niet tot de geleedpotigen behoren, gevonden in de Muschelkalk (Midden-Trias, Anisien) van Winterswijk. We kennen 18 soorten tweekleppigen, twee soorten gastropoden, twee soorten brachiopoden, één soort ammoniet en mogelijke kwallen. Foto's van vijf bivalvensoorten uit Winterswijk die nog niet eerder zijn gefotografeerd, zijn toegevoegd. Invertebraten uit de Laat-Trias schalies en Vroeg-Jura kleien van Winterswijk worden kort genoemd. De invertebraten uit de Muschelkalk wijzen op een hypersalien en verstoord milieu.

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