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The oldest (Middle Triassic, Anisian) lobsters from the Netherlands: taxonomy, taphonomy, paleoenvironment, and paleoecology

Adiël A. Klompmaker and René H.B. Fraaije

ABSTRACT

Fossil lobsters from the Netherlands have been described only rarely. This article describes the oldest, marine lobsters from the Netherlands in Middle Triassic Anisian (Muschelkalk) sediments cropping out in the Winterswijk quarry complex. The lobsters include the erymids *Clytiopsis argentoratensis* and *Oosterinkia neerlandica* n. gen., n. sp., and the mecochirid *Pseudoglyphea* cf. *P. spinosa*. They lived in a low energy, stressed environment with fluctuating salinity levels. This fluctuation might have caused the limited size of the specimens of *Clytiopsis argentoratensis* compared to related stratigraphically younger and older lobsters. In addition, the low number of specimens collected over decades and the low number of crustacean species is likely to be caused by a combination of the environment itself and a limited preservation potential.

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KEY WORDS: Muschelkalk; paleoecology; paleoenvironment; taphonomy; Vossenveld Formation; new species; new genus

PE Note: high-resolution versions of Figures 2, 4, and 5 are available online in a zipped folder at palaeo-electronica.org/2011_1/220/figures.zip.

INTRODUCTION

The Winterswijk quarry complex (Figure 1) contains Triassic (Anisian and Rhaetian), Jurassic (Hettangian), and Cenozoic (Oligocene, Pleistocene, and Holocene) sediments (e.g., Oosterink 1986; Diedrich 2001; Herngreen et al. 2005; Klompmaker and Van den Berkmortel 2007; Klompmaker et al. 2010) of which the Anisian (Muschelkalk) sediments predominate. These sediments are part of the Vossenveld Formation that

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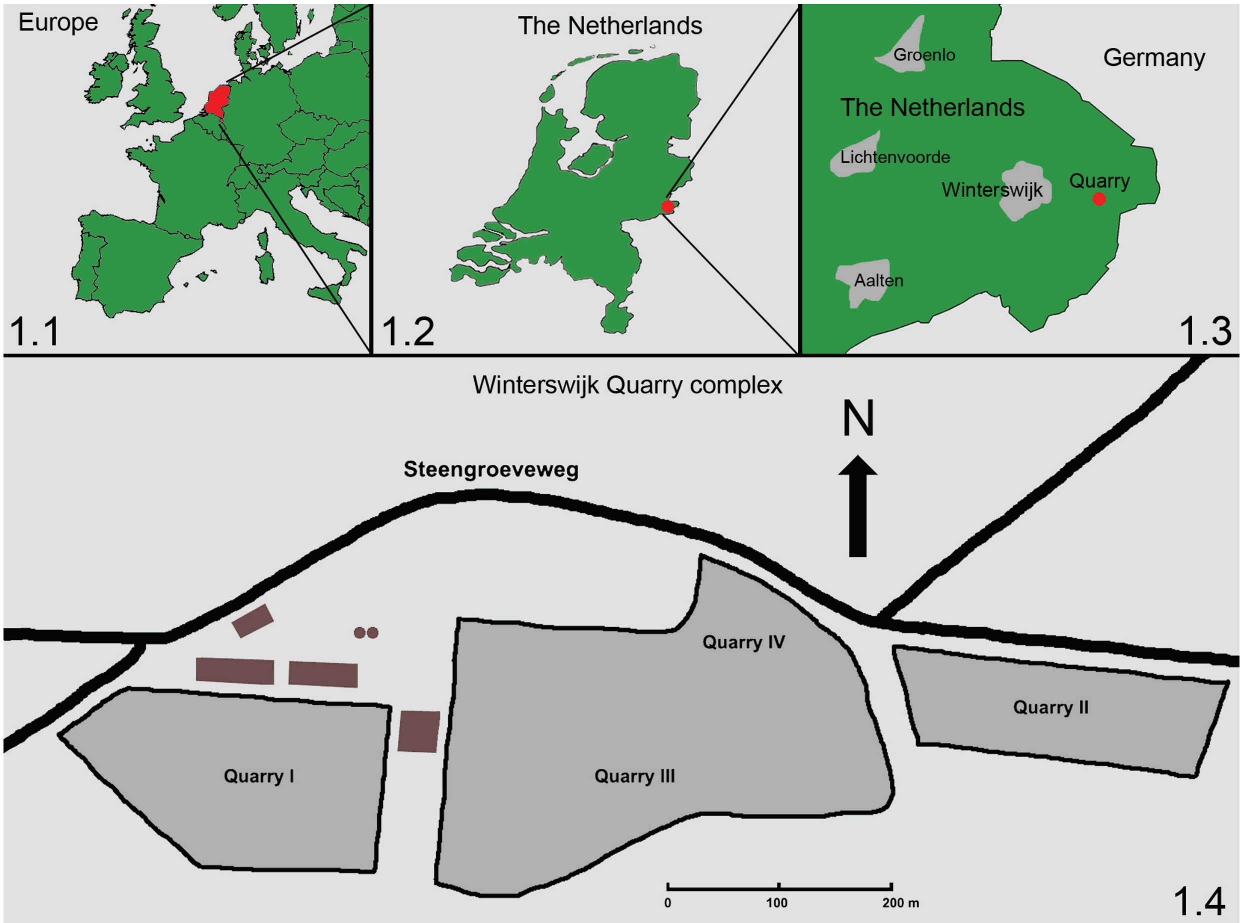

FIGURE 1. The location of the Winterswijk quarry complex in 2008. 1.1) The location of the Netherlands in Europe. 1.2) The location of the quarry in the Netherlands. 1.3) The location of the quarry in the neighborhood of Winterswijk. 1.4) The Winterswijk Quarry complex. Strongly modified after Klompmaker and Van den Berkmortel (2007).

has been erected recently (Subkommission Perm-Trias 2008). Within these predominantly marine sediments, numerous fossils have been found such as reptiles, reptile footprints, other trace fossils, fishes, bivalves, ammonites, a brachiopod, bivalves, gastropods, rare plant fossils, chelicerates, and crustaceans (e.g., Oosterink 1986; Oosterink et al. 2003). This article focuses on decapods (lobsters) from Winterswijk quarry which have never been described in detail. Moreover, fossil lobsters from the Netherlands are extremely rare. This article describes and discusses the oldest lobsters from the Netherlands.

Other, younger fossil lobsters include *Meyeria ornata* (Phillips 1829) from the Hauterivian of Losser (Anderson 1980), late Maastrichtian *Oncopareia bredai* Bosquet 1854 (sensu Tshudy 1993; = *Hoploparia beyrichi* Schlüter 1862), and *Jagtia kunradensis* Tshudy and Sorhannus 2000 from the Kunrade area (Jagt and Fraaije 2002), and undeterminated lobsters from the Eocene (Bartonian-Lutetian) of Losser (Spaink et al. 1978, p. 12).

The freshwater *Pygocephalus dubius* (Milne-Edwards 1840) from the Carboniferous strata in the southern part of the province of Limburg (Van der Heide 1951) belongs to the superorder Eocarida, and, therefore, is not a lobster that is part of the Decapoda.

PREVIOUS WORK ON CRUSTACEANS FROM WINTERSWIJK

Oosterink (1978) assigned one specimen, found in the first quarry of the complex, to either *Litogaster* von Meyer 1847, *Pseudoglyphea* Oppel 1861, or *Pseudopemphix* Wüst 1903. Later on, Oosterink (1979) ascribed the same specimen to *Clytiopsis* sp. In the same article he mentioned *Pseudoglyphea* cf. *spinosa*. Oosterink (1986) mentioned that even more specimens of *Clytiopsis* sp. were found (about five, Oosterink, personal com-

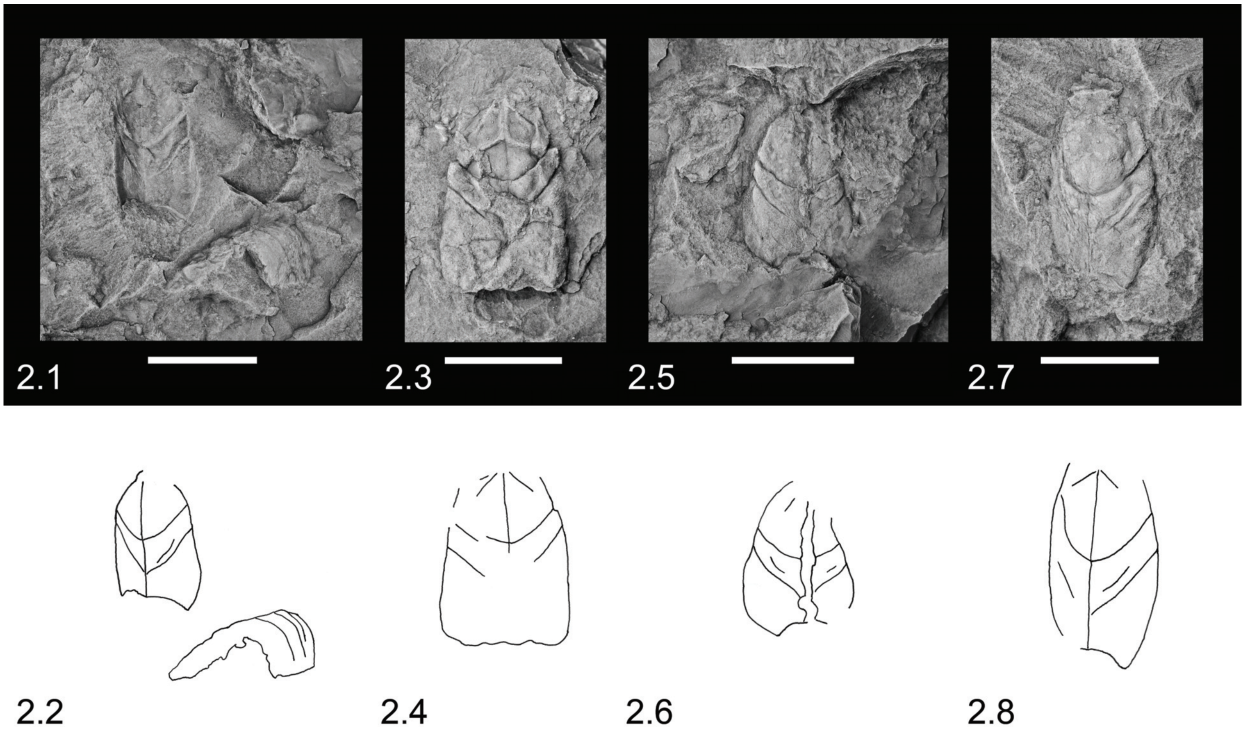

FIGURE 2. Photos of the four specimens of *Clytiopsis argentoratensis* and their line drawings of the outline and grooves. 2.1, 2.2) MAB k2855; 2.3, 2.4) MAB k2856; 2.5, 2.6) MAB k2857; 2.7, 2.8) MAB k2858. The scale bar equals 10 mm.

mun., 2008). Since the 1980s more specimens have been found. Other known arthropods from Winterswijk include a limulid (Hauschke et al. 2009) and the cycloid *Halicyne* cf. *agnota* (Oosterink 1986).

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1802
Suborder PLEOCYEMATA Burkenroad, 1963
Infraorder GLYPHEIDEA Winckler, 1882
Superfamily ERYMOIDEA van Straelen, 1924
Family ERYMIDAE van Straelen, 1924
Subfamily CLYTIOPSINAE Beurlen, 1928
Genus CLYTIOPSIS Bill, 1914

Type Species. *Clytiopsis argentoratensis* Bill, 1914

Included Species. *Clytiopsis argentoratensis* Bill, 1914; *C. thuringica* Förster, 1967

Discussion. Bill (1914) erected a genus and two species: *Clytiopsis argentoratensis* and *Clytiopsis elegans.* Differences between the two were minimal which led Gall and Fisher (1965) to conclude that *C. elegans* is synonymous with *C. argentoratensis*. Förster (1966, 1967) and Gall (1971) supported that view. *Clytiopsis argentoratensis* and *Clytiopsis thuringica* are the only two species described within *Clytiopsis* so far. Several authors have reported *Clytiopsis* sp. (e.g., Bill 1914; Förster 1966, 1967; Diedrich and Schulz 2003).

Clytiopsis argentoratensis Bill, 1914
Figure 2

* 1914 *Clytiopsis argentoratense* Bill, p. 298, pl. 10, fig. 1, pl. 11, fig. 1.

1914 *Clytiopsis elegans* Bill, p. 300, pl. 10, fig. 3, pl. 11, fig. 2, pl. 12, figs. 2, 3.

1928 *Clytiopsis argentoratensis* Bill; Schmidt, p. 323, fig. 883.

1928 *Clytiopsis elegans* Bill; Schmidt, p. 324, fig. 884.

1965 *Clytiopsis argentoratense* Bill; Gall and Fischer, p. 44, fig. 1, pl. 1, 2.

1966 *Clytiopsis argentoratensis* Bill; Förster, p. 83, fig. 10, pl. 13, figs. 1, 2, 3.

1967 *Clytiopsis argentoratensis* Bill; Förster, p. 146, fig. 4, pl. 9, fig. 3.

1971 *Clytiopsis argentoratensis* Bill; Gall, p. 52, figs. 12, 13, pl. 12, fig. 4, pl. 13, figs. 1, 2.

1999 *Clytiopsis argentoratensis* Bill; Hauschke and Wilde, fig. 10.

TABLE 1. Measurements of the six studied specimens (in mm).

	max. cephalothorax length	max. cephalothorax width	length/ width	max. abdomen length	max. tailfan width
MAB k2855 (*Clytiopsis argentoratensis*)	15	8	1.88		
MAB k2856 (*C. argentoratensis*)	17	11	1.55		
MAB k2857 (*C. argentoratensis*)	16	9	1.78		
MAB k2858 (*C. argentoratensis*)	15	9	1.67		
MAB k2854 (*Oosterinkia neerlandica* n. gen., n. sp.)	15	9	1.67	25	
MAB k2859 (*Pseudoglyphea* cf. *P. spinosa*)				33	16

Diagnosis. Cephalothorax cylindrical; rostrum triangular; faint median groove; postorbital ridge and antennal ridge with spines; strong cervical groove; faint postcervical groove partly parallels branchiocardiac region; strong branchiocardiac groove and cervical groove connected by two-lobed hepatic groove; ventral groove connects to branchiocardial groove; antennal groove curves forward from cervical groove. Mostly pits on branchial region, sometimes granules; granules on cardiac region, gastric and antennal region. Abdomen longer than cephalothorax; first somite small; epimeres rounded with pointed tips. Telson spade-shaped; exopods with diaeresis. First three pereiopods with opposing dactylus and propodus.

Description. Cephalothorax cylindrical; wider posteriorly. Front narrowing anteriorly. Rostrum not preserved. Median line is faint furrow. No intercalated plate observed. Boundary of gastric and antennal region is postorbital ridge composed of small spines. Cervical groove marks end of both regions. Posteriorly directed postorbital ridge makes a 40–50° angle to median line. Anteriorly directed cervical groove arises at median line with an angle of about 30°, curving to about 40°; stronger than median line. Gastroorbital groove very faint to invisible. Postcervical groove does not reach median line; in between cervical and branchiocardiac groove; weaker than cervical and branchiocardiac grooves; extends parallel to branchiocardiac groove in middle part but curves to cervical groove ventrally; approaches branchiocardiac groove near median line. Branchiocardiac and cervical grooves define a trapezoid region consisting of medial cardiac and ventral hepatic regions. Posteriorly directed branchiocardiac groove originates at about median line; starts at a very low angle to median line, curves to an angle of 30–40° to median line, then curves slightly forward at about midlength in dorsal view; stronger than postcervical groove; slightly weaker than cervical groove. Two-lobed hepatic furrow connects cervical and branchiocardiac groove. Branchial region ended by groove along rim of cephalothorax. Groove about as strong as branchiocardiac groove; starts about perpendicular to median line; more ventrally it curves posteriorly. Mostly pits on branchial region, sometimes granules; granules on cardiac region, gastric and antennal region. Abdomen only partly preserved in one specimen (Figure 2.1); same for a part of an appendage; one part of uropod preserved; no telson preserved. Few granules or pits visible on abdominal segments. State of preservation of epimeres does not allow further description. For measurements see Table 1.

Material examined. Four specimens (MAB k2855–2858) deposited at Oertijdmuseum De Groene Poort, Boxtel, The Netherlands. The exact stratigraphic level at which the specimens were collected is unknown.

Discussion. The cephalothorax of four specimens can be assigned to *Clytiopsis argentoratensis*. Although not all details as described by Förster (1966) are visible, all the characters that are visible are the same. The type species description of Bill (1914) is not useful because it does not describe the cephalothorax in detail.

The antennal ridge, the ventral groove, and the bifurcation at the most dorsal position of the postcervical groove were invisible due to the preservation state.

Differences with *Clytiopsis thuringica* from the Ladinian of Straußfurt (Germany) are numerous. The postcervical groove does not approach the cervical groove as it does in *C. thuringica*. The postorbital ridge is smaller than that of *C. thuringica*. The ornamentation of the specimens from Winterswijk does not show pits followed by larger

FIGURE 3. The location of various finds of *Clytiopsis* spp. and *Pseudoglyphea* (cf. *P.*) *spinosa*. Red dots are localities where *Clytiopsis* spp. is found: Schachten, Anisian (*Clytiopsis* sp., Diedrich and Schulz 2003); Straußfurt, Ladinian (*Clytiopsis thuringica*, Förster 1967); Bust, Anisian (*Clytiopsis argentoratensis*, Gall 1971); Schoenbourg, Anisian (*C. argentoratensis*, Gall 1971); Vilsberg, Anisian (*C. argentoratensis*, Gall 1971); Arzviller, Anisian (*C. argentoratensis*, Gall and Fisher 1965); Wasselone, Anisian (*Clytiopsis* cf. *argentoratensis*, Bill 1914); Soultz-les-Bains (Königsgrube), Anisian (*C. argentoratensis*, Bill 1914; *Clytiopsis* sp., Förster 1966, 1967); Gresswiller, Anisian (*C. argentoratensis*, Bill 1914); Breuches (near Luxeuil), Anisian (*Clytiopsis* sp., Förster 1967). Green dot is the locality where the holotype of *Pseudoglyphea spinosa* is found (Dinkelberg, Anisian, Assmann 1927). The blue dot is the locality of the specimens from this study. The size of the dots seeks to denote the number of localities with finds in that area.

granules posteriorly, as is the case for *C. thuringica*.

Of special note is specimen MAB k2856 (Figure 2.2). The trifurcated ridge in the gastric was probably caused by diagenetic pressure differences. Ridges are rare on lobsters from the Triassic and, if present, are usually formed by aligned bumps, which is not the case here. The median groove does not follow the anteriormost branch of the trifurcation closely. Lastly, the two posteriormost ridges are unequal in size and length. Therefore, the trifurcated ridge is considered as having been formed after burial.

Gall and Fischer (1965) studied the 50 specimens of *Clytiopsis* from the Anisian of the Vosges Mountains in France on which Bill (1914) based his descriptions. They rectified the groove pattern of *C. argentoratensis* (see their figure 1). The main difference between the reconstruction of Förster (1966, 1967), who did not address Gall and Fischer's (1965) reconstruction, and theirs is the postcervical groove. Their figure 1 shows that the dorsal bifurcation is far more extended than in Förster (1966, 1967). The posteriormost branch reaches the median line. The ventral part connects to the cervical groove and the gastroorbital groove. This type of postcervical groove is not present in our specimens. On the other hand, they also stated that the postcervical groove varies. Thus, the reconstruction of Gall and Fischer (1965) should be interpreted with caution.

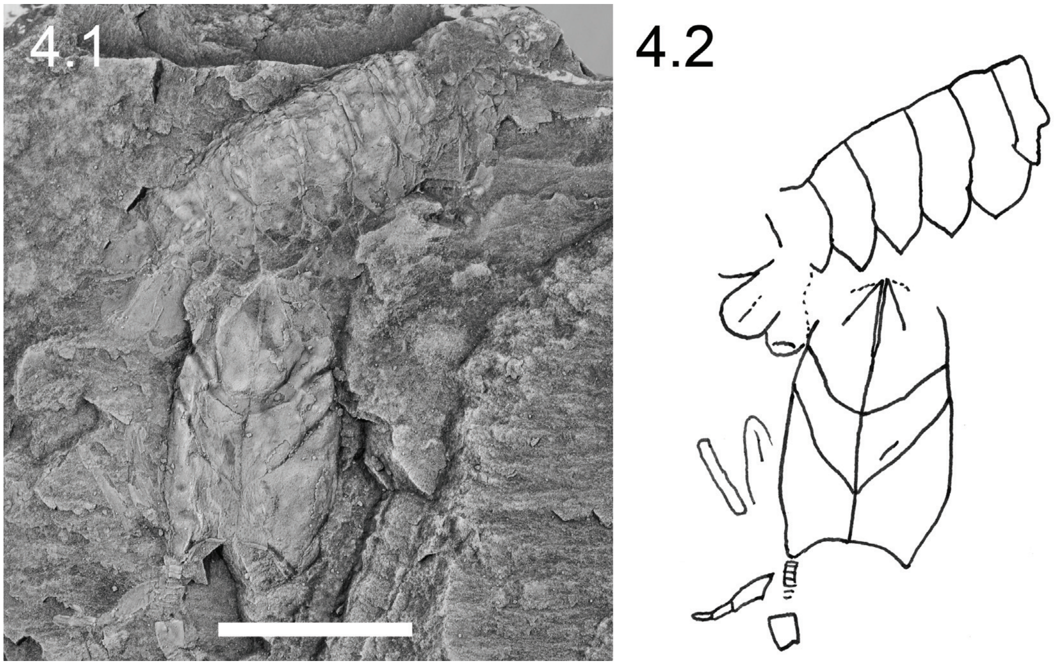

FIGURE 4. A picture of the specimen of *Oosterinkia neerlandica* n. gen., n. sp and the line drawing depicting the outline and grooves (MAB k2854). The scale bar equals 10 mm.

Occurrence and age. The studied specimens are all from the Middle Triassic (Anisian) strata from the Winterswijk quarry complex, the eastern Netherlands. Specimens MAB k2856–2858 were found in Quarry III; MAB k2855 was found in Quarry II. Other specimens have been found in Anisian strata in the Vosges Mountains of France (Figure 3).

Subfamily ERYMINAE van Straelen, 1924

Genus OOSTERINKIA n. gen.

Diagnosis. Cephalothorax cylindrical; triangular rostrum; median line present; intercalated plate on gastric part; strong cervical groove; small, faint postcervical groove parallels stronger branchiocardiac groove; cephalothorax partly smooth or pitted. Terga and epimeres pitted; epimeres with pointed, slightly posteriorly directed tip. Spade-shaped telson with longitudinal groove but without bristle structure; exopod with diaeresis.

Description. As for type species.

Etymology. The name is derived from a specialist on the geology and paleontology of the Winterswijk quarry complex, and collector of the specimens described herein: Henk Oosterink.

Oosterinkia neerlandica n. sp.

Figure 4

1978 *Litogaster* sp., *Pseudoglyphea* sp., or *Pseudophemphix* sp., Oosterink, p. 5, fig. 6.

1979 *Clytiopsis* sp., Oosterink, fig. 1.

1986 *Clytiopsis* sp., Oosterink, p. 57, fig. 17.

Diagnosis. As for genus.

Description. Cephalothorax cylindrical; widest part at half to two thirds of length. Front narrowing. Rostrum triangular. Median line is faint groove from posterior to slightly anterior of cervical groove; on anterior half of gastric region median line becomes a 0.3 mm wide ridge, which is an intercalated plate; becoming groove again on rostrum. Postorbital ridge covered with a row of four more or less equal-sized, forwardly oriented spines**.** Left antennal ridge extends more posteriorly than postorbital ridge; approaches cervical groove; extends parallel to postorbital ridge; exhibits strong spines. Strong cervical groove arises at median line at an angle of about 30° and curves ventrally to about 40°; becomes stronger ventrally. Small, very faint postcervical groove parallels branchiocardiac groove; neither reaches median line nor curves to cervical groove. Sinuous branchiocardiac groove arises at median line at a very low angle, increases to about 40°, then increases to about 50°; about as pronounced as cervical groove; more pronounced ventrally. Branchial region ends in groove along rim of cephalothorax. Groove about as strong as branchiocardiac groove; starts near and about perpendicular to median line; ventrally curving more posteriorly and more pronounced ventrally. Cephalothorax party smooth and pitted except few isolated, aligned nodes just posterior of cervical groove. Pits on branchial, posterodorsal part of branchiocardiac region, and anterior part of antennal and gastric region. First of six somites reduced; epimere not visible. Sixth somite longest. Epimeres convex in anterior part and initially convex and becoming downward more concave at posterior part; sides merge to form an apex directed slightly posteriorly. Epimere of sixth somite smallest. Epimeres and most ventral part of terga with pits. Spade-shaped telson with small row of nodes in middle part surrounded by smaller ones; some pits on the sides; longitudinal groove in middle; no bristles visible at distal rim. Right uropod only partly preserved. Endopod with longitudinal lines at distalmost part and small, faint, transverse ridges in the middle. Exopod with transversal, curved diaeresis. Part of exopod or antennae close to posteriormost left part of branchial region. At least two parts of thoracic appendage to left of cephalothorax. For measurements see Table 1.

Etymology. The name is derived from the country in which the specimen was found.

Type. The holotype (MAB k2854) and sole specimen is stored at Oertijdmuseum De Groene Poort, Boxtel, The Netherlands. The exact stratigraphic level at which the specimen was collected is unknown.

Discussion. *Oosterinkia neerlandica* exhibits a deep groove anterior to the cervical groove which is present on both sides of the median line. The groove approaches very close to the cervical groove on the left side of the cephalothorax and bifurcates on the right side. This groove is not symmetrical and, therefore, must be considered to be a taphonomic feature.

There are several genera within the family Erymidae: *Clytiella* Glaessner 1931; *Clytiopsis* Bill 1914; *Enoploclytia* McCoy 1849; *Eryma* von Meyer 1840; *Galicia* Garassino and Krobicki 2002; *Lissocardia* von Meyer 1851; *Palaeastacus* Bell 1850; *Paraclytiopsis* Oravecz 1962; *Protoclytiopsis* Birshtein 1958; *Pustulina* Quenstedt 1857.

At first sight *Oosterinkia neerlandica* resembles *Clytiopsis* spp. However, differences from *Clytiopsis thuringica* may be observed. First, the postcervical groove is longer and more pronounced in *C. thuringica*. The ornamentation differs: *C. thuringica* has nodes posterior to pits, while *O. neerlandica* has only pits in the gastric region. The postorbital ridge of *C. thuringica* has spines that increase in height posteriorly, while *O. neerlandica* shows no spines. The median furrow is continuous in *C. thuringica* but is not continuous in *O. neerlandica*. The furrow becomes an intercalated plate in the posterior part of the gastric region. Differences in the postcephalothracic parts cannot be given because the description of the sole specimen of *C. thuringica* is based on a cephalothorax only.

Oosterinkia neerlandica differs from *Clytiopsis argentoratensis* in several aspects. The median line is only present as a faint groove posterior from about the cervical groove and is a ridge on the anteriormost part of the gastric. The median groove does not turn into an intercalated plate in specimens of *C. argentoratensis*; it remains a groove. The postcervical groove of *O. neerlandica* is smaller and fainter than in *C. argentoratensis*. The cervical and branchiocardiac groove are very clear in *O. neerlandica*, even more pronounced than in other specimens. Therefore, a clearer postcervical groove would be expected if it were to be *C. argentoratensis*. Furthermore, the cephalothorax is pitted in the gastric and antennal region, but exhibits granules in *C. argentoratensis*. The telson shows no bristle structure that is present in *C. argentoratensis* according to Gall (1971). Gall and Fisher (1965), however, mentioned that it might not have been present in some specimens of *C. argentoratensis* due to the nature of fossilization. The telson shows a small groove, a feature not reported on *C. argentoratensis*.

The new genus differs from *Paraclytiopsis* by the presence of a median line and the intercalated plate, which are present in *Oosterinkia neerlandica*. *Clytiella* also does not exhibit an intercalated plate, and, moreover, has a row of spines on the median keel. This is not observed in *O. neerlandica*. It differs from *Protoclytiopsis* by its stronger branchiocardiac groove compared to the postcervical groove, which is the opposite in *Protoclytiopsis*. *Enoploclytia* and *Palaeastacus* have a more pronounced ornamentation with nodes on the gastic and cardiac regions. *Oosterinkia neerlandica* is smooth to pitted on the whole cephalothorax. The new genus differs from *Eryma* by the branchiocardiac groove that is about as strong as the cervical groove, the pitted abdomen, and the smooth to pitted cephalothorax. *Eryma* has a weaker branchiocardiac groove compared to the cervical groove, a smooth abdomen, and a granulated cephalothorax.

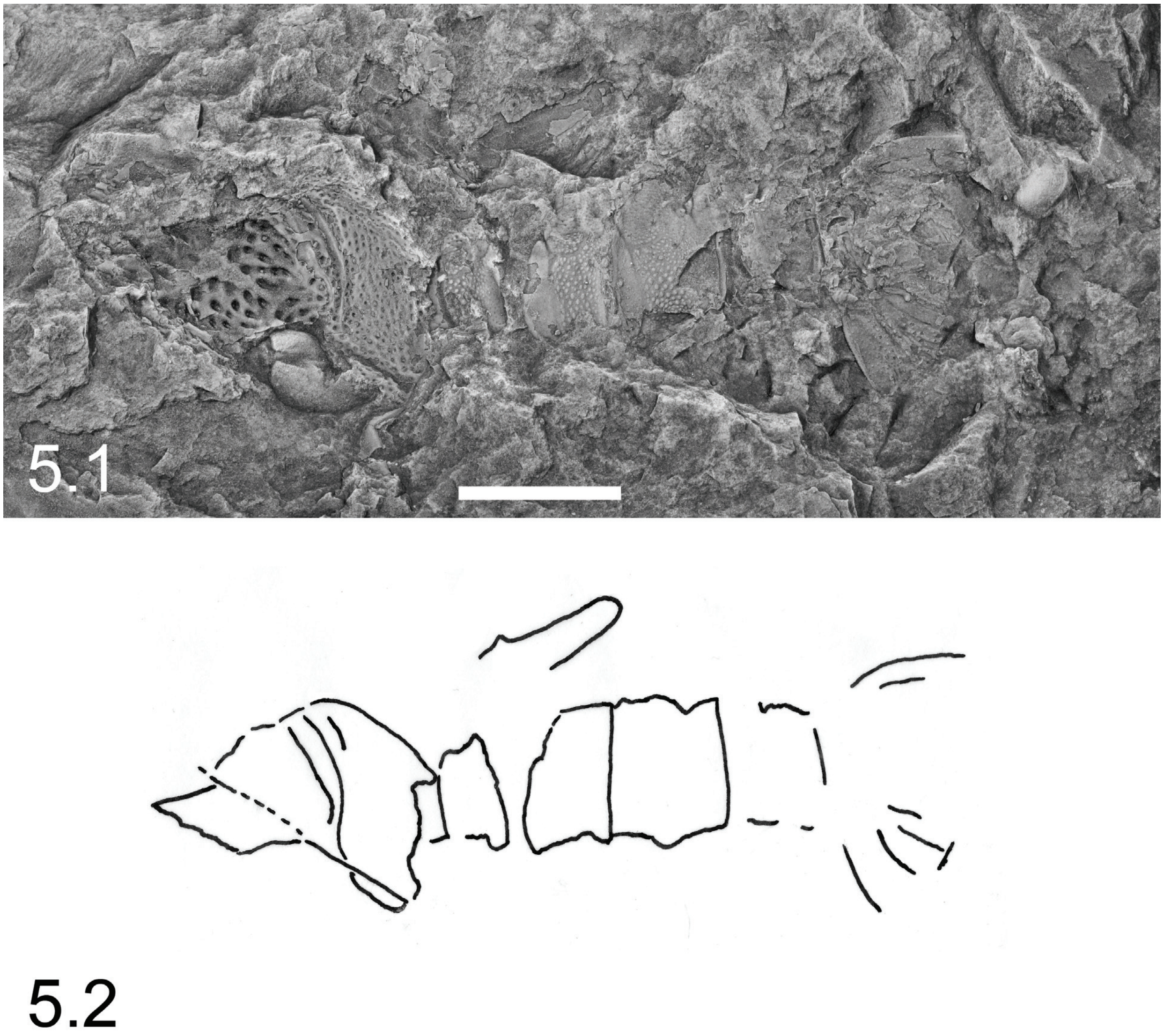

FIGURE 5. A picture of the specimen of *Pseudoglyphea* cf. *P. spinosa* and the line drawing depicting the outline and grooves (MAB k2859). The scale bar equals 10 mm.

Lissocardia differs from *Oosterinkia* by having longitudinal ridges in the gastric region instead of an oblique ridge and a weaker branchiocardiac groove. *Galicia* is granulated on the cephalothorax and has a stronger postcervical groove that joins the branchiocardiac groove, while the new genus has a smooth to pitted cephalothorax and a very weak postcervical groove that does not join the branchiocardiac groove. *Pustulina* bears a strong gastroorbital groove, has a granulated cephalothorax, a strong postcervical groove, and a small branchiocardaic groove. On the other hand, *O. neerlandica* exhibits no gastroorbital groove, has a smooth to pitted cephalothorax, and bears a strong branchiocardiac, but a faint postcervical groove.

The specimen, thus, shows numerous differences compared to the known genera and species. We, therefore, erect *Oosterinkia neerlandica* n. gen., n. sp.

Occurrence. One specimen from Anisian sediments from Quarry I of the Winterswijk quarry complex, eastern Netherlands.

Superfamily GLYPHEOIDEA Winckler, 1882
Family MECOCHIRIDAE van Straelen, 1924
Genus PSEUDOGLYPHEA Oppel, 1861

Emended diagnosis. Subcylindrical carapace; long rostrum; cephalic region with longitudinal ridges reduced or absent; well marked cervical groove; postcervical and branchiocardiac grooves closely spaced and parallel, approaching or extending to median line; well-marked hepatic groove extends in smooth arc defining posterior, ventral, and anterior margins of "adductor testis" muscle attachment; inferior groove absent or weakly marked; strong and subchelate pereiopod I; subchelate pereiopods II–III; abdominal terga pitted, smooth, or with granules; uropodal exopod with or without diaeresis (modified from Feldmann et al. 2002 and Garassino and Rigo 2008).

Type Species. *Glyphea grandis* von Meyer, 1837, by original designation

Included Species. *Pseudoglyphea grandis* (von Meyer 1837); *P. numismalis* (Oppel 1853); *P. eximia* (Oppel 1861); *P. amalthea* Oppel 1861; *P. terquemi* Oppel 1861; P. *etalloni* Oppel 1862; *P. ancylochelis* (Woodward 1863); *P. jourdani* (Dumortier 1867); *P. paronae* (Colosi 1921); *P. spinosa* (Assmann 1927); *P. mulleri* (van Straelen 1936); *P. straeleni* (Théobald 1953); *P. alpina* (Förster 1971); *P. gigantea* Garassino and Teruzzi 1993; *P. foersteri* Feldmann, Crisp, and Pirrie 2002; *P. friulana* Garassino and Rigo 2008.

Pseudoglyphea cf. *P. spinosa*
Figure 5

* 1927 *Pseudopemphix spinosus*, Assmann, p. 340, pl. 9, fig. 1.

1928 *Pseudopemphix spinosus* Assmann; Schmidt, p. 319, fig. 878.

1932 *Pseudoglyphea spinosa* (Assmann); Glaessner, p. 113-114, fig. 2C.

1960 *Pseudoglyphea spinosa* (Assmann); Glaessner, p. 40, fig. 19.1.

1966 *Pseudoglyphea spinosa* (Assmann); Förster, fig. 36.

1967 *Pseudoglyphea* ? *spinosa* (Assmann); Förster, p. 163, fig. 10a, pl. 11, fig. 1.

1979 *Pseudoglyphea* cf. *spinosa* (Assmann); Oosterink, p. 115.

1986 *Pseudoglyphea* cf. *spinosa* (Assmann); Oosterink, p. 62.

Description. Left part of cephalothorax best preserved; only cardiac region preserved on right part. Possible part from gastric and/or rostrum with small granules, possibly accompanied by bases of antennules. Longitudinal axis is faint ridge on branchial region; on cardiac region it is a furrow formed by position of large nodes on both sides. Strong cervical groove (only visible on right side) forms about a 40° angle with longitudinal axis. Strong postcervical groove parallels weaker branchiocardiac groove dorsally, then curves slightly toward it and parallels it again; ventralmost part as strong as cervical groove; dorsalmost part less pronounced; does not connect to longitudinal axis. Branchiocardiac groove arises near axis and gradually curves forward from 30° to about 50°. Faint groove posterior and parallel to branchiocardiac groove distal from longitudinal axis. Marginal groove marks end of branchial region; arises perpendicular to longitudinal axis, curves forward followed by sharp curve backwards. Strong nodes on cardiac region and in region between postcervical and branchiocardiac groove. Smaller granules on branchial region. Five granular terga visible of which first is mostly hidden beneath the cephalothorax. Second and third visible terga separated. Last tergum longest. One part of epimere preserved on right side of last or next to last somite; at least partly granular. Telson broken into many pieces. Left uropod granular; endopod overlapping exopod; furrow in middle does not reach diaeresis; diaeresis with small spines directed posteriorly; distalmost part of uropod not preserved. Exopod with thickened lateral margin exhibiting pits. Granular endopod only preserved on right uropod. Part of possible thoracic appendage preserved right of abdomen. For measurements see Table 1.

Material examined. This specimen (MAB k2859) is stored at Oertijdmuseum De Groene Poort, Boxtel, The Netherlands. The exact level at which the specimen was collected is unknown.

Discussion. The described specimen resembles *Pseudopemphix albertii* (von Meyer 1840) due to the fact that only a part of this specimen is preserved. Förster (1967) pointed out that *Pseudopemphix* and *Pseudoglyphea* have similarities, and Assmann (1927) assigned *P. spinosa* to *Pseudopemphix* when he erected the species. However, there are some major differences between *P. spinosa* and *Pseudopemphix albertii*, type species of the genus. Schulz (2002) mentioned that the abdomen of *Pseudopemphix albertii* has pits, which is not the case in this specimen from the Netherlands. Unfortunately, the type specimen of *Pseudoglyphea spinosa* is known only from the cephalothorax. The distribution and number of large nodes is critical. There are fewer large nodes on *Pseudopemphix albertii* (see Schmidt 1928, figure 876; Förster 1967, figure 12; Schulz 2002) than on the specimen at hand. Moreover, the large nodes are also present between the postcervical and the branchiocardiac groove in this specimen. This applies to *P. spinosa*, but not to the type of

Pseudopemphix (see Schmidt 1928, figure 878; Förster 1967, figure 10, 12; Schulz 2002). In addition, the cardiac region of *Pseudopemphix albertii* bears both large and small nodes, which is not the case in this specimen. It bears large nodes only. Furthermore, this specimen does bear a thickening just before the end of the branchial region which is not observed in *Pseudopemphix*. In conclusion, this specimen is better referred to *Pseudoglyphea* than to *Pseudopemphix*.

We favor assignment to *Pseudoglyphea* over other genera within the Mecochiridae and over *Pseudopemphix*. The specimen bears all the characters described by Förster (1967), Feldmann et al. (2002), and Garassino and Rigo (2008) as far as they are visible in this specimen. The only exceptions are the terga, which would be pitted or smooth in most species of *Pseudoglyphea*, but have nodes in this specimen. It clearly differs from *Mecochirus* (Germar 1827), *Meyeria* (McCoy 1849), *Huhatanka* (Feldmann and West 1978), and *Jabaloya* (Garassino et al. 2009) by its less oblique grooves posteriorly from the cervical grooves. It differs from *Pseudopemphix* by exhibiting spines on the cardiac region of *Pseudoglyphea* that do not appear to form rows and the absence of pits on the cephalothorax. This specimen can, thus, best be assigned to *Pseudoglyphea*.

It differs from *Pseudoglyphea foersteri* by its large spines on the cardiac region, which are absent in *P. foersteri*. *Pseudoglyphea friulana* has weaker postcervical and branchiocardiac grooves. The postcervical groove is more pronounced than in specimens of *P. grandis* and *P. alpina*. The cardiac region has stronger spines than on specimens of *P. mulleri*, *P. amalthea*, *P. terquemi*, and *P. gigantea.* The postcervical and branchiocardiac groove of *P. staeleni, P. numismalis,* and *P. jourdani* do not approach the median line, which can be observed from this specimen. The preservation of the cephalothorax of *P. paronae* allowed identification of a strong cervical groove, the hepatic groove, and a part of the postcervical groove only (van Straelen 1924). The assignment of that species to *Pseudoglyphea*, thus, is doubtful. The postcervical appears to be fairly weak and, as a result, differs from the described specimen. *Pseudoglyphea etalloni* differs from the specimen by possessing a distinct bifurcation of the postcervical groove dorsally and by the presence of larger nodes on the dorsal part of the branchiocardiac region. The described specimen does not show a distinct bifurcation in the postcervical groove and has a weak granulation on the branchiocardiac region. *Pseudoglyphea eximia* has a smaller branchiocardiac region and has weaker nodes on the cardiac region. The specimen has more large nodes in the cardiac region than specimens of *P. ancylochelis*. It is very similar to *P. spinosa* based on the cardiac region being covered by strong nodes, the presence of strong nodes between the postcervical and branchiocardiac groove, the relative strength of the groove, and the relatively large, granulated branchiocardiac region. In addition, Assmann (1927) and Schmidt (1928) mentioned that the holotype of *Pseudoglyphea spinosa* has a thickening just before the end of the branchial region. The thickening is observed in the specimen from Winterswijk. There are, however, some minor differences. Förster (1967) mentioned that the longitudinal axis of *Pseudoglyphea* (?) *spinosa* has large spines and Assman (1927) stated that they appeared on the anterior part of the cardiac region. This is not observed in this specimen. It has a ridge in the branchial region and a groove on the cardiac region. Furthermore, Assmann (1927) mentioned that the nodes at the anterior of the cardiac region are larger in *P. spinosa*, which is not clear from this specimen. The differences are, however, too few to warrant erecting a new species. Therefore, we refer to it as *Pseudoglyphea* cf. *P. spinosa*.

Occurrence and age. One specimen found in Anisian sediments from Quarry III of the Winterswijk quarry complex, the eastern Netherlands. The holotype was found in Anisian sediments of Dinkelberg, Germany (Figure 3).

TAPHONOMY, PALEOENVIRONMENT, AND PALEOECOLOGY

At least a couple of the specimens are very likely to be molts. *Pseudoglyphea* cf. *P. spinosa* and *Clytiopsis argentoratensis* (Figure 2.1) have their cephalothoraxes and abdomina misaligned, and the abdomen is facing upward while the cephalothorax is upside down. This is interpreted as an indication of a molt. Furthermore, one specimen of *C. argentoratensis* (Figure 2.5) has its cephalothorax split along the median line. This is a way some lobsters molt (Glaessner 1969, R431). One other specimen, *Oosterinkia neerlandica*, has its abdomen misaligned with the cepahalothorax as well, typically known as the Salter's position (Schäfer 1951) or Open Molt Position (Bishop 1986). This is likely to happen typically in the case of a molt (see Bishop 1986; Feldmann and Tshudy 1987). Moreover, Glaessner (1969, R431) mentioned that some lobsters molt by opening up between the transition from cephalothorax to the first abdominal somite and split along the median line, thereby leaving the cephalothorax and abdomen behind separately. The configuration of the remains of *Oosterinkia neerlandica* also resembles figure 29 in Mertin (1941). The author described molts of *Oncopareia* Bosquet 1854 with an open carapace split and misalignment of the cephalothorax and abdomen. However, the split is not observed in this specimen. The other specimens from this study could be either a molt or a fossilized part of a dead lobster.

The majority of the lobsters exhibits no cuticle implying that the exoskeleton has been dissolved due to diagenesis. Bivalve shells are also preserved without the actual shell. As a result, the preservation is moldic since the lobsters are preserved with relief.

None of the specimens is complete. If nearly complete, the cephalothorax and abdomen are separated. The specimens, therefore, could not have been buried alive or very fast after their death by high sedimentation rates. Lobsters buried under these circumstances should be complete and articulated for the most part. The specimens, thus, have been lying on the bottom for a while after death or were disintegrated molts. If some of the remains are actual corpses, then they must have been exposed for an extended period of time, and, hence, experienced considerable decomposition that allowed the disarticulation of the lobsters. Disarticulation took mainly place between the cephalothorax and the abdominal region as none of those region are still connected (Figures 2, 4, 5).

Allison (1986) demonstrated that a freshly killed lobster of *Nephrops* Leach 1841 and the shrimp *Palaemon* Weber 1795 were hardly affected by strong rotation in a barrel (125 rpm for 5 hrs), while the same animals were severely damaged after they had decomposed for two weeks before being subjected to the same experiment. Other indications of a low-intermediate sedimentation rate are the presence of epi- and infaunal organisms, the horizontal orientation of most of the fossils found in the quarry, and the thin layers of sediment surrounding the lobsters.

Plotnick (1986) studied the taphonomy of modern shrimp and suggested that scavengers and infaunal organisms could be important in the destruction of buried arthropod remains. The number of epifaunal scavengers in the Muschelkalk sea was probably limited given the very limited crustacean fauna in terms of total specimens (<10) and number of species (5). On the other hand, burrows are found (e.g., *Rhyzocorallium*) in the Winterswijk quarry complex. Bioturbation might, thus, have limited the preservation potential of lobsters.

Decomposition due to microbial activity has a profound effect on the preservation potential of the lobsters as well. Chan (1970) observed highest densities of chitinoclastic bacteria on molted arthropod skeletons in intertidal and fresh-water sediments, which could suggest enhanced decomposition. Plotnick (1986) observed that fresh remains of modern shrimp were resistant to rough handling; when decomposition proceeded, the remains disarticulated by moderate disturbance. The lobsters from this study were, thus, probably not buried quickly but the corpses or molts were able to disintegrate at least by decomposition. The low-intermediate sedimentation rate enhanced microbial decay in this case.

Not a single specimen is complete and some show possible signs of wear exemplified by the absence of most rostra (Figures 2, 5) and the incompleteness of the cephalothorax and abdomen (Figure 5). Most of the specimens are, however, not severely damaged suggesting limited transport. The presence of a number of nearly complete fish (see Oosterink and Poppe 1979) also indicates a limited energy level. On the other hand, the vast number of loose bones of vertebrates (see Oosterink et al. 2003) suggests that it was not completely still water. The bones might have been displaced by various scavengers or hunters that were active on the carcasses of the reptiles. Lankamp (2002) documented bite marks on a nothosaur bone, possibly caused by a *Nothosaurus*. Reptile bones might, thus, be more susceptible to transport than other smaller animals of the Anisian time period of Winterswijk due to scavengers and predators that move part of the carcass. In addition, the bones are more susceptible to transport when the bones themselves are not connected anymore by organic tissue after predation, scavenging, and decomposition. The hypothesis of limited transport is further strengthened by the completeness of the vast majority of the bivalves. Also, sometimes the valves are still connected.

In summary, a low-intermediate sedimentation rate caused the decay of the lobsters epifaunally, while bioturbation might have caused further decay infaunally. Limited hydrological activity, on the other hand, enhanced the preservation. Although other paleoenvironmental factors also had a major negative impact on the diversity and number of individuals of lobsters (see discussion below), the low number of finds over decades of collecting is also likely to be in part caused by the low preservation potential.

Fossils of the Anisian strata of Winterswijk are dominated by marine fossils such as ammonites, fishes, bivalves, gastropods, brachiopods, and stromatolites (Oosterink 1986). Amphibians and famous aquatic reptiles from this site such as *Nothosaurus*, *Cymatosaurus*, and *Anarosaurus* are also associated with marine strata from other localities (Oosterink et al. 2003). In one case (MAB k2859) a bivalve is found in association with a lobster (*Pseudoglyphea* cf. *P. spinosa*). The presence of numerous fossil footprints (Demathieu and Oosterink 1983) together with fossil mudcracks, and wave ripples (Oosterink et al. 2003) imply a very shallow sea and periods of exposure. Thus, sea level was not constant. The oldest layers of the quarry (Röt and lowermost Muschelkalk) in particular were terrestrially influenced (Diedrich 2001). The arid climate permitted no huge influx of freshwater and caused high levels of evaporation followed by higher salinities (Oosterink et al. 2003). The presence of the crustacean *Halycine* cf. *agnota* and the minerals dolomite and celestine also indicate a higher salinity (Oosterink 1981). In addition, absence of corals, echinoids, and crinoids, and the presence of only few brachiopods indicates an unstable environment, possibly with changing salinities. The rare presence of the mineral gypsum (Oosterink and Winkelhorst 2003) might also indicate higher salinities, although the authors stated that it might have been derived from alteration of pyrite. The common occurrence of pyrite crystals suggests oxygen depletion.

The described lobsters were also inhabitants of this shallow marine realm. They are, however, small (cephalothorax lengths without rostrum vary from 11 to 17 mm for *Clytiopsis* spp. and about 25 mm for *Pseudoglyphea* cf. *P. spinosa*). This is comparable to lengths given in Förster (1967) for the two taxa (7.6–15.5 and 35 mm, respectively). Förster (1967) mentioned *Clytiopsis thuringica* to have a length of 13.2 mm. Interestingly, species of the presumed predecessor and descendent of *Clytiopsis*, the Upper Permian *Protoclytiopsis antiqua* Birshtein 1958 and the Carnian *Paraclytiopsis hungaricus* Oravecz 1962 (see Förster 1967), are notably larger than *Clytiopsis* spp. (62 and 23 mm, respectively). The reduced length of *Clytiopsis* spp. may also be due to the ecological stress of high salinities. A common bivalve from the Anisian strata from Winterswijk , *Myophoria vulgaris*, was also considered small (Faber 1959) and Oosterink (1981) mentioned that ammonites, lobsters, fishes, and reptiles were relatively small. Gall (1971) noted that the early Anisian fauna found in the French Vosges Mountains also consisted of small specimens, even compared to the French Muschelkalk fauna. Finally, Urlichs (2001) mentioned a dwarfed fauna in Anisian strata of the German localities Rübersdorf and Borgholzhausen, and from upper Ladinian strata of St. Kassian, Italy. Gall (1971) explained that negative ecological stress caused by high salinities might be a reason for the dwarfed fauna. Oosterink et al. (2003) provided additional causes such as food scarcity, high temperatures, and toxic levels because of, for example, pyrite formation. The first two causes are related to a high salinity. Thus, the small lobsters support earlier suggestions of ecological stress caused by high salinities.

The environment during the deposition of the Muschelkalk differs from the preceding Grès à Voltzia deposits (early Anisian) found in France in which most of the specimens of *Clytiopsis* have been found. In addition, the diversity of crustaceans was higher in the French occurrence: 15 genera versus four from Winterswijk (see Gall and Grauvogel-Stamm 2005). The shale lenses of the Grès à Voltzia were deposited in a deltaic environment, where terrestrial, freshwater/brackish, and marine fossils were found that have suffered from changes in salinity, temperature, and oxygen content (Gall and Grauvogel-Stamm 2005). The crustaceans would have lived in a freshwater to brackish environment (Gall 1985; Gall and Grauvogel-Stamm 2005). *Clytiopsis*, thus, must have been able to live in different environments and under a stressed regime.

Having a combination of very weak chelae, a relatively thin and smooth cephalothorax, and strong abdomen, *Clytiopsis* probably did not burrow, but, most likely, had a mixed crawling-swimming mode of life. Indeed, no definite infilling of a burrow was found surrounding or in the close proximity of the lobsters.

The predators of the lobsters must have been either fishes, like today, or the various aquatic reptiles that inhabited the Winterswijk area at that time. Diedrich and Schulz (2003) mentioned reptiles that would have preyed upon the lobsters in leftover, small water bodies. The lobsters might have fed on the various bivalves and gastropods and/or stromatolites found in the Winterswijk quarry complex.

CONCLUSIONS

Lobster specimens found in Middle Triassic (Anisian) sediments from the Dutch Winterswijk quarry complex are assigned to *Clytiopsis argentoratensis*, *Oosterinkia neerlandica* n. gen., n. sp., and *Pseudoglyphea* cf. *P. spinosa*. The lobsters lived in a low energetic, stressed environment with fluctuating salinity levels. The low number of lobster specimens is probably related to their low fossilization potential and the stressed habitat. The four specimens assigned to *Clytiopsis argentoratensis* are markedly smaller than stratigraphically younger and older relatives, suggesting that their limited size could be related to the stressed environment.

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