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# A decapod crustacean assemblage from the Middle Triassic Upper Muschelkalk of Großenlüder (Hessen, Germany)

## Kurzfassung

Im Oberen Muschelkalk des Großenlüderer Grabens (Osthessen) wurden aus Brockelkalk 4a (Trochitenkalk-Formation, Kraichgau-Subformation; *atavus*-Biozone; Anis, Oberillyr) in der näheren Umgebung von Großenlüder zahlreiche Exuvien und Körperfossilien dekapoder Krebse geborgen. Am häufigsten ist darin *Lissocardia silesiaca* v. Meyer,

1847. Wesentlich seltener sind in der Fossilagerstätte die Gattungen *Aspidogaster*, *Litogaster* und *Pseudopemphix*. Das flächenhafte (mehrere km<sup>2</sup>), auf eine einzige Lage begrenzte Vorkommen der *Lissocardia*-Bank wird als Ergebnis von populationsdynamischen Prozessen gedeutet. Eine Erklärung ausschließlich durch günstige diagenetische Prozesse ist

weniger wahrscheinlich. Hinweise auf Baue oder andere Lebensspuren von Krebsen liegen nicht vor. Das hervorragend erhaltene Material ermöglicht erstmals eine vollständige Beschreibung der Morphologie von *Lissocardia* und die sichere Zuordnung zur Familie Nephropidae (Ordnung Astacidea).

## Abstract

Many exuviae and body fossils of decapod crustaceans have been collected in the Upper Muschelkalk of the Großenlüder Graben (eastern Hessen, Central Germany). The decapod bed is a single layer in Brockelkalk 4a (Trochitenkalk-Formation, Kraichgau-Subformation; *atavus* Biozone; Anisian, Late Illyrian) in the vicinity of Großenlüder.

The most common decapod of this fossil lagerstätte is *Lissocardia silesiaca* v. Meyer, 1847. In addition, *Aspidogaster*, *Litogaster*, and *Pseudopemphix* occur, although they are much less abundant in the *Lissocardia* Bed. The mass occurrence of decapods in this fossil lagerstätte extending over at least several km<sup>2</sup> is interpreted as a result of unusually favorable local

environmental conditions rather than as a taphonomic process. Burrows or other traces of decapod activity have not yet been observed. The excellent preservation makes possible the first comprehensive morphological description of *Lissocardia* and its definite attribution to the family of Nephropidae (order Astacidea).

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## 1. Introduction

Decapod crustaceans, many well preserved in limestone nodules, have been collected from the Germanic Muschelkalk since the pioneer period of paleontology, early in the 19<sup>th</sup> century. As the first species, the large spiny lobster *Palinurus suevi* was described by Desmarest (1822). Later, v. Meyer (1840) established the genus *Pemphix* for this crustacean, which is most common in the Upper Muschelkalk of Southwest Germany. Until now, it remained the best-known of all Muschelkalk decapods (Förster 1967). Due to their rarity, other genera of reptant Muschelkalk decapods have been added later: *Litogaster* by v. Meyer (1844), *Lissocardia* by v. Meyer (1847), *Pseudopemphix* by Wüst (1903), *Clytiopsis* by Bill (1914), *Aspidogaster* and *Piratella* by Assmann (1927). A fragmentary carapace has been attributed to *Pseudoglyphica* by Förster (1967), a genus established for Jurassic decapods by Oppel (1861). It was Assmann (1927) who studied the decapod material housed in major German collections and discussed their systematic positions and geographical and stratigraphical distribution. In his comprehensive study, Förster (1967) revised the reptant decapods that were then known from Triassic strata worldwide. His monograph clearly demonstrated that the most complete and diverse reptant decapod faunas of the entire Middle Triassic (Anisian, Ladinian) are found in the Upper Buntsandstein (Votziensandstein) of eastern France and Southwest Germany and in the Upper Muschelkalk of Southwest Germany. However, the type material of some of the genera listed above has been collected from the Lower Muschelkalk of Upper Silesia (now Poland) and – once again – of Southwest Germany.

Decapod faunas from the Triassic of the Tethys realm and phylogeny of early Mesozoic decapods have been discussed in a number of papers by Glaessner (comp. Glaessner 1960). In recent years, knowledge of Triassic decapod diversity has been significantly enlarged by systematic investigation of rich conservation lagerstätten, which have yielded decapod crustaceans in Lombardy and elsewhere, conducted by the Invertebrate Paleontology Department of the Museo di Storia Naturale di Milano. Included in this research programme are the Triassic faunal assemblages of the Ambilobè region (NW-Madagascar; Garassino & Teruzzi 1995), of Cene (Seriana Valley, Bergamo – N-Italy; Pinna 1974), of Prati di Rest

(Valvestino, Brescia – N-Italy; Pinna 1976), of Ponte Giurino (Imagna Valley, Bergamo – N-Italy; Garassino & Teruzzi 1993), and of Carnia (Udine, NE-Italy; Garassino et al. 1996, Garassino, in press).

Private collecting activity in many Muschelkalk sections in Germany since publication of Förster's monograph has resulted in a great number of new specimens many of which have been excavated from measured sections and skillfully prepared from hard limestone nodules by means of pneumatic chisels. These new specimens allow more detailed morphological description of some of the less well known genera and discussion of systematic position. Moreover, they also allow discussion of paleoecology, stratigraphical range, and geographical distribution of Muschelkalk decapod crustaceans.

One of the most productive decapod beds yielding an association both diverse and rich in individuals has been discovered by one of us (Manfred Schulz) at the base of the Upper Muschelkalk of eastern Hessen (Central Germany). The most common species in this fossil lagerstätte is *Lissocardia silesiaca* v. Meyer, 1847, hitherto mostly known from the Lower Muschelkalk from a few more or less fragmentary specimens. The excellent preservation of relatively complete specimens allows a full morphological description of *Lissocardia* and confirmation of its attribution to the family Nephropidae Dana, 1852 (order Astacidea Latreille, 1803). The new specimens of *Aspidogaster* and *Litogaster* (Glyphidae), and *Pseudopemphix* (Pemphicidae) collected in the Großenlüder *Lissocardia* Bed do not provide additional morphological information. Therefore, they were not described in this paper.

The specimens studied in this publication are part of the private collection of Manfred Schulz (acronym CSG). Additional material referred to in this paper is housed in the Museum für Naturkunde an der Humboldt-Universität Berlin (MB), the Staatliches Museum für Naturkunde Stuttgart (SMNS), the Muschelkalkmuseum Hågdom, Ingelfingen (MHI) and in the private collection of M. Hartinger (CHK), Krautheim (Baden-Württemberg, Germany). It is guaranteed that none of the figured or referred to specimens will be given to another than a public collection. The Muschelkalkmuseum Ingelfingen will be informed about any change of specimen repository.

## 2. The Großelüder *Lissocardia* Bed

### 2.1 Localities

*Lissocardia* and other decapod crustaceans have been collected in four outcrops around the town of Großelüder near Fulda (Hessen, Central Germany; Fig. 1). Generally, the Muschelkalk in this region is preserved in the Großelüder Graben, a minor tectonic structure striking SE-NW. Along this graben, small downfaulted Muschelkalk blocks are quarried for lime and portland cement. Each of the few localities exposing the section under study has yielded decapod specimens. These localities are:

- (1) Großelüder, quarry of Kalkwerk Meister. TK 25 Sheet Nr. 5423 Großelüder, R 35 36 85, H 56 06 36
- (2) Großelüder-Müs, road cutting of the Umgehungsstraße Müs. TK 25 Sheet Nr. 5423 Großelüder, R 35 36 08, H 56 06 05
- (3) Großelüder-Müs, landfill of Firma Hillenbrand. TK 25 Sheet Nr. 5423 Großelüder, R 35 36 11, H 56 05 91
- (4) Fulda-Rodges, quarry of Firma Wende. TK 25 Sheet Nr. 5423 Großelüder, R 35 43 18, H 56 02 60

In 1999, only Locality 1 is still accessible; Localities 2–4 were only temporarily open and have been refilled.

### 2.2 Stratigraphy

The *Lissocardia* Bed is a single layer of uniform expansion in the Großelüder area (Fig. 2). The Kalkwerk Meister quarry (Fig. 3) exposes a complete profile from the dolomitic marls of the Middle Muschelkalk Diemel For-

mation up to the Upper Muschelkalk Meißner Formation (Hagdorn & al. 1987: pl. 2). Lithostratigraphically, it belongs to the Trochitenkalk Formation (Kraichgau Subformation) at the base of the Upper Muschelkalk Subgroup. Biostratigraphically, its position is exactly the base of the *atavus*-Biozone, which is of Late Anisian (Late Illyrian) age.

Traditionally, the Germanic Muschelkalk is subdivided by a number of isochronous marker beds, many of which can be traced over wide areas of the Muschelkalk basin. In terms of this extremely detailed marker bed stratigraphy, the Großelüder *Lissocardia* Bed is a distinct layer in Brockelkalk 4a, 20 cm below the base of Trochitenbank 1 (Fig. 2, 4). Brockelkalk 4a is a 50–65 cm thick horizon of nodular limestone (calcilutite, mudstone) interbedded with marlstone. This horizon was originally identified and described as a marker bed some 200 km farther to the South in Baden-Württemberg (Southwest Germany; Wirth 1957, Ockert 1992). The same is true for Trochitenbank 1, an 80 cm thick set of limestone beds (calcirudite, packstone) with abundant bivalve and brachiopod shells and echinoderm sclerites (mostly crinoid columnals, the so-called Trochiten).

One layer in Trochitenbank 1 contains shells of *Tetractinella trigonella*. In the entire 70 to 80 m thick column of the Upper Muschelkalk, this brachiopod only occurs in this marker bed, the *Tetractinella*-Bank, which can be traced from the Black Forest to the Subhercynian Hills over 500 km in a wide zone along the eastern coast of the Muschelkalk sea (Hagdorn & Simon 1993). Isochrony of

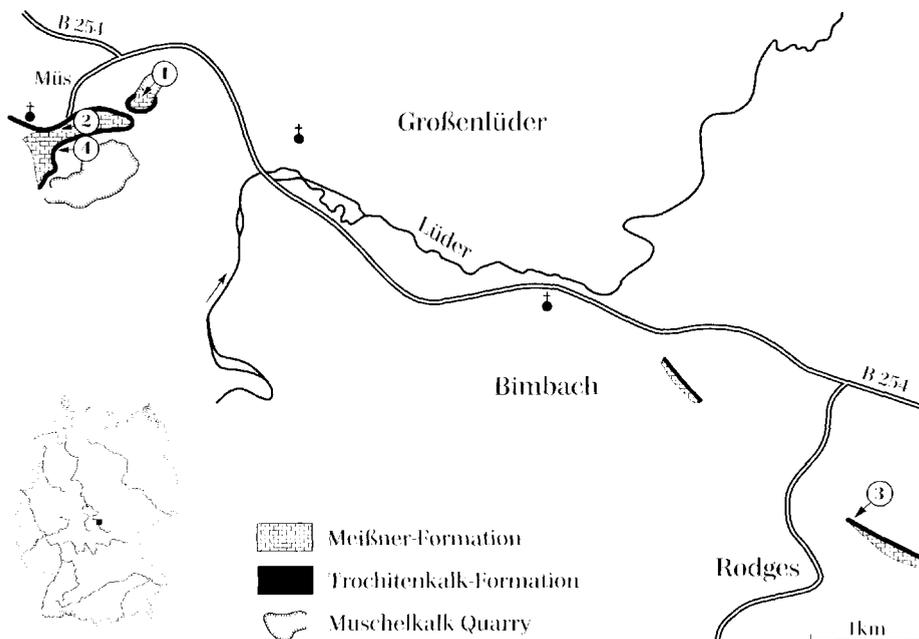


Fig. 1. Geographical position of *Lissocardia* fossil sites and Upper Muschelkalk outcrop around Großelüder.

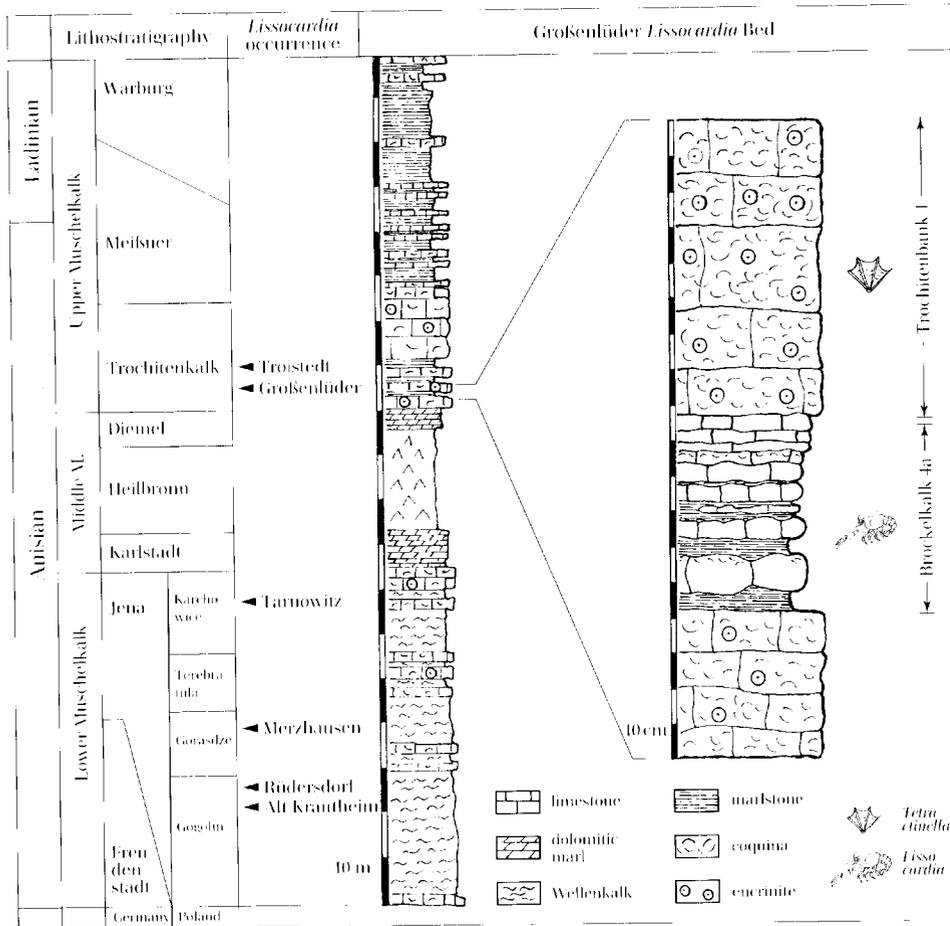


Fig. 2. Stratigraphical position of the Großenlüder *Lissocardia* Bed and additional *Lissocardia* occurrences.

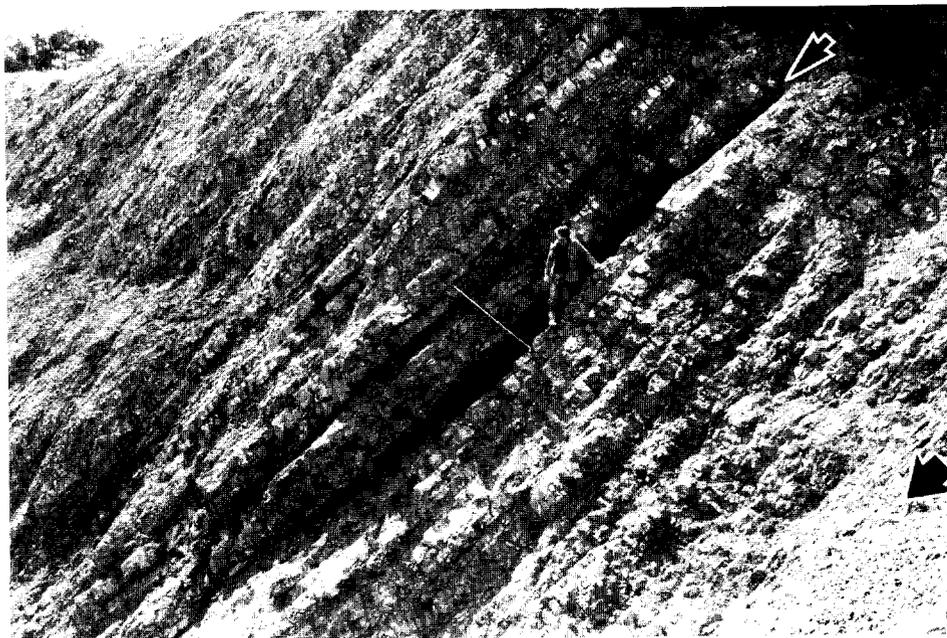


Fig. 3. Overview of Kalkwerk Meister near Großenlüder-Müs with *Lissocardia* Bed (thin arrow). The Middle/Upper Muschelkalk boundary is indicated by a thick arrow.



Fig. 4. Detail of *Lissocardia* Bed in Kalkwerk Meister (arrow).

the *Tetractinella*-Bank is corroborated biostratigraphically by the first occurrence of *Paracratites atavus* and *P. flexuosus* in the Germanic Basin directly below it, in Brockelkalk 4a (Geisler 1939, König 1920). Thus, the stratigraphical position of the *Lissocardia* Bed can be exactly fixed and easily compared with other decapod occurrences in the basal Upper Muschelkalk.

### 2.3 Sedimentology and paleosynecology

The *Lissocardia* Bed is a 5–6 cm thick layer of nodular limestone in the upper part of Brockelkalk 4a (Figs. 2, 4). The nodules containing the crustaceans are irregular, often longitudinal, up to 15 cm long and 6–8 cm wide lensoid bodies of a grey, micritic, marly limestone. Their lime content decreases towards the surfaces of the nodules and therefore there are no distinct boundaries between concretion and marly matrix. Many of the crustaceans are positioned close to the upper or lower surface of the nodules, however, others may also be found in the interior parts of the nodules. The typical preservation

of the crustaceans with carapace and abdomen separated or slightly displaced indicates that most of the fossils are exuviae. Some intact specimens could also have been embedded as carcasses. The three-dimensional and uncompressed preservation of both carcasses and exuviae indicates early diagenetic cementation of the nodules. It is supposed that the early diagenetic cementation of the nodules was triggered by decay of the crustaceans.

We also discussed whether the nodules originally represented crustacean burrows that were later infilled with lime-mud and subsequently cemented. However, the nodules are not likely to be burrow fills because (1) the shape of the nodules is too irregular for crustacean burrows, (2) we did not find fecal pellets in the nodules and (3) because some nodules may also contain actinopterygian fish skeletons and are thus definitely concretions formed during decay of animal skeletons.

The *Lissocardia*-Bed around Großenlüder yielded the following fossils, most of which are rare:

- Brachiopoda: *Lingula* cf. *tenuissima*  
*Discinisca discoides*
- Bivalvia: *Pleuromya musculoides*  
*Myophoria vulgaris*  
*Entolium discites*  
*Hoernesia socialis*  
*Plagiostoma striatum*
- Crustacea: *Lissocardia silesiaca*  
*Litogaster ornata*  
*Aspidogaster limicola*  
*Pseudopemphix meyeri*
- Vertebrata: Actinopterygian fish indet.

Crustaceans are the most abundant fossils in the *Lissocardia* Bed. Until April 1999, the four localities yielded the following numbers of decapod specimens:

Tab. 1: Number of decapod crustaceans from the Großenlüder *Lissocardia* Bed

Locality	1	2	3	4
<i>Lissocardia silesiaca</i>	24	15	3	17
<i>Litogaster ornata</i>	1	-	-	-
<i>Aspidogaster limicola</i>	1	-	2	-
<i>Pseudopemphix meyeri</i>	-	1	-	-

On average, one specimen is found per m<sup>2</sup>. In patches, the fossil density is greater (up to five per m<sup>2</sup>). Below and above the *Lissocardia* Bed, no crustacean fossils have been found. A thin tempestitic shellbed a few cm upsection contains abundant shells of the bivalves *Palaconucula*, *Myophoria*, *Entolium* and the small gastropod ?*Neritaria* or ?*Ampullina*. The above faunal list indicates that in the *Lissocardia* Bed, fossils with chitinous or phosphatic skeletons are over-represented in both abundance and diversity. Among the bivalves, the same is true for genera with calcitic shells, whereas genera with originally arago-

nitic shells are rare. Due to early diagenetic cementation of coquinas with high pore volume between the shells, aragonitic shells have increased fossil potential in tempestite beds. Therefore, the fossil content of the *Lissocardia* Bed and of the entire Brockelkalk 4a represents only a small part of the original community. Thus, diagenetic extinction of aragonite shells and diagenetic overprint of the sediment makes it difficult to comment on paleoecology and sedimentary environment.

The benthic fauna suggests a soft substrate. As there are no clasts or large shells, it can be concluded that the crustaceans must have burrowed in a slightly firm sediment, possibly in a level a few decimeters below the seafloor. However, there is no definite sedimentological evidence for burrowing activity, such as scratch marks or doubtless burrows.

Around Großenlüder, *Lissocardia* and the other decapod crustaceans are limited to a single layer of Brockelkalk 4a, however, this layer extends over at least several km<sup>2</sup>. This striking decapod occurrence can be interpreted (1) as an episodic event of extreme population growth or (2) as a short period of time with unusually favorable conditions for preservation of crustacean skeletons. Given the second case, the decapods inhabited the Muschelkalk seafloor over longer periods and their skeletons usually were dissolved by diagenetic processes. We favor the first inference and explain the mass occurrence as an explosive local or regional population increase. In the Muschelkalk, episodic mass occurrences of fossils also have been described from ophiuroids, asteroids, and brachiopods. *Aspidogaster* also occurs hundreds of kilometers distant in the same horizon at Neidenfels, Baden-Württemberg (MHI 1631).

The marl layers of the Hassmersheim Subformation

(which follows upsection and which are very similar in fauna and sediments) yielded *Aspidogaster*, *Litogaster* and rare *Lissocardia* and *Pseudopenphix*. Localities are Eschelbronn, Baden-Württemberg (König 1920), Künzelsau and Neidenfels, Baden-Württemberg (MHI 1477, 787), Rottershausen, Bavaria (MHI 1673), Troistedt, Thuringia (MHI 1634, CHK 22017, 22019). *Aspidogaster* and *Pseudopenphix* have also been recorded from the upper part of the Trochitenkalk Formation and from the Meißner Formation (comp. Assmann 1927, Förster 1967). However, *Lissocardia* has been previously recorded from the Upper Muschelkalk only in one specimen from the shaft of the Friedrichshall salt mine (SMNS 4401/658, Alberti-Collection). These records in different strata indicate that the decapods inhabited the Muschelkalk sea over a longer period. Episodic events of mass reproduction may have caused local or regional mass occurrences such as the Großenlüder *Lissocardia* Bed.

The Kraichgau and Hassmersheim Subformations of the Trochitenkalk Formation are characterized by stacked parasequences (or high frequency sequences, comp. Aigner & Bachmann 1993). The thickly bedded limestones such as Trochitenbank 1 are interpreted as transgressive peaks during high sea levels and their stenohaline echinoderms and articulate brachiopods are exotic immigrants from Tethys (Hågdom & Simon 1993). The marlstone and nodular limestone intercalations such as Brockelkalk 4a or the three marlstone horizons of the Hassmersheim Subformation were deposited during low sea level and increased input of fine clastics. Decrease of echinoderms in these horizons might indicate salinity changes that were tolerated by the decapods. The Trochitenbänke have not yielded decapods because the coarse skeletal beds were unfavorable for crustacean preservation.

### 3. Systematic paleontology

Order Decapoda Latreille, 1803

Infraorder Astacidea Latreille, 1803

Family Nephropidae Dana, 1852

Genus *Lissocardia* v. Meyer, 1847

- 1847 *Lissocardia* v. Meyer: 575
- 1851 *Lissocardia* v. Meyer – v. Meyer: 254
- 1903 *Lissocardia* v. Meyer – Wüst: 11
- 1927 *Lissocardia* v. Meyer – Assmann: 335
- 1927 *Piratella* n. gen. – Assmann: 337
- 1930 *Lissocardia* v. Meyer – Beuerlen & Glaessner: 53
- 1930 *Piratella* Assmann – Beuerlen & Glaessner: 53
- 1930 *Lissocardia* v. Meyer – Beuerlen: 326
- 1930 *Piratella* Assmann – Beuerlen: 326
- 1967 *Lissocardia* v. Meyer – Förster: 174

The genus *Piratella* has been established by Assmann (1927) because of alleged lack of cristae on the gastrical region and a shallow abdominal notch, however, he emphasized its similarity with *Lissocardia*. Förster (1967) treated *Piratella* as a synonym of *Lissocardia*. The new material corroborates Förster's decision.

**Generotype:** *Lissocardia silesiaca* v. Meyer, 1847

**Diagnosis:** Carapace cylindrical, relatively high, compact. Rostrum narrow. Longitudinal dorsal keel with spines from rostrum to the posterior margin. Cervical groove deep, gastroorbital groove short. Postcervical groove weaker than branchiocardial groove, dorsally strongly reduced, becoming deeper downward completely separating the posterior, reduced part of the hepatic region. Anterior part of the hepatic groove horizontal, appearing only in outlines. Gastrical region with two

longitudinal carinae. Second carina on anterior side strongly bent upwards towards the rostrum. Antennal region on anterior side constricted by a depression originating from the antennal groove. Keel and carinae with spines, posterior antennal region and cardial region with coarser granules, otherwise uniform granulation. Abdomen weakly ornamented; epimeres separated from tergum by granulated longitudinal bulge. Pereiopod I with elongate merus, short carpus and strong propodus, chelate, elongate index and dactylus with long, dagger-like spines on opposite internal edges. Pereiopods II and III chelate. Pereiopods IV and V with terminal dactylus. Extended diagnosis modified after Förster (1967).

*Lissocardia silesiaca* v. Meyer, 1847

Figs. 5–10

1847 *Lissocardia silesiaca* – v. Meyer: 575

1847 *Lissocardia magna* – v. Meyer: 575

1851 *Lissocardia silesiaca* v. Meyer – v. Meyer: 254, Taf. 32, Fig. 34–35, 37–39

1864 *Lissocardia magna* v. Meyer – v. Alberti: 196

1865 *Lissocardia silesiaca* v. Meyer – Eck: 108

1927 *Lissocardia silesiaca* v. Meyer – Assmann: 336, Taf. 8, Fig. 4–8, Taf. 13, Fig. 1

1927 *Piratella badensis* n. gen. no. sp. – Assmann: 338, Taf. 8, Fig. 2–3

1928 *Lissocardia silesiaca* v. Meyer – Schmidt: 318, Fig. 874

1929 *Piratella badensis* Assmann, 1927 – Schmidt: 318, Fig. 875

1929 *P. badensis* Assmann, 1927 – Glaessner: 317

1937 *Lissocardia silesiaca* v. Meyer – Assmann: 110, Taf. 22, Fig. 6–8

1960 *Lissocardia silesiaca* v. Meyer – Glaessner: 40, Fig. 18, 1

1965 *Lissocardia silesiaca* v. Meyer – Förster: 160, Taf. 36, Fig. 1

1967 *Lissocardia silesiaca* v. Meyer – Förster: 175, Taf. 9, Fig. 6; Fig. 14.

1967 *Lissocardia badensis* (Assmann, 1927) – Förster: 176

**Lectotype:** v. Meyer 1851: Taf. 32, Fig. 37 (same specimen as Assmann 1927: Taf. 8, Fig. 6–7) Museum für Naturkunde an der Humboldt-Universität zu Berlin MB.A.936.

**Locus typicus:** Tarnowitz, Upper Silesia (now Tarnowskie Góry, Poland), abandoned Böhm quarry.

**Stratum typicum:** Lower Muschelkalk, upper part of Karchowice Formation (Anisian, Early Illyrian).

**Geographical occurrence:** Lower Muschelkalk: Upper Silesia (Poland), Brandenburg (East Germany), Baden-Württemberg (Southwest Germany). Upper Muschelkalk: Baden-Württemberg (Southwest Germany), Hessen, Thüringen (Central Germany).

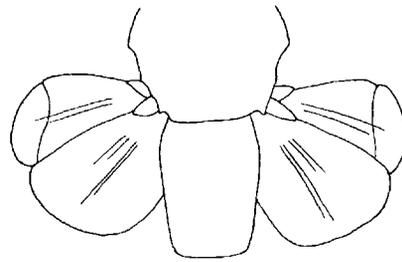


Fig. 5. *Lissocardia silesiaca* v. Meyer, 1847. Tail fan reconstruction in dorsal view.



Fig. 6. *Lissocardia silesiaca* v. Meyer, 1847. Reconstruction.

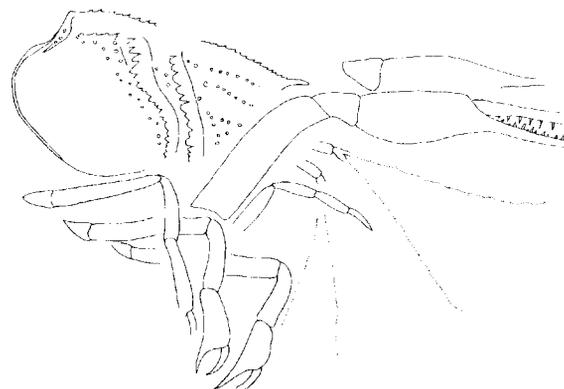


Fig. 7. *Lissocardia silesiaca* v. Meyer, 1847. Specimen CSG 1/1. Carapace, pereopods and antennulae of a large specimen; exuvia, right side, lateral view, x 1.5.

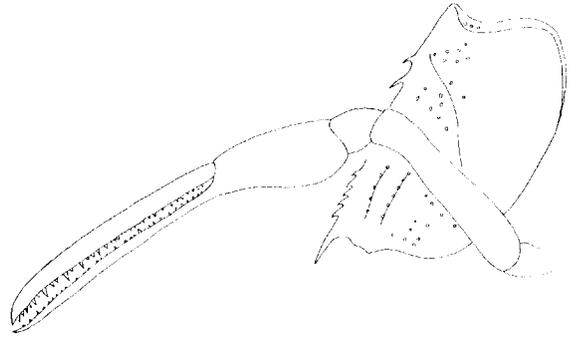
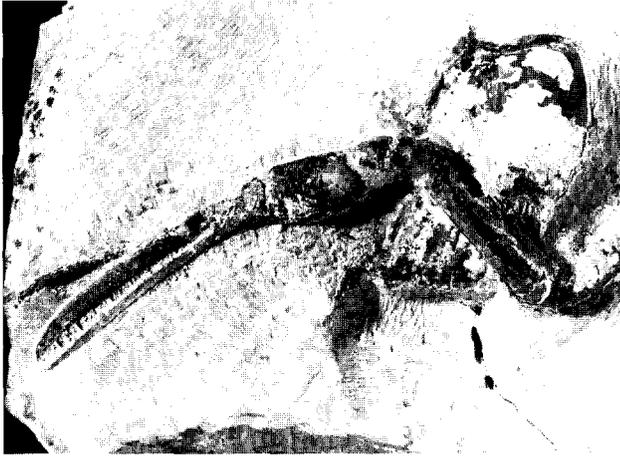


Fig. 8. *Lissocardia silesiaca* v. Meyer, 1847. Specimen CSG 1/2. Carapace and chelate pereiopod I with dagger-like teeth on inner edges: exuvia, right side, lateral view, x 2.

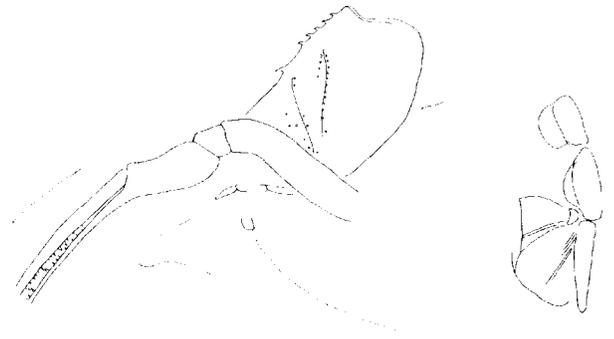


Fig. 9. *Lissocardia silesiaca* v. Meyer, 1847. Specimen CSG 1/3. Carapace, chelate pereiopod I and tail fan: probably an exuvia, left side, lateral view, x 0.9.

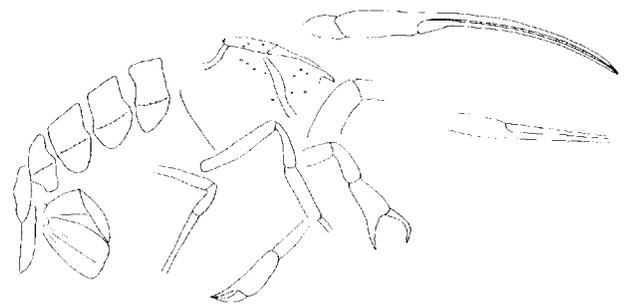
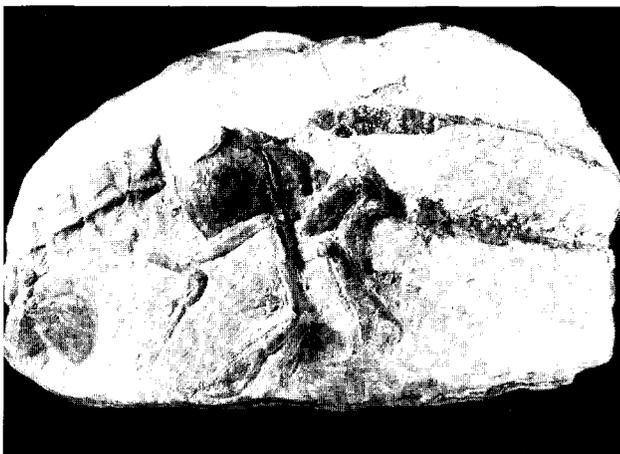


Fig. 10. *Lissocardia silesiaca* v. Meyer, 1847. Specimen CSG 2/1. Almost complete specimen showing carapace, abdomen with tail fan and pereiopods; body specimen, right side, lateral view, x 1.3.

**Stratigraphical occurrence:** Lower Muschelkalk, Jena Formation, Freudenstadt Formation, Karchowice Formation (Anisian, Bithynian to Early Illyrian); Upper Muschelkalk, Trochitenkalk Formation (Kraichgau Subformation, Brockelkalk 1a and contemporaneous Troistedt Subformation), *atavus* Biozone (Anisian, Late Illyrian).

**Material:** The originals of *Lissocardia* (M.B.A. 936, 937) and *Piratella* from the Lower Muschelkalk have been so carefully described by Assmann (1927) and Förster (1967) that a restudy was not necessary. The same is true for the specimen mentioned by v. Alberti (1864: 196) from the Upper Muschelkalk of Friedrichshall (SMNS 4401/658). Due to their poor preservation, a number of very fragmentary and compressed *Lissocardia* specimens from the Lower Muschelkalk Freudenstadt Formation (Lower Anisian) of Altkrautheim (Hohenlohekreis, Baden-Württemberg) in M. Hartinger's collection (CHK 22036–22042) have not been studied in detail. The same is true for a typical *Lissocardia* chela from the Lower Muschelkalk Jena Formation of Rüdersdorf (Brandenburg, East Germany); W. Tornow (Berlin) kindly sent a photo of this specimen in his private collection (uncatalogued). However, these specimens provide additional data on stratigraphical and geographical range of the species. A fragmentary specimen (carapace, chela) from the Lower Muschelkalk Jena Formation of Buchen-Bödighheim (MH 1674) is much better preserved. Among 59 more or less complete and well preserved specimens from the Großenlütter *Lissocardia* Bed, 17 have been selected for study. After skillfull preparation, they are visible either in lateral or in dorsal view. Certainly, most of the specimens are exuviae showing the typical separation between carapace and abdomen. Two specimens (CSG 2/2, CSG 4/4) are full body fossils. An additional specimen from the Trochitenkalk Formation (Troistedt Subformation, *atavus* Biozone) of Troistedt (Thüringen) in M. Hartinger's collection (CHK 22019) has also been studied.

The excellently preserved specimens from Großenlütter make possible for the first time a full morphological description of *Lissocardia silesiaca*, which was known before by a few fragmentary specimens only.

**Description:** *Lissocardia silesiaca* is a medium-sized astacidean of 4 to 6 cm length, with a coarsely tuberculate carapace and strongly elongate index and dactylus of chelate pereiopod I.

**Carapace:** In lateral view in almost all specimens, the carapace has a subrectangular shape, which becomes slightly more narrow towards the anterior margin be-

cause of the slight curvature of the ventral margin. Over its total extension, the straight dorsal margin forms a crista with a row of equal-sized spines pointing forward. The rostrum is short, without supra- and subrostral teeth and with a pointed distal extremity. The posterior margin is sinuous and strengthened by a strong marginal carina with a row of spines in its upper part. The ocular incision is narrow and shallow and the antennal and pterygostomial angles are not very marked. Two strongly barbed carinae extend along the antennal region of the carapace, joining together at the base of the rostrum. Moreover, the surface of the carapace has deep cervical and branchiocardic grooves with exterior margins ornamented by rows of equal-sized spines. Generally the largest part of the carapace is smooth; strong spines are located only near the grooves, and small tubercles are located near the carinae.

**Abdomen:** The subrectangular somites are equal in length. The triangular pleurae are strengthened by a coarse tuberculate transverse median carina, and the margins have a row of similar small spines. Somite VI has a subrectangular shape and is slightly longer than the others. The telson (Fig. 5) has a triangular shape with a rounded distal extremity; it is strengthened by two thin median longitudinal carinae. The uropods have the same length as the telson. The exopodite, with rounded diaeresis, is crossed by a strong median longitudinal carina. The median carina crossing the endopodite longitudinally bifurcates at its anterior extremity. The surface of the abdomen and of the tail fan is slightly tuberculate.

**Cephalic appendages:** None of the specimens has the eyes preserved. The antennular peduncle is composed of three articula; the 1° and the 2° are thin and elongate, and the 3° is short and stocky; two long flagella are articulated with it. The antennal peduncle is composed of three thin and elongate articula. The flagellum is twice the body length. The scaphocerite is not preserved.

**Thoracic appendages:** The maxilliped III is composed of thin, elongate and barbed articula. Pereiopod I has an elongate merus, short and stocky carpus and strong propodus with strongly elongate and curved distal extremity of dactylus and index (Fig. 8). The interior margins of the dactylus and the index have alternating strong and small teeth. Pereiopods II–III are chelate. The exterior margins of pereiopods I–III have sparse and strong spines. Pereiopods IV–V have a terminal dactylus.

**Abdominal appendages:** The pleopods have a subrectangular sympodite; two long multiarticulate flagella are attached to the sympodite.

## 4. Discussion

### 4.1 Systematic position of *Lissocardia*

In his revision of the Triassic reptant decapod crustaceans, Förster (1967) emphasized the most important characters of *Lissocardia*: subrectangular carapace, dorsal margin of carapace with a longitudinal keel with spines from rostrum to the posterior margin, deep cervical and branchiocardial grooves, antennal region with two longitudinal carinae and pereiopod I chelate with strongly elongate dactylus and index. These features could be found in the examined specimens.

Due to the fragmentary preservation of v. Meyer's specimens, the systematic position of *Lissocardia* has been controversial for a long time. Assmann (1927) ascribed *Lissocardia* to the Nephropsidae whereas Förster (1967) compared it with the Glypheidae Zittel, 1885, the Erymidae van Straelen, 1924, and the Pemphicidae van Straelen, 1928, and stated its intermediate position between these families. Glaessner (1969) ascribed this genus to the family Erymidae van Straelen, 1924 (subfamily Clytiopsinae Beurlen, 1927).

The complete and perfect preservation of many of our specimens made possible a more precise statement of its systematic position. Certainly, *Lissocardia* is not an erymid because this family has a cylindrical carapace, cervical and branchiocardial grooves devoid of spines and a pereiopod I with short and stocky chelae. *Lissocardia* has a longitudinal keel with spines in the dorsal margin of the carapace, longitudinal carinae in the antennal region and long and strong chelae of pereiopod I. This character is diagnostic enough to exclude an ascription of *Lissocardia* to the family Erymidae.

Zariquiey-Alvarez (1968:199–201) and Holthuis (1991: 19) pointed out the main characters of the family Nephropidae Dana, 1852: subrectangular carapace, longitudinal keel with spines in the dorsal margin of carapace, tuberculate longitudinal carinae in the antennal region, deep cervical and branchiocardial grooves, abdominal somite with a transverse median carina and pereiopod I with elongate and strong chelae with long and small teeth along the interior margins of dactylus and index. Because these characters are clearly developed in the studied specimens we ascribe the genus *Lissocardia* to the Nephropidae.

Two species of *Lissocardia* have been established from the Muschelkalk: *L. silesiaca* v. Meyer, 1851 and *L. magna* v. Meyer, 1851, both of them from the Lower Muschelkalk Karchowice Formation of Upper Silesia. They only dif-

fer in size and are certainly conspecific. Förster (1969) also assigned the poorly known *Piratella badensis* Assmann, 1927 to *Lissocardia*. However, he kept this species, which is based on two compressed specimens (Lower Muschelkalk, South Baden, Southwest Germany), as a separate species because he could not decide with certainty whether or not its diagnostic characters (shallow abdominal notch, no cristae on the gastrical region) are only a matter of poor preservation. A specimen recently collected in contemporaneous Lower Muschelkalk strata of Buchen-Bödighheim (northern Baden; MH 1674) has typical cristae on its gastrical region and does not substantially differ from *Lissocardia silesiaca* in the shape of the the abdominal notch. Therefore, we do not hesitate to treat *Piratella badensis* as a junior synonym of *Lissocardia silesiaca*.

### 4.2 Life habit

The small size of *Lissocardia* with its slender carapace and abdomen and its elongate and strong chelae give evidence that, like other astacideans, it was a benthic crustacean burrowing in muddy or slightly consolidated sediment. Its long and slender chelae with dagger-like spines on the interior edges of index and dactylus indicate food gathering specialization. However, the low diversity of other invertebrate fossils in the Großenlüder *Lissocardia* Bed does not indicate any kind of specialized predator-prey relationship. *Lissocardia* can be compared to the extant astacideans *Thaumastocheles* and *Acanthacaris* that live as burrowers on muddy bottoms and have chelae similar to those of *Lissocardia* (Holthuis 1991).

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