

UPPER OLIGOCENE BRACHIOPODS FROM NW GERMANY, WITH DESCRIPTION OF A NEW PLATIDIINAE GENUS, *GERMANOPLATIDIA* N. GEN.

ALFRÉD DULAI¹ & FRITZ VON DER HOCHT²

¹Department of Palaeontology and Geology, Hungarian Natural History Museum, H-1083 Budapest, Ludovika Square 2, Hungary.
E-mail: dulai.alfred@nhmus.hu
²G.-Hoensbroech-Str. 100, D-50169, Kerpen, Germany. E-mail: von.der.Hocht@gmx.de

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Abstract. Upper Oligocene brachiopods of NW Germany were studied in two collections: the Naturalis Biodiversity Center (Leiden, the Netherlands) and the F. von der Hocht private Collection (Kerpen, Germany). Overall, six taxa have been identified. Generic attributions of “*Rhynchonella*” *supraoligocaenica* Görges, 1952 (*Aphelesia*) and “*Terebratula*” *pusilla* Philippi, 1843 (*Germanoplatidia* n. gen) have been solved. The Chattian occurrence of *Aphelesia* is the first confirmed record of the genus in the Paleogene. Chattian record of the well-known Neogene *Disciniscia fallens* (Wood, 1872) confirms that faunal change within brachiopods happened before the Paleogene/Neogene boundary. Similarly to the Mediterranean *Terebratula*-*Aphelesia* association, *Aphelesia* occurs also together with a large terebratulide genus (*Pliothyris*) in the upper Oligocene Pre-North Sea. Along with some previously recognized genera (*Orthothyris*, *Bronnothyris*, *Rugia*), a further brachiopod evolutionary lineage was found to survive from the Mesozoic to the Paleogene (*Aemula*-*Germanoplatidia* n. gen.). According to the morphological characters of the genus and sedimentological characters of the surrounding deposits, *Germanoplatidia* n. gen. species lived on sandy bottom environments, and attached to small hard objects in the fine sediment by a pedicle longer than that of *Aemula*. Half of the identified species are endemic in Pre-North Sea. Here we document the first record of *Argyrotheca bitnerae* Dulai in Dulai & Stachacz, 2011 from the Pre-North Sea; this recently described species shows a cosmopolitan distribution in the Cenozoic.

INTRODUCTION

The Cenozoic brachiopod fauna of Europe has been studied for a long time but is far from being perfectly known. Most of the large-sized forms were discovered earlier, however, their generic attributions were only rarely solved. Therefore, new results can be achieved even on large brachiopods, on the basis of investigation of their internal morphological characters. The lack of knowledge is more conspicuous in the case of the micromorphic brachiopods, as their study was neglected in several cases because of their size. As a result, washed or dissolved Cenozoic samples yield important new

taxonomic results even nowadays. The brachiopod fauna of different Cenozoic stages is also unevenly known. While several papers deal with Eocene and Miocene faunas, we have much fewer data on Oligocene brachiopods. Therefore, Oligocene brachiopods even with limited specimen numbers are always worthwhile to study.

The Oligocene brachiopod fauna of the North Sea is still largely unknown. Bosquet (1862) described Oligocene brachiopods from the Netherlands and Belgium (Limbourg). Sandberger (1862-1863) has found a surprisingly rich fauna in the lower Oligocene of the Mainz Basin (S Germany), including *Terebratula*, *Terebratulina* and some megathyridid species (*Argiope subradiata* Sandberger, 1862, *A. crenata* Sandberger, 1862, *A. megaloccephala*

Sandberger, 1862). Vincent (1893, 1923) reported *Terebratulina* from the Oligocene of Belgium. More recently, Bitner & Kroh (2011) revised one of Sandberger's (1862-1863) species, and *Argiope subradiata* was transferred into the genus *Bronnothyris*. Bitner & Müller (2015) described six species from the upper Eocene to lower Oligocene Silberberg Formation of Atzendorf in Central Germany.

A few Chattian brachiopods from Germany were found by A.D. in the collection of Naturalis Biodiversity Center (Leiden, the Netherlands) in 2016. Although the specimen number was rather limited, the 13 specimens from two localities (Krefeld-Gellep and Glimmerode) represented four different taxa. One of them, a small platidiid species from Krefeld-Gellep was especially interesting with well-preserved internal morphological characters. According to the collection labels, this material was collected by Fritz von der Hocht (the second author of this paper) in 1973. Later it turned out that the Krefeld-Gellep specimens were donated to Arie W. Janssen and Naturalis by F.v.d. Hocht, and he possesses a much larger brachiopod collection from Krefeld-Gellep and other localities of the Lower Rhine Embayment, as well as from some other Chattian localities of Germany. This paper summarizes the upper Oligocene (Chattian) brachiopod fauna record of NW Germany, on the basis of Naturalis collection (Leiden, the Netherlands) and the F.v.d. Hocht private collection (Kerpen, Germany).

GEOLOGICAL SETTINGS

The Chattian stage in northern Germany.

The Sternberger Gestein was selected by Beyrich (1854) as the highest member when he established the Oligocene stage. Fuchs (1894) named the upper Oligocene interval "Chattische Stufe" (= Chattian). The Chattian can be found in five distinct areas in northern Germany. From North to South these are: Mecklenburg-Vorpommern, a region encompassing Hildesheim and Söllingen to Magdeburg, the "Osnabrücker Bergland" and the nearby "Ostwestfalen-Lippe" district, locations near Kassel, and finally the "Niederrhein" (Lower Rhine area).

The Chattian is commonly subdivided based on Pectinidae bivalves and comprises the Eochattian and Neochattian in the definition of Hubach (1957) or Chattian A, B, C according to Anderson (1961).

The studied area in NW Germany was part of the Pre-North Sea Basin (Diedrich 2012: figs. 4, 15).

Sülstorf Formation. The Sülstorf Formation is composed of about 80 m of thick micaceous, calcareous and glauconitic fine- to medium-sized sands with sandstone intercalations. The sandstone intercalations are thin layers with well-preserved mollusc coquinas and the remains of several marine fossils (Suhr & Braasch 1991). These sandstones are also the source of erratic rocks in glacial fluvial sediments in Mecklenburg (=Sternberger Gestein). Until now, the rich fauna of the Sternberger Gestein has not yielded any brachiopods.

Diekholzen Formation. According to Rust's (1999) modern review of the Chattian from Diekholzen, this formation starts with a glauconitic, green-grey sands and sandstones at the base (9-19 m, Chattian A). It is conformably overlain by 30 m thick, fine- to medium-sized glauconitic sands containing many bioclasts. This interval is overlain by a sandy, fossiliferous limestone composed primarily of remains of pectinids, cirripeds and echinoderms (Ritzkowski in Rust 1999). The stratigraphic position of the middle and upper intervals encompasses part of the Chattian A and Chattian B and C. Platidiidae brachiopods (*Germanoplatidia* n. gen.) have been found in the basal green sands, while the higher levels have yielded *Pliothyridina* specimens (Rust 1999: 74).

Söllingen Formation. Richly fossiliferous Chattian sediments of the Söllingen Formation were first excavated in 1857 during building of a railway track between Söllingen and Jerxheim. The lower part consists of grey, silty-clayey and glauconitic fine sands, and it is overlain by at least 2 m of thick yellow, fossil-rich fine- to medium-sized sands. They were originally considered to be early Oligocene (Rupelian) in age. Janssen (1979) identified these sands as representing the lower part of the Chattian A based on *Pecten soellingensis* von Koenen, 1868. Two species of brachiopods have been described from the grey, clayey fine sands by Speyer (1860, 1864); however, his species, *Terebratulina subrhomboidea* Speyer, 1860 is revised in this paper (see below).

Doberg Formation. This formation consists of 53 well defined layers at the type locality Doberg (Anderson 1969: 45). Layers 1-10 consist of slightly clayey, moderate to strongly glauconitic and very fossiliferous sands. Layers 11-24 are most-

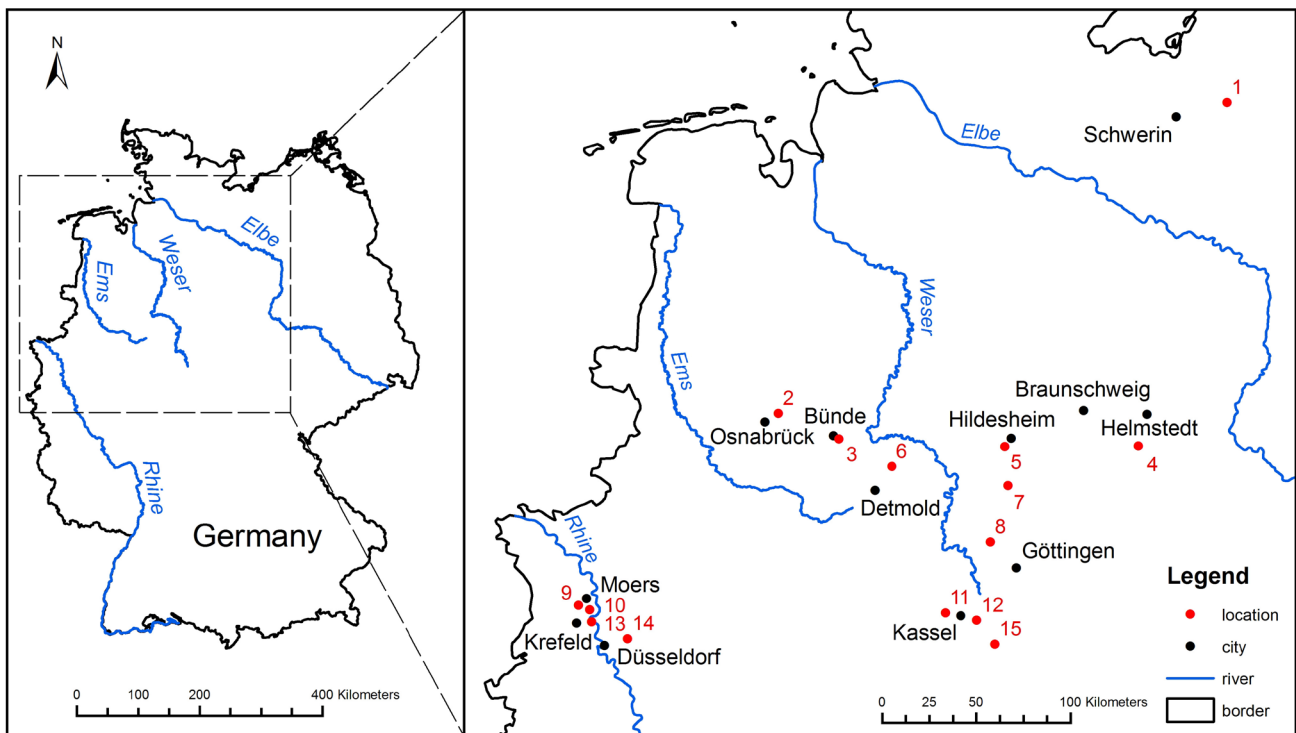


Fig. 1. Map of Chattian brachiopod occurrences in NW Germany. Localities: 1 - Kobrow; 2 - Astrup; 3 - Doberg; 4 - Söllingen; 5 - Diekhöfen; 6 - Göttentrup; 7 - Freden; 8 - Volpriehausen; 9 - Kapellen; 10 - Rumeln; 11 - Ahnatal; 12 - Niederkaufungen; 13 - Krefeld-Gellep; 14 - Mettmann; 15 - Glimmerode.

ly sandy to conglomerate bearing marls. Starting with layer 25 loose or slightly consolidated fossiliferous sands occur again. The entire stratigraphic sequence of the Chattian A through C is represented at Doberg (1-32: Eochattian, 32-53: Neochattian). Doberg has been selected as the neostratotype for the Chattian (Anderson et al. 1971). The brachiopod *Pliothyridina grandis* (Blumenbach, 1803) has been found through the entire sequence, but it is particularly common in layers 7, 27 and 42, where they built three massive shell beds with single and double valued specimens (Diedrich 2012). *Aphelesia supraoligocaenica* has been found primarily in layer 27, and one specimen in layer 9.

Another classic location of the Doberg Formation is the marl pit at Astrup, NE of Belm. About 20 m of glauconitic calcareous sand or consolidated sandstone of Chattian A and B have been mined in this pit. *Pliothyridina grandis* is common here, and a single valve of “*Rhynchonella*” has also been found (Dallmann 1996: 41).

Chattian A (Philippi 1843) and Chattian B (Janssen 1986) have also been recorded from Freden. Sediments from the Chattian B were retrieved from a temporary excavation for a construction.

They consist of glauconitic fine- to medium-sized sands and fine gravels.

Kassel Formation. Wilhelmshöhe and Brandkopf are the classical localities of the upper Oligocene of Kassel, located south of the Ahnatal in the Habichtswald. The Kassel Formation consists of light yellow to brown, glauconitic, micaceous and coquina-rich fine- to medium-sized sand. Another classical location in the Kassel embayment is the “Gelber Berg” near Niederkaufungen. Rich fossil faunas have been collected from yellow fine- to medium-sized sands of the Chattian A. The lignite mining at Höllkopf near Glimmerode has excavated large outcrops of Oligocene and Miocene strata overlying the coal beds. The total thickness of the Kassel Formation is 63 m (Janssen 1986: 332), and the age of the entire sequence corresponds to the Chattian A. Megathyridid brachiopods (*Argyrotheca*, *Bronnothyris*?) are known from Höllkopf Mine.

Grafenberg Formation. The Grafenberg Formation represents the Chattian in the Lower Rhine Embayment. On average, it consists of about 100 m thick green-grey, fine- to medium-sized glauconitic sands. Its sediments are found at or near to the surface along the western margin of the Em-

Tab. 1 - Location and coordinates of localities in NW Germany, where Chattian brachiopods were found. Legend: NRW - North Rhine-Westphalia; NS - Lower Saxony; H - Hesse; MVP - Mecklenburg-Vorpommern.

Locality	State	TK_25	Easting	Northing	Easting GK 2	Northing GK 2	Number	UTM_Easting	UTM_Northing
Mettmann	NRW	4707 (Mettmann)	2566460	5680450	2566460	5680450	14	357045	5680181
Kr-Gellep	NRW	4606 (Ddf.-Kaiserswerth)	2547325	5689415	2547325	5689415	13	338295	5689919
Kapellen	NRW	4505 (Moers)	2540320	5698240	2540320	5698240	9	331657	5699022
Rumeln	NRW	4605 (Krefeld)	2546270	5695870	2546270	5695870	10	337505	5696411
Diekholzen	NS	3825 (Hildesheim)	3561300	575800	2766735, 786	5782582, 446	5	561203	5773929
Freden	NS	4025 (Groß-Freden), Winzenburger Str.	3562180	5755140	2768469, 558	5761959, 254	7	562082	5753277
Astrup	NS	3614 (Wallenhorst)	3442040	5798340	2646582, 147	5800176, 632	2	441991	5796462
Doberg	NRW	3817 (Herford-West)	3473560	5783480	2678700, 007	5786630, 093	3	473498	5781607
Göttrtrup	NRW	3920 (Bödingfeld)	3501050	5767770	2706828, 511	5772062, 93	6	500977	5765903
Volpriehausen	NS	4324 (Hardegsen)	3551710	5725650	2759214, 803	5732038, 912	8	551616	5723799
Ahnatal	H	4622 (Kassel-West)	3526200	5688900	2735215, 085	5694246, 513	11	526116	5687064
Niederkaufungen	H	4723 (Oberkaufungen)	3542760	5684200	2751965, 339	5690224, 596	12	542669	5682366
Glimmerode	H	4824 (Hess.-Lichtenau)	3551770	5671200	2761506, 206	5677593, 551	15	551675	5669371
Kobrow	MVP	?	4488650	5949400	2884893, 966	5965181, 829	1	686703	5951159
Söllingen	NS	3931 (Jerxheim)	4426600	5772050	2837791, 531	5782983, 692	4	632115	5771395

bayment (Viessen-Süchteln) and in the East near Düsseldorf. Calcareous fossils are dissolved with only a few exceptions, e.g. the Freudenberg sandpit in the Karlsberg near Süchteln.

The Grafenberg Formation is overlain by 10-70 m thick Pleistocene sands and gravels. Therefore, Chattian marine sands have only been found in shafts of coal measures and wells. Rarely they have been temporarily exposed during large construction excavations, (e.g., enlargement of the Rhine harbour at Krefeld in 1973) or during the construction work of the highway A 44 near Meerbusch in 2000. Many specimens of *Germanoplattidia pusilla* have been collected from the harbour enlargement at Krefeld. *Argyrotheca* valves have been obtained from wells near Mettmann from gravel-bearing marine sands, which is nearly identical in composition with that of Glimmerode of the Kassel Formation (see above). Brachiopods have been reported in literature from the coal measure shafts of Rumeln (Görges 1940) and Kapellen and Tönisberg (Strauch 1967). The Grafenberg Formation encompasses all three substages of the Chattian (A-C). The Chattian C (=Neochattian) was observed by F.v.d. Hocht not only in the northern part of the Lower Rhine Embayment, but also in the region of Krefeld and Düsseldorf directly below the Pleistocene rocks.

The upper Oligocene brachiopod occurrences in NW Germany are indicated in Fig. 1, and the exact location of these localities are summarized in Tab. 1.

MATERIAL AND METHODS

The smaller part of the studied brachiopods is from the Naturalis Biodiversity Center (Leiden, the Netherlands); these specimens are indicated with inventory numbers prefixed by NBC RGM (Rijksmuseum van Geologie en Mineralogie, Leiden inventory numbers). The majority of the studied fauna is from the F.v.d. Hocht private collection. The studied and illustrated specimens in the present work are kept in the collection of Hungarian Natural History Museum, Budapest. These specimens are indicated with inventory numbers prefixed by HNHM INV (Hungarian Natural History Museum, Invertebrate Collection, Budapest inventory numbers). Additional specimens of all described species are housed in the private collection of Fritz von der Hocht (Kerpen, Germany).

Abbreviations used in the text: A - articulated specimen; D - dorsal valve; V - ventral valve; fr - fragment; juv. - juvenile.

A complete list of the material investigated is listed below:

1. Specimens from Naturalis Biodiversity Center (Leiden, the Netherlands)

Krefeld-Gellep (Germany, North Rhine-Westphalia), construction pit diver pipe at port; MTB 4606, coordinates: r = 47.290, h = 89.490. Oligocene, Chattian B, Grafenberg Sand, Leg.: F.v.d. Hocht, 1973.

Discinisca fallens (Wood, 1872) (2 D, 2 fr), NBC RGM.800513

Germanoplatidia pusilla (Philippi, 1843) (3 A, 1 V), NBC RGM.800512.

Glimmerode (Germany, Hessen), open-cast mine at Höllkopf, MTB 4824, coordinates: r = 51.900, h = 71.100. Oligocene, Chattian A, Kassel marine sand, Leg.: M. van den Bosch, June 1973.

Argyrotheca bitnerae Dulai in Dulai & Stachacz, 2011 (1 A juv., 2 V juv., 5 fr), NBC RGM.801079.

Bronnothyris? sp. (4 fr), NBC RGM.801078.

2. Specimens from F.v.d. Hocht private collection, donated to HNHM, Budapest

Krefeld-Gellep, excavation pit at new harbor basin, Oligocene, Chattian B, Grafenberg Formation.

Discinisca fallens (Wood, 1872) (4 D), HNHM INV 2019.70-71.

Kaarst, borehole, 37-41 m depth, Oligocene, Neochattian, Grafenberg Formation.

Discinisca fallens (Wood, 1872) (3 D, 4 fr), HNHM INV 2019.68-69.

Kapellen near Moers, Oligocene, Chattian B, Grafenberg Formation.

Germanoplatidia pusilla (Philippi, 1843) (3 A, 3 D), HNHM INV 2019.86-90.

Mettmann (13 km ENE of Düsseldorf), Oligocene, Chattian A, Grafenberg Formation.

Discinisca fallens (Wood, 1872) (5 D, 15 fr), HNHM INV 2019.72-75.

Pliothyrina grandis (Blumenbach, 1803) (7 fr), HNHM INV 2019.91.

Argyrotheca bitnerae Dulai in Dulai & Stachacz, 2011 (3 A, 1 D, 1 V), HNHM INV 2019.83-85.

Astrup near Osnabrück, Oligocene, Chattian A

Pliothyrina grandis (Blumenbach, 1803) (1 A, 2 V, 1 D), HNHM INV 2019.79-82.

Doberg, south of the city of Bünde

Aphelesia supraoligocaenica (Görge, 1952) (1 A, 1 V, 1 D), HNHM INV 2019.76-78.

The Paleogene is covered by fluvio-glacial and glacial deposits of the Pleistocene in the Lower Rhine Basin, therefore no natural outcrops of the marine upper Oligocene occur in the area. Generally drilling boreholes (for water wells, geothermal energy and building ground exploration) excavate the Chattian. Fossils of the Chattian fine and medium sands were collected directly from the drilling fluid current of the large auger machine with a sieve of mesh size 1mm (Mettmann, Kapellen). In the laboratory, the residue was washed partially in 1% H₂O₂ solution, then dried and fractionated in sieves (1-4, 4-10 and > 10 mm).

Germanoplatidia pusilla specimens were extracted from bulk samples of the excavation for an extension of the Rhine harbour at Krefeld-Gellep in 1973. Grey-green fine sands of the Chattian B were accessible at the bottom of this building pit. Rust (1999: 16) reports that he has received the fossil content of the Chattian green sand (Diekholzen Formation) from Diekholzen-Neuhof, Lower Saxony, with coarse-mesh sieves directly in the water of the Eichteiche creek. After preparation in the laboratory, he found 50 specimens of *Germanoplatidia pusilla* in this residue.

SYSTEMATIC PALEONTOLOGY

Phylum **BRACHIOPODA** Duméril, 1805
 Subphylum **LINGULIFORMEA** Williams, Carlson, Brunton, Holmer & Popov, 1996
 Class **LINGULATA** Gorjansky & Popov, 1985
 Order **Lingulida** Waagen, 1885
 Superfamily Discinoidea Gray, 1840
 Family Discinidae Gray, 1840
 Genus *Discinisca* Dall, 1871
 Type species - *Orbicula lamellosa* Broderip, 1833 by original designation of Dall (1871).

Discinisca fallens (Wood, 1872)

Pl. 1, Figs. 1-12

1852 *Orbicula lamellosa?* Brod. - Davidson, p. 7, pl. I, fig. 9.

1872 *Discina fallens* - Wood, p. 172, pl. 11, fig. 6.

2011 *Discinisca* sp. - Müller, p. 20, pl. 2, fig. 28.

2013 *Discinisca fallens* (Wood) - Dulai, pp. 27-28, figs. 15-24.

Material: NBC (Leiden): Krefeld-Gellep, Chattian B (2 D, 2 fr); F.v.d. Hocht Collection donated to HNHM: Krefeld-Gellep, Chattian B (4 D); Mettmann, Chattian A (lowermost) (5 D, 15 fr); Kapellen-Moers, Chattian B (fr); Kaarst borehole, 37-41m (3 D, 4 fr).

Other materials: Neukirchen-Vluyn, shaft Niederberg-5, Chattian A (fr).

Dimensions (in mm).

	length	width
RGM.800513a (D)	3.4	2.9
RGM.800513b (D)	4.8	3.1
INV 2019.68. (D)	2.5	2.4
INV 2019.70. (D)	1.6	1.5
INV 2019.75. (D)	3.3	3.1

Description. The available fragmentary discinide specimens from the Chattian of Germany are small (less than 5 mm in diameter), and characterised by rounded and smooth dorsal valves. The shells are ornamented only by concentric growth lines (Pl. 1, Fig. 4). The subcircular or more or less elongated (Pl. 1, Figs. 1, 2, 5, 8) shells are thin-walled and conical with central-subcentral apex (situated at the third of the length) (Pl. 1, Figs. 9, 10, 11). The internal side of fragmentary dorsal valves is generally badly preserved, and the muscle scars characteristic for *Discinisca* cannot be seen (Pl. 1, Fig. 12). The colour of shells is reddish dark brown.

Remarks. Discinide brachiopods of the North Sea Basin are known both from the Paleogene (e.g., Muir-Wood 1929, 1939) and the Neogene

(e.g., Wood 1872; Davidson 1874a; Radwańska & Radwański 2003; Dulai 2013; Dulai et al. unpublished data). Muir-Wood (1929, 1939) identified four different Discinidae species from the British Paleogene. *Discinisca ferroviae* Muir-Wood, 1929 is relatively large-sized (10 mm in diameter) and its surface is ornamented by several finely raised radial ribs. *Discinisca davisii* Muir-Wood, 1939 is similar in size (3 mm) to the studied Chattian specimens, but it is also covered by numerous small radial ribs. *Discinisca insularis* Muir-Wood, 1939 differs from the previous two species in having no ornament of radial ribs, and in this way is similar to the studied specimens. However, the German upper Oligocene specimens are significantly smaller with less elevated conical valve, and have more regular concentric growth lines. Their shells are much thinner than the rather thick *D. insularis*. Muir-Wood's (1939) unidentified species, *Discinisca* sp., has a very depressed conical valve and is ornamented by nine narrow concentric rugae. Radwańska & Radwański (1989) described *Discinisca steiningeri* Radwańska & Radwański, 1989 from the upper Oligocene of Austria. It is obviously different from the studied specimens with the dense radial ribbing pattern and therefore should be transferred to the genus *Discradisca*, as it was suggested by Bitner & Cahuzac (2013). The German upper Eocene - lower Oligocene *Discradisca* sp. (Bitner & Müller 2015) and the Ukrainian Eocene *Discradisca* sp. (Bitner & Müller 2017) can be also clearly separated by the radial ribs.

Regarding the European Neogene discinide species, some of them have a radial ribbing pattern and therefore can be easily distinguished from the German Chattian specimens. One ribbed discinide is known from the Atlantic Province: *Discradisca multiradiata* (de Morgan, 1915) (de Morgan 1915; Bitner & Cahuzac 2013; Dulai 2013), while the Central Paratethyan fauna seems to be more diverse: *D. scutellum* (Dreger, 1889) (Dreger 1889; Kroh 2003), *D. carpathica* (Čtyroký & Fejfar, 1963) (Čtyroký & Fejfar 1963), *D. polonica* (Radwańska & Radwański, 1984) (Radwańska & Radwański 1984; Dulai 2015, 2017).

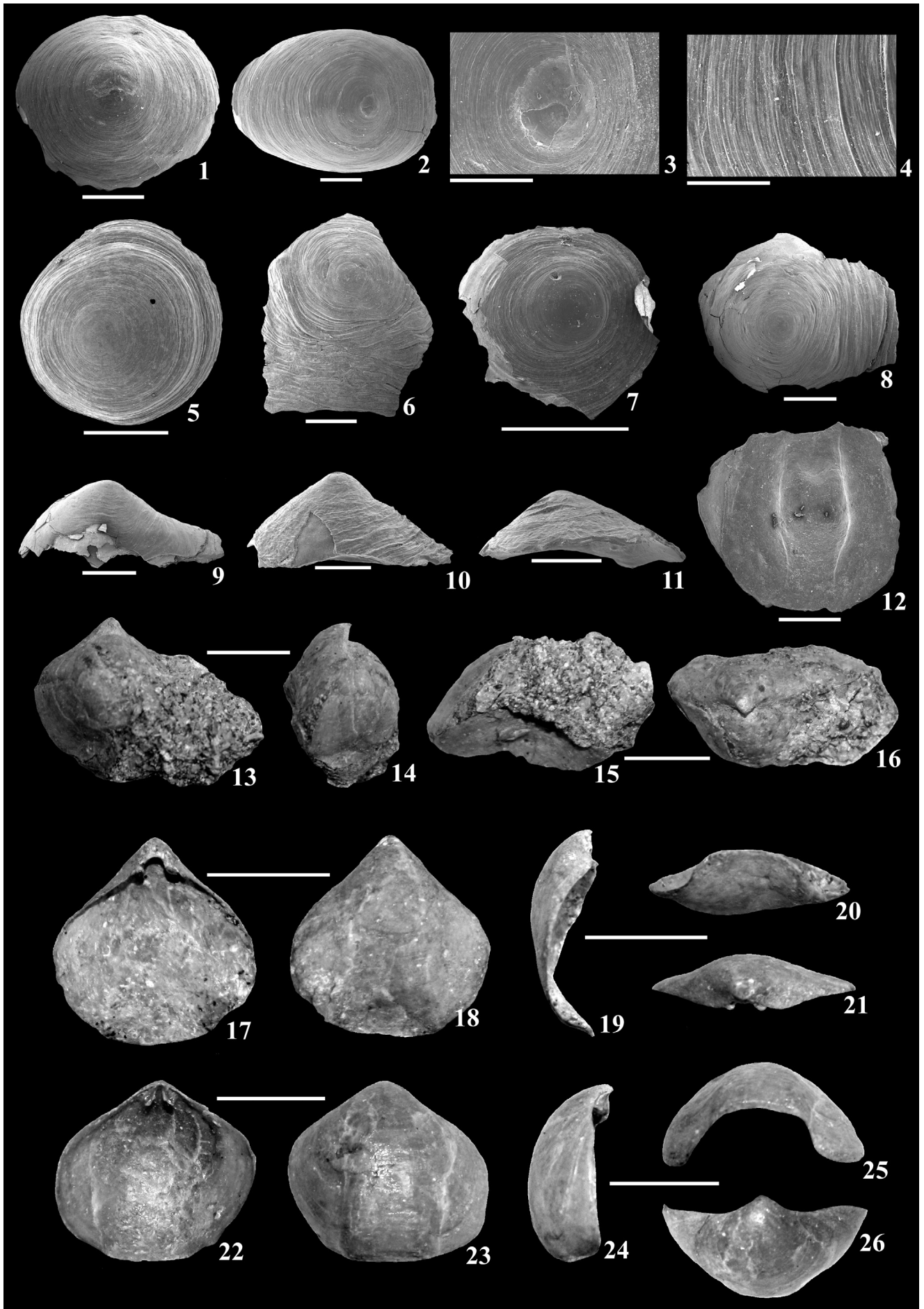
There are three European Neogene discinide species, which are ornamented only by growth lines. *Discinisca leopolitana* (Friedberg, 1921) is known from the middle Miocene of the Central Paratethys (Friedberg 1921; Schmid et al. 2001; Radwański & Wysocka 2004; Dulai 2015). It seems to be thicker

and larger than the studied Chattian brachiopods: Friedberg (1921) mentioned a 7×9 mm specimen, while the Naturalis collection from Poland contains a 5.5×6.6 mm one (Dulai 2015). The largest specimen of the studied Chattian material is 4.5 mm long. *D. elsloensis* Radwańska & Radwański, 2003 known from the middle Miocene Elsloo Conglomerate of the Netherlands is medium-sized, quadrangular, thick-walled, low conical with subposterior-posterior apex and almost devoid of ornamentation (Bosquet 1862; Radwańska & Radwański 2003), therefore different in many characters from the studied material.

The German Chattian specimens can be attributed to *Discinisca fallens*, described from the Pliocene Coralline Crag of Great Britain (Sutton). A single dorsal shell was found by S. Wood, and some different names were given to it [*Discina norvegica*?

PLATE 1

- 1-12 - *Discinisca fallens* (Wood, 1872). 1 - Dorsal valve, Krefeld-Gellep, NBC RGM.800513a, external view; 2-4 - Dorsal valve, Krefeld-Gellep, NBC RGM.800513b, 2 - External view, 3 - Detail of protogulum, 4 - Detail of dense concentric growth lines; 5 - Dorsal valve with protogulum, Kaarst, F.v.d. Hocht Collection, HNHM INV 2019.68., external view; 6 - Slightly irregular, fragmentary dorsal valve, Kaarst, F.v.d. Hocht Collection, HNHM INV 2019.69., external view; 7 - Fragmentary dorsal valve, Krefeld-Gellep, F.v.d. Hocht Collection, HNHM INV 2019.70., external view; 8 - Fragmentary dorsal valve, Krefeld-Gellep, F.v.d. Hocht Collection, HNHM INV 2019.71., external view; 9 - Slightly asymmetrical, fragmentary dorsal valve, Mettmann, F.v.d. Hocht Collection, HNHM INV 2019.72., lateral view; 10 - Irregular dorsal valve, Mettmann, F.v.d. Hocht Collection, HNHM INV 2019.73., lateral view; 11 - Dorsal valve, Mettmann, F.v.d. Hocht Collection, HNHM INV 2019.74., lateral view; 12 - Dorsal valve, Mettmann, F.v.d. Hocht Collection, HNHM INV 2019.75., internal view with muscle scars;
- 13-26 - *Aphelesia supraoligocaenica* (Görges, 1952). 13-16 - Articulated specimen partly in matrix, Doberg, F.v.d. Hocht Collection, HNHM INV 2019.76., 13 - Dorsal view, 14 - Lateral view, 15 - Anterior view, 16 - Posterior view; 17-21 - Ventral valve, Doberg, F.v.d. Hocht Collection, HNHM INV 2019.77., 17 - Internal view, 18 - External view, 19 - Lateral view, 20 - Anterior view, 21 - Posterior view; 22-26 - Dorsal valve, Doberg, F.v.d. Hocht Collection, HNHM INV 2019.78., 22 - Internal view, 23 - External view, 24 - Lateral view, 25 - Anterior view, 26 - Posterior view.
- Scale bars: 1, 2, 5, 6, 7, 8, 9, 10, 11, 12: 1 mm; 3, 4: 0.5 mm; 13-26: 1 cm.



(Sowerby, 1822) by Wood 1840; *Orbicula lamellosa*? Broderip, 1833 by Davidson 1852], while Wood (1872) described it as a new species, *Discina fallens*. Davidson (1874a) accepted the name *D. fallens*. After a long time, Dulai (2013) published several *D. fallens* specimens from the Miocene of the North Sea. Some hundreds fragmentary specimens and fragments were found in Haamstede borehole samples (the Netherlands) and some additional specimens at other localities: Winterswijk-Miste, Delden (the Netherlands) and Dingden (Germany). A single dorsal valve was also identified from the Atlantic Province (Cacela Velha, Portugal; Dulai 2013).

Occurrence. *Disciniscia fallens* is known from the upper Oligocene (this paper), the Miocene (Dulai 2013) and the Pliocene (Wood 1872; Davidson 1874a) of the North Sea and probably from the Miocene of the Atlantic Ocean (Dulai 2013).

Subphylum **RHYNCHONELLIFORMEA**

Williams, Carlson, Brunton, Holmer & Popov, 1996

Class **RHYNCHONELLATA** Williams, Carlson, Brunton, Holmer & Popov, 1996

Order **Rhynchonellida** Kuhn, 1949

Superfamily Pugnacoidea Rzhonsnitskaya, 1956

Family Basiliolidae Cooper, 1959

Subfamily Aphelesiinae Cooper, 1959

Genus *Aphelesia* Cooper, 1959

Type species - *Anomia bipartita* Brocchi, 1814, by original designation of Cooper (1959: p. 41).

Aphelesia supraoligocaenica (Görges, 1952)

Pl. 1, Figs. 13-26, Pl. 2, Figs. 1-4

1909 *Rhynchonella* sp. - von Koenen, p. 92.

1952a "*Rhynchonella*" *supraoligocaenica* n. sp. - Görges, pp. 5-6, pl. 2, figs. 10a-b.

1996 *Rhynchonella supraoligocaenica* Görges - Dallmann, p. 41, pl. 6, fig. 5.

2014 *Rhynchonella supraoligocaenica* Görges - Kaiser & Ebel, p. 136, fig. 228a, b.

Material: F.v.d. Hocht Collection, donated to HNHM: Doberg (1 A, 1 D, 1 V).

Other collections and museum materials: Geowissenschaftliches Museum Göttingen: Uslar-Volpriehausen (1 fr), Collection v. Koenen; Senckenberg Museum Frankfurt /M.: Doberg, Chattian A, Schicht 9-10, (1 A), Collection Görges; Doberg Museum Bünde (3 A), inventory numbers: 2003/934-936, Collection Dallmann and (1 A) in the exhibition of the museum; Astrup, Chattian A (1 A), Collection Dallmann, (the whereabouts are unknown); Collection Droege, Detmold: Doberg, Chattian B, Schicht 27 (5 A, 3 fr).

Dimensions (in mm).

	length	width	thickness
INV 2019.76. (A)	20.0	18.1	14.2
INV 2019.77. (V)	16.2	16.5	5.3
INV 2019.78. (D)	16.8	18.6	9.3

Description. Middle-sized dorsibiconvex shell (maximum observed length 20.0 mm). Dorsal valve much more convex (Pl. 1, Figs. 25-26) than the ventral one (Pl. 1, Figs. 20, 21); subcircular in outline (Pl. 1, Figs. 13, 17-18, 22-23). Maximum width and maximum thickness near to mid-length. Shell surface smooth with some inconspicuous growth lines. Lateral commissure ventrally curved (Pl. 1, Fig. 19), anterior commissure strongly uniplicate. Uniplication wide, rounded trapezoidal, its dorsal side maybe straight (Pl. 1, Fig. 20) or arched (Pl. 1, Fig. 25). Beak of ventral valve high, suberect, with weak beak ridges (Pl. 1, Figs. 14, 16). Apical angle of ventral valve 85-95°. Foramen small, elongate, oval and hypothyril (Pl. 1, Figs. 13, 17, Pl. 2, Fig. 1). Conjunct, slightly auriculate deltidial plates (Pl. 1, Fig. 17, Pl. 2, Fig. 1). Ventral valve interior with small teeth supported by dental plates (Pl. 2, Fig. 2). Dorsal valve interior with long inner socket ridges; long and deep dental sockets, with grooves (Pl. 2, Figs. 3-4). No cardinal process. Crura broken, probably attached directly to the inner socket ridges. No hinge plates. Short and very low median ridge (Pl. 2, Fig. 3).

Remarks. Rhynchonellides are rare in the Chattian of Germany. Von Koenen (1909) mentioned an unidentified fragmentary *Rhynchonella* sp. from the upper Oligocene of Volpriehausen. Later, the same form was described as a new species ("*Rhynchonella*" *supraoligocaenica*) by Görges (1952a) from the lower layers of Doberg. Its dimensions (length: 21 mm, width: 20 mm, thickness: 11 mm) are very similar to the specimens described here. As Görges (1952a) had a single specimen with articulated valves, the internal morphological characters were not visible; therefore, the exact generic identification of his species was not possible. Later, Dallmann (1996) and Kaiser & Ebel (2014) have also reported this species with very wide collective generic attribution, as *Rhynchonella*.

The studied three specimens from the F.v.d. Hocht Collection (1 articulated specimen, 1 dorsal and 1 ventral valve) are from the same locality as the Görges material (Doberg near Bünde). Both

the external morphology (smooth surface, conjunct, slightly auriculate deltidial plates, small, elongate and oval foramen, uniplicate anterior margin) and the internal morphological characters (dental plates, long inner socket ridges, long and deep dental sockets, lack of cardinal process, short and low median ridge) refer to the genus *Aphelesia* described by Cooper (1959). *Aphelesia* is common and well-known from the Miocene and the Pliocene and ranges also in the Pleistocene in the Mediterranean (Mediterranean: Pedley 1976; Gaetani & Saccà 1985; Bitner & Martinell 2001; Bitner & Moissette 2003; Dulai 2016; Central Paratethys: Meznerics 1944, Bitner & Dulai 2004; Bitner & Schneider 2009). Both Cooper (1959) and Savage et al. (2002) mentioned its occurrence from the Eocene but without any details or arguments of the Paleogene records. None of the species assigned to *Aphelesia* by Cooper (1959) [*A. bipartita* (Brocchi, 1814), *A. plicatodentata* (Costa, 1852), *A. saccoi* (Maugeri Patané, 1923), *A. acuta* (Meznerics, 1944) and *A. pseudobipartita* (Maugeri Patané, 1923)] are older than Miocene. Cooper (1959) listed “*Rhynchonella*” *supraoligoaenica* among “unplaced species” mentioning its similarity to *Aphelesia bipartita*, but the lack of knowledge of the internal characters did not allow a generic identification. Savage et al. (2002) mentioned Germany with a question mark among the distributional areas, but Görge (1952a) is not in the cited references. Therefore, this Chattian record from NW Germany seems to be the first confirmed occurrence of *Aphelesia* from the Paleogene.

Aphelesia supraoligoaenica can be clearly distinguished from the five Neogene *Aphelesia* species so far known. The smooth Chattian form clearly differs from *A. pseudobipartita* (Sacco, 1902) and *A. margineplicata* (Philippi, 1844) because both latter species have some radial ribs at the anterior margin (Gaetani & Saccà 1985). The smooth *Aphelesia bipartita* is the most similar form to *A. supraoligoaenica*; however, it has a subtrigonal outline rather than a subcircular outline, and its plication is lower and more angular. *Aphelesia acuta* (Meznerics, 1944) was described from the Miocene of Hungary by Meznerics (1944), but most probably it is synonymous with *A. bipartita* (see Bitner & Dulai 2004). *Aphelesia winebergeri* Bitner & Schneider, 2009 from the Burdigalian of the Upper Marine Molasse of Germany has a subtriangular-subpentagonal and more irregular outline with an angulation in the lateral outline, and frequently with a concave part at the anterior end, while *A. supraoligo-*

caenica has a regular outline. Another significant difference is the shallow sulcus on both the dorsal and ventral valves (Bitner & Schneider 2009, fig. 2B, E, and F). *Aphelesia winebergeri* has higher and narrower uniplication.

Occurrence. Until now *Aphelesia supraoligoaenica* seems to be endemic, it is known only from the Chattian of NW Germany.

Order **Terebratulida** Waagen, 1883

Suborder **Terebratulidina** Waagen, 1883

Superfamily Terebratuloidea Gray, 1840

Family Terebratulidae Gray, 1840

Subfamily Terebratulinae Gray, 1840

Genus *Pliothyryna* van Roy, 1980

Type species - *Terebratula sowerbyana* Nyst, 1843 by original designation of van Roy (1980: p. 2)

Pliothyryna grandis (Blumenbach, 1803)

Pl. 2, Figs. 5-25

- 1803 *Terebratulites grandis* - Blumenbach, p. 18, pl. 1, fig. 4.
- 1860 *Terebratula grandis* Blum. - Speyer, p. 492.
- 1860 *Terebratula subrbomboidea* n. sp. - Speyer, p. 492, pl. XI, fig. 5a-c.
- 1863 *Terebratula* cf. *grandis* Blumenbach - von Koenen, p. 616.
- 1864 *Terebratula grandis* Blumenb. - Speyer, p. 321.
- 1864 *Terebratula subrbomboidea* nov. spec. - Speyer, p. 322.
- 1869 *Terebratula grandis* Blumenbach - von Koenen, p. 110.
- 1891 *Terebratula grandis* Blumenbach - Lienenklaus, p. 134.
- 1894 *Terebratula grandis* Blumenbach - von Koenen, p. 1339, pl. XCVI, figs. 1a-c, 2a-c, 3a-d.
- 1909 *Terebratula grandis* Blum. - Nahnsen, p. 94.
- 1967 *Terebratula grandis* Blumenbach - Strauch, p. 37.
- 1983 *Pliothyryna grandis* (Blumenbach) - Cooper, p. 237, pl. 5, figs. 5, 6.
- 1996 *Terebratula grandis* Blumenbach - Dallmann, p. 41, pl. 6, figs. 1, 2, 3, 4, 6.
- 1999 *Terebratula grandis* Blumenbach - Rust, p. 74, pl. 12, figs. 2a-c.
- 2003 *Terebratula grandis* Blumenbach - Aue, p. 34, fig. 5.
- 2011 “*Terebratula*” *grandis* (Blumenbach, 1803) - Müller, p. 20, pl. 2, figs. 29a-b, 30, 31a-b, pl. 3, figs. 1a-b, 2a-b.
- 2012 *Pliothyryna grandis* (Blumenbach) - Diedrich, p. 177, fig. 12.10.
- 2014 *Terebratula grandis* Blumenbach - Kaiser & Ebel, p. 136, figs. 224, 225.
- 2015 *Pliothyryna* sp. cf. *P. grandis* (Blumenbach, 1803) - Bitner & Müller, pp. 676-677, fig. 3e-h.

Material: F.v.d. Hocht Collection, donated to HNHM: Mettmann (7 fr); Astrup (1A, 2V, 1D); Doberg (1A).

Other specimens from Doberg: Doberg Museum, Bünde, Chattian A-C (33 A), No. 2003/937-969, in Collection Dallmann; (9 A, 5 D, 24 V, 5 fr) in Collection Witte; (4 A) and a concretion with at least 6 ventral valves in the exhibition of the museum. Ruhr Museum, Essen (3 A, 1 fr), RE 551.781.53 A017/1, A122, A0470, RE 551.781.53 A017/2. Many specimens can be found also in numerous private collections.

Other specimens from Astrup: Meckert, Osnabrück, (now Vancouver/Canada) (6 A, 1 D, 1 V); Collection F.v.d. Hocht, Kerpen.

Other specimens from Niederrhein: Mettmann, Chattian A (lowermost) (1 A, 24 fr), Collection F.v.d. Hocht, Kerpen; Moers-

Kapellen, shaft Niederberg-3, (1 A) in a FeS₂-concretion; Kempen-Tönisberg, shaft Niederberg-4 (1 A), Collection Strauch, Münster.

Other materials from Diekholzen: Neuhof (1 A), Collection of Roemer-Museum, Hildesheim; Diekholzen (2 A, 1 V, 6 fr.), Collection of Roemer-Museum, Hildesheim; (1 D), Collection Köneke, Bodenburg.

Dimensions (in mm).

	length	width	thickness
INV 2019.79. (A)	61	36	36
INV 2019.80. (V)	46	33	18
INV 2019.81. (V)	32	22	10
INV 2019.82. (D)	47	41	15

Description. Large terebratulides with elongated, oval outline (Pl. 2, Figs. 5, 10, 16, 21). Lateral commissures are nearly straight (Pl. 2, Figs. 18, 23), or curved ventrally at anterior third (Pl. 2, Figs. 12-13). Shells ornamented only by growth lines. Anterior commissure rectimarginate or slightly plicate in juvenile specimens (Pl. 2, Fig. 20), sulcinate in adult specimens (Pl. 2, Figs. 9, 15). Suberect beak strongly truncated (Pl. 2, Figs. 7-8, 12-13, and 18). Large mesothyrid foramen and short pedicle collar (Pl. 2, Figs. 10, 14, 19).

Remarks. Large-sized terebratulides may represent a brachiopod group with a problematic systematic position. All large and smooth terebratulides were identified as “*Terebratula*” for a long time. The genus *Pliothyridina* was erected by van Roy (1980) on the basis of Pliocene material from Belgium (*P. sowerbyana*). The only short-looped terebratulide species known from the Oligocene of the North Sea Basin is *Pliothyridina grandis* (Davidson 1874b; Vincent 1886; von Koenen 1894; Cooper 1983; Müller 2011; Diedrich 2012; Bitner & Müller 2015). Speyer (1860) described another species, *Terebratula subrhomboidea*, on the basis of a single small-sized (16 mm long) dorsal valve; however, it seems to be a juvenile specimen of *P. grandis*.

Cooper (1983) illustrated two specimens of *T. grandis* from Doberg, Bünde (Chatian glauconitic sandy marl) and ascribed the species to the genus *Pliothyridina*. However, several subsequent regional publications dealing with geology of the given areas neglected the generic attribution of *grandis* to *Pliothyridina* and mentioned or illustrated “*Terebratula*” *grandis* (see synonymy list). Most probably, the authors of these papers (Dallmann 1996; Rust 1999; Aue 2003; Müller 2011; Kaiser & Ebel 2014) were not aware of the voluminous Cooper’s monogra-

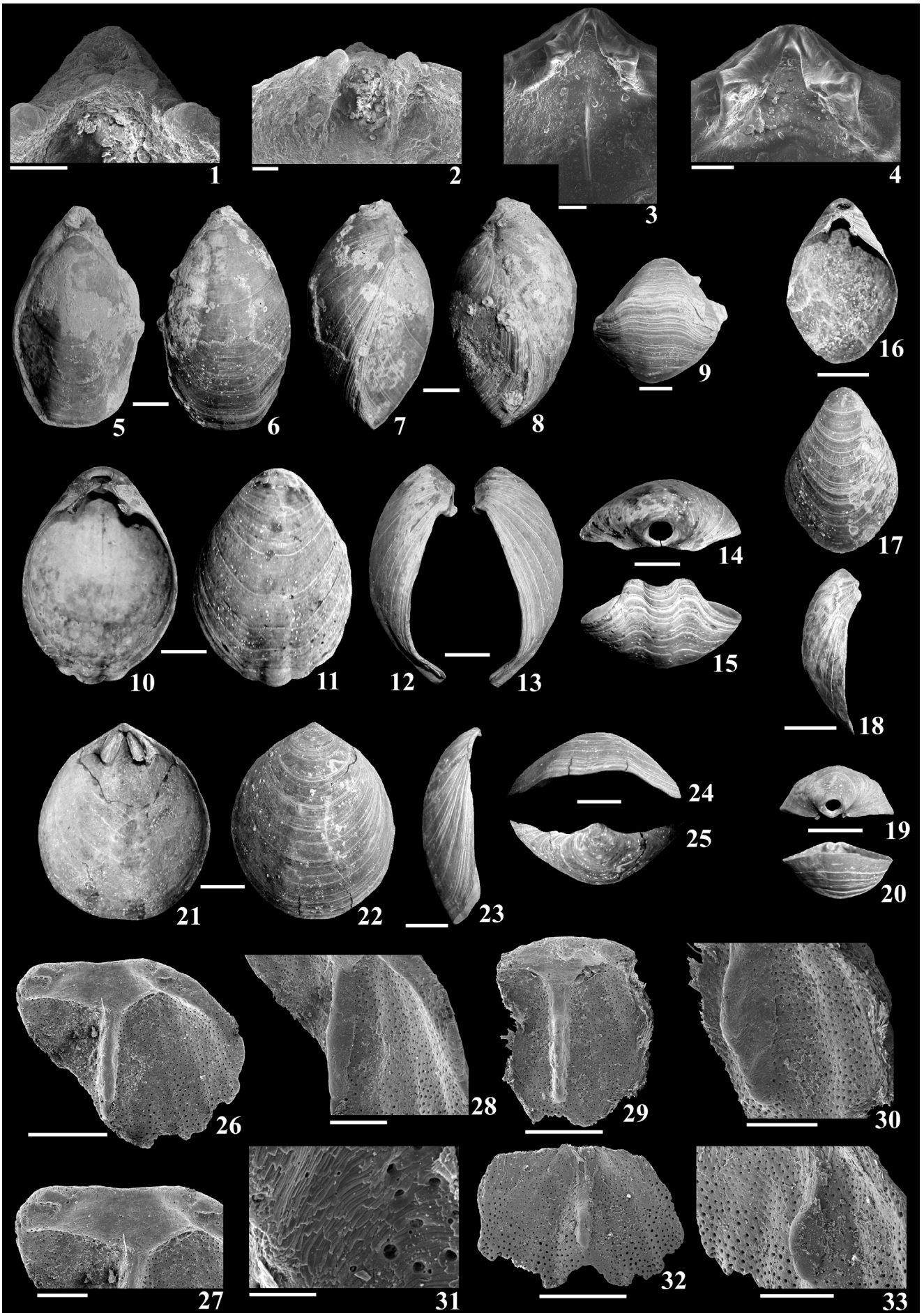
phy. García Ramos (2006) re-illustrated Blumenbach’s (1803) and von Koenen’s (1894) original figures in his review paper. Most recently, Bitner & Müller (2015) mentioned some juvenile *P. grandis* specimens from the upper Eocene-lower Oligocene Silberberg Formation.

There are several Neogene *Terebratula grandis* records in the literature both from the North Sea and the Mediterranean-Central Paratethys area. These occurrences probably refer to another species, maybe another genus, but their necessary revision has not been done yet. *Terebratula grandis* was described from the Pliocene of the North Sea several times (e.g., Davidson 1852; Wood, 1872; Davidson 1874a), but these specimens represent another species of *Pliothyridina*. Most commonly, the name of the type species, *P. sowerbyana* is used for these materials, but recently the validity of this species name was questioned. Moerdijk (2016) discussed

PLATE 2

- 1-4 - *Aphelesia supraoligocaenica* (Görges, 1952). 1-2 - Ventral valve interior, Doberg, INV 2019.77., 1 - Detail of beak, foramen and deltidial plates, 2 - Detail of dental plates in oblique anterior view; 3-4 - Dorsal valve interior, Doberg, INV 2019.78., 3 - Detail of dorsal beak with short and low median ridge, 4 - Detail of dorsal beak with long and deep dental sockets and long inner socket ridges;
- 5-25 - *Pliothyridina grandis* (Blumenbach, 1803). 5-9 - Articulated specimen, Astrup, F.v.d. Hocht Collection, HNHM INV 2019.79., 5 - Dorsal view, 6 - Ventral view, 7 - Lateral view, 8 - Lateral view, 9 - Anterior view; 10-15 - Ventral valve, Astrup, F.v.d. Hocht Collection, HNHM INV 2019.80., 10 - Internal view, 11 - External view, 12 - Lateral view, 13 - Lateral view, 14 - Posterior view, 15 - Anterior view; 16-20 - Ventral valve, Astrup, F.v.d. Hocht Collection, HNHM INV 2019.81., 16 - Internal view, 17 - External view, 18 - Lateral view, 19 - Posterior view, 20 - Anterior view; 21-25 - Dorsal valve, Astrup, F.v.d. Hocht Collection, HNHM INV 2019.82., 21 - Internal view, 22 - External view, 23 - Lateral view, 24 - Anterior view, 25 - Posterior view;
- 26-33 - *Bronnothyris?* sp. 26-28 - Fragmentary dorsal valve, Glimmerode, NBC RGM.801078a, 26 - Internal view, 27 - Detail of broad and fused hinge plates, 28 - Oblique lateral view of median septum; 29-31 - Fragmentary dorsal valve, Glimmerode, NBC RGM.801078b, 29 - Internal view, 30 - Oblique lateral view of median septum, 31 - Detail of shell structure; 32-33 - Fragmentary brachial valve, Glimmerode, NBC RGM.801078c, 32 - Internal view, 33 - Oblique lateral view of dorsal median septum.

Scale bars: 1, 2, 3, 4, 26, 29, 32: 1 mm; 27, 28, 30, 33: 0.5 mm; 31: 0.1 mm; 5-25: 1 cm.



in detail the complex and difficult nomenclatural problems of Neogene *Pliothyryna* assemblages of the North Sea. The species *Pliothyryna grandis* has been reported from the middle Miocene Central Paratethys (e.g., Friedberg 1921; Popiel-Barczyk & Barczyk 1990) and from the Miocene of the Mediterranean of Spain (Calzada Badía 1978). Most probably, these terebratulid records belong to different species of the genus *Terebratula*; however, in the absence of information on the internal morphological characters their generic attribution remains uncertain. One of the Central Paratethyan middle Miocene terebratulid species from the Hartl Formation of the Vienna Basin was mentioned as *Pliothyryna macrescens* (Dreger, 1889) by Kroh et al. (2003) but without any arguments on this generic attribution.

Occurrence. The presence of *P. grandis* is confirmed in the Oligocene of the Pre-North Sea Basin, but probably had a wider European distribution.

Suborder **Terebratellidina** Muir-Wood, 1955

Superfamily Megathyridoidea Dall, 1870

Family Megathyrididae Dall, 1870

Genus *Bronnothyris* Popiel-Barczyk & Smirnova, 1978

Type species - *Terebratula bronni* Roemer, 1841 by original designation of Popiel-Barczyk & Smirnova (1978: p. 41)

***Bronnothyris?* sp.**

Pl. 2, Figs. 26-33

2011 *Argyrotheca* sp. - Müller, pl. 3, figs. 9a-b, 10a-b.

Material: NBC (Leiden): Glimmerode, Chattian A (4 fr).

Dimensions (in mm).

	length	width
RGM.801078a (D)	2.4	(2.8)
RGM.801078b (D)	2.5	-
RGM.801078c (D)	(1.6)	2.4

Remarks. Some moderately preserved megathyridid specimens in the Naturalis collection are clearly different from another megathyridid species of this assemblage, *Argyrotheca bitnerae* (see below). The wider than long dorsal valves are coarsely punctate. The shell surface is covered with 5-6 low, rounded ribs. Hinge plates are broad and fused mid-dorsally to form a single coherent plat-

form (Pl. 2, Figs. 26, 27, 29). The dorsal median septum is strongly eroded in all specimens, and the original shape of septum is invisible.

Bronnothyris was erected by Popiel-Barczyk & Smirnova (1978) for the Upper Cretaceous megathyridid brachiopods and five species were attributed to this genus [*B. bronni* (Roemer, 1841), *B. coniuncta* (Steinich, 1965), *B. lacunosa* (Steinich, 1965), *B. obstinata* (Steinich, 1965), *B. stevensis* (Nielsen, 1928)]. An Ukrainian lower Paleocene species, *Argyrotheca rugicosta* Zelinskaya, 1975, was also transferred to *Bronnothyris* by Smirnova et al. (1983). The genus was mentioned from the Upper Cretaceous and lower Danian of Western Europe in the Treatise (Lee et al. 2006), but later it was also recorded from the lower Oligocene of Germany [Bitner & Kroh 2011; *B. subradiata* (Sandberger, 1862)] and from the upper Eocene of Ukraine (Bitner & Müller 2017; *B. danaperensis*). *Bronnothyris* is also present in the Eocene brachiopod fauna of the Thrace Basin (Turkey; Dulai et al. unpublished data).

The main distinguishing character of *Bronnothyris* is the presence of short septal flanges extending ventrally from the dorsal septum (Lee et al. 2006; Bitner & Kroh 2011). The preservation of the studied specimens is rather poor, and the septal flanges cannot be observed on the eroded septa; therefore, their attribution to *Bronnothyris* is uncertain. However, on the studied dorsal valves (Pl. 2, figs. 26, 27, 29), the hinge plates are broad and fused mid-dorsally in a single platform, similarly to lower Oligocene *B. subradiata* from the Mainz Basin (Bitner & Kroh 2011) or to the Upper Cretaceous *B. coniuncta* (Steinich, 1965). The upper Paleocene *Argyrotheca wansinensis* Vincent, 1923 from Belgium also shows this kind of fused hinge plates; however, the insufficient illustrations and the missing type material so far have prevented its attribution to *Bronnothyris* (Vincent 1923; Bitner & Kroh 2011).

Occurrence. *Bronnothyris?* sp. is known from the Chattian of NW Germany.

Genus *Argyrotheca* Dall, 1900

Type species - *Terebratula cuneata* Risso, 1826, by original designation of Dall (1900: p. 44)

Argyrotheca bitnerae Dulai in Dulai & Stachacz, 2011

Pl. 3, Figs. 1-8

- p 2011 *Argyrotheca* cf. *cordata* (Risso, 1826) - Müller, p. 20, pl. 3, figs. 3-4 (non figs. 5-6).
 2011 *Argyrotheca bitnerae* n. sp. - Dulai in Dulai & Stachacz, pp. 285-289, figs. 3: 1-11, 4: 1-6. (cum syn.).
 2013 *Argyrotheca bitnerae* Dulai in Dulai & Stachacz - Bitner et al., pp. 588-589, fig. 5A-M, table 5.
 2014 *Argyrotheca bitnerae* Dulai - Hladilová et al., fig. 4E-J.
 2015 *Argyrotheca bitnerae* Dulai in Dulai & Stachacz - Dulai, pp. 196-197, pl. 4, figs. 6-9.
 2018 *Argyrotheca bitnerae* Dulai - Kopecká et al., fig. 9F-I.
 2019 *Argyrotheca bitnerae* Dulai in Dulai & Stachacz - Pedramara et al., p. 243, fig. 5B-F.

Material: NBC (Leiden): Glimmerode, Chattian A (1 A juv., 2 V juv., 5 fr); F.v.d. Hocht Collection, donated to HHNM: Niederrhein, Mettmann (Chattian A, lowermost part) (2 A, 2 D, 1 V).

Dimensions (in mm).

	length	width
RGM.801079a (V)	1.6	1.3
RGM.801079b (V)	1.7	1.4
INV 2019.83. (A)	1.8	1.7
INV 2019.84. (A)	2.1	1.8
INV 2019.85. (D)	1.9	2.1

Remarks. Some small-sized subpentagonal megathiridid specimens from Glimmerode and Mettmann represent a recently erected *Argyrotheca* species. It was described from the Central Paratethys, but it was confirmed within a few years, that, although *A. bitnerae* is generally not very numerous, it has a wide distribution both stratigraphically and geographically. *A. bitnerae* was originally found in the Polish part of the middle Miocene Central Paratethys by Dulai & Stachacz (2011) and Dulai (2015). Soon after, it was identified in other part of the Central Paratethys (Czech Republic: Hladilová et al. 2014; Kopecká et al. 2018) and also in the upper Oligocene of the Atlantic (France, Aquitaine Basin: Bitner et al. 2013) and upper Miocene (Tortonian) of the Mediterranean (Maltese Islands: Dulai et al. unpublished data). Müller (2011) illustrated some *Argyrotheca* cf. *cordata* from the lower Oligocene of Mammendorf (North Sea), from which a complete specimen (fig. 3) and a ventral valve (fig. 4) seem to be identical with *A. bitnerae*. The other two specimens, a rounded oval dorsal valve (fig. 5), and a slightly ribbed ventral valve (fig. 6) are closer to *Joaquia cordata*.

Occurrence. *A. bitnerae* is known from the upper Oligocene of the Atlantic (Bitner et al. 2013); lower and upper Oligocene of the Pre-North Sea Basin (Müller 2011; this paper); lower Miocene of Iran (Pedramara et al. 2019); middle Miocene

of the Central Paratethys (Dulai & Stachacz 2011; Hladilová et al. 2014; Dulai 2015; Kopecká et al. 2018); upper Miocene of the Mediterranean (Dulai et al. unpublished data).

Superfamily Platidioidea Thomson, 1927

Family Platidiidae Thomson, 1927

Subfamily Platidiinae Thomson, 1927

Genus *Germanoplatidia* n. gen.

Type species - *Terebratula pusilla* Philippi, 1843 (by monotypy)

Derivation of name: It refers to Germany, the country of the type locality of the new Platidiinae genus.

Diagnosis: Small-sized Platidiinae, with very regularly subcircular outline. Smooth shells, without any spines or tubercles on the ventral valve. Wide and straight hinge line mostly horizontal, sometimes slightly inclined outwards. High suberect beak, wide and finely striated interarea. Two narrow, divergent deltidial plates. Amphithyrid foramen, with very shallow dorsal notch (L/W: 0.3). Long but low myophragm. No hinge plates, crura and descending branches. High triangular septal pillar with widening base. Short septal flanges parallel to the septal pillar.

Comparison with related genera. Based on ventribiconvex shells, with dorsal valve almost flat, amphithyrid foramen, high and triangular septal pillar and septal flanges at the apex of septal pillar, *Germanoplatidia* n. gen. belongs to the subfamily Platidiinae Thomson, 1927.

The most common genus of the subfamily is *Platidia* Costa, 1852 which has more irregular outline, shorter beak and hemispherical notch (L/W: 0.75, vs. 0.3 at *Germanoplatidia* n. gen.). The internal morphological characters of *Germanoplatidia* n. gen. are significantly different to *Platidia*. *Germanoplatidia* n. gen. lacks crura, crural processes and descending branches. *Platidia* has high blade-like septal pillar with U-shaped septal flanges, while *Germanoplatidia*'s septal pillar is triangular with widening base, and its septal flanges are short and parallel with septal pillar. Their common character is the lack of hinge plates.

Regarding the internal morphology, the most similar genus within the subfamily is *Aemula* Steinich, 1968, but even so there are several differences. *Aemula* is very frequently irregular in dorsal view (e.g., Steinich 1968, fig. 1; Surlyk 1972, pl. 3, figs. e, f, h; Surlyk 1974, pl. 2, figs B-F; Žitt et al. 2002, figs. 2-4) possibly due to the short massive pedicle, because in this way the dorsal valve was pressed against the substrate (Surlyk 1974). On the contrary, all known specimens of *Germanoplatidia* n.

gen. (about hundred specimens) show very regular, subcircular outline in dorsal view. *Germanoplatidia* n. gen. generally longer than wide, while *Aemula* is wider than long (MacKinnon & Lee 2006). The surface of the ventral valves never bears any fine spines in *Germanoplatidia* n. gen. In the case of *Aemula* spines are common, although not always present: according to Steinich (1968) 68% of the ventral valves were tuberculate and 32% smooth. However, there is a definite separation according to the size (and age) of the shells: all shells under 1 mm shell width are non-tuberculate, while shells greater than 2 mm are predominantly tuberculate. The studied German shells are far larger than 2 mm, but none of them is tuberculate. The beak of ventral valve is much higher and more regular in *Germanoplatidia* n. gen., and the dorsal notch is significantly shallower (L/W: 0.3 vs. 0.72 at *Aemula*). In contrast to *Aemula*, there are no hinge plates in *Germanoplatidia* n. gen. A long but low myophragm can be seen in the new genus, which is lacking in *Aemula*. The septal pillar of *Germanoplatidia* n. gen. has a much wider base, and its posterior end near to the notch. The septal flanges are divergent in *Aemula*, while short and parallel in *Germanoplatidia* n. gen.

Holocene *Amphithyris* Thomson, 1918 from SW Pacific (MacKinnon & Lee 2006; Bitner 2006, 2008, 2019; Nauendorf et al. 2014) is broadly separated from *Germanoplatidia* n. gen. both in time and place; however, it is worth mentioning that recently MacKinnon et al. (2008) confirmed Thomson's (1918) opinion that *Terebratulina seminula* Philippi, 1836 from the Mediterranean may belong to *Amphithyris*. The outer morphological characters with subcircular outline are very similar, except the hemispherical notch (L/W: 0.72) in *Amphithyris*, and very shallow notch (L/W: 0.3) in the German specimens. The internal morphological characters are clearly different: unlike the high triangular septal pillar of *Germanoplatidia* n. gen., *Amphithyris* has a very low median septum.

Annuloplatidia Zvezina, 1981 has similar smooth and subcircular shell, and its relatively shallow notch is the most similar to *Germanoplatidia* n. gen. within subfamily Platidiinae (L/W 0.46 vs. 0.3 in *Germanoplatidia* n. gen.). However, the inner morphological characters are significantly different. *Annuloplatidia* has anteriorly projecting crura, transverse band connecting distal extremities of divergent septal flanges and descending branches as in *Platidia* (MacKinnon

& Lee 2006); all of these features are lacking in *Germanoplatidia* n. gen. The long and divergent septal flanges also differ from short and parallel flanges of the German specimens.

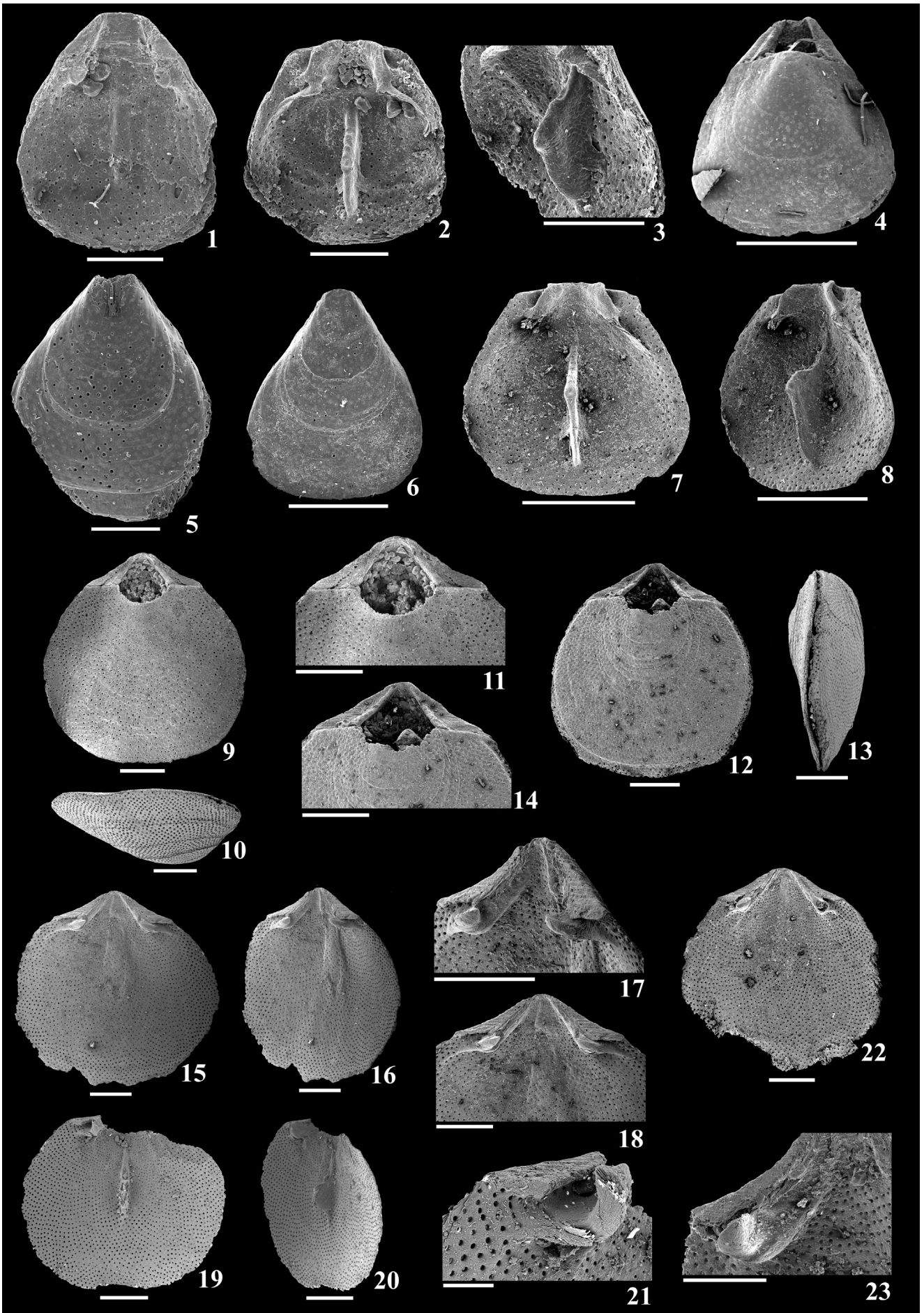
Scumulus Steinich, 1968 has subtriangular to elongate-oval outline and hypothyriform foramen in adult specimens. Its brachidium is represented by descending branches that extend between crura and narrow, high, subtriangular septal pillar (MacKinnon & Lee 2006). The septal pillar is low, and its apex is truncated.

Neoemula MacKinnon et al. 2008 was described recently from the Fiordland of New Zealand. Its shells have subrectangular, and slightly irregular outline, with short beak, and hemispherical dorsal notch (L/W: 0.71). Small tubular spines appear at the periphery of larger, more mature specimens. Similarly to *Aemula* and *Germanoplatidia* n.

PLATE 3

- 1-8 - *Argyrotheca bitnerae* Dulai in Dulai & Stachacz, 2011. 1-3 - Separated ventral and dorsal valve of the same specimen, Glimmerode, NBC RGM.801079a, 1 - Internal view of ventral valve, 2 - Internal view of dorsal valve, 3 - Oblique lateral view of dorsal median septum; 4 - Articulated specimen, Mettmann, F.v.d. Hocht Collection, HNHM INV 2019.83., dorsal view; 5 - Ventral valve, Glimmerode, NBC RGM.801079b, external view; 6 - Articulated specimen, Mettmann, F.v.d. Hocht Collection, HNHM INV 2019.84., ventral view; 7-8 - Dorsal valve, Mettmann, F.v.d. Hocht Collection, HNHM INV 2019.85., 7 - Internal view, 8 - Oblique lateral view of dorsal median septum;
- 9-23 - *Germanoplatidia pusilla* (Philippi, 1843). 9-11 - Articulated specimen, Kapellen, F.v.d. Hocht Collection, HNHM INV 2019.86., 9 - Dorsal view, 10 - Oblique anterior view, 11 - Detail of beak region showing the amphithyrid foramen, wide interarea, diverging deltidial plates and shallow dorsal notch; 12-14 - Articulated specimen, Kapellen, F.v.d. Hocht Collection, HNHM INV 2019.87., 12 - Dorsal view, 13 - Lateral view, 14 - Detail of beak region, showing hinge line slightly inclined outwards; 15-18 - Fragmentary ventral valve, Kapellen, F.v.d. Hocht Collection, HNHM INV 2019.88., 15 - Internal view, 16 - Oblique lateral view, showing the long diaphragm, 17 - Oblique lateral view of beak region, showing the pedicle collar, deltidial plates and small rectangular teeth, 18 - Detail of beak region, showing the posterior part of diaphragm and the horizontally striated area; 19-21 - Fragmentary dorsal valve, Kapellen, F.v.d. Hocht Collection, HNHM INV 2019.89., 19 - Internal view, 20 - Oblique lateral view, showing the broken septal pillar; 21 - Oblique lateral view showing the short and nearly horizontal outer socket ridge, and the broken inner socket ridge; 22-23 - Fragmentary ventral valve, Kapellen, F.v.d. Hocht Collection, HNHM INV 2019.90., 22 - Internal view, 23 - Detail of tooth and horizontally striated area.

Scale bars: 1-20, 22: 1 mm; 21, 23: 0.25 mm.



gen., no hinge plates, crura or descending bands. The septal pillar of *Neoemula* is shorter and closer to the posterior notch, it is blade-like and T-bar shaped, without a basal widening. The septal flanges are narrow and laterally directed, while the short septal flanges of *Germanoplatidia* n. gen. are short and parallel to the septal pillar.

Range. *Germanoplatidia* n. gen. is known from the upper Oligocene (Chattian) of NW Germany.

Germanoplatidia pusilla (Philippi, 1843)

Pl. 3, Figs. 9-23, Pl. 4, Figs. 1-26

1843 *Terebratulula pusilla* n. sp. - Philippi, p. 17, pl. 2, fig. 15.

1884 *Morrisia pusilla* Philippi - Speyer, pl. 31, figs. 11-14.

1940 *Morrisia pusilla* Philippi - Görge, p. 60.

1952b *Argiope pusilla* Philippi - Görge, pl. 3, figs. 102, 103.

1999 *Platidia pusilla* (Philippi) - Rust, p. 74, pl. 13, figs. 1a-b.

Material: NBC (Leiden): Krefeld-Gellep (3 A, 1 V); F.v.d. Hocht Collection, donated to HNHM: Kapellen (3 A, 3 D).

Other materials from Niederrhein: Senckenberg Museum Frankfurt /M.: Rumeln, Chattian A (1 A), Collection Görge; Krefeld-Gellep, Chattian B (69 A, 16 V, 10 D), Collection F.v.d. Hocht, Kerpen; Moers-Kapellen, Chattian B (4 A), Collection F.v.d. Hocht, Kerpen.

Other materials from Diekholzen: (10 A, 40 fr.), Collection of Roemer-Museum, Hildesheim, (occurring only in the glauconitic sands).

Dimensions (in mm).

	length	width
INV 2019.86. (A)	4.7	4.6
INV 2019.87. (A)	4.3	4.1
INV 2019.88. (V)	4.7	4.7
RGM.800512a (A)	4.6	4.5
RGM.800512b (A)	4.4	4.2
RGM.800512c (V)	4.1	(3.6)
RGM.800512d (A)	4.6	4.7

Description

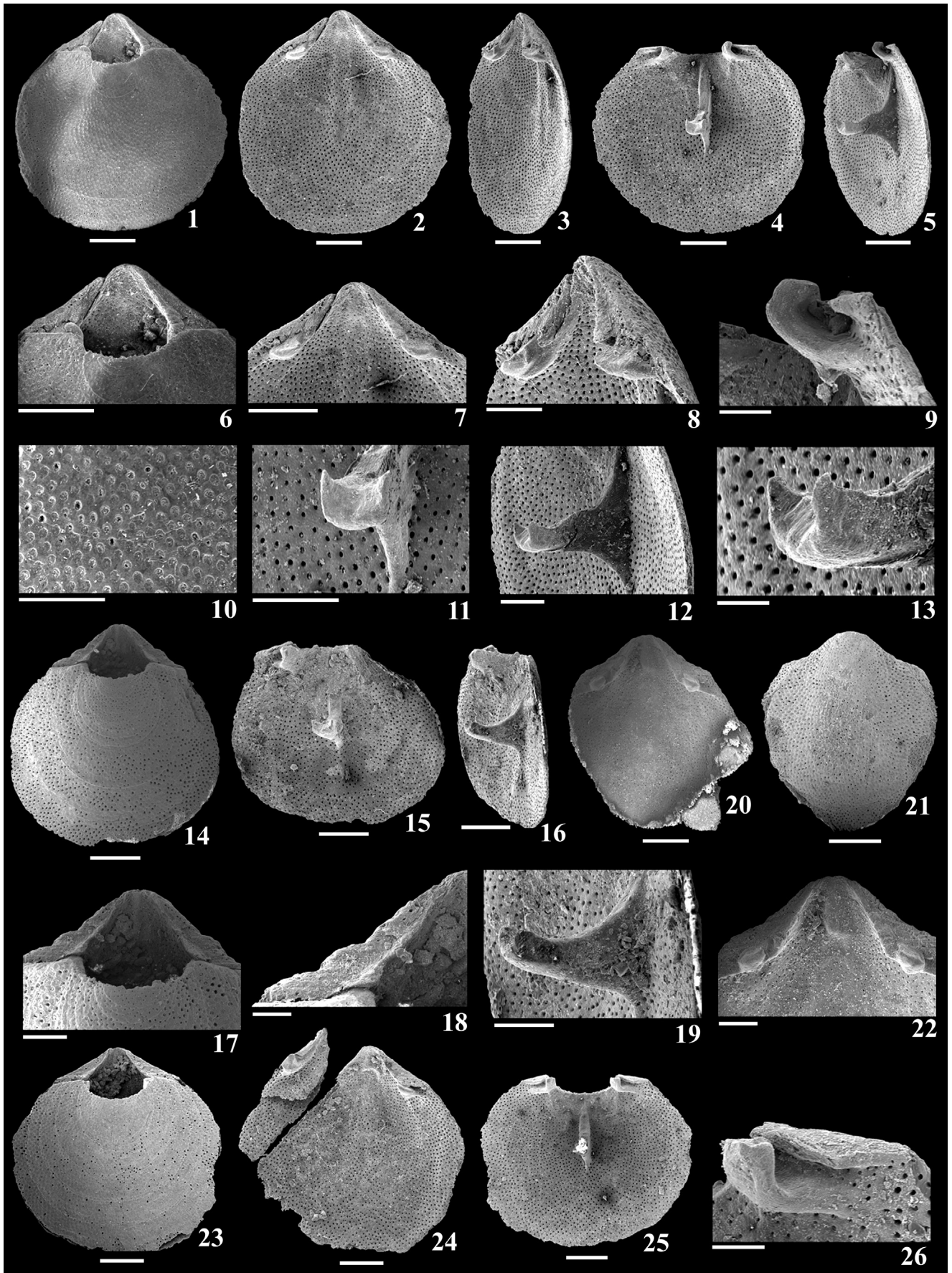
External characters. Small-sized, thin shells (maximum observed length 5.5 mm), with very regularly subcircular outline (Pl. 3, Figs. 9, 12, Pl. 4, Figs. 1, 14, 23). Ventribiconvex, dorsal valve almost flat, except for the posterior thickening around the notch (Pl. 3, Fig. 13). Generally longer than wide. Maximum width at the mid-length, maximum thickness at the posterior third. Lateral commissures straight (Pl. 3, Fig. 13), anterior commissure recrimarginate with an inconspicuous unisulcation (Pl. 3, Fig. 10). Coarsely endopunctate smooth shells (Pl. 4, Fig. 10), shell surface ornamented only by some indistinct growth lines (Pl. 3, Fig. 12, Pl. 4, Figs. 1, 14). Hinge line wide (55-66% of total width)

and straight; mostly horizontal (Pl. 3, Figs. 9, 11, Pl. 4, Fig. 1), or slightly inclined outwards (Pl. 3, Figs. 12, 14, Pl. 4, Fig. 14). Ventral beak suberect (Pl. 4, Figs. 3, 8), relatively high (Pl. 3, Figs. 9, 12, 17, Pl. 4, Figs. 1, 6, 14). Sharp beak ridges subtending at an angle of about 110° (102°-118°) at umbo (Pl. 3, Figs. 9, 12, 15, Pl. 4, Figs. 1, 6, 14). Wide interarea, sometimes finely striated transversely (Pl. 3, Figs. 11, 14, 18). Two narrow, slightly widening, distinct, strongly diverging deltidial plates (Pl. 3, Figs. 11, 14, 17, 18, Pl. 4, Figs. 7, 8). Pedicle foramen wide and amphithyrid, dorsal notch very shallow, L/W ratio of notch about 0.3 (0.27-0.34) (Pl. 3, Figs. 9, 11, 12, 14, Pl. 4, Figs. 1, 6, 14, 17, 23). Pedicle collar short and wide (Pl. 3, Figs. 17, 18, Pl. 4, Figs. 2, 7).

PLATE 4

1-26 - *Germanoplatidia pusilla* (Philippi, 1843). 1-13 - Complete specimen and its separated valves, Krefeld-Gellep, NBC RGM.800512a, 1 - Dorsal view, 2 - Internal view of pedicle valve, 3 - Oblique lateral view of pedicle valve interior, showing the long myophragm, 4 - Internal view of brachial valve, 5 - Oblique lateral view of brachial valve, showing the septal pillar and septal flanges, 6 - Detail of beak area, showing the amphithyrid foramen, dental plates and shallow dorsal notch, 7 - Detail of pedicle valve interior, showing the pedicle collar and teeth, 8 - Oblique lateral view of pedicle valve interior showing the teeth and deltidial plates, 9 - Oblique lateral view of dorsal valve, showing the socket, the short outer socket ridge and angularly reclined inner socket ridge, 10 - Detail of shell surface of dorsal valve, 11 - Detail of apex of septal pillar with the short and parallel septal flanges, 12 - Lateral view of dorsal valve, showing the septal pillar, 13 - Detail of septal flanges; 14-19 - Complete specimen and its separated valves, Krefeld-Gellep, NBC RGM.800512b, 14 - Dorsal view, 15 - Internal view of brachial valve, 16 - Lateral view of dorsal valve, showing the septal pillar, 17 - Detail of beak area, showing foramen and dorsal notch, 18 - Detail of horizontally striated area, deltidial plate and slightly inclined hinge line, 19 - Detail of septal pillar and septal flanges; 20-22 - Pedicle valve, Krefeld-Gellep, NBC RGM.800512c, 20 - Internal view, 21 - External view, 22 - Detail of beak area, showing pedicle collar, deltidial plates and teeth; 23-26 - Complete specimen and its separated valves, Krefeld-Gellep, NBC RGM.800512d, 23 - Dorsal view, 24 - Internal view of broken pedicle valve, 25 - Internal view of dorsal valve, 26 - Detail of socket, subhorizontal outer socket ridge and angularly reclined inner socket ridge.

Scale bars: 1, 2, 3, 4, 5, 6, 7, 14, 15, 16, 20, 21, 23, 24, 25: 1 mm; 8, 10, 11, 12, 17, 19, 22: 0.5 mm; 9, 18, 26: 0.25 mm; 13: 0.2 mm.



Genus	Outline	Shell	Ventral valve	Beak	Notch, L/W	myo-phragm	hinge plates	crura	descending branches	median septum/septal pillar	Septal flanges
<i>Platidia</i>	subcircular, subquadrate, irregular	planoconvex	smooth, or spinules	short	hemispherical, 0.75	short	no	long and slender	strongly arcuate	high, blade-like SP	U-shaped
<i>Aemula</i>	oval, irregular, subcircular	planoconvex	fine spines	short	hemispherical, 0.72	no	weak	no	no	triangular SP	small divergent
<i>Amphithyris</i>	broadly subcircular	planoconvex	smooth or faint capillae	apiculate	hemispherical, 0.72	no	no	no	no	low MS	no
<i>Annuloplatidia</i>	subcircular	planoconvex, concavoconvex	smooth	short	shallow, 0.46	no	no	projecting anteriorly	arcuate	septal pillar	long, divergent
<i>Scumulus</i>	subtriangular, elongate, oval	flattened biconvex	smooth	short, straight	hemispherical, 0.57; hypothryd in adults	no	no	ventrally directed	between crura and septal pillar	subtriangular SP	no truncated apex
<i>Neoaemula</i>	subrectangular irregular	planoconvex	spines on larger specimens	short	hemispherical, 0.71	no	no	no	no	T-bar shaped, blade-like SP	narrow, laterally directed
<i>Germanoplatidia</i> n. gen.	regularly subcircular	ventri-biconvex	smooth	high	shallow, 0.3	long	no	no	no	high triangular SP	short, parallel

Tab. 2 - Comparison of some significant morphological characters of different genera of subfamily Platidiinae (MacKinnon & Lee 2006; MacKinnon et al. 2008)

Internal characters. Small rectangular teeth (Pl. 3, Figs. 17, 18, 23, Pl. 4, Figs. 2, 3, 7, 8, 22), no cardinal process (Pl. 4, Figs. 2, 7). Long but low myophragm, nearly invisible in dorsal view of the ventral valve (Pl. 4, Fig. 2), but markedly well-visible in oblique lateral view (Pl. 4, Fig. 3). Short and subhorizontal outer socket ridges, high and angularly reclined inner socket ridges (Pl. 3, Figs. 19, 22, Pl. 4, Figs. 4, 5, 9, 25, 26). No hinge plates, crura and descending branches (Pl. 3, Fig. 19, Pl. 4, Figs. 4, 15, 25). Septal pillar narrow triangular; anterior side of the pillar concave; the posterior side strongly widening at the base of the pillar; after a mild inclination the posterior side steeply ascends with a small shoulder (Pl. 4, Figs. 4, 5, 12, 16, 19). The short and nearly parallel septal flanges are oriented posteroventrally (Pl. 4, Figs. 4, 5, 11, 12, 13, 19).

Remarks. *Terebratulula pusilla* was described in the mid 19th century by Philippi (1843), but its generic attribution was unsolved until recently. Speyer (1884) and G6rges (1940) were near to the correct solution, as they considered *T. pusilla* as belonging to the genus *Morrisia* Davidson, 1852, which later was regarded as junior synonym of *Platidia* Costa, 1852. However, some years later G6rges (1952b) attributed *T. pusilla* to *Argiope* (= *Argyrotheca*). Rust

(1999) referred again the species *pusilla* to the genus *Platidia*. Most probably, the identifications of Speyer (1884), G6rges (1940) and Rust (1999) were based only on external characters when they attributed this species to the genus *Platidia*. However, the internal morphological characters of *T. pusilla* are rather different from the complicated brachidium of *Platidia*, and much more similar to *Aemula*, with the simple septal pillar and septal flanges. After the detailed comparison it turned out that the Chat-tian specimens show several differences even from *Aemula*, which justify the erection of a new genus (see above, at description of the genus).

Stratigraphic distribution of family Platidiidae is known from the Upper Cretaceous to the Recent (MacKinnon & Lee 2006). Subfamily Phaneroporinae contains only Holocene genera, while subfamily Platidiinae has both Holocene and fossil representatives. The earliest record of platidiid brachiopods (?*Aemula*) are from the middle Turonian (Upper Cretaceous) of the Bohemian Basin (Žitt et al. 2002). Now, the subfamily is complemented with a new upper Oligocene member which seems to belong to the evolutionary lineage of *Aemula*.

As far as *Argyrotheca cuneata* (Risso, 1826) (Álvarez et al. 2008a, b), *Argyrotheca schrammi* (Crosse &

Fischer, 1866) (Álvarez et al. 2008b) and *Bronnothyris* (Bitner & Kroh 2011) are concerned, the laterally directed prongs or the septal flanges were interpreted as possible rudimentary ascending branches. A similar interpretation can also be suggested for *Germanoplatidia* n. gen. (and other Platidiinae genera as *Aemula* and *Neoemula*).

Occurrence. Until now, *Germanoplatidia pusilla* is known only from the Chattian of Germany (Pre-North Sea).

DISCUSSION

Taxonomic results. The upper Oligocene (Chattian) brachiopod fauna of NW Germany is not very diverse; six taxa could be identified in the studied material. “Inarticulate” brachiopods are represented by a few discinide specimens. All of them belong to a single species, *Discinisca fallens*, and its fragmentary remains could be found at several localities or boreholes. Rhynchonellides are generally rare in the Cenozoic, so their limited occurrence in the German upper Oligocene is not a surprise. Görge (1952a) identified a new rhynchonellide species (“*Rhynchonella supraoligocaenica*”), but his description remained mostly unknown to brachiopodologists; only Cooper (1959) mentioned it very shortly among the “unplaced species”. The species was only rarely mentioned by local geologists, correctly identified, but not correctly attributed to the genus. On the basis of external and internal morphological characters, this species belongs to the genus *Aphelesia*. Large-sized, short-looped terebratuloides (*Pliothyryna grandis*) are the most common and best known brachiopods of the studied formations. They were found at several localities and were mentioned in several papers, at least in the faunal lists. Although Cooper (1983) recognized correctly its attribution to the genus *Pliothyryna*, the German Chattian terebratulide occurrences in regional geological papers were mostly identified as *Terebratula*, even recently. The small-sized megathyridid brachiopods are rare, but represented by two different taxa. The well-preserved and characteristic specimens of *Argyrotheca bitnerae* could be easily identified with the previous records of this species. Similarly to some earlier occurrences, its specimen number is limited at both known German localities. *Bronnothyris?* sp. was found only in a single sample and its poor and

fragmentary preservation prevents its identification at the species level. The small-sized Platidiidae specimens of the Chattian of NW Germany were found and described already at the mid-19th century, but their generic attribution was unsolved until nowadays. The external and internal characters of the very well-preserved specimens justify the erection of a new genus, *Germanoplatidia* n. gen. within the subfamily Platidiinae.

Evolutionary significance. The upper Paleogene discinides of the Pre-North Sea Basin have more affinity to the Neogene discinides of the area, than to the older Eocene forms. Recently similar observations were published on other upper Oligocene brachiopod faunas. Along with the long stratigraphical ranging Paleogene-Neogene-Recent species as *Megathyris detruncata* and *Lacazella mediterranea*, both Bitner et al. (2013) and Dulai (2010) have found characteristic Neogene (to Recent) species in the French and Hungarian upper Oligocene localities [e.g. *Novocrania anomala* (Müller, 1776), *Terebratulina retusa* (Linnaeus, 1758), *Argyrotheca cuneata*, *A. bitnerae*, *Joania cordata*, *Megerlia truncata* (Linnaeus, 1767)]. The record of *Discinisca fallens* in the Pre-North Sea Basin Chattian confirms that faunal change within brachiopods did not happen at the Paleogene/Neogene boundary, but before the late Paleogene.

Occurrence of *Aphelesia* in the Chattian of the Pre-North Sea Basin yielded important data for European Cenozoic rhynchonellides. Although both Cooper’s (1959) description and the revised Treatise (Savage et al. 2002) mentioned its occurrence from the Eocene, we did not find any data on the Eocene or Oligocene record. It means that this German Chattian occurrence is the first confirmed record of *Aphelesia* from the Paleogene.

The end-Cretaceous event was one of the most important mass extinctions in the history of Earth; however, brachiopods were not so strongly affected at generic and higher level. Recently some Cretaceous (e.g., *Orthothyris*, *Rugia*) or Cretaceous-basal Paleocene (e.g., *Bronnothyris*) genera were found in different Paleogene successions, indicating that even fewer genera were affected by the extinction. The Chattian Platidiidae material from NW Germany also confirms these results. At a first sight, the studied specimens are very similar to species of *Aemula* (known also from Cretaceous and

basal Paleocene). However, our detailed morphological comparison led to the erection of a new genus, *Germanoplatidia* n. gen. It seems very probable that *Germanoplatidia* n. gen is a descendant of *Aemula*, and therefore this evolutionary lineage has also survived at least until the Chattian.

Paleoecology. *Disciniscar*. With the exception of deep-water *Pelagodiscus*, discinides are mainly restricted to the continental shelves and strongly attached to various hard substrates by a very short and highly muscular pedicle (Emig 1997). Discinides sometimes live in clusters; this is the main reason of their commonly seen irregular shape (La Barbera 1985). Some of them occur even in the intertidal zone, but generally they are more abundant in subtidal depths. Their occurrence in Chattian of NW Germany fits very well with the generally accepted shallow-water paleoenvironmental reconstruction of this area (Diedrich 2012).

Aphelesia. Extinct *Aphelesia* seems to be restricted to the circalittoral environments on sandy or calcarenitic bottoms. In the Neogene of the Mediterranean, it is usually associated with species of *Terebratula* and bryozoans (Pedley 1976; Gaetani & Saccà 1985). Within the famous Maltese *Terebratula-Aphelesia* Bed, *A. bipartita* is restricted to the top of the bioherm, under turbulent conditions at depths of less than 30 m (Pedley 1976). Although the occurrence of *Aphelesia* is very limited in the Chattian of Germany, it is remarkable that similarly to the Mediterranean *Terebratula-Aphelesia* association, a *Pliothyryna-Aphelesia* co-occurrence can also be observed. *Aphelesia* was found at two localities of the Doberg Formation: in Doberg section *Aphelesia* occurs in layer 27, where *Pliothyryna* is also particularly common and produces a shell bed (Anderson 1969). Another known locality of *Aphelesia* is the marl pit at Astrup, where *Pliothyryna* is again common (Dallmann 1996).

Pliothyryna. Diedrich (2012) distinguished a brachiopod-bryozoan littoral fauna in glauconitic fine gravels at Astrup and Doberg sections. This assemblage was dominated by the large brachiopod *P. grandis*, which forms three shell beds at Astrup. Additional fossil elements are red algae and different bryozoan species. The shells are commonly encrusted by balanids, bryozoans and serpulids. This environment was characterized by very shallow, oxygen rich water and high energy conditions (Diedrich 2012). As the small gravels were not optimal for at-

tachment of terebratulides, most probably they attached to large red algae or other brachiopod shells.

Argyrotheca. Representatives of Recent *Argyrotheca* occur in neritic to upper bathyal environments, but they are most common in cryptic shallow water habitats (Logan 1979, 2007; Logan et al. 2004; Álvarez & Emig 2005). Various *Argyrotheca* species live attached by a very short pedicle to firm substrates of cryptic habitats, such as lower surface of boulders and corals, submarine caves, and coralligène (Logan 1975, 1977; Álvarez et al. 2005). Their very limited occurrence in the studied area is connected to the very shallow environments and especially the lack or paucity of cryptic environments.

Bronnothyris. Recent megathyridids are commonest in shallow-water environment, preferring cryptic habitats (Logan 2007). However, Cretaceous representatives of *Bronnothyris* all come from the white chalk facies (Popiel-Barczyk & Smirnova 1978). The Cenozoic representatives of the genus also come from soft sediments, as detrital sands (Smirnova et al. 1983; Bitner & Kroh 2011; Bitner & Müller 2017). The German Chattian specimens were also collected from fine marine sands of the Kassel Formation. Surlyk (1972) suggested that small size of micromorphic brachiopods in chalk facies may be an adaptation to the occurrence of numerous, but small-sized hard substrates on a generally soft bottom.

Germanoplatidia. A significant difference between *Germanoplatidia* n. gen. and *Aemula* is the very regular subcircular outline. According to Surlyk (1974), the extinct *Aemula* had a very short and massive pedicle and therefore lived with its dorsal valve pressed against the hard substrate. This life position means that rather high percentage of *Aemula* (and also *Platidia*) species shows very irregular outline in dorsal view. On the contrary, all available specimens of *G. pusilla* are very regularly subcircular in outline, they do not show any irregularity. This probably suggests that the pedicle of the species of *Germanoplatidia* was longer than in *Aemula*, and its dorsal valve did not press strongly against a hard substrate. *Germanoplatidia pusilla* specimens were found in the basal green sands of the Diekholzen Formation and in the glauconitic fine sands of the Grafenberg Formation. On the basis of the lithology, the species of *Germanoplatidia* n. gen. lived in sandy bottom environments, and attached to small hard objects in the fine sediment.

Paleobiogeography. Compared with the Eocene and Miocene brachiopod faunas, the Oligocene ones are less diverse and less well-known. Due to the few and not satisfactorily known data, paleobiogeographic analyses of Oligocene brachiopods are more difficult to achieve. It is true also for the Chattian fauna of NW Germany. Only six taxa were identified, from which *Bronnothyris* is identified only at generic level. This genus is a survivor from the Mesozoic, and until now only a few records are known from the lower Paleocene (Zelinskaya 1975; Ukraine), upper Eocene (Bitner & Müller 2017; Ukraine) and lower Oligocene (Bitner & Kroh 2011; Germany). The German Rupelian *Bronnothyris subradiata* may have some relations with the studied Chattian material.

Two other identified species (*Aphelesia supraoligocaenica*, *Germanoplatidia pusilla*) seem to be endemic, because until now they are known only from the German part of the late Oligocene Pre-North Sea. Regarding the Paleogene, *Disciniscia fallens* is also known only from this area; however, it had a wider distribution in the Neogene. Although most data come from different parts of the North Sea Basin (England, the Netherlands, Germany: Wood 1872; Davidson 1974a; Dulai 2013), there is an uncertain record also from the Miocene of the Atlantic Province (Portugal; Dulai 2013).

Identification of large terebratulides may be uncertain not only in the Chattian of Germany, but practically in the whole European Cenozoic. As until recently “*Terebratula*” *grandis* was frequently mentioned from the German Oligocene, the poor preservation or the unknown internal morphological characters caused similar identification problems in many other cases. The confirmed distribution of *P. grandis* is in the Oligocene of the Pre-North Sea, but its Paleogene occurrence is possible also at other European areas. At the same time, there are several Neogene “*Terebratula grandis*” records in the literature both from the North Sea and the Central Paratethys, which probably belong to other species or even other genera.

The only identified species, which has a wide distribution, is *Argyrotheca bitnerae*. Although it was described only in recent years (Dulai & Stachacz 2011), additionally to the type area in the middle Miocene Central Paratethys, it has been found in the upper Oligocene of the Atlantic (Bitner et al. 2013), in the upper Oligocene of the North Sea (this pa-

per), in the lower Miocene of Iran (Pedramara et al. 2019) and in the upper Miocene of the Mediterranean (Dulai et al. unpublished data). Despite the fact that it is everywhere much less frequent than the other megathyridid *Argyrotheca cuneata* or *Joania cordata*, its distribution seems to be similarly cosmopolitan in the European Cenozoic; moreover, it extends to the lower Miocene of Iran too (Pedramara et al. 2019).

CONCLUSIONS

Although the studied Chattian brachiopod fauna from NW Germany was limited in specimens and not very diverse, several important taxonomical, stratigraphic, evolutionary, paleoecological and paleobiogeographical results were achieved:

The generic attribution of “*Rhynchonella*” *supraoligocaenica* has been solved: the external and internal morphological characters allow to refer the species *Aphelesia*.

The generic attribution of “*Terebratula*” *pusilla* has been solved: the internal morphology is similar to *Aemula*, but several differences justify the erection of a new genus, *Germanoplatidia* n. gen. within the subfamily Platidiinae.

The Chattian record of the Neogene *Disciniscia fallens* confirms that faunal change within brachiopods did not happen at the Paleogene/Neogene boundary, but before the late Paleogene.

The Chattian occurrence of *Aphelesia* in Germany seems to be the first confirmed record of the genus in the Paleogene.

Similarly to *Orthothyris*, *Rugia* and *Bronnothyris*, a further micromorphic brachiopod evolutionary lineage (*Aemula*-*Germanoplatidia* n. gen.) has been shown to survive from the Mesozoic to the late Paleogene.

Aphelesia occurs together with a large terebratulide genus (*Pliothyridina*) in the upper Oligocene North Sea, at Doberg and Astrup. This is similar to the record of the *Terebratula*-*Aphelesia* association in the Mediterranean region.

The regularly subcircular outline, and the surrounding fine sandy deposits indicate that species of *Germanoplatidia* n. gen. lived in sandy bottom environments, and attached to small hard objects in the fine sediments by a longer pedicle than that of the species of *Aemula*.

Half of the identified species seems to be endemic to the Pre-North Sea Basin (*D. fallens*, *A. supraoligocaenica*, *G. pusilla*).

The first record of *Argyrotheca bitnerae* from the Pre-North Sea Basin has been reported. *Argyrotheca bitnerae* thus shows a cosmopolitan distribution in the Cenozoic (Atlantic upper Oligocene, North Sea upper Oligocene, Central Paratethys middle Miocene, Mediterranean lower and upper Miocene).

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