Geologie

Middle and Upper Devonian Cryptodonta (Bivalvia) from the Pelagic Hercynian Facies - Taxonomy, Stratigraphy, and Paleoecology

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I Abstract

The Middle and Upper Devonian pelagic facies is rich in peculiar bivalves. Despite their great quantity in several different horizons, neither their life habits nor their correct stratigraphic rang have been well understood. Additionally, no systematic concept was available for classification, and their geographical distribution was also unknown. Our knowledge mostly dated back to Münster (1840), Barrande (1881), and Clarke (1904) who erected most of the taxa from the Bohemian and the Laurussian region. But apart from the introduction of names, no details of the internal morphology or species concepts have been presented until now.

This study presents a basic systematic revision of Givetian and Upper Devonian pelagic bivalve taxa. It is based on museum collections, including all available type specimens and originals, and on new material from Germany, France, Morocco, and North America. Other records are from Russia, Poland, and Australia. Furthermore, for the first time data on the morphology, paleoecology, and biostratigraphy of Givetian and Upper Devonian pelagic bivalves is provided. As in associated faunal groups, it suggests a control of global events on their distribution in space and time.

The studied Devonian pelagic facies realm is characterized by condensed limestones of outer shelf ramps and seamounts that grade into nodular limestones and fine siliclastics, including black shales. Bivalves were part of the low-diverse but very characteristic deeper and cooler-water benthos association that inhabited these depositional environments on the outer shelf south to the Laurussia Continent.

In this study, *Deltacardium* n. gen. is introduced for taxa that earlier have been placed into the Silurian praecardiids. Therefore, previously assumed continuation of pelagic bivalve taxa from the Upper Silurian of Bohemia into the Upper Devonian of Germany does, in this case, not withstand scrutiny. *Deltacardium* was probably restricted to the Lower Famennian of the western Prototethys and of the Appalachians, and can be used as a biostratigraphic marker for the lower Nehden-Stage. It appeared during the main radiation phase after the global Upper Kellwasser Event and its extinction coincided with a regressive phase of the Condroz Event.

The Loxopteriinae n. subfam. is erected and assigned to the revised Dualinidae. The genera *Loxopteria* and *Elasmatium* are included into the Loxopteriinae, and a new *Loxopteria* species *Loxopteria meioklina* has been identyfied. The loxopteriids occurred in the basalmost Famennian and disappeared in the Hembergian-Stage, at the end of the hypoxic global *Annulata* Event. These bivalves provided many soft-body information. Therefore, their mode of life can be interpreted as pleurothetic suspension feeders.

The lunulacardiids are re-studied, and the included taxa *Lunulacardium*, *Prosochasma*, *Chaenocardiola*, and their type species are finally defiened herein. Especially, controversal

questions concerning the actual bauplan, such as the orientation of the valves, the presence of a gap, and the location and function of the characteristic truncation are clarified.

Ontaria and its type species *Ontaria suborbicularis* are re-studied. It appears to be certain that taxa commonly assigned to this genus and often used as marker for the uppermost Famennian/lowermost Carboniferous are no ontariids. These taxa are characteristic faunal elements of the Frasnian Adorf-Stage that occurres in large quantities covering whole bedding planes.

II Kurzfassung

Die pelagische Fazies des Devon ist durch Serien auf dem äußeren Schelf abgelagerter, kondensierter Kalksteine gekennzeichnet. Die Abfolge geht in knollige Kalke und feine siliziklastische Sedimente, inklusive Schwarzschiefer, über.
Gegenstand dieser Studie ist die reichhaltige Bivalvenfauna der pelagischen Fazies des Mittel- und Oberdevon wurde, die Teil einer typischen aber wenig diversen benthischen Lebensgemeinschaft des Tief- und Kaltwasser-Milieus ist. Diese wurde bislang hinsichtlich ihrer geographischen- und stratigraphischen Reichweite sowie ihrer Ökologie wenig erforscht. Erschwert wurde die Untersuchung der Muschelfauna durch das Fehlen einer einheitlichen taxonomischen Systematik. Der bisherige Kenntnisstand geht auf Arbeiten von Münster (1840), Barrande (1881) und Clarke (1904) zurück, die ihre Taxa und Artabgrenzungen jedoch auf keiner einheitlichen/gemeinsamen Grundlage aufstellten. Bisher bestanden zudem keine detaillierten Beschreibungen der internen Morphologie und die Untersuchungsgebiete der vorherigen Bearbeiter beschränkten sich auf das Prager Becken und Teile des Old Red Kontinents.
Mit dieser Arbeit wird nun erstmals eine systematische Revision der Bivalvenfauna der pelagischen Fazies des Givet und Oberdevons vorgelegt. Untersucht wurden Exemplare aus Museums Sammlungen, inklusive aller verfügbaren Orginaltypen, und Material aus jüngst beprobten Profilen Deutschlands, Frankreichs, Marokkos, Nord-Amerikas, Russlands, Polens und Australiens.
Die Untersuchungsergebnisse der der Morphologie, Paläoökologie und Biostratigraphie der pelagischen Bivalven deuten auf die Steuerung ihrer räumlichen und zeitlichen Verbreitung durch globale Events hin.

Die Gattung *Deltacardium* n. gen. wird hier für Taxa eingeführt, die bisher zu den silurischen Praecardiiden gestellt wurde. Die bisher angenommene Reichweite der pelagischen Taxa vom Obersilur des Prager Beckens bis zum Oberdevon Deutschlands ist für dies Gattung somit hinfällig. *Deltacardium* war räumlich und zeitlich wahrscheinlich auf das untere Famennian der westlichen Paläotethys und der Appalachen beschränkt, womit sie als biostratigraphischer Markerfossil der unteren Nehden-Stufe eingesetzt werden kann. Die Gattung tritt erstmals im

Zuge der Radiationsphase nach dem Kellwasser-Event auf und stirbt zum Zeitpunkt der regressiven Phase des Condroz-Events aus.

Die aufgestellte Subfamilie Loxopteriinae n. subfam. wurde in die hier revidierte Dualinidae eingegliedert. *Loxopteria* und *Elasmatium* wurden zu den Loxopteriinae gestellt, die neue Art *Loxopteria meioklina* n. sp. wurde beschrieben. Die Loxopteriiden treten erstmals im basalen Famennian auf und sterben zur Zeit der Hangenberg-Stufe aus, die das Ende des globalen hypoxischen *Annulata*-Events darstellt. Aufgrund der häufig guten Weichteilerhaltung dieser Taxa ist es möglich diese ökologisch als pleurothetische Suspensionsfiltrierer einzuordnen.

Die Lunulacardiiden wurden revidiert und die Taxa *Lunulacardium, Prosochasma* und *Chaenocardiola* sind untersucht und neu definiert worden. Bislang kontrovers diskutierte Aspekte des Bauplanes (die Orientierung der Klappen, klaffende oder nicht klaffende Klappen, sowie die Position und Funktion des charakteristischen abgestutzten Randes) wurden spezifiziert.

Das Genus *Ontaria* und seine Typus-Art *Ontaria suborbicularis* wurden näher untersucht. Es scheint gesichert, dass Taxa, die bislang zu diesem Genus gestellt und oft als Marker für die Zeit des obersten Famennian/basales Karbon verwendet worden sind, *nicht* zu den Ontariiden gestellt werden dürfen. Die Ontariiden gehören zu den charakteristischen Faunenelementen der Adorf-Stufe (Frasnium), die dort in großen Individuenzahlen auftreten.

III Acknowledgment

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IV Index

1 Introduction

Upper Devonian bivalves from the pelagic facies have been reported from all over the world. They occur in various German regions including the Rhenish Massif (Figs. 1, 2), the Hercynian Mountains, Thuringia, Saxony and the Franconian Forest. Furthermore, they are widely distributed in many Devonian localities of southern Morocco (Maider and Tafilalt), France (Armorican Massif, Montagne Noire), Poland (Holy Cross Mountains) and in closely related faunas from western New York State (Fig. 1). Bivalves from many other regions of Russia (Timan, Ural Mountains, Sibiria), Iran, Nothern and Southern China, and Australia have rarely been studied, but the overall pelagic assemblages, which occur in those regions, are rather similar to those known from the classical Devonian localities and, therefore, the presence of congeneric bivalve taxa may be expected. This is supported by a study of the Buchiolinae by Grimm (1998), the only pelagic bivalve group that has so far been investigated in detail.

Despite their abundance in the fossil record, the current knowledge about the pelagic Upper Devonian bivalves dates back to the beginning of the 20th century. Due to the chaotic systematic situation of this group, the bivalve taxa appear in faunal lists often summarized as "Lamellibranchiata div.", or were placed within taxa, which act as diffuse collective for more or less undefined morphological groups. The lack of any modern studies or revisions prevents an appropriate understanding of the evolutionary history, diversity, biostratigraphy, and biostratigraphy of this group. Interesting phenomena, such as the often reported "bloom" of certain bivalve taxa during small to large scale, global environmental perturbations and extinction events, such as black shale events (e.g., House, 1985, 2002; Walliser, 1985; Becker, 1993b) have been neglected for a long time. Therefore, the taxonomic review, which has been accomplished in this study, provides an essential basis for first further biostratigraphic and paleoecologic investigations, which are presented herein. In this respect, the present study must be seen as a pioneering work that yet cannot resolve all outstanding questions.

2 History

The Upper Devonian bivalves from the pelagic facies have been almost completely neglected in the past hundred years, and Clarke (1904) was the last author who studied them closely.

Prior, in the 19th century, they have been in the focus of scientific interest, but documenation was often insufficiant and many species are based on poorly preserved preserved material. In the course of his study of Devonian localities from the Franconian Forest (southeastern Germany), Münster (1840) was the first author, who conducted a systematic study. Later, Frech (1891) and Beushausen (1895) achieved monographs exclusively treating Devonian bivalves from Germany. Hall (1843, 1883, 1885) studied contemporaneous North American faunas and, as mentioned above, Clarke (1904) contributed his comprehensive work on the Late Devonian Naples Fauna. The study of Upper Silurian and Lower Devonian taxa of the Bohemian

Facies from the Prague Basin (Czech Republic) is, although dealing with older taxa, very important. Generally, these Bohemian taxa have been aligned with Upper Devonian species and genera, due to their occurence in a similar outer shelf facies. Therefore, many genera and species described from the Upper Devonian have been placed in Upper Silurian taxa for a long time. Barrande (1881) produced a tremendous amount of names for Silurian and Lower Devonian forms, which mostly remained un-revised until today. In the following, studies focusing on Late Devonian pelagic faunas mentioned the presence of bivalves, but they were simply enclosed in the faunal lists (e.g., Schmidt, 1922; Lange, 1929). Only few new species were added (e.g., Schmidt, 1924; Grüneberg, 1925; Schindewolf, 1923), but these studies did not include any taxonomic work.

The taxonomy, the stratigraphic distribution as well as the ecology of these taxa have been neglected and, thus, no insight in the paleontological significance of this group has been gained. La Rocque (1950) and McAlester (1962a) made an approach on some bivalve associations from the Devonian of North America, but these are from shallower, benthic facies. Recently a lot of information on Upper Devonian shallow marine taxa was provided by the work of Amler (e.g., 1995, 1996, 2004), and Grimm (1998) re-studied the buchioliids. The bulk of species and genera, especially from the pelagic realm, remains unstudied, even on a global scale.

Futhermore, the constant introduction of new taxa in the 19th century created serious taxonomic confusion with a lack of clear distinction between erected taxa, mostly as a consequence of insufficiant comparision of material, or even of ignorance of previous work. Further progress in the perception of these diverse bivalves stagnated afterwards. Only Neumayr (1884, 1891) provided a classification of the bivalves with particular emphasize on Paleozoic groups. Conrath (1887) examined the hinge morphology of some Late Paleozoic taxa and correlated them with high-level bivalve systematics. In the course of their compendia of mollusks, Zittel (1881-1885) and Fischer (1880-87) compiled an overview on Paleozoic bivalve taxa that was mostly based on Neumayr´s work (1884). Later, no new information was added. The “Treatise on Invertebrate Paleontology” (Moore, 1969) resumed the poor state of knowledge, but failed to establish clarification and a review of Paleozoic and, especially, of the Upper Devonian bivalve taxa.

In summary, the taxonomy and systematics of Upper Devonian bivalves is, despite their significance in many ecosystems of their time, a hughe mess and the common taxonomic monographs, such as the Treatise, allow no overview and form no base of identification.

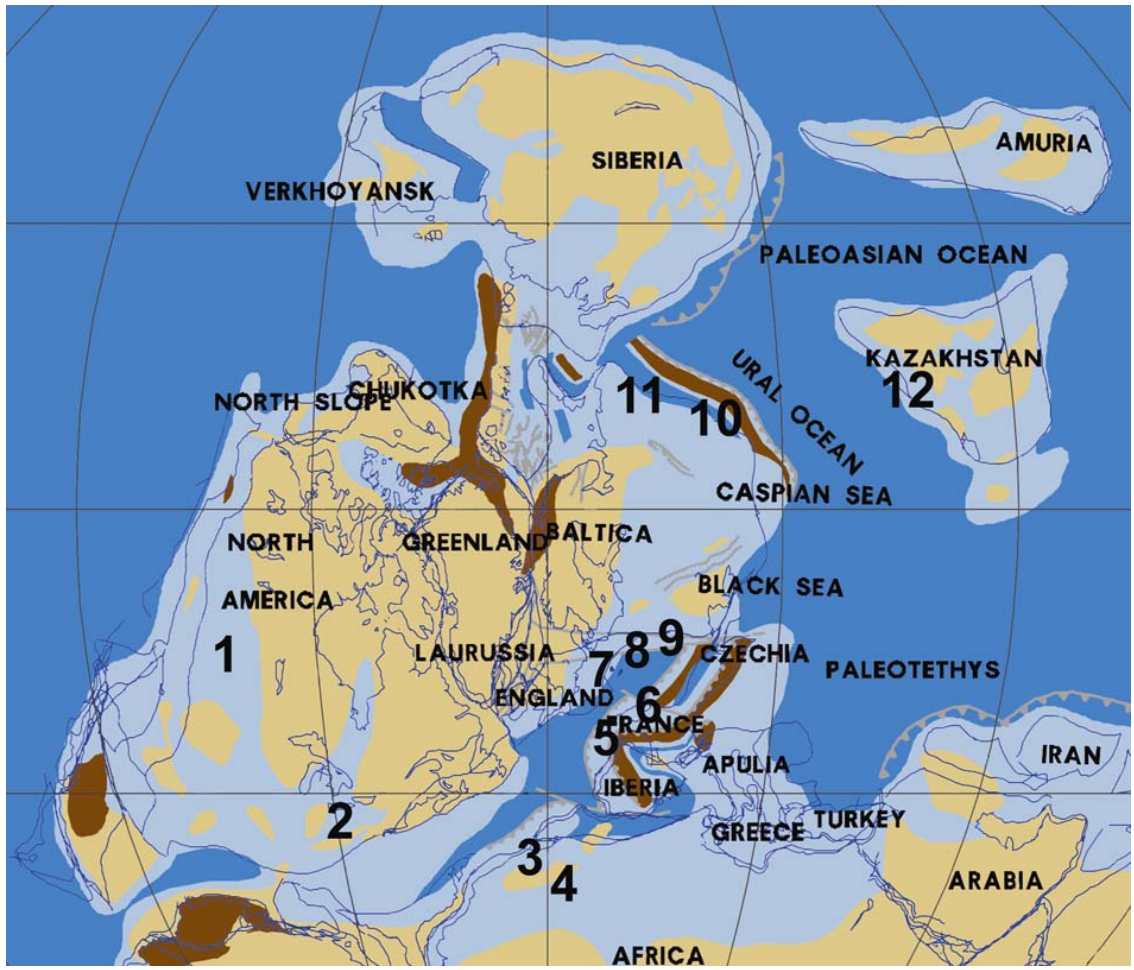


Figure 1 Paleogeographical distribution of investigated pelagic bivalve occurrences from the Givetian to Famennian (paleogeographical map based on Golonka, 2000).
1 - Montana, USA; 2 - New York State, USA; 3 - Meseta, Morocco; 4 - Tafilalt and Maider, Morocco; 5 - Rhenish Massif, Germany; 6 - Hercynian Mountains, Germany; 7 - Armorican Massif, France; 8 - Franconia Forest, Germany; 9 - Holy Cross Mountains, Poland; 10 - Ural Mountains, Russia; 11 - Timan, Russia; 12 - Kazachstan.

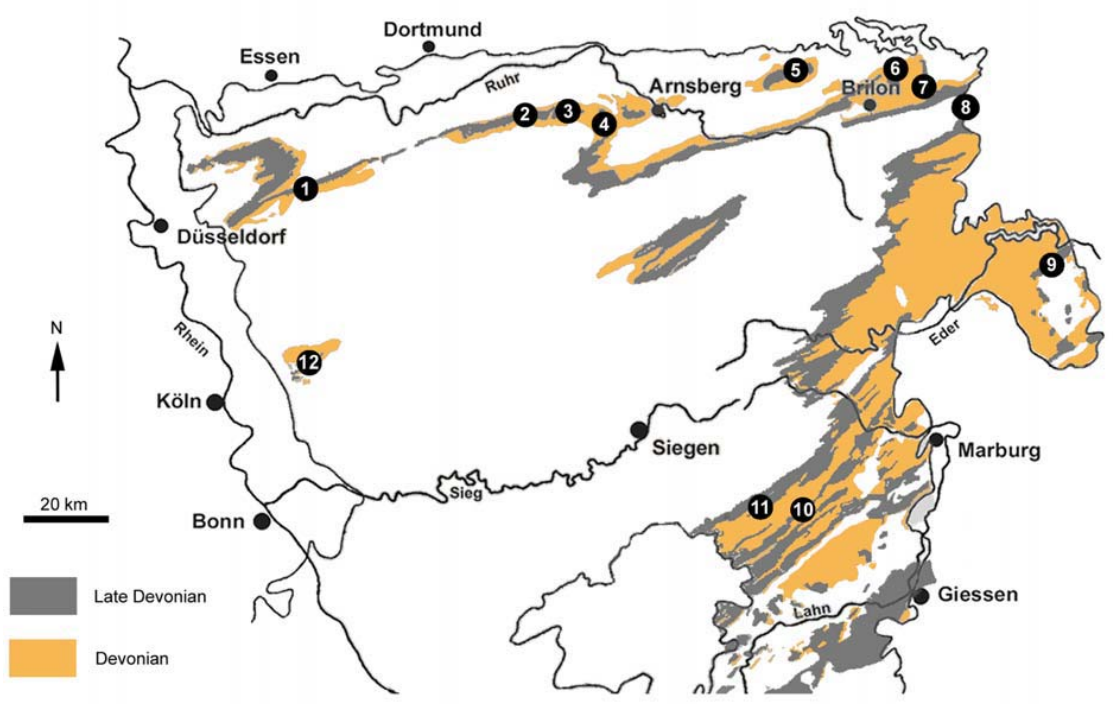


Figure 2 Frequent occurrences of bivalves in outcrops of the Upper Devonian from the eastern Rhenish Massif; (1-Eskesberg; 2-Reitenberg; 3-Beul; 4-Dasberg; 5-Biesenberg; 6-Nehden; 7-Enkeberg; 8-Martenberg; 9-Wildungen; 10-Langenaubach; 11-Oberscheld; 12-Bergisch Gladbach).

3 Methods / Material

The examined material comprises about thousandtwohundret specimens from all available museum collections and additional type material of several publications on the Upper Devonian. A better part of the material is housed in the Museum für Naturkunde, Berlin. This collection comprises specimens from various German regions, collected over a period of 150 years. Furthermore, it contains material collected during the first geological mapping carried out in the eastern Rhenish Massif in the 1930th (e.g., Paeckelmann and Kühne, 1936a, b; Paeckelmann, 1938). Many types of monographs from different Upper Devonian localities and faunas (e.g., Clarke, 1904; Born, 1912; Jux and Krath, 1974) have also been re-studied. Especially, the important types of Beushausen (1895), who compiled a still unique outline of the Devonian bivalve faunas of Germany, were re-examined.

As a basis of the systematic review all available type specimens were examined and documented to ensure an acceptable systematic concept for the genera and the species. These originals have been located in the Bayerische Staatssammlung Munich, the Geowissenschaftliches Zentrum der Universität Göttingen, the National Museum, Prague, the New York

State Museum, Albany, and the American Museum of Natural History, New York. In addition, partly unpublished collections by R.T. Becker (Universität Münster) from Southern France, Morocco, the Rhenish Massif, and North America were made available. Important specimens from Bergisch Gladbach belong to the collection of V. Ebbighausen.
An overview of all species and genera described from the Rhenish Massif has been compiled. All known monographs and comments to geological mappings have been searched for bivalve taxa in order to obtain a complete review of occurences in time and space for Germany, and specimens have been, as far as possible, correlated with the listed references.

The material shows rather different preservation modes. Steinkerns dominate, but rarely original shell material is preserved. Specimens occur as internal, external or composite moulds. The state of preservation is one of the most significant but often neglected aspects in the study of pre-Carboniferous bivalve faunas (McAlester, 1962b). Due to the preservation of a single individual, the morphological features of species can vary considerably (e.g., Amler, 1995; Rogalla and Amler, 2003). This instance has led to a lot of taxonomic and morphological confusion in the past.
The examination of pyritic steinkerns, which occur in e.g., the Knoppenbissen Formation (Bergisch Gladbach, eastern Rhenish Massif, Germany), revealed many morphological details, which have never been observed before. This provided new information concerning the supposed ecology of these bivalves and allowed to clarify the actual bauplan of some taxa.

Specimens needed mechanically preparation, to get a correct impression of details such as, e.g., the outline or the hinge area. Due to the embedding of many specimens in rather solid limestone matrix, they had to be manually dissected. Some fossils, which were covered with hard encrustations of marl and clay, were treated with the tenside Rewoquat to remove these components from the specimens.
For documentation the material was coated with ammonium chloride. The photographs were taken with an Olympus SZX9 microscope and a Color View II camera. The data were processed with the photosoftware analySIS of Soft Imaging System and Adobe Photoshop and Adobe Illustrator provided further image processing.

4 Pelagic Facies

Classically, two main facies types ("magnafacies") are distinguished in the Devonian, the Rhenish Facies and the Hercynian Facies (e.g., Schmidt, 1962). The Rhenish Facies is represented by coarse-grained sandy or silty and mostly carbonate-free sediments, which were deposited in well oxygenated, relative shallow, nearshore areas (Erben, 1964). These regions were located within the photic zone and were influenced by strom waves. The pelagic facies of the Devonian is known as the Hercynian Facies. It includes mostly carbonates and fine-grained siliciclastic sediments, which have been accumulated below the photic zone. These deeper water deposits originated in lower to middle latitudes on the outer shelf south to the Laurussia Continent. Due to the subsidence in Central Europe during the Devonian, the Hercynian sediments often overlie older shallow-water carbonates (reefs) and clastic sediments, which have been deposited in shelf basins (Krebs, 1979).

In the Lower Devonian the Rhenish Facies was predominant in the Rhenish Massif, while the Bohemian Facies of the Prague Basin (Czech Republic) represented the pelagic facies realm. From the Middle Devonian onward, the input of clastics transported from the Laurussia Continent into the shelf decreased allowing the growth of reefs in shallow marine but still rapidly subsiding areas. In the Middle and Upper Devonian, the margin between the Rhenish and Hercynian Facies shifted with sea-level change from the southeast to the northwest (Langenstrassen, 1983; Krebs, 1979).

The depositional environment of the Upper Devonian pelagic facies is characterized by submarine topographic elevations subdividing the basin (Fig. 3). Tectonic rises bounded by block faults, volcanic seamounts, and drowned reefs flanked deeper water basins (e.g., Krebs, 1979, Franke and Walliser, 1983; Wendt and Aigner, 1985, Devleeschouwer et al., 2002). The bathymetrical succession from the inner shelf region, which is characterized by currents and storm events, to the calmer outer shelf areas is represented by typical lateral sedimentary depositional systems (Fig.3).

- Condensed micritic reddish or grey cephalopod limestones accumulated on submarine rises, such as submerged reefs or volcanic rises (Tucker, 1974). They include a low-diverse benthonic fauna, such as distinctive gastropods, small solitary rugose corals, specific brachiopods (rhynchonellids, small orthids, and chonetids), crinoids, small-sized often reduced-eyed trilobites, and the eponymous cephalopods.
- Red or grey nodular limestones intercalated with shales, which contain slumps, are characteristic for intra-shelf basin slopes or marginal basin slopes.
- Rocks originated by mass flows, such as allodapic limestones (Flinz Limestone) and sediments containing reef detritus, which are especially present in the Givetian rock succession, were generated at slopes of drowned reefs.

- Fine-grained siliciclastic sediments, such as banded, gray or black shales, tentaculite shales or entomozoid shale ("Cypridinenschiefer") were deposited in outer intrashelf basins. In inner shelf basins goniatite shales were the predominant sediments. The faunal elements of these rocks are mostly pelagic organisms, such as, conodonts, tentaculites, entomozoid ostracodes, goniatites, bivalves, small gastropods, and blind trilobites. Especially the dark shales contain a pyritic fauna adapted to low-oxygen conditions.

Apart from these sediments, there are layers, which originated by short-term events, such as bentonites, which represent volcanic ash layers, or black shales as the result of hypoxic events (e.g., Kellwasser Beds, black shales of the *annulata* and Hangenberg Events).
Numerous hiati and condensation horizons characterize the often extremely reduced and discontinuous sedimentation (Wendt and Aigner, 1985) on the outer shelf seamounts. Transgressive phases caused sediment starvation of basins, but allowed the settling of fine mud detritus on morphological highs due to decreased bottom turbulences. Regressions resulted either in non-deposition and reworking of sediments by bottom currents (on seamounts) or in turbiditic sandstones (e.g., “Plattensandstein” or “Hangenberg Sandstein”), which were also deposited during phases of sea level falls.
Volcanic rocks are also important in the Upper Devonian rock succession (e.g., Bottke, 1965, Sunkel, 1990). Ironstones, tuffites, pillow lavas, and volcanic breccia represent the volcanism of this time. Pyroclastic beds may also yield various fossils.

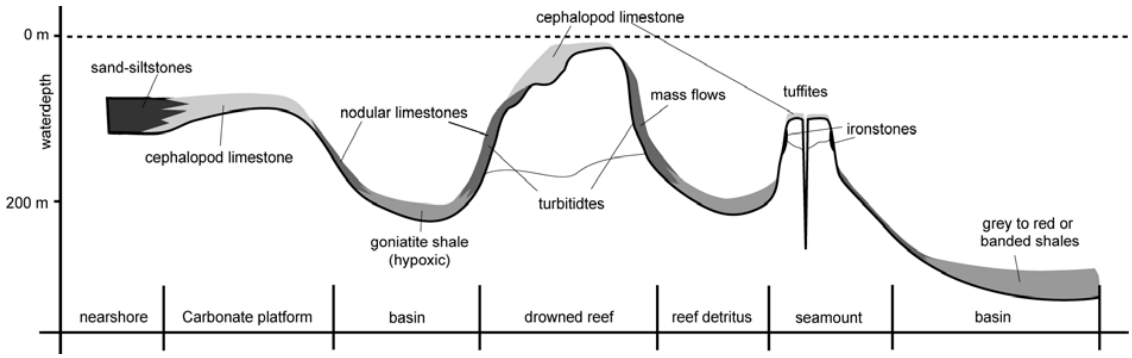


Figure 3 Simplified view of the deposition environment of the Upper Devonian Hercynian Facies in Central Europe (after Becker, 2001).

Pelagic organisms dominate all Hercynian deposits. The planktonic fauna consists of embryonic to juvenile cephalopods, dacryoconarids and entomozoid ostracods while the nekton is represented by conodonts, nautiloid, ammonoids, armored fish (placoderms, agnathans), and

sharks. Apart from bivalves, the low-diverse deeper water benthos includes typically single rugose corals, small gastropods, small-eyed to blind trilobites, crinoids, and brachiopods (e.g., Wendt and Aigner, 1985).

The environmental conditions during the Upper Devonian are, apart from the faunal information, in many points controversial. The reconstruction of the climate of the Upper Devonian is issue of a lot of discussion (e.g., Joachimski and Buggisch, 1993; Goddéris and Joachimski, 2004; Denison et al., 1997). The most recent calculation of the paleotemperature of the ocean during the Eifelian and early Givetian is based on the oxygen isotope values of brachiopod calcite and conodont apatite, and ranges from 22°C to 25°C (Joachimski et al., 2004). Temperatures increased during the Upper Givetian and Frasnian, reconstructed by conodont apatite, up to approximately 25°C and reached probably 32°C in the early Famennian (Joachimski et al., 2004). Thus the water temperature of the Upper Devonian corresponds to a subtropical to tropical climate during a supposed hot greenhouse phase. It is important to mention that these data probably refer to the upper water layers of the ocean and the environment of the deeper water fauna, studied herein, was not as highly affected by this increase of the temperature than organisms living closer to the water surface. It has to be taken into account that the temperature in the basins may have been lower than at the top of the water column similar to the thermocline of modern tropics, where the temperature drops down immediately in hundred meters water depth (Schmitt et al., 1987; Philander and Federov, 2003). On the other hand, the reconstruction of seawater temperatures from similar greenhouse periods during the Cretaceous showed the presence of rather warm bottom water with temperatures increasing to a maximum of 20°C (Gustafsson et al., 2003; Huber et al., 2002).

The water depth in which the pelagic sediments were originated ranges from shallow bathyal (deeper than 200 meters) to middle to deep sublittoral (50-200 meters; Krebs, 1979). Especially the depositional depth of the cephalopod limestones is discussed controversially. These Devonian deeper water limestones, which were deposited on topographical elevations, were widespread over Central Europe. Paleobathymetric data range from some 10´s to some 100´s of meters (Tucker, 1973, 1974; Franke and Walliser, 1983; Wendt and Aigner, 1985). The observable sedimentary structures are not truly diagnostic of their depositional environment (Tucker, 1974). The main evidence that they are true deeper water limestones is the pelagic fauna. One limitation for the depth is the implosion depth of goniatite shells, which ranges from 100-300 meters (Hewitt, 1996). This depositional depth did not range below this value, because ammonoid shells found in the cephalopod limestones are not imploded. Furthermore, the environment was located in the subphotic zone of the ocean, which ranges from below 60 to 80 meters, because the observed fauna lacks any typical photic elements, such as biohermal corals, stromatoporoids or photic green and red algae. Therefore, the general agreement on the depositional depth of the cephalopod limestones is between 60 and approx. 300 meters.

5 Stratigraphy

This study deals with bivalves from the Middle and Upper Devonian. The oldest included stage is the Givetian (upper Middle Devonian). Its lower boundary is marked by the earliest occurrence of the conodont *Polygnathus hemiansatus*, and the *Maenioceras* Stufe commences a little below (Walliser et al., 1995). The Frasnian Stage is defined by the entry of oldest *Ancyrodella rotundiloba pristina* (Aboussalam and Becker, 2004). The GSSP level corresponds to the base of Montagne Noire zone MN 1 (Klapper, 1989) and falls within the *falsiovalis* conodont Zone of Sandberg and Ziegler (1996). The oldest occurrence of the goniatite genus *Neopharciceras* is observed at the base of the Frasnian, too (House et al., 2000a). The Frasnian/Famennian boundary is characterized by the Upper Kellwasser horizon and by a major, global extinction event. The Famennian starts just above the Upper Kellwasser level, at the boundary between the *Palmatolepis linguiformis* and *Pa. triangularis* zones (Klapper et al., 1994). All Gephuroceratidae became extinct at this boundary (Becker and House, 1994; Becker, 2004).

The Devonian/Carboniferous boundary is characterized by the first occurrence of the conodont *Siphonodella sulcata* (Paproth et al., 1991; Feist et al., 2000). Just below this boundary, during the Hangenberg Event, major ammonoid groups, such as almost all goniatites and clymeniids, became extinct (e.g., Becker and House, 2000). The main extinction of the multiphase Hangenberg Event lies at the onset of the Hangenberg Black Shales (Becker, 1996) and affected globally all ecosystems (Kaiser et al., 2004; Kaiser, 2005).

Many biostratigraphic zonations have been established whereas reliable absolute ages for rocks of this period are less numerous. For a long time the scale of Harland et al. (1990) was in use. They set ages of 380.8 ma for the start of the Givetian, 377.4 ma for the start of the Frasnian, 367.0 ma for the start of the Famennian, and proposed an end of the Devonian period at 362.5 ma. These ages contrast with the more recent scale of Tucker et al. (1998) who estimated 387.5 ma for the start and 382.5 ma for the end of the Givetian, 376.5 ma for the Frasnian/Famennian boundary and 362 ma for the Devonian/Carboniferous boundary. These ages were challenged by Streel (2000) who expressed doubts about the accuracy of their biostratigraphic correlation.

Other authors calculated an distinct younger age for the end of the Devonian period. Claoué-Long et al. (1995) estimated an age of 353.7 ± 4.2 ma for the Devonian/Carboniferous boundary from the stratotype section at the Hasselbachtal (Rhenish Massif, Germany) by U-Pb SHRIMP-dating of zircons from metabentonites. Recently, Trapp et al. (2004) reinterpolated the age of the Devonian/Carboniferous boundary to 360.7 ± 0.7 ma by re-studying zircons from the same outcrop using U-Pb ID-TIMS analysis. Kaufmann et al. (2004) provided new ID-TIMS data from Steinbruch Schmidt (Kellerwald, Germany), which allows an estimation of 376.1 ± 1.7 ma for the Frasnian/Famennian boundary. House and Gradstein (2004) compared and compiled previous radiometric timescales, but lack the recent ages of Trapp et al.

(2004), and Kaufmann et al. (2004). House and Gradstein (2004) also summarized the high resolution biostratigraphy for the pelagic facies of the Givetian and Upper Devonian, which is mainly based on conodonts and ammonoids.

The classical Givetian conodont zonation (e.g., Ziegler et al., 1976; Klapper, 1989) was updated by Bultynck (1987), Aboussalam and Becker (2001, 2004), and Becker (2005). Following the most recent divisions, the Givetian is subdivided in the successive *hemiansatus*, *timorensis*, *rhenana*/*varcus*, *ansatus semialternans*, *hermanni*, *christatus ectypus*, *disparilis*, *dengleri*, and *norris* Zones (Fig. 5).

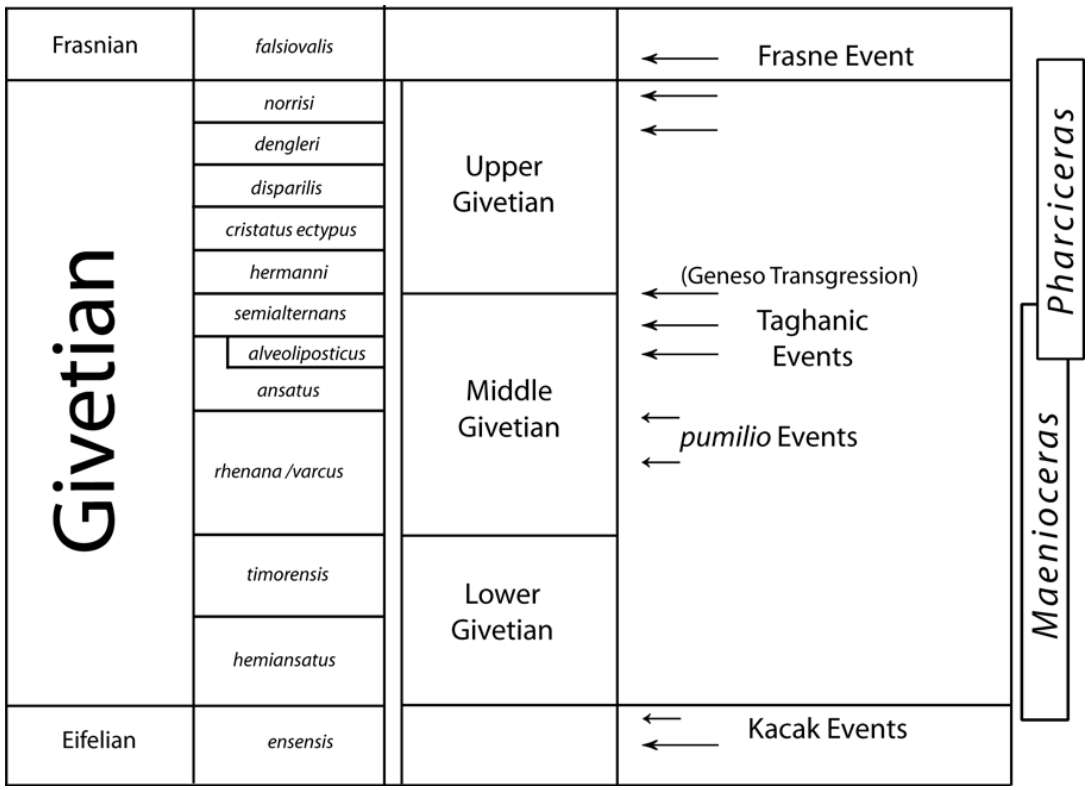


Figure 5 Stratigraphic table of the Givetian (after Becker, 2005).

The *Maenicoceras* and *Pharciceras* ammonoid Stufen divide the Givetian into two major units, but the stage will be subdivided into three substages, Lower (*hemiansatus* Zone to *timorensis* Zone), Middle (*rhenana* to *ansatus* Zone) and Upper (*semialternans* to *semialternans* Zone) Givetian (Bultynck and Gouwy, 2002; Becker, 2005) (Fig. 5).

For the Frasnian two different conodont zonations are available, the Montagne Noire zonation of Klapper (1989) and the so-called "standard zonation" of Sandberg and Ziegler (1996). Both conodont successions have been correlated by Klapper and Becker (1999) in the German Martenberg type-section of Ziegler and Sandberg (1990). The "standard zonation" is seriously affected by taxonomic difficulties and since the Montagne Noire zonation is more detailed and has been applied successfully on a global scale and in modern graphic correlation schemes (Klapper, 1997) preference should to be given to the MN zones (Fig. 6).

The Famennian zonation follows revisions summarized by Ziegler and Sandberg (1990), but some zones (*postera* Zone, Middle *praesulcata* Zone) are poorly recognizable (Becker, 1996; Kaiser, 2005) and revisions for the lower Famennian are available (Schülke, 1999).
The Famennian is divided into three *triangularis* Zones, four *crepida* Zones, two *rhomboidea* Zones, three *marginifera* Zones, two *trachytera* Zones, two *postera* Zones, three *expansa* Zones, and two *praesulcata* Zones. The top of the latter coincides with the Devonian/Carboniferous boundary.
The ammonoid zonation of the Middle and Upper Devonian is revised and discussed in Becker and House (2000). The Upper Devonian includes the traditional *Manticoceras* Stufe, which represents the Frasnian or Upper Devonian I, and the *Cheiloceras* (Upper Devonian II), *Prolobites* (Upper Devonian III), *Platyclymenia* (Upper Devonian IV), *Clymenia* (Upper Devonian V), and the *Wocklmeria* (Upper Devonian VI) Stufen in the Famennian. All these levels are subdivided in ammonoid genozones and regional zones named after species (Fig. 6).
Other organisms, such as corals, brachiopods, or crinoids, are mostly present in shallow-water facies. Bivalves and gastropods, due to their poor state of knowledge, have not shown their biostratigraphic potential yet.

The Givetian and Upper Devonian was a time of major biotic turnovers and extinctions, which are documented in drastic lithological and faunal changes. The biostratigraphic classification of this period is supported by event stratigraphic horizons, which can be used as correlation markers (Fig. 4). General reviews have been given, e.g., by Walliser (1985, 1996), House (1985, 2002) and Becker (1993b) and showed close relationships of extinction and radiation with rapid eustatic changes and sudden hypoxic events caused by shelf entrophications.

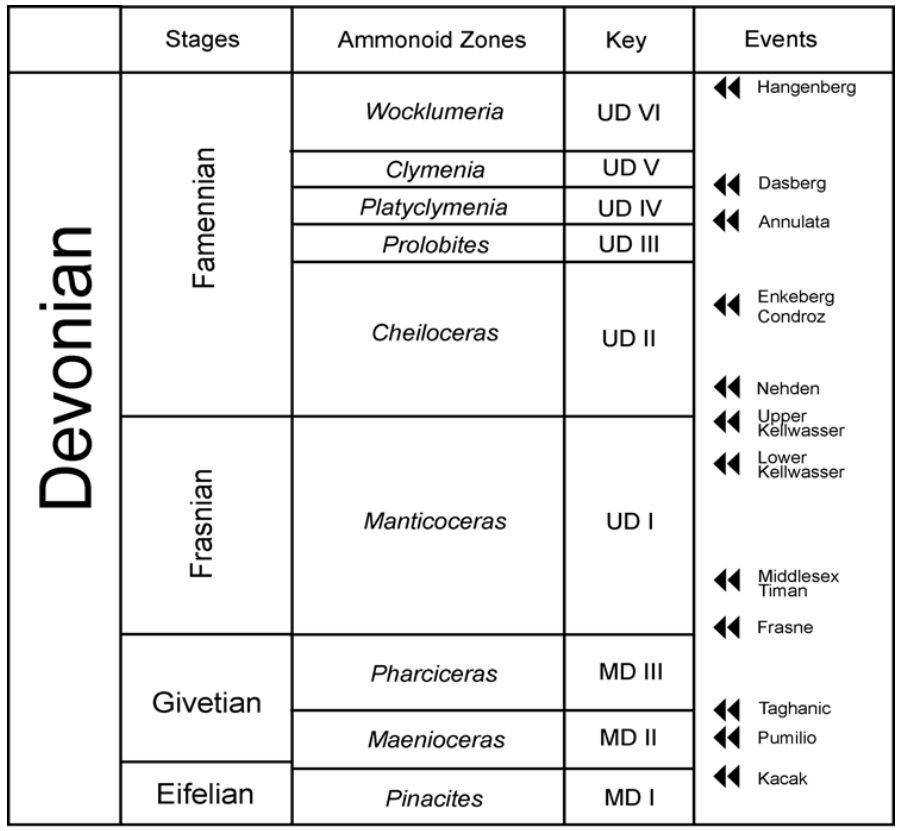


Figure 4 Stratigraphic distribution of Givetian and Upper Devonian Events correlated with ammonoid zones (after House et al. 2002).

Several major and minor event levels occur in the rock succession of the Givetian and Upper Devonian, including at the Eifelian/Givetian boundary the Kačák Event (Budil, 1995; House, 1996; Schöne, 1997), the Taghanic Event (Aboussalam, 2003), the *pumilio* Events (Lottmann, 1990), the Frasne Event (Ebert, 1993, Aboussalam and Becker, 2004; Lüning et al., 2004), the Timan Event (Becker and House 1997, House et al., 2000c), the Middlesex Event (Becker et al., 1993; House and Kirchgasser, 1993), the Kellwasser Events (e.g., Schindler 1990, 1993; Becker and House, 1994), the Nehden Event (Schülke and Popp, 2005), the Condroz Event (Becker, 1993a, 1993b), the Enkeberg Event (House, 1985; Becker, 1993a), the *Annulata* Event (Becker, 1992, Becker et al., 2004; Korn, 2002, 2004; Hartenfels and Becker 2005), the Dasberg Event (Becker, 1993b; Hartenfels and Becker 2005), and the Hangenberg Event (Caplan and Bustin, 1999; Becker, 1996; Kaiser, 2005) (Fig. 4).

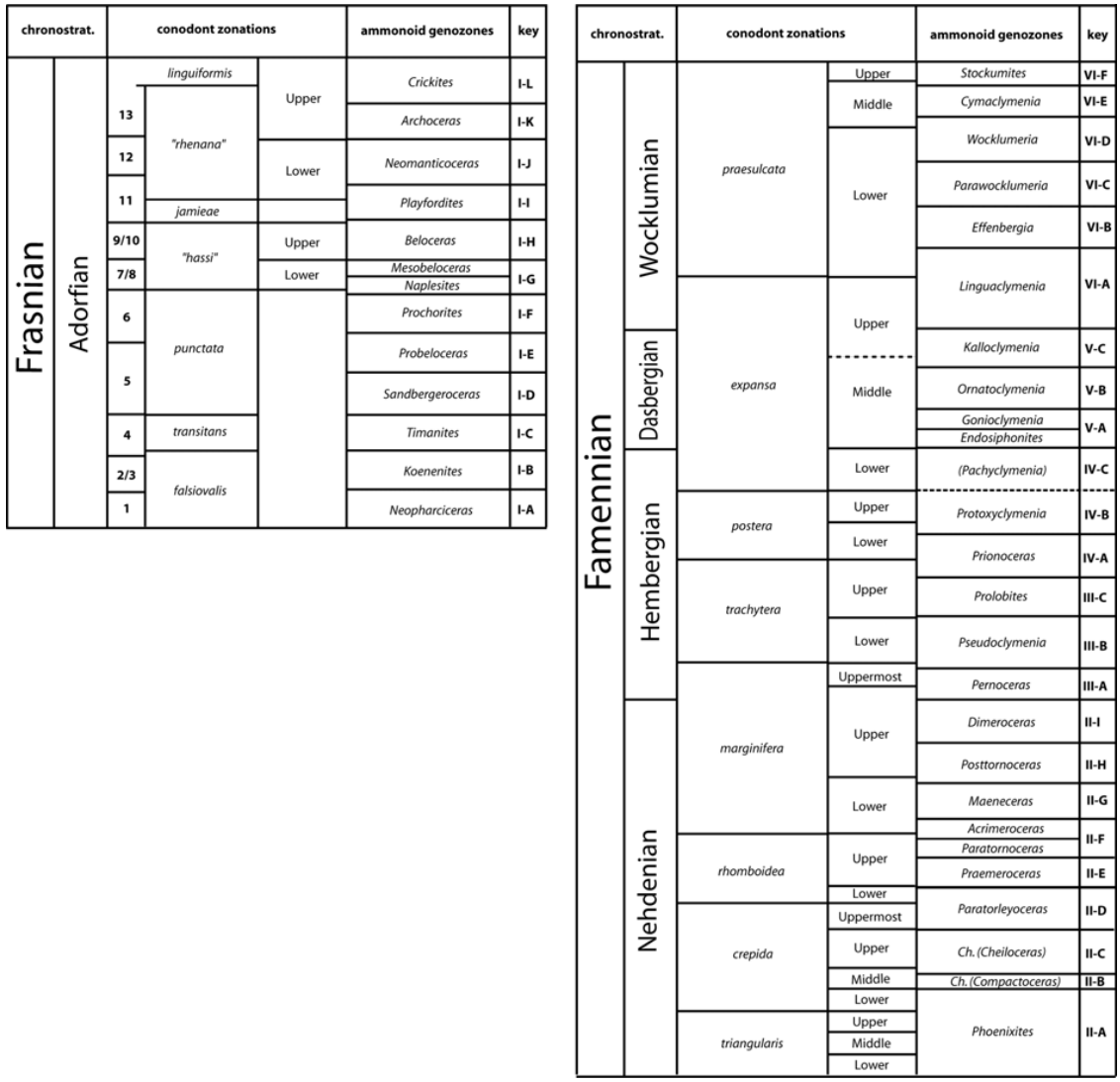


Figure 6 Stratigraphic table of the Upper Devonian (after Becker et al., 2004).

6 Localities

Upper Devonian bivalve taxa from Hercynian Facies appear in various localities representing outer shelf depositional environments. They have been reported from German outcrops of the Rhenish Massif (Fig. 2; e.g., Beushausen, 1895; Schmidt, 1922, 1924; Grüneberg, 1925), the Hercynian Mountains (e.g., Born, 1912), Saxony (Freyer, 1957), Thuringia (Meyer, 1920), and the Franconian Forest (e.g., Münster, 1840; Wurm, 1961). They also occur in contemporaneous faunas of the Holy Cross Mountains (Sobolew, 1911; Gunia, 1968), the Ural Mountains (Rozmann, 1962), and Kazakhstan (Sadykov, 1962). Furthermore, they are abundant in many Devonian outcrops of the Moroccon Meseta (Termier and Termier, 1951), southern Morocco (e.g., Becker et al., 2000), the Montagne Noire (e.g., Becker, 1993a; Kriz, 2005), and the Armorican Massif (Babin, 1966), and have been described from western New York State (e.g., Clarke, 1904) and from Montana (e.g., Raymond, 1909). Further outcrops of the Late Devonian pelagic facies, such as western Australia (Becker et al., 1991) and Iran (Becker et al., 2004), offer similar faunal assemblages, but, apart from *Buchiola*, bivalves from these areas are yet unnoticed.

In the following a brief overview of the main localities, which provided specimens of revised groups, is given. All references quoting the occurrence of bivalve taxa and important classical biostratigraphical studies dealing with these outcrops are listed. The beds containing bivalves are specified. Further appearing bivalve taxa are mostly unreviesed and, therefore, summarisied on a higher systematic level.

6.1 Germany

The northern and northeastern portion of the Rhenish Massif is abundant in classical Upper Devonian outcrops (Fig. 1). The Kellerwald is located in the east of the Rhenish Massif, and the Lahn-Dill Syncline attaches south of it, both providing further Upper Devonian localities.

Numerous studies and monographs on Rhenish localities and faunas have been published in the last 160 years (e.g., Wedekind, 1913; Schmidt, 1924; Lange, 1929; Becker, 1992; Devleeschouwer et al., 2002). An overview on the stratigraphic research history of the Rhenish Massif is given by Korn (2002). Becker (1993a) re-studied many of the classical Lower Famennian localities.

Bergisch Gladbach (Western Rhenish Massif, Paffrather Syncline)

Map sheet 5009 Overath

General literature: Jux, 1975; Jux, 1982; Hartkopf-Fröder et al., 2004.

Literature with bivalve references: Paeckelmann, 1913; Jux and Krath, 1974.

Beds: grey, silty mudstones and limestone nodules, with diverse pyritic fauna ("Knoppenbiessener Schichten").
Stratigraphy: Nehden-Stage (UD II-C/E).
Examined bivalve taxa: *Loxopteria dispar*, *Loxopteria problematica*, *Elasmatium gowandense*, *Elasmatium elongata*, *Deltacardium vetustum*, *Deltacardium duplicatum*, *Deltacardium clymeniae*.
Further bivalve taxa: *Mytilarca, Eutydesma*, *Leptodesma*, *Ptychopteria*, *Guerichia*, buchiolids, nuculoids.

Eskesberg (Northern Rhenish Massif)
Map sheet 4708 Wuppertal-Elberfeld

Literature with bivalve references: Paeckelmann, 1913; Grüneberg, 1925.

Beds: red to green entomozoid shales ("Cypridinenschiefer").
Stratigraphy: Nehden-Stage (UD II-D/E).
Examined bivalve taxa: *Loxopteria dispar*, *Elasmatium gowandense*, *Elasmatium elongata*, *Deltacardium vetustum*, *Deltacardium duplicatum*, *Deltacardium clymeniae*.
Further bivalve taxa: *Guerichia*, *Paracyclas*, *Myophoria*, *Cardiomorpha*, *Dolabra*,"praecardioids gen. et sp. indet", buchiolids, nuculoids.

Barmen (Northern Rhenish Massif)
Map sheet 4709 Wuppertal-Barmen

Literature with bivalve references: Paeckelmann, 1913; Paeckelmann, 1922; Grüneberg, 1925; Kaever et al., 1980.

Beds: red to green entomozoid shales ("Cypridinenschiefer").
Stratigraphy: Nehden-Stage (UD II-D/E).
Examined bivalve taxa: *Loxopteria dispar*, *Deltacardium duplicatum*.

Beds: brown, marly, shales ("Untere Matangne Schichten").
Stratigraphy: Adorf-Stage (UD I-J/K).
Examined bivalve taxa: *Chaenocardiola koeneni*.
Further bivalve taxa: *Ctenodonta*, *Opisthocoelus*, *Paracyclas*, *Pterochaenia*, *Paraptyx*, buchiolids, nuculoids.

Reitenberg (Northern Rhenish Massif)
Map sheet 4611 Hagen-Hohenlimburg

General literature: Denckmann, 1901c; Kamp, 1972; Korn, 2004.
Literature with bivalve references: Becker, 1992.

Beds: red, nodular shales with entomozoids, fossils preserved as nodules
Stratigraphy: Hemberg-Stage (UD III-C).
Examined bivalve taxa: *Loxopteria* sp. (due to the resolved shell).
Further bivalve taxa: *Guerichia*.

Beds: dark grey, greenish-grey or brown weathering black, calcareous, laminated mudstone ("*Annulata*-Schiefer").
Stratigraphy: Hemberg-Stage (UD IV-A).
Examined bivalve taxa: *Loxopteria gibbosa*, *Loxopteria inflata.*
Further bivalve taxa: *Pterinea*, *Guerichia*, ?*Paleolima*, buchiolids.

Beul (Northern Rhenish Massif)
Map sheet 4613 Balve

General literature: Denckmann, 1901b; Paeckelmann, 1938; Becker, 1993a.
Literature with bivalve references: Denckmann, 1901a; Schindewolf, 1923; Paeckelmann, 1924, 1936a; Lange, 1929; Kaever et al., 1980.

Beds: red, grey nodular or thin bedded limestones ("Adorfer Kalk").
Stratigraphy: Adorf-Stage (UD I).
Examined bivalve taxa: *Ontaria concentrica.*
Further bivalve taxa: buchiolids.

Beds: grey, platy limestones with lenticular, black limestone and dark marly shales.
Stratigraphy: Adorf-Stage, Upper Kellwasser Beds (UD I-L).
Examined bivalve taxa: *Ontaria concentrica.*
Further bivalve taxa: buchiolids.

Beds: grey, grey-reddish, sometimes marly limestones ("Cephalopoden Kalke").
Stratigraphy: Nehden-Stage (UD-II).
Examined bivalve taxa: *Ontaria suborbicularis*, *Loxopteria dispar*, *Loxopteria gibbosa*, *Elasmatium gowandense*, *Elasmatium elongata*.

Further bivalve taxa: buchiolids, nuculoids.

Beds: grey-reddish or red, platy or nodular limestones.
Stratigraphy: lower Hemberg-Stage (UD-III).
Examined bivalve taxa: *Loxopteria dispar*, *Loxopteria gibbosa*, *Loxopteria problematica*, *Loxopteria inflata*, *Elasmatium gowandense*, *Elasmatium elongata*.
Further bivalve taxa: *Guerichia*, buchiolids.

Beds: grey-blue, platy limestones with some nodular layers.
Stratigraphy: upper Hemberg-Stage, *annulata*-zone (UD IV-A).
Examined bivalve taxa: *Loxopteria dispar*, *Loxopteria gibbosa*, *Loxopteria problematica*, *Loxopteria inflata*, *Chaenocardiola tetragonum*.
Further bivalve taxa: *Guerichia*, *Opisthocoelus*, *Cardiomorpha*, buchiolids.

Dasberg (Northern Rhenish Massif)
Map sheet 4613 Balve

General literature: Denckmann, 1901; Lange, 1929; Paeckelmann, 1938; Schäfer, 1976; Korn and Luppold, 1987.
Literature with bivalve references: Schmidt, 1924; Paeckelmann, 1924; Kaever et al., 1980.

Beds: grey to red, platy to nodular limestones.
Stratigraphy: upper Hemberg-Stage (UD IV).
Examined bivalve taxa: *Ontaria concentrica*, *Loxopteria gibbosa*, *Loxopteria problematica*, *Elasmatium gowandense*.
Further bivalve taxa: buchiolids, nuculoids.

Wettmarsen (Northern Rhenish Massif)
Map sheet 4613 Balve

Literature with bivalve references: Paeckelmann, 1924; Paeckelmann, 1938.

Beds: red, entomozoid shales with limestone nodules.
Stratigraphic unit: lower Hemberg-Stage (UD III).
Examined bivalve taxa: *Ontaria concentrica*, *Loxopteria gibbosa*, *Loxopteria problematica*, *Loxopteria inflata*, *Elasmatium elongata*.
Further bivalve taxa: *Guerichia*.

Nehden-Schurbusch (Northeastern Rhenish Massif)
Map sheet 2659 Brilon

General literature: Sandberger and Sandberger, 1856; Denckmann, 1896; Frech, 1887, 1902; Wedekind, 1908, 1911; Paeckelmann, 1926; Schindewolf, 1937; Becker, 1984.
Literature with bivalve references: Schülke, 1867; Beushausen, 1895; Drevermann, 1901; Grüneberg, 1925; Lange, 1929; Matern, 1931; Paeckelmann and Kühne, 1936a; Jux and Krath, 1974; Kaever et al., 1980; Becker, 1993a.

Beds: black to grey, laminated, silty, foliated mudstones or shales, with abundant pyritic (secondary goethitic) fauna (Nehden Goniatite Shale).
Stratigraphy: Nehden-Stage (UD II-C/E).
Examined bivalve taxa: *Loxopteria dispar*, *Elasmatium gowandense*, *Elasmatium elongata*, *Deltacardium vetustum*, *Deltacardium duplicatum*, *Deltacardium clymeniae*.
Further bivalve taxa: *Myalina*, *Guerichia*, buchiolids, nuculoids, rare pectinids, other poorly preserved bivalves.

Enkeberg (Northeastern Rhenish Massif)
Map sheet 4518 Madfeld

General literature: Denckmann, 1896; Wedekind 1908, 1911; Matern, 1931; Korn and Ziegler, 2002; Korn, 2004.
Literature with bivalve references: Schülke, 1867; Kayser, 1873; Holzapfel, 1895; Drevermann, 1901; Schmidt, 1924; Lange, 1929; Paeckelmann and Kühne, 1936b; Kaever et al., 1980; Becker, 1993a.

Beds: grey, platy to massive limestones with Manticoceras-Fauna.
Stratigraphy: Adorf-Stage (UD I-J/K).
Examined bivalve taxa: *Ontaria concentrica*.
Further bivalve taxa: buchiolids.

Beds: grey, red, greenish, sometimes dolomitic, nodular, platy to massive cephalopod limestones ("Clymenien Kalk").
Stratigraphy: Nehden-Stage to lower Hemberg-Stage (UD II/III).
Examined bivalve taxa: *Loxopteria problematica*, *Loxopteria dispar*, *Loxopteria gibbosa*, *Loxopteria inflata*, *Elasmatium elongata*, *Elasmatium gowandense*, *Deltacardium vetustum*, *Deltacardium duplicatum*, *Deltacardium clymeniae*.

Further bivalve taxa: "*Myalina*", *Guerichia*, *Paracyclas*, "praecardioids gen. et sp. indet", buchiolids, nuculoids.

Beds: base: brown, yellow sandy limestones; top: purple to greyblue limestones.
Stratigraphy: upper Hemberg-Stage, *Platyclymenia annulata*-Zone (UD IV).
Examined bivalve taxa: base: *Elasmatium elongata*; top: *Loxopteria dispar.*
Further bivalve taxa: *Guerichia*.

Martenberg (Northeastern Rhenish Massif)
Map sheet 4618 Adorf

General literature: Denckmann, 1896; Wedekind, 1913; House and Ziegler, 1977; Ziegler and Sandberg, 1990; Klapper and Becker, 1999; Aboussalam, 2003.
Literature with bivalve references: Holzapfel, 1882; Holzapfel, 1895; Bottke, 1965; Paeckelmann, 1979.

Beds: red, massive limestones or red iron stones.
Stratigraphy: Givetian (MD II/III).
Examined bivalve taxa: *Ontaria concentrica.*
Further bivalve taxa: buchiolids.

Beds: light grey or reddish (secondarily haematized), platy, partly nodulare limestones, partly dolomitized ("Adorfer Kalk").
Stratigraphy: Adorf-Stage (UD I).
Examined bivalve taxa: *Ontaria suborbicularis*, *Ontaria concentrica*, *Prosochasma pyriforme*, *Prosochasma muelleri*, *Prosochasma mytiloides*, *Prosochasma bickense*, *Chaenocardiola conalifer*, *Chaenocardiola koeneni*.
Further bivalve taxa: *Myalina*, *Guerichia*, *Pterinea*, *Cardiomorpha* sp., buchiolids.

Beds: dark, marly shales or grey-black shamarlsles with pyrite (Kellwasser Beds).
Stratigraphy: upper Adorf-Stage (UD I-K/L).
Examined bivalve taxa: *Deltacardium vetustum*, *Lunulacardium semistriatum*, *Prosochasma pyriforme*, *Prosochasma bickense*, *Chaenocardiola koeneni*.
Further bivalve taxa: buchiolids.

Beds: greenish or dark grey, calacreous shales, with layers of grey nodulare limstones
Stratigraphy: lower Nehden-Stage (UD II-A/B).

Examined bivalve taxa: *Loxopteria dispar*, *Chaenocardiola koeneni*, *Ontaria concentrica*.
Further bivalve taxa: buchiolids.

Wildungen/ Ense (Kellerwald, Southeastern Rhenish Massif)
Map sheet 4820 Bad Wildungen

General literature: Denckmann, 1902; Pusch, 1935; Schneider, 1969, Lotmann, 1990; Schöne, 1997.
Literature with bivalve references: Denckmann, 1893; Denckmann, 1896; Denckmann, 1901c.

Beds: black, organogene limestones ("Odershäuser Kalk").
Stratigraphy: upper Eifelian to basalmost Givetian MD I-F/II-A.
Examined bivalve taxa: *Ontaria concentrica*, *Chaenocardiola tetragonum*, *Chaenocardiola carinata*, *Chaenocardiola koeneni*, *Chaenocardiola denckmanni*.

Beds: grey to reddish, thin-bedded, sometimes nodular limestones ("Adorfer Kalk").
Stratigraphy: Adorf-Stage (UD I).
Examined bivalve taxa: *Lunulacardium semistriatum*, *Prosochasma bickense*, *Chaenocardiola koeneni*, *Ontaria suborbicularis*, *Prosochasma bickense*.
Further bivalve taxa: buchiolids.

Beds: reddish or grey, platy cephalopod limestones ("Clymenien Kalk").
Stratigraphy: Nehden-Stage (UD II).
Examined bivalve taxa: *Loxopteria gibbosa*, *Loxopteria dispar*, *Loxopteria inflata*.
Further bivalve taxa: buchiolids, nuculoids, other poorly preserved bivalves.

Langenaubach (Lahn Dill Syncline)
Map sheet 5215 Dillenburg

General literature: Drevermann, 1901; Schindewolf, 1921; Becker, 1993a.
Literature with bivalve references: Denckmann, 1896; Denckmann, 1901; Drevermann, 1905.

Beds: Volcanoclastic breccia with mixed Famennian goniatite fauna.
Stratigraphy: lower and middle Famennian (UD II-VI).

Examined bivalve taxa: *Loxopteria inflata*, *Loxopteria dispar*, *Elasmatium gowandense*, *Elasmatium elongata*, *Prosochasma muelleri*.
Further bivalve taxa: buchiolids.

Weilburg, Kirchhofen (Lahn Dill Syncline)
Map sheet 5515 Weilburg

General literature: Schindewolf, 1921; Ahlburg, 1918.
Literature with bivalve references: Kegel, 1922.

Beds: red to green entomozoid shales with limestones nodules.
Stratigraphy: Nehden-Stage (UD II).
Examined bivalve taxa: *Loxopteria gibbosa*, *Loxopteria inflata*.

Grube Joseph at Graeveneck (Lahn Dill Syncline)
Map sheet 5515 Weilburg

General literature: Ahlburg, 1918; Becker, 1993a.

Beds: red to green entomozoid shales with limestones nodules.
Stratigraphy: Nehden-Stage (UD II).
Examined bivalve taxa: *Loxopteria gibbosa*, *Loxopteria dispar*.

Oberscheld (Lahn Dill Syncline)
Map sheet 5216 Oberscheld

General literature: Beyrich, 1837; Kayser, 1907; Ziegler, 1958; Buggisch et al., 1978; Schindler, 1990; Becker, 1993a; Schindler et al., 1998.
Literature with bivalve references: Sandberger and Sandberger, 1856; Kegel, 1922; Matern, 1931; Kaever et al., 1980.

Beds: Red ironstones and deep red cephalopod limestones ("Adorfer Kalk").
Stratigraphy: upper Adorf-Stage (UD I-J/L).
Examined bivalve taxa: *Lunulacardium semistriatum*, *Prosochasma muelleri*, *Prosochasma mytiloides*, *Prosochasma bickense*, *Chaenocardiola koeneni*, *Ontaria suborbicularis*.

Further bivalve taxa: *Opisthocoelus*, *Euthydesma*, *Guerichia*, *Myalina*, buchiolids, "praecarioids sp. et gen. indet".

Beds: grey, partly reddish, platy limestone.
Stratigraphy: upper Adorf-Stage; lower and upper Kellwasser beds (UD I-K/L).
Examined bivalve taxa: *Prosochasma muelleri*, *Prosochasma mytiloides*, *Prosochasma bickense*, *Lunulacardium semistriatum*, *Ontaria suborbicularis*.
Further bivalve taxa: *Opisthocoelus*, *Euthydesma*, *Guerichia*, *Myalina*, buchiolids, "praecarioids sp. et gen. indet".

Beds: Red to green entomozoid shales ("Cypridinenschiefer").
Stratigraphy: Nehden-Stage (UD II).
Examined bivalve taxa: *Loxopteria dispar*.
Further bivalve taxa: *Opisthocoelus*, *Euthydesma*, *Guerichia*, *Myalina*, buchiolids, "praecarioids sp. et gen. indet".

Beds: Red to green cephalopod limestones ("Clymenien Kalk" or "Goniatiten Kalk").
Stratigraphy: Nehden-Stage to Hemberg-Stage (UD II/IV).
Examined bivalve taxa: *Loxopteria problematica*, *Elasmatium gowandense*, *Elasmatium elongata*, *Deltacardium vetustum*, *Prosochasma bickense*, *Prosochasma muelleri*, *Ontaria concentrica*, *Chaenocardiola koeneni*.
Further bivalve taxa: *Opisthocoelus*, *Euthydesma*, *Guerichia*, *Myalina*, buchiolids, "praecarioids sp. et gen. indet".

Schübelhammer (Franconian Forest, Southeastern Germany)
Map sheet 5734 Wallenfels

General literature: Gandl, 1981, 1998; Hartenfels, 2003; Hartenfels and Tragelehn, 2001.
Literature with bivalve references: Münster 1840; Gümbel, 1879; Schindewolf, 1923; Wurm, 1961.

Beds: grey, reddish platy cephalopod limestones ("Clymenien Kalk").
Stratigraphy: Nehden-Stage to Hemberg-Stage (UD II/IV).
Examined bivalve taxa: *Loxopteria gibbosa*, *Loxopteria inflata*, *Lunulacardium excrescens*, *Prosochasma pyriforme*, *Prosochasma muelleri*, *Chaenocardiola tetragonum*, *Chaenocardiola conalifer*, *Chaenocardiola carinata*.

Further bivalve taxa: *Guerichia*, *Modioptera*, *Actinoptera*, "mytiloids gen. et sp. indet", "praecardioids gen, et sp. indet", buchiolids.

Geuser (Franconian Forest, Southeastern Germany)
Map sheet 5734 Wallenfels

General literature: Gandl, 1981, 1998; Hartenfels, 2003; Hartenfels and Tragelehn, 2001.
Literature with bivalve references: Münster 1840; Gümbel, 1879; Schindewolf, 1923.

Beds: grey, reddish platy cephalopod limestones ("Clymenien Kalk").
Stratigraphy: Nehden-Stage to Hemberg-Stage (UD II/IV).
Examined bivalve taxa: *Loxopteria gibbosa*, *Loxopteria problematica*, *Elasmatium elongata*, *Chaenocardiola tetragonum*.
Further bivalve taxa: *Pompeckjina*, *Guerichia*, *Enkebergia*, *Myalina*, *Modioptera*, *Actinoptera*, "mytiloids gen. et sp. indet", "praecardioids gen, et sp. indet",buchiolids.

Aeketal (Hercynian Mountains, Central Germany)
Map sheet Clausthal-Zellerfeld 4128

General literature: Beushausen and Denckmann, 1894; Fuhrmann, 1955; Schindler, 1990.
Literature with bivalve references: Beushausen, 1900; Born, 1912.

Beds: Red to green cephalopod limestones ("Clymenien Kalk").
Stratigraphy: Nehden-Stage to Hemberg-Stage (UD II/IV).
Examined bivalve taxa: *Loxopteria dispar*, *Loxopteria gibbosa*, *Deltacardium vetustum*.
Further bivalve taxa: *Myalina*, *Guerichia*, *Euthydesma*, *Aviculopecten*, buchiolids, "praecardioids sp. et gen. indet".

Beds: grey-blue cephalopod limestones ("Kramenzelkalk").
Stratigraphy: Hemberg-Stage (UD III-C).
Examined bivalve taxa: *Loxopteria dispar*, *Loxopteria gibbosa*, *Loxopteria problematica*, *Elasmatium elongata*.
Further bivalve taxa: *Myalina*, *Guerichia*.

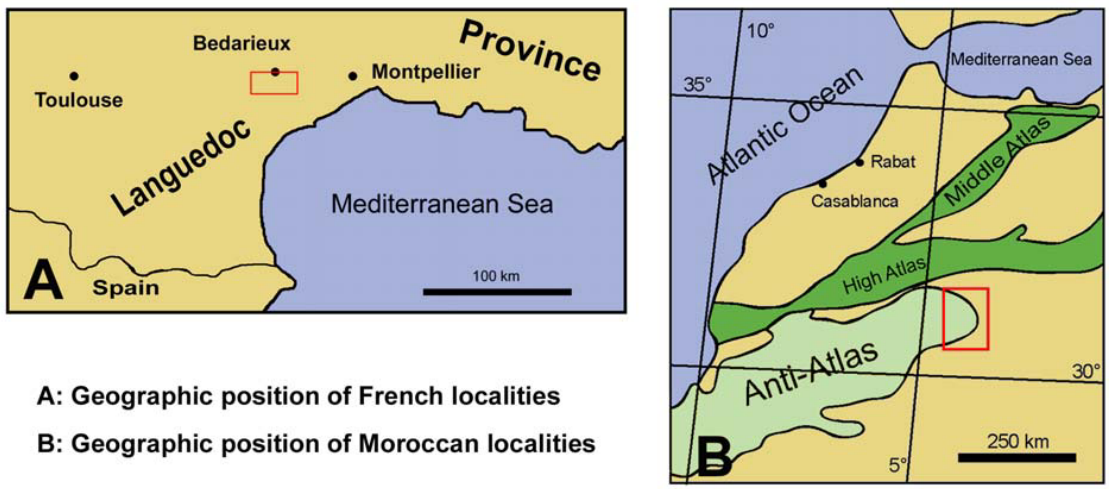
6.2 France

Outcrops from the Montagne Noire (southern France) provide sediments that represent a slightly different depositional regime than observed in the Hercynian Facies of the Rhenish Massif. These rocks are a transitional facies between the pelagic sediments of the Rhenish Massif and the parahemipelagic realm of Morocco (see below). They are supposed to be deposited on a deep carbonate platform or ramp with a comparatively low paleo-relief (Schindler, 1990; Schülke, 1999). The Montagne Noire, which is located at the southern margin of the Massif Central, is composed of southbound transported nappes (Feist, 1985) and olistolites. Due to its complex tectonical situation, its paleogeographic position is still ambiguous (Young, 1987). Generally, a position close to Northwestern Gondwana is assumed (Scotese, 1986).

The Upper Devonian outcrops of the Montagne Noire (southern France) have been studied for a long time. Frech (1887) was one of the first to investigate the "Klippen" of Cabriéres.

The Montange Noire includes the GSSP sections for the Middle/Upper Devonian boundary (Col de Puech de la Suque, Klapper, 1987), for the Frasnian/Famennian booundary (Klapper et al., 1994), and for the Devonian/Carboniferous boundary (Paproth et al., 1991).

Further studies of this area have been compiled by, e.g., Schindler (1990), Becker (1993a), and Becker and House (1994).



A: Geographic position of French localities

B: Geographic position of Moroccan localities

Figure 7 French (Montagne Noir) and Moroccan (Tafilalt and Maider) regions with Upper Devonian bivalve faunas studied herein.

Côl de Puèche de la Suque (Montagne Noire, Armorican Massif)

General literature: House et al., 1985; Klapper, 1989; Feist et al., 1986; House, et al., 2000a.
Literature with bivalve references: Becker, 1993a.

Beds: yellowish grey weathering, calcareous, nodular shales, with haematitic faunas. (base of the "Griotte Kalke").
Stratigraphy: lower Nehden-Stage (UD II-A/B).
Examined bivalve taxa: *Lunulacardium semistriatum*, *Deltacardium vetustum*.
Further bivalve taxa: *Leptodesma*, buchiolids, other poorly preserved bivalves.

Mentaresses (Montagne Noire)

General literature: Feist, 1985; House et al., 1985.
Literature with bivalve references: Becker, 1993a; Kriz, 2005.

Beds: dark grey, partly argillaceous mudstones, with limestone nodules.
Stratigraphy: lower Nehden-Stage (UD II-B/E).
Examined bivalve taxa: *Chaenocardiola tetragonum*, *Deltacardium vetustum*, *Deltacardium duplicatum*, *Ontaria concentrica*.
Further bivalve taxa: *Guerichia*, *Karkulum*, *Leptodesma*, *Cheioptera*, buchiolids.

La Serre (Montagne Noire, Armorican Massif)

General literature: Schindler, 1990; Lethiers et al., 1998; Girard and Feist, 1997; Tribovillard et al., 2004.
Literature with bivalve references: Becker, 1993a; Becker and House, 1994; Kriz, 2005.

Beds: dark grey to black, pyrite rich mudstones, with single, marly limestones layers or fossiliferous, black limestone nodules (Upper Kellwasser beds).
Stratigraphy: upper Adorf-Stage (UD I-L).
Examined bivalve taxa: *Chaenocardiola koeneni*.
Further bivalve taxa: *Leptodesma*, *Cabricardium*, buchiolids.

Beds: Haematite rich, dark grey shales, and marly limestones.

Stratigraphy: Nehden-Stage (UD II-A).
Examined bivalve taxa: *Deltacardium duplicatum*, *Chaenocardiola koeneni*.
Further bivalve taxa: *Guerichia*, *Leptodesma*, *Cabricardium*, buchiolids, other poorly preserved, and juvenile bivalves.

Combe de Izarne (Montagne Noire)

General literature: De Rouville, 1868; Schindewolf, 1921; Wendt and Aigner, 1985.
Literature with bivalve references: Frech, 1887; Becker, 1993a; Kriz, 2005.

Beds: light to dark grey, massive limestones.
Stratigraphy: Adorf-Stage (UD I).
Examined bivalve taxa: *Chaenocardiola koeneni*, *Prosochasma bickense*.
Further bivalve taxa: *Leptodema*, buchiolids.

Beds: black, argillaceous limestones (Upper Kellwasser beds).
Stratigraphy: Adorf-Stage (UD I-L).
Examined bivalve taxa: *Deltacardium duplicatum*.
Further bivalve taxa: *Cabricardium*, *Disarnella*, *Karkulum*, *Leptodesma*, *Cheioptera*, buchiolids.

Beds: dark, grey limestone nodules, dark mudstones.
Stratigraphy: lower Nehden-Stage (UD II-A/B).
Examined bivalve taxa: *Deltacardium vetustum*.
Further bivalve taxa: *Guerichia*, *Karkulum*, *Leptodesma*, *Cheioptera*, *Cabricardium*, buchiolids, nuculoids.

6.3 Morocco

The Moroccan localities included in this study were situated on the northwestern margin of Gondwana and belong to the eastern Anti-Atlas (Gnoli, 2003; Becker et al 2002). Towards the end of the Middle Devonian, in relation with the emerging early Variscan orogeny, a basin and platforms developed by block faults (Wendt and Aigner, 1985). The Tafilalt Platform and the Maider Basin provide various localities, which provided examined material. On the platform the pelagic facies is characterized by reduced sedimentation rates. Condensed cephalopod limestones are the predominant rocks (e.g., Wendt and Aigner 1985; Bensaid et al., 1985;

Becker, 1993a). The Maider Basin is characterised by dysoxic, thicker shales with pyritic faunas.
The first comprehensive monograph on the Moroccan Devonian fauna was compiled by Termier and Termier (1950). Recently, the stratigraphic potential of the little altered or folded rocks from Morocco, and the exceptionally well preservation faunas led to numerous publications on pelagic assemblages (e.g., Korn, 1999; Becker et al., 2000; Becker and House, 2000; Becker et al., 2002)

Mrakib (Southern Maider, Morocco)

General literature: Korn, 1999; Becker et al., 2002, 2004.
Literature with bivalve references: Becker et al., 2000; Webster et al., 2005.

Beds:

- green shales and limestones (bed D, Becker et al., 2000).
- fossiliferous shale with red rubbly limestone at top (bed E_1, Becker et al. 2000).

Stratigraphy: lower Hemberg-Stage (UD III-A/B).
Examined bivalve taxa: *Loxopteria problematica*, *Loxopteria meioklina*.
Further bivalve taxa: *Myalina*, *Guerichia*, buchiolids, nuculoids.

Beds:

- green shale with thin red nodular limestone at top (beds H_2/H_3, Becker et al., 2000).
- green shale with limestone at top (top of bed I, Becker et al., 2000).

Stratigraphic unit: lower Hemberg-Stage (UD III-C).
Examined bivalve taxa: *Loxopteria problematica*, *Loxopteria gibbosa*.
Further bivalve taxa: *Leptodesma*, buchiolids.

Beds:

- alternation of three marly units and three limestone nodule beds, with haematitic fauna (bed N_2, Becker et al., 2000).

Stratigraphy: upper Hemberg-Stage (UD IV-A).
Examined bivalve taxa: *Loxopteria problematica*.
Further bivalve taxa: *Guerichia*, other poorly preserved bivalves.

Rich Bou Kourazia (Southern Maider, Morocco)

General literature: Becker et al., 2002; Becker et al., 2004; Webster et al., 2005.

Beds: green shales and subordinate marls with limestone nodules, and pyritic (secondary goethitic) fauna.
Stratigraphy: Hemberg-Stage (UD III/IV).
Examined bivalve taxa: *Loxopteria gibbosa*.

Jebel Amelane (Western Tafilalt, Southern Morocco)

General literature: Becker, 1993a; Becker and House 1994; Becker and House, 2000; Becker et al., 2002.
Literature with bivalve references: Becker, 1993a.

Beds: at the base black limestones, subsequent more argillaceous, dark grey, nodular limestones.
Stratigraphy: Nehden-Stage (UD II-D).
Examined bivalve taxa: *Loxopteria dispar*.
Further bivalve taxa: *Guerichia*, buchiolids, bivalve shell beds.

Bou Tchrafine (Central Tafilalt, Morocco)

General literature: Buggisch and Clausen, 1972; Bensaid et al, 1985; Becker and House, 2000; Becker et al., 2002.
Literature with bivalve references: Becker, 1993a.

Beds: green shale with red nodulare limestones, haematitic fauna.
Stratigraphy: Nehden-Stage (UD II-B/D).
Examined bivalve taxa: *Ontaria concentrica*, *Deltacardium vetustum*.
Further bivalve taxa: *Guerichia*, buchiolids.

6.4 North America

The specimens from North America, especially from the Upper Devonian of the Three Forks Shale, Montana, and from the Gowanda Shale of Northwestern New York State, reveal a striking similarity with the Central European taxa. The incorporated material is mostly original types of species and genera. Additional unpublished material from Montana was made available from the collection of R.T. Becker, in order to complete an overview of the spatial distribution as far as possible.

Due to the much discussed situation of Upper Devonian paleogeography (e.g., Robardet, 2003) questions such as, e.g., the migration paths of European faunas, are far from being understood. But the striking similarities between the North American and the European bivalve fauna described by Bailey (1978) from the Middle Devonian and observed herein for the Upper Devonian confirm the close relation between both.

The western Appalachian region was located on the south-western margin of the Old Red Continent (Fig. 1). An epicontinental sea covered this region, which was the depositional environment for pelagic shales and marls (Smith and Jacobi, 2003). Due to the Acadian orogeny in the east during the Upper Devonian, the epicontinental sea became a foreland basin, which was progressively filled with terrigenous deposits and the coastline prograded westwards (Baird and Lash, 1990).

Walnut Creek, Forestville, Correll´s point, Portage
(Chautauqua province, New York State)

General literature: Chadwick, 1935a, 1935b; Rickard, 1975; Smith and Jacobi, 2003.
Literature with bivalve references: Hall, 1843, 1885; Clarke, 1904; Baird and Lash, 1990.

Beds: green, grey, sitly, laminated mudstone (Gowanda Shale or "Naples Beds"), with pyritic fauna.
Stratigraphy: Nehden-Stage (UD II-C).
Examined bivalve taxa: *Deltacardium melletes*, *Deltacardium vetustum*, *Loxopteria dispar*, *Loxopteria inflata*, *Elasmatium gowandense*, *Elasmatium elongata*.
Further bivalve taxa: *Pterinopecten*, *Pterinea*, *Actinoptera*, *Leptodesma*, *Pterochaenia*, *Paraptyx*, *Schizodus*, *Honeoyea*, buchiolids, nuculoids.

Three Fork Shale (Montana)

General literature: House, 1962.
Literature with bivalve references: Raymond, 1907, 1909.

Beds: dark grey shales with haematitic fauna (Three Forks Member of the Trident Formation).
Stratigraphy: upper Hemberg-Stage (UD IV-A).
Examined bivalve taxa: *Loxopteria dispar*, *Loxopteria gibbosa*, *Loxopteria problematica*.
Further bivalve taxa: *Actinoptera*, *Paracyclas*, *Mytilarca*, *Guerichia*, pectinids, nuculids, "modiomorphoids gen. et sp. indet".

7 Systematics

The taxonomy of the Bivalvia has always been a matter of controversy (e.g., Boss, 1978, Amler, 1999). One of the general problems in the systematics of Paleozoic bivalves are genus and species names that were proposed in studies of local faunas, usually within single geologic systems. This created for the rather slowly evolving bivalves a vast amount of synonyms throughout their stratigraphic range. McAlester (1962a) observed this phenomenon in his study of the Upper Devonian Chemung fauna of New York State and not much has changed since. It is unlikely that bivalves survived without evolutionary changes through the complex sequences of global extinction events and ecological crises, which affected other contemperouos benthic groups. First indications of a connection between extinction events and the stratigraphic distribution of the bivalve taxa are discussed in Chapter 8.

Silurian taxa have also been re-studied herein. It is important to mention that this provides just a small part of the Silurian bivalve fauna, and is not the main focus of this study. Unfortunately, due to the outdated state of knowledge of the Silurian and lower Devonian bivalve faunas, there is no data bases that allows an interpretation of their evolutionary development.

The following systematics treats the taxonomic groups individually. Their state of preservation is rather ariable, and the specific characters of their bauplan such as e.g., the hinge development or the orientation of the valves have to be considered. Therefore, four main groups are discussed in the following, loxopteriids, praecardiids, lunulacardiids, and ontariids.

As mentioned above, are the systematic categories of these taxa currently rather confused and lack well defined type species and type genera. Therefore, the classification in higher categories within the Cryptodonta of the here revised genera is of a tentative nature and follows Amler (1999, p. 246). This subclass was abandonded for a long time and was re-activated by Johnston and Collom (1998), and Amler (1999) presented it as an alternative classification. Although its relationships and its position within a higher bivalve classification is partly uncertain, it is adequate for including the herein re-studied taxa.

Abbreviations:

+	new taxon
*	original description
e.p.	ex pate, partial
v	vide, specimens of this reference have been re-studied
non	does not belong to this taxon
nom. dub.	nomen dubium
nom. nud.	nomen nudum
SD	subsequent designation
OD	original designation
LV	left valve
RV	right valve
RM	Rhenish Massif
NYSM	New York State Museum, Albany
AMNH	American Museum of Natural History, New York
MB.M	Museum für Naturkunde, Berlin
NMP	National Museum, Praha
GZG	Geowissenschaftliches Zentrum der Universität Göttingen
BSPG	Bayerische Staatssammlung, München
NWS	Landesmuseum Wiesbaden
SMF	Senckenberg Museum, Frankfurt
GIK	Geologisches Institut Köln
B6A-35.	identifies specimens, which are located collection in the Westfälische-Wilhelms-Universität Münster.

7.1 Loxopteriids

Morphology of Loxopteria Frech, 1881

The shell morphology of the Loxopteriinae is quite peculiar. Especially the development of left and right valves, which do not resemble each other at first sight, created a lot of confusion. Authors tried to correlate the valves and, type series often include more than one taxon because the bauplan of articulated specimens was not known. The development of the right valve in relation to the left valve was always the reason for misinterpretations. The shell morphology of *Loxopteria* Frech is described in detail separately, because the species included in this genus differ, as in other bivalve taxa (e.g. Pecten), mostly in their ornamentation while the characters of their bauplan are more or less alike. This is shown in Fig. 10, which illustrates the lack of markedly differences in the morphological range of variation between the species. In the following the valves are orientated with the ventral commissure line horizontal, forming the sagittal plane (Fig. 7). The left valve (LV) and the right valve (RV) are described individually and measured values refer to the left valves of the specimens.
The following characters indicate a loxopteriid shell morphology.

The subtrigonal LV is highly convex. It inclines posteriorly, developing the highest inflation in the posterior half of the valve. The posterior third of the shell is bent downwards with an angle wider than 90° from the sagittal plane. This deflection generates a roundly arched edge, which runs from the umbo to the ventral margin. The posterior portion of the valve is slightly concave and develops a smooth ridge running from the umbo towards the posterior margin.
The umbo is incurved, projecting distinctly above the hinge line and is situated slightly posterior of the centre of the valve.
The RV is transversely oval in outline, lid-shaped and slightly convex. It slightly inclines anteriorly, developing the highest inflation in the anterior half of the valve. The posterior third of the shell is bent upwards, corresponding to the LV. The small umbo is slightly to distinctly situated anterior of the centre of the valve, somewhat above the hinge line and barely incurved. The antero-dorsal margin of the valve is elevated from the actual comissure by a fringe. This delays the umbo slightly back towards the centre of the valve.
Loxopteria Frech appears not bilateral symmetrical in proportions. Its beaks are antigyrate developed and point in contrary directions. Furthermore, the point of maximum convexity of the valves is located in opposing shell portions (Fig. 8). The LV inclines anteriorly, whereas the RV is inclined posteriorly. Therefore, considering the convexity and the orientation of the umbo, they appear to be reflected through a point, which is located on the hinge line between the beaks. Both valves preserve a relatively large, well developed prodissoconch. The LV displays a less conspicuous larval stage, whereas the RV presents a marked prodissoconch, which is clearly separated from the body of the shell. Furthermore, a second growth stage is

observable on the RV, which can be interpreted as the prodissoconch II; it can also be faintly detected on the LV. This knob-like development of the beak is characteristic for the RV, whereas it is not as strikingly evident on the strongly inflated and incurved umbo of the LV. This is similarly developed in *Elasmatium* Clarke (Fig. 11).

The development of the loxopteriids is, like many other aberrant taxa, quite variable. The degree of convexity and angles can differ to a certain extent and is not specific to a certain species (Fig. 10). Especially the development of the RV is highly variable. Often individual RV´s cannot be certainly assigned to a species, because their range of variation in ornamentation, inflation and development of the posterior part of the shell is different. Therefore, the determination of most specimens is mainly based on the LV.

The loxopteriid hinge is edentulous, but instead of true hinge teeth the dorsal margins develop dents, which interlock with the terminations of the corresponding valve.

The ornamentation of *Loxopteria* includes radial and comarginal elements. In *Loxopteria*, fine, unequal and irregular radial ribs are present. These are often associated with fine, unequal and irregular comarginal growth lines (Pl. 3, Figs. 11-16). The growth lines intersect the radial ribs and generate small elevations (Pl. 3, Fig. 14). Originally, these areas were scaly developed (Pl. 3, Fig. 15-16), but due to the preservation mode they appear as small nodes on most of the specimens. Therefore, the radial ribs often resemble a string of pearls (Pl. 3, Figs. 12, 14). This fine ornamentation, if displayed in a specimen usually covers the whole valve. Additional, coarser elements can be developed in *Loxopteria*. Strong, irregular, comarginal rugae are displayed as well as strong radial undulations. Due to the combination or the lack of all these elements species can be distinguished. Thus, shell preservation or steinkerns, which display imprints of the ornamentation, are needed to definitely assign specimens on the species level.

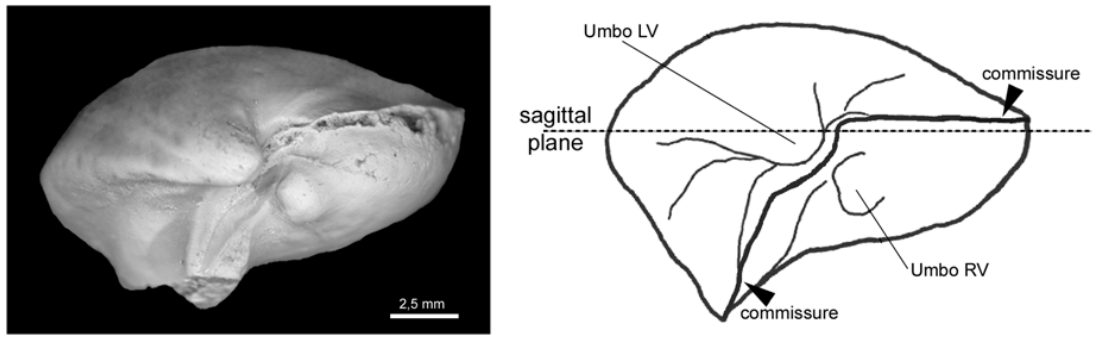


Figure 8 Dorsal view of *L. dispar* showing orientation of loxopteriid valves (MB.M.2222.2 from Nehden).

Soft body organization of Loxopteriinae

The state of preservation of some specimens of the Loxopteriinae offers the rare chance to observe the organization of the soft body. Some steinkerns display the soft tissue attachment structures as elevated subtle ridges. But the more striking preservation are black marks, which the soft body left on the pyritic steinkerns from the Koppenbissen Formation (Bergisch Gladbach, Eastern Rhenish Massif, Germany). This preservation mode of soft tissue attachment areas has already been reported from ammonoids (e.g., Richter, 2002), but was never examined on bivalves before. The genesis of this phenomenon is probably attributed to a first phase of pyritisation, which took place while the decay of the soft body started. In little pores and cavities, where the epithelial layer of the muscles attaches on the shell, an anoxic microenvironment developed and a first, short phase of pyritisation took place (Richter, 2002). At this point the calcareous parts of the bivalve remained unchanged. Sulphide was originated from the bacterial decomposition of the soft body and not from the sediment. Later, when the sediment was completely anoxic the actual steinkern was formed, by sulphide, which was derived from the surrounding sediment (Berner, 1984; Richter, 2002). These first shortly generated pyrite layers, which trace the soft tissue attachment areas of the bivalve, are observable as black marks on the steinkern.

The soft body preservation clearly shows a broad pallial line (Figs. 9.1, 8.6), which runs parallel to the comissure. It is traceable on both sides up to the hinge line underneath the umbo (Figs. 9.2-3). Some specimens show little pits in the course of the pallial line, which can be interpreted as the attachment areas of the pallial muscles. Posterior a small, but markedly developed pallial sinus is observable (Figs. 9.2, 8.4-6). Adductor attachment zones are completely missing. Pallial muscles probably took over the function of the adductors. This is supported by the unusual broad and strong pallial line, which leaves an elevation on most of the steinkerns (Pl. 1, Figs. 4, 14).

At the anterior side of the pallial sinus a line is developed, which leads upwards to the beak. This structure occurs as black trace on the Knoppenbissen specimens and as ridge on several other steinkerns. In some specimens this ridge is already clearly visible in the growth stage of the prodissoconch II. The origin of this morphological feature is dubious, but as it seems to be linked to the pallial sinus, the presence of a strong siphonal retractor muscle can be assumed.

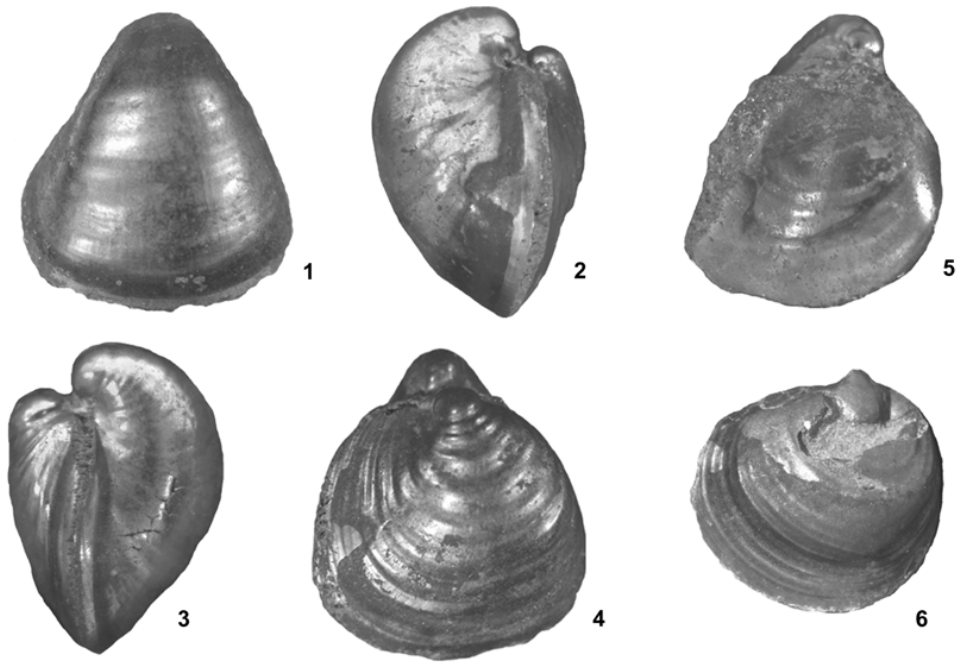


Figure 9 Soft tissue attachment areas on pyrite-steinkerns from Koppenbissen Formation (Northeastern Rhenish Massif). **1-4** *Elasmatium elongata,* B6A.35.52, x 4; **5** RV, *Loxopteria dispar* B6A.35.41, x 4; **6**, RV, *Elasmatium gowandense*, B6A.35.65, x 4.

7.1.1 Dualinidae

Class BIVALVIA Linnaeus, 1758
Subclass CRYPTODONTA Neumayr, 1884
Order PRAECARDIOIDEA Newell, 1965
Family DUALINIDAE Conrath, 1887

Type genus: *Dualina* Barrande, 1881.

Included subfamilies: Dualininae Conrath, 1887, Antipleurinae Conrath, 1887, Vlastinae Neumayer, 1891, Loxopteriinae nov. subfam.

Diagnosis:

Shell slightly to strongly inequivalve, thin, often antipleural.

Hinge line edentulous, sometimes with corresponding denticulate indentations in dorsal margin of valves as interlocking terminations.

Discussion:

Conrath (1887) identified the Dualinidae as family of the Cryptodonta Neumayr, 1884. He divided the taxon into the subfamilies Antipleurinae and Dualininae. This classification (Conrath, 1887) was based on the development of the hinge of these taxa. Neumayr (1891) modified the systematics and described, amongst others, "Vlastiden" and "Dualiniden" as subdivisions of the Cryptodonta Neumayr, 1884. In his list of subdivisions (1891, p. 724) he named "Antipleuriden", which include *Antipleura* Barrande, *Dualina* Barrande and *Dalila* Barrande. In the following he refers to the family as "Dualiniden", which he explicitly used by following Conrath (1887). Probably the term "Antipleuriden" (p. 724) was not corrected in the manuscript before it was published shortly after Neumayr´s death.

Newell and La Rocque (1969) revised Neumayr´s classification. They adopted his subdivision Antipleuridae (p. 724; Neumayr, 1891) and ignored the older term Dualinidae Conrath, 1887 (p. 728; Neumayr, 1891). Therefore, Antipleuridae Neumayr (corrected and translated by Newell and La Rocque, 1969) is a subjective synonym of Dualinidae Conrath, 1887.

The type genus of the Dualinidae is *Dualina* Barrande (1881). This genus includes more than one hundred species and has never been re-studied since its first description (Barrande, 1881). The type species of *Dualina* is *Dualina comitans* Barrande, 1881 (Figs. 14.9-13), which is defined by a lectotype figured in Barrande (1881, pl. 22, figs. 17-21) both subsequently designated by Ruzicka and Prantl (1960).

Unfortunately, Barrande´s monograph does not include description of species. The lectotype was chosen without any comments or figures (Ruzicka and Prantl, 1960). According to the illustrations of Barrande (1881), it displays a strongly inflated and a lid-shaped valve and its umbos are antipleurally developed. Its ornamentation consisits of fine comarginal and radial elements.

Heritsch (1929) reported the occurrence of *Dualina comitans* from the Silurian of the Alps and stated that his specimens match the Barrande figures, but he likewise gave no description of this taxon.

Later, Kriz and Serpagli (1993) mention the occurrence of *Dualina comitans* Barrande from Sardinia (Italy), but again, no description neither of the genus, nor of the species has been accomplished. Babin (1966) contributed the first and only description of this taxon. He described *D. comitans* as inequivalve and inequilateral and the beak of the highly inflated valve as strongly arched and projecting far above the hinge line.

Another subfamily, which is included in the Dualinidae, is the Vlastinae, which was described by Neumayr (1891). Type genus is *Vlasta* Barrande, 1881. Ruzicka and Prantl (1960) identified the type species, *Vlasta bohemica* Barrande, 1881, and likewise its lectotype (Barrande, 1881, pl. 2, figs. 1-2).

Furthermore, Neumayr (1891) included *Vevoda* Barrande in the Vlastinae. He denominated this genus as *Dux*, because he felt that the Czech term *Vevoda* was not appropriate. The type species *Vevoda expectans* Barrande, 1881, as well as the lectotype for *V. expectans* (Barrande 1881, pl. 13, figs. 10-11), was subsequently designated by Ruzicka and Prantl (1960).

The Vlastinae was identified as strongly inequivalve with a markedly developed umbo, slightly gaping (Neumayr, 1891) and judging from the figures of Barrande´s monograph (1881) these taxa are certainly related to the Dualininae Conrath and Antipleurinae Conrath. This is supported by Neumayr´s (1891) observation of transitional forms between *Antipleura* Barrande and *Vlasta* Barrande. He stated that especially juvenile specimens appear to be rather similar.

It should be mentioned that Newell and La Rocque (1969) described the Vlastinae Neumayr as equivalve, which contradicts the definition of this subfamily as given by Neumayr (1891). Probably this was based on Barrande´s statements (1881) who noted the peculiar instance that he identified either just RV or just LV of one taxon. Barrande (1881), although not completely convinced, described them as probably more or less equivalve. Neumayr´s re-study (1891) of e.g., *Vlasta* Barrande showed that Barrande (1881) separated *Vlasta bohemica* Barrande and *Vlasta pulchra* Barrande, which actually represent the RV and LV of one single species. Furthermore, Kriz (1998) re-studied *Vlasta bohemica* Barrande. He figured and described articulated specimens, which finally prove the inequivalve shell of this taxon and, thus, of the subfamily. Therefore, the definition given by Newell and La Rocque (1969) is wrong, but the Vlastinae Neumayr fit even better in the Dualinidae Conrath with the correct description of their morphology.

7.1.2 Loxopteriinae

Class BIVALVIA Linnaeus, 1758
Subclass CRYPTODONTA Neumayr, 1884
Order PRAECARDIOIDEA Newell, 1965
Family DUALINIDAE Conrath, 1887
Subfamily LOXOPTERIINAE nov. subfam.

Type genus: *Loxopteria* Frech, 1891.

Diagnosis:
Valves are strongly inequilateral, not gaping.
LV: more or less triangular in outline, strongly convex.
RV: circular to transversely oval in outline, lid-shaped, faintly convex; knob-like umbo separated from shell-body.

Included genera: *Loxopteria* Frech, 1891, *Elasmatium* Clarke, 1904.

Discussion:
The Loxopteriinae nov. subfam. includes strongly inequivalve taxa from the Upper Devonian. Some of these display an antipleural morphology, which strongly resembles the bauplan of Upper Silurian taxa, which are included in the Dualinidae Conrath. The characteristic strongly convex LV with the lid-shaped, slightly convex RV is not as markedly developed in the Upper Silurian species, although parallel morphologies are present. This aberrant bauplan is singular in Paleozoic bivalves and its reoccurrence as an analogue morphology in the Upper Devonian is highly unlikely, and hence, relationships are presumed. A final conclusion of their relationships cannot be drawn yet, due to the dubious and confused taxonomic situation of the Silurian taxa.
The assumed affiliation of *Loxopteria* Frech and *Elasmatium* Clarke with the Kochiidae Maillieux, 1931 (Newell and La Rocque, 1969) does not withstand scrutiny, because the kochiids develop a flat to concave RV, unlike the convex RV of the Loxopteriinae. Therefore, due to the similarities, such as, e.g., the development of the umbo or valve symmetry (see following paragraph), the Upper Devonian Loxopteriinae is assigned to the Dualinidae Conrath.

7.1.3 *Loxopteria*

Subfamily LOXOPTERIINAE nov. subfam.

Genus *Loxopteria* Frech, 1891

Type species: *Avicula dispar* Sandberger and Sandberger, 1856 (SD Newell and La Rocque, 1969).

Included species:
Loxopteria dispar (Sandberger and Sandberger), *Loxopteria gibbosa* (Münster), *Loxopteria inflata* (Münster), *Loxopteria problematica* (Münster), *Loxopteria meioklina* n. sp.

Diagnosis (revised):
Small to medium size loxopteriid shell. Angle in posterior shell portion differs from over 90° to more or less 10°. Ornamentation ranges from comarginal to radial-comarginal lines and rugae. Umbos antigyrate.
LV: umbo opisthogyrate to strongly prosogyrate, located behind centre of valve. Posterior part of shell strongly to slightly concave.
RV: transversely to rounded oval in outline, umbo almost orthogyrate to opisthogyrate, located somewhat to distinctly behind the centre of the valve.
Species differ mostly in ornamentation.

Discussion:
The type species *Avicula dispar* Sandberger and Sandberger, 1856 (Pl. 1, Fig. 18) was designated by Newell and La Rocque (1969). Münster (1840) described a group of bivalves from the Franconian Forest (Southeastern Germany) he assigned to *Avicula*, which comprise strongly inequivalve taxa. These taxa certainly belong to the loxopteriids and have been completely neglected by Frech (1891), when he first identified the genus *Loxopteria*, and likewise by all later authors.
For a long time the loxopteriids have been aligned with the kochiids. Frech (1891) established both, *Loxopteria* and *Kochia*. He felt that the kochiids were the Lower Devonian predecessors of the loxopteriids, but conceded that there was no real evidence for his assumption. However, Frech (1891) placed *Loxopteria* as subgenus within *Kochia*. But the lid-shaped valve of the kochiids is supposed to be concave (comments to pl. 6; Frech, 1891), while loxopteriid shells are convex. Especially the development of the hinge region contradicts an affiliation of these taxa. The straight hinge line and the large, triangular area underneath the beak of *Kochia* Frech are not displayed in *Loxopteria* Frech. Furthermore, there is no posterior or anterior

wing, as described for *Kochia* Frech, developed in the loxopteriids and its typical knob-like prodissoconch is not present in the kochiids. Consequently, it is believed herein that these taxa are truly related

Clarke (1904) raised *Loxopteria* Frech to the genus level. He included *Sluzka* Barrande (1881) as a subgenus of *Loxopteria* Frech. Clarke (1904) stated that this subgenus avoids the erection of a new genus and he, furthermore, noted that it does not imply the reappearance of this Silurian genus in the Upper Devonian or its integrity.

The species *Sluzka amygdala* Barrande (Barrande, 1881; pl. 358), to which Clarke (1904) refers, shows a similar development of the umbo, which is set off from the body of the shell, like the RV of *Loxopteria* Frech. But the valves are almost equilateral, subcircular to oval in outline. This and the differences in ornamentation of *S. amygdala* Barrande clearly indicate the separation of these two taxa. However, the type species of *Sluzka* Barrande is *Sluzka pulchella* Barrande, 1881 (pl. 185, figs. 4.1-3), subsequently designated by Ruzicka and Prantl (1960). This species is equivalve, more or less equilateral, subcircular in outline and develops a small, central umbo. It does not resemble any *Loxopteria* species. Therefore, a direct relationships of *Sluzka* and *Loxopteria* is highly unlikely. This misapprehension, like many concerning the loxopteriids, is the result of the differing development of the valve morphology. Clarke (1904) was not aware of any articulated specimens. Therefore, he did not assume that the triangular LV is the counterpart of a rounded, transversely oval RV. Another Bohemian genus Clarke (1904) compared with *Loxopteria* is *Vevoda* Barrande, 1881, with the type species *Vevoda expectans* Barrande, 1881 (pl. 13, figs. 10-11), subsequently designated by Ruzicka and Prantl (1960). This species also resembles features of loxopteriid RV. Especially the development of the prodissoconch and the oval, slightly lateral drawn-out outline are similar to loxopteriid RV´s. According to Neumayr (1891) and Newell and La Rocque (1969), *Vevoda* Barrande is included together with *Vlasta* Barrande in the Vlastidae and an affiliation of the loxopteriids with *Vevoda* on generic level is not likely.

Although the Bohemian taxa which Clarke (1904) compared with *Loxopteria* Frech are not suitable to show any relationships between these groups, there are specimens figured by Barrande (1881), which suggest some kind of affiliation.

Schmidt (1924) mentioned a variation of *Loxopteria* Frech, *Loxopteria* ? *dispar*. He described it as close to *L. laevis* with strong concave RV, which shows fine comarginal lines and/or more pronounced comarginal rugae. A loxopteriid RV can appear concave, if the posterior portion of the valve is markedly bent upwards, the specimen is poorly preserved, and its outline is not completely visible. No variation of loxopteriids with concave valves has been observed, therefore, Schmidt's assumption is probably based on the mode of preservation. The valves he described as having strong comarginal rugae on the RV probably belong to *Elasmatium* Clarke or to *L. problematica*, but without examining the specimens and more information about their morphology, a correct assignment is impossible.

Occurrence:

Loxopteria Frech is reported from the UD I-J up to the UD V from various outcrops. Matern (1931) mentioned the oldest occurrence from the Upper Frasnian. This appearance cannot be supported by any examined specimens nor other quotes of Frasnian representatives of this genus. Therefore, until there is a certain proof of specimens from the Frasnian, the first occurrence of this genus is assumed to be basal Famennian. In Germany, it occurs in the Rhenish Massif (Central Germany), the Harz Mountains (Central Germany) and Franconian (Southeastern Germany). Furthermore, it extends from the Holy Cross Mountains (Poland), the Ural Mountains (Kazakhstan), and Morocco (Meseta, Tafilalt, Becker, 1993a) to New York State (North America). Further studies of Upper Devonian pelagic bivalves will probably reveal a wider range of distribution of this genus.

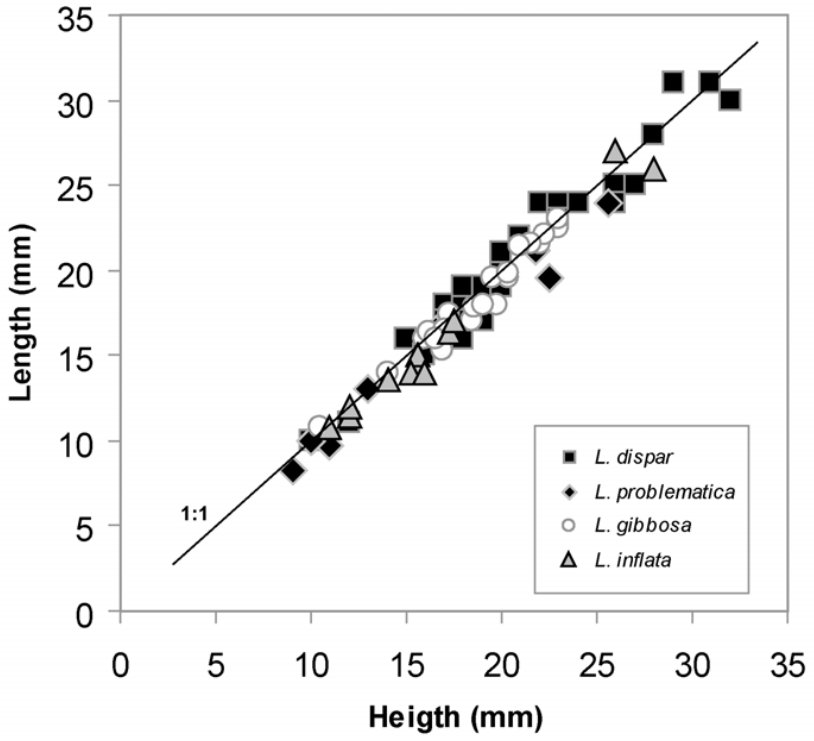


Figure 10 Length / height ratio of *Loxopteria* species showing isometric growth and restricted shape variability.

Loxopteria dispar (Sandberger and Sandberger, 1856)
Figs. 8-9; Pl. 1, Figs. 1-15; Pl. 3, Figs. 11-18

* + v	1856	*Avicula dispar* SANDBERGER AND SANDBERGER, p. 284, pl. 39, fig. 14a.
	1867	*Avicula dispar*.- SCHÜLKE, p. 145.
	1873	*Avicula dispar*.- KAYSER, p. 636.
	1896	*Loxopteria dispar*.- DENCKMANN, p. 14, 38, 39.
v	1891	*Kochia* (*Loxopteria*) *dispar*.- FRECH, p. 77, pl. 6, fig. 4.
	1895	*Loxopteria dispar*.- BEUSHAUSEN, p. 361.
	1900	*Kochia dispar*.- BEUSHAUSEN, p. 175, 180, 186.
	1901	*Kochia dispar*.- DREVERMANN, p. 146, pl. 16, fig. 1.
	1901a	*Kochia dispar*.- DENCKMANN, p. 12.
	1901b	*Kochia dispar*.- DENCKMANN, p. 43, 44, 46.
v	1904	*Loxopteria dispar*.- CLARKE, p. 272, pl. 13, figs. 8-17.
	1905	*Loxopteria dispar*.- DREVERMANN, p. 389.
v	1912	*Kochia* (*Loxopteria*) *dispar*.- BORN, p. 577.
+	1912	*Kochia* (*Loxopteria*) *Clarkei* BORN, p. 577, pl. 18, fig. 5.
	1911	*Kochia* (*Loxopteria*)*dispar*.- SOBOLEW, p. 36, 37.
	1913	*Loxopteria dispar*.- PAECKELMANN, p. 246.
	1913	*Loxopteria* n. sp.- PAECKELMANN, p. 246, pl. 4, fig. 6.
	1922	*Loxopteria dispar*.- SCHMIDT, p. 274, 277, 291.
	1922	*Loxopteria dispar*.- KEGEL, p. 39.
	1924	*Loxopteria dispar*.- SCHMIDT, p. 109, 110, 143.
	1923	*Loxopteria dispar*.- SCHINDEWOLF, p. 283.
	1922	*Loxopteria dispar*.- PAECKELMANN, p. 63, 64, 69, 70.
v	1929	*Kochia* (*Sluzka*) *dispar*.- LANGE, p. 14, 17.
	1931	*Loxopteria dispar*.- MATERN, p. 124.
	1935	*Loxopteria dispar*.- CHADWICK, p. 324.
v	1936b	*Loxopteria dispar*.- PAECKELMANN AND KÜHNE, p. 26, 27, 30.
	1936a	*Loxopteria dispar*.- PAECKELMANN AND KÜHNE, p. 18.
	1938	*Loxopteria dispar*.- PAECKELMANN, p. 24, 25.
	1961	*Loxopteria dispar*.- WURM, p. 119.
	1962	*Lotopteria dispar*.- ROZMAN, p. 28.
	1968	*Loxopteria dispar*.- GUNIA, p. 177, pl. 10, fig. 7.
	1974	*Loxopteria dispar*.- JUX AND KRATH, p. 134, pl. 6, figs. 4-5.
	1980	*Kochia* (*Loxopteria*) *dispar*.- KAEVER et al., p. 160, pl. 28, fig. 3.
	1985	*Loxopteria dispar*.- BECKER, p. 29.
v	1993a	*Loxopteria dispar*.- BECKER, p. 48, 132.

Holotype: NWS 240.
Type locality: Oberscheld (Lahn-Dill Syncline, Germany).
Type stratum: "Cypridinenschiefer" (Nehdenian, lower Famennian, UD II).

Material:
see Tab. 2.

Diagnosis:
Small to medium sized loxopteriid shell. Ornamentation consisting of fine, unequal radial lines, fine comarginal growth lines intersecting radial ribs; intersection point partly generating small nodes.
LV: subtrigonal in outline, strongly convex; two to five strong radial undulations developed, either shortly just at umbo present or covering the total length of valve, posterior ribs generally stronger developed.

RV: transversely oval in outline. Ornamentation consisting of variable number of radial ribs, comarginal rugae. Comarginal growth lines mostly dorsally sinuous. Umbo located anteriorly to centre of the valve.

Description:

Loxopteriid shell, postero-dorsal margin is slightly convex, antero-dorsal margin is roundly declining.

Area-like development posterior to beak present (Fig. 7; MB.M.2222.1-2, Pl. 1, Figs. 16-17):

- LV develops large, somewhat triangular surface with longitudinal sulcus in its centre
- RV develops rounded ridge.
- On both valves the area is tapering off towards the ventral margin; along the commissure line a markedly depression is developed.

On LV, directly anterior to the beak, a tiny bulge in dorsal margin present.

Hinge line edentulous, deviating shortly before umbo, generating interlocking dents between umbos (Fig. 2; MB.M.2222.1-2, Pl. 1, Figs. 16-17).

Pallial line is parallel to ventral margin and runs anterior and posterior upwards to the umbo, pallial sinus present (Fig. 9.5). No adductor scars are observable. On RV a fine, radial, linear muscle scar runs from umbo to the anterior portion of the ventral margin (e.g., MB.M.2222.1, Pl. 1, Fig. 14; B6A-35.54, Pl. 1, Fig. 4).

Prodissoconch is clearly separated from body of shell (e.g., B6A-35.57, Pl. 1, Fig. 13; B6A-35.54, Pl. 1, Fig. 2). Prodissoconch II is markedly observable on umbo of RV (e.g., MB.M.789, Pl. 1, Fig. 7).

The holotype NWS 240 is LV, preserving the posterior central portion of the shell, lacking umbo and outline. Strong undulations and typical loxopteriid fine comarginal and radial ornamentation clearly observable.

Variation of length/height ratio see Fig. 10

Largest specimen (MB.M.4218): height, 31.1 cm; length, 31.0 cm.

Smallest specimen (B6A-35.55): height, 10.0 cm; length, 10.0 cm.

Discussion

Avicula dispar Sandberger and Sandberger has been introduced for specimens from the Cypridinenschiefer of Oberscheld, Enkeberg and Nehden. Out of all these specimens just one original survived in the Naturwissenschaftliche Sammlung, Museum Wiesbaden (NWS 240, Pl. 1, Fig. 18). This specimen, which is falsely declared as steinkern is the holotype of this species. It clearly displays the fine ornamentation of the loxopteriids and three to four of the rough, radial undulations, which are the main characteristics of *L. dispar*. The umbo, outline and hinge area are, unfortunately, not visible (Pl. 1, Fig. 18).

Frech (1891) designated *Kochia* and its subgenus *Loxopteria*. He re-assigned *Avicula dispar* Sandberger and Sandberger to this subgenus. *Kochia*, with its type species *Avicula capuliformis* Koch, 1881 from the Lower Devonian, is, as discussed above, not related to *Loxopteria*. The Frech types are specimens MB.M.2220.1-2 (Pl. 3, Figs. 11-16).

Drevermann (1901) reported *L. dispar* (Sandberger and Sandberger) from the volcaniclastic brekzie at Langenaubach (Lahn Dill Syncline) and discussed the problem of the misleading assignment of RV and LV. He figured a well preserved RV of *L. dispar* from Oberscheld (Lahn Dill Syncline) to finally clarify its morphology (1901, pl. 16, figs. 1, 1a).

Paeckelmann (1913) reported *Loxopteria* n. sp. from the Dorper Kalk of Beek at Elberfeld (Western Rhenish Massif). He described it as circular in outline and noted that the umbo is not as far located anterior as in *L. laevis*, which was erected by Frech (1891). Judging from his figure (pl. 4, fig. 6), the impression of the outline is received by the orientation of the valve. Furthermore, the umbo of the loxopteriids is actually located posteriorly. Paeckelmann (1913) mentioned radial undulations and comarginal growth lines. This supports a re-assignment of this poorly preserved specimen within *L. dispar*. The described differences are assumed to be in the normal range of variation of *L. dispar*.

Born (1912) described a new species from the Aektal (Hercynian Mountains), *Kochia* (*Loxopteria*) *clarkei*. This taxon is an invalide homonym of *Loxopteria clarkei* Raymond, 1909 from the Three Fork Shale of Montana. The figured Born specimen (1912, pl. 18, fig. 5) has to be re-assigned to *L. dispar*, because the variation of the outline of the valve and the degree of deflection of the posterior portion of the valve, which were supposed to be the distinctive characters of Born´s species, are clearly in the range of variation of the RV of *L. dispar*.

Loxopteria clarkei Raymond is re-assigned to *L. problematica* herein (see following paragraph).

Occurrence:

Upper Devonian UD II-?V (Tab. 1; Tab. 2).

In the literature the youngest occurence of *L. dispar* is of quoted to be from the UD V (Tab. 4; e.g., Drevermann, 1901; Schmidt, 1922). The corresponding material could not be traced in the course off this study. Therefore, until it is confirmed that the described material actually belongs to this species, this referrences have to be treated cautiously. Thus, the last occurence of *L. dispar* is assumed to be from the UD IV-C after the *annulata* Event.

Locality	Region	Reference	Stratigraphic level
Aeketal	Hercynian Mountains	Beushausen, 1900	UD II/IV
Aeketal	Hercynian Mountains	Born, 1912	UD III-C
Balve area	Northeastern RM	Denckmann, 1901a	UD II-C
Balve area	Northeastern RM	Kaever et al., 1980	UD I-IV
Balve area	Northeastern RM	Paeckelmann, 1924	UD III-C
Balve area	Northeastern RM	Paeckelmann, 1924	UD IV-A
Balve area	Northeastern RM	Paeckelmann, 1938	UD III
Balve area	Northeastern RM	Paeckelmann, 1924	UD II
Beul	Northeastern RM	Denckmann, 1901a	UD II-C
Beul	Northeastern RM	Kaever et al., 1980	UD I-IV
Beul	Northeastern RM	Paeckelmann, 1924	UD III-C
Beul	Northeastern RM	Paeckelmann, 1924	UD IV-A
Beul	Northeastern RM	Paeckelmann, 1938	UD III
Beul	Northeastern RM	Paeckelmann, 1938	UD IV
Biesenberg	Northeastern RM	Denckmann, 1896	UD II
Biesenberg	Northeastern RM	Kaever et al., 1980	UD I-IV
Biesenberg	Northeastern RM	Schmidt, 1924	UD II
Braunau	Kellerwald, Eastern RM	Denckmann, 1896	UD II/V
Dasberg	Northeastern RM	Kaever et al., 1980	UD I-IV
Drewer Quarry	Northeastern RM	Schmidt, 1922	UD III-C
Drewer Quarry	Northeastern RM	Schmidt, 1924	UD III-C
Enkeberg	Northeastern RM	Becker, 1993a	UD II-H
Enkeberg	Northeastern RM	Drevermann, 1901	UD V
Enkeberg	Northeastern RM	Kaever et al., 1980	UD I-IV
Enkeberg	Northeastern RM	Kayser, 1873	UD II
Enkeberg	Northeastern RM	Lange, 1929	UD III
Enkeberg	Northeastern RM	Lange, 1929	UD II D/H
Enkeberg	Northeastern RM	Paeckelmann and Kühne, 1936b	UD IV-A
Enkeberg	Northeastern RM	Paeckelmann and Kühne, 1936b	UD II-III
Enkeberg	Northeastern RM	Schülke, 1867	UD II
Eskesberg	Wuppertal area, Northern RM	Paeckelmann, 1913	UD II
Eulenspiegel	Northeastern RM	Schmidt, 1922	UD IV/V
Fichtelgebirge	Northern Bavaria	Drevermann, 1901	UD V
Gattendorf	Franconian Forest, South-eastern Germany	Schindewolf, 1923	UD III-C
Gattendorf	Franconian Forest, South-eastern Germany	Wurm, 1961	UD III-C
Gehöft Frankenburg	Northeastern RM	Schmidt, 1922	UD IV/V
Gowanda Shale, Forestville	Chautauqua County, New York State	Chadwick, 1935	UD II-C
Gowanda Shale, Forestville	Chautauqua County, New York State	Clarke, 1904	UD II-C
Grasberg	Balve area, Northeastern RM	Paeckelmann, 1924	UD III-C
Grube Joseph,	Lahn Dill Syncline	Kegel, 1922	UD II

Graeveneck			
Hahnenfurth	Wuppertal area, Northern RM	Paeckelmann, 1913	UDII
Hauern	Kellerwald, Eastern RM	Denckmann, 1896	UD II/V
Hemberg	North of Iserlohn, Northeastern RM	Schmidt, 1924	UD III/IV
Hönnevalley	Northeastern RM	Schmidt, 1922	UD III/IV
Hönnevalley	Northeastern RM	Schmidt, 1924	UD III/IV
Jebel Amelande	Central Tafilalt, Southeastern Morocco	Becker, 1993a	UD II-D
Kahlenbergköpfe	West of Warstein, Northeastern RM	Schmidt, 1922	UD III
Kalvarienberg	Northeastern RM	Schmidt, 1924	UD II
Kielce-Sandomierze	Holy Cross Mountains, Poland	Sobolew, 1911	UD II-C / III-C
Knoppenbiessener Schichten	Bergisch Gladbach	Jux and Krath, 1974	UD II-C/E
Langenaubach "Schalsteinbrekzie"	Lahn Dill Syncline	Denckmann, 1901b	Famennian
Lubiechowa	Swiebodzice-Syncline, Poland	Gunia, 1968	Famennian
Mädler´s Länder	Warstein area, Northeastern RM	Schmidt, 1922	UD II-F/G
Mokrzesowa	Swiebodzice-Syncline, Poland	Gunia, 1968	Famennian
Nassau	Lahn Dill Syncline	Drevermann, 1901	UD V
Nehden	Northeastern RM	Becker, 1993a	UD II-C/E
Nehden	Northeastern RM	Drevermann, 1901	UD II-C/E
Nehden	Northeastern RM	Kaever et al., 1980	UD I-IV
Nehden	Northeastern RM	Kayser, 1873	UD II-C/E
Nehden	Northeastern RM	Paeckelmann and Kühne, 1936a	UD II-C/E
Nie Brickwork Quarry	North of Letmathe, Northeastern RM	Becker, 1985	UD III-C
Oberrödinghausen	Northeastern RM	Kaever et al., 1980	UD I-IV
Oberrödinghausen	Northeastern RM	Kaever et al., 1980	UD I-IV
Oberscheld	Lahn Dill Syncline	Kaever et al., 1980	UD I-IV
Oberscheld	Lahn Dill Syncline	Kegel, 1922	UD II-IV
Oberscheld	Lahn Dill Syncline	Matern, 1931	UD II/III
Oberscheld	Lahn Dill Syncline	Matern, 1931	UD I H-J/K
Oberscheld	Lahn Dill Syncline	Sandberger and Sandberger, 1856	UD II
Ural Mountains	-	Rozman, 1962	UD II/IV
Various outcrops	Kellerwald, Eastern RM	Denckmann, 1901b	UD II/V
Warstein area	Northeastern RM	Kaever et al., 1980	UD I-IV
Wildungen	Kellerwald, Eastern RM	Drevermann, 1901	UD V

Table 1 References quoting the occurrence of *Loxopteria dispar*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Aeketal	Clymenien Kalk	Born, 1909	UD III-C	GZG 462-21	
Aeketal	Clymenien Kalk	Born, 1909	UD III-C	GZG 462-22	
Aeketal	Clymenien Kalk	Born, 1909	UD III-C	GZG 462-23	
Aeketal	Clymenien Kalk	Born, 1909	UD III-C	GZG 462-24	
Aeketal	Clymenien Kalk	Born, 1909	UD III-C	GZG 462-25	
Aeketal	Clymenien Kalk	Born, 1909	UD III-C	GZG 462-6	
Aeketal	Clymenien Kalk	Born, 1909	UD III-C	GZG 462-11	
Aeketal	Clymenien Kalk	Born, 1909	UD III-C	GZG 462-19	
Aeketal	Clymenien Kalk	Born, 1909	UD III-C	GZG 462-20	
Aeketal	Clymenien Kalk, Bank 8	Born, 1909	UD III-C	GZG 462-16	
Aeketal	Clymenien Kalk, Bank 8	Born, 1909	UD III-C	GZG 462-17	
Aeketal	Clymenien Kalk, Bank 8	Born, 1909	UD III-C	GZG 462-7	
Barmen, Nordpark	togt	Paeckelmann, 1921	UD II	MB.M.4210	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.43	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.41	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.45	
Bergisch Gladbach/ Aushub Kreishaus	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.44	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.86	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.55	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.42	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.46	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Weber	UD II-C/E	B6A-35.47	
Beul	Enkeberger Kalk	Denckmann, 1900	UD II/III	MB.M.4212	
Biesenberg	-	Denckmann, 1894	UD II	MB.M.4205	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II	MB.M.4206	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II	MB.M.4207	
Braunau	tocl b	Denckmann, 1899	UD II	MB.M.4237	
Enkeberg	v. Koenen Schurf	Denckmann/ Lotz, 1900	UD II/IV	MB.M.4213	
Enkeberg	Oberdevon III	Lange, 1922	UD III	MB.M.2271.7	
Enkeberg	Schicht 18/ Obere Cheiloceras-Zone	Paeckelmann	UD II-E/F	MB.M.4214	
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II-E/F	MB.M.4216	
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II-E/F	MB.M.4218	
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II-E/F	MB.M.4220	
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II-E/F	MB.M.4221	
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II-E/F	MB.M.4222	

Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II-E/F	MB.M.4224	
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II-E/F	MB.M.4225	
Enkeberg	Schicht 20/ Untere Cheiloceras-Zone	Paeckelmann	UD II-A/E	MB.M.4227	
Enkeberg	Schicht 20/ Untere Cheiloceras-Zone	Paeckelmann	UD II-A/E	MB.M.4217	
Enkeberg	Schicht 20/ Untere Cheiloceras-Zone	Paeckelmann	UD II-A/E	MB.M.4226	
Enkeberg	Schicht 20/ Untere Cheiloceras-Zone	Paeckelmann	UD II-A/E	MB.M.4228	
Enkeberg	Schicht 14/ Prolobites-Zone	Paeckelmann, 1925	UD III	MB.M.4215	
Enkeberg	Schicht 14/ Prolobites-Zone	Paeckelmann, 1925	UD III	MB.M.4219	
Enkeberg	Schicht 14/ Prolobites-Zone	Paeckelmann, 1925	UD III	MB.M.4244	
Enkeberg	Oberdevon	Schülcke Grube	UD II/IV	MB.M.4230	
Enkeberg	Schicht 4	Paeckelmann, 1925	UD IV-C	MB.M.4223	
Enkeberg/ Schurf Paeckelmann	Schicht 18	Paeckelmann	UD II-E/F	MB.M.4229	
Enkeberg/ Schurf Paeckelmann	Schicht 18	Paeckelmann	UD II-E/F	MB.M.4242	
Enkeberg/ Schurf Paeckelmann	Schicht 18	Paeckelmann	UD II-E/F	MB.M.4241	
Hauern/Wildungen	Unterer Clymenien Kalk	Denckmann	UD II	MB.M.4211	
Langenaubach	-	Denckmann, 1896	Famennian	MB.M.4245	
Martenberg-Klippe	-	Paeckelmann, 1928	UD II	MB.M.4240	
NE Nehden	to2	Paeckelmann, 1924	UD II-C/E	MB.M.4228	
Nehden bei Brilon	Oberdevon	Amelung	UD II-C/E	MB.M.2222.1	
Nehden bei Brilon	Oberdevon	Amelung	UD II-C/E	MB.M.2222.2	
Nehden bei Brilon	Oberdevon	von Buch	UD II-C/E	MB.M.2220.1	
Nehden bei Brilon	Oberdevon	von Buch	UD II-C/E	MB.M.2220.2	
Oberscheld	-	-	UD II/IV	MB.M.4233	
Oberscheld	-	-	UD II/IV	MB.M.4281	
Oberscheld	Oberdevon	Beyrich, 1837	UD II/III	MB.M.789	
Oberscheld	Oberes Oberdevon	Bolle, 1874	UD II/IV	MB.M.4232	
Oberscheld	Oberes Oberdevon	Bolle, 1874	UD II/IV	MB.M.4236	
Oberscheld	Clymenien Kalk	Lotz, 1902	UD II/III	MB.M.4231	
Oberscheld	Clymenien Kalk	Lotz, 1902	UD II/III	MB.M.4235	
Oberscheld	Clymenien Kalk	Lotz, 1902	UD II/III	MB.M.4243	
Oberscheld	Clymenien Kalk	Lotz, 1902	UD II/III	MB.M.4234	
Oberscheld	Cypridinenschiefer	Sandberger and Sandberger	UD II	NWS 240	Holotype *A. dispar*
Riefsnei, Warstein-Hirschberg	verkiester Clymenien Kalk	Wiemeyer, 1909	-	MB.M.4208	
Schurbusch East of Nehden	goniatite slate	Becker	UD II-A	B6A-35.49	
Schurbusch, East of Nehden	goniatite slate	Becker	UD II-A	B6A-35.51	
Schurbusch, East of Nehden	goniatite slate	Becker	UD II-A	B6A-35.54	
Schurbusch, East of Nehden	goniatite slate	Becker	UD II-A	B6A-35.57	

Schurbusch, east of Nehden	Nehden	Becker	UD II-C/E	B6A-35.48
Schurbusch, east of Nehden	Nehden	Becker	UD II-C/E	B6A-35.50
Schurbusch, east of Nehden	Nehden	Becker	UD II-C/E	B6A-35.52
Schurbusch, east of Nehden	Nehden	Becker	UD II-C/E	B6A-35.53
Schurbusch, East of Nehden	Nehden	Becker	UD II-C/E	B6A-35.56
St. Claas/Repetal	Nehdener Schiefer	-	UD II-C/E	MB.M.4239

Table 2 Examined specimens of *Loxopteria dispar*.

Loxopteria gibbosa (Münster, 1840)
Pl. 4, Figs. 10-14

* + 1840 *Avicula gibbosa* MÜNSTER, p. 52, pl. 11, fig. 4.
+ v 1842 *Cardium problematicum* MÜNSTER, p. 119, pl. 11, fig. 8.
v non 1850 *Avicula laevis*.- ROEMER, p. 165.
+ 1891 *Kochia* (*Loxopteria*) *laevis* FRECH, p. 76, pl. 6, fig. 3
1907 *Loxopteria* aff. *dispar*.- RAYMOND, p. 118.
+ 1909 *Loxopteria holzapfeli* RAYMOND, p. 145, pl. 5, figs. 1-7, 11.
+ 1912 *Kochia* (*Loxopteria*) *Losseni* BORN, p. 579, pl. 18, fig. 6.
1920 *Cardiola* (*Kochia*) *laevis*.- MEYER, p. 29.
+ 1923 *Loxopteria radiata* SCHINDEWOLF, p. 286.
1924 *Loxopteria* ? *dispar*.- SCHMIDT, p. 143, 161.
v 1922 *Loxopteria laevis*.- KEGEL, p. 39.
v 1929 *Loxopteria radiata*.- LANGE, p. 17, 24.
1951 *Kochia laevis*.- TERMIER AND TERMIER, p. 65.
1961 *Avicula* ? *gibbosa*.- WURM, p. 119.
1961 *Loxopteria radiata*.- WURM, p. 120.
1968 *Loxopteria Losseni*.- GUNIA, p. 77, pl. 10, fig. 8.
1992 *Loxopteria radiata*.- BECKER, p. 10.
1992 *Loxopteria* cf. *losseni*.- BECKER, p. 10.
v 1993a *Loxopteria radiata*.- BECKER, p. 48.

Neotype (selected herein): B6A-35.126.
Type locality: Schübelhammer (Franconiann Forest, Southeastern Germany).
Type stratum: "Wagner Bank" (basis *postera*-Zone, Famennian, Upper Devonian IV-A).

Material:
see Tab. 4.

Diagnosis:
Small to medium sized loxopteriid shell.
Ornamentation consisting of fine, unequal radial lines and fine comarginal growth lines, comarginal lines intersecting radial ribs; intersection points partly generating small nodes.

Description:

In comparision to *Loxopteria dispar*:

LV: often somewhat rounder in outline, without rough undulations; umbo more dull; radial edge more rounded (Pl. 4, Fig. 9).

RV: more circular in outline (Pl. 4, Fig. 12), sometimes not as elongated.

Ornamentation often quite subtle, may appear almost smooth due to preservation mode (e.g., B6A-35.120, Pl. 4, Figs. 10-11).

Neotype B6A-35.126 (Pl. 4, Fig. 12), LV with partial shell preservation; fine radial and comarginal ornamentation on shell remains, smooth surface on steinkern. Hinge line not observable.

Variation of length/height ratio see Fig. 10.

Largest specimen (MB.M.4355): height, 23.0 cm; length, 21.5 cm.

Smallest specimen (MB.M.4373): height, 10.5 cm; length, 10.8 cm.

Discussion:

Münster (1840) designated *Avicula gibbosa* based on a series of strongly inequivalve bivalves from the Clymenienkalk of Geuser (Franconian Forest, Southeastern Germany). He mentioned that they show a highly inflated and a corresponding, lid-shaped valve, which he observed on one articulated specimen. Therefore, this is the only species, which was established after examining an articulated specimen. Unfortunately, the types and likewise the knowledge of its morphology were lost afterwards. Münster (1840) clearly described the ornamentation as consisting of fine comarginal and radial ribs and he, furthermore, noted the knob-like development of the umbo. Therefore, *A. gibbosa* can be unequivocally identified by Münster´s description as *Loxopteria* species with fine ornamentation.

Unfortunately, no original specimen survived, neither in the collection of the Bayrische Staatssammlung München nor in the Urwelt-Museum in Bayreuth. The only other specimens (MB.M.3641.1-6) from Geuser, which are designated as *Avicula gibbosa,* were 1846 collected by Lemaire. This material is poorly preserved steinkerns. MB.M.3641.1 and MB.M.3641.3 can be determinated as *Loxopteria* aff. *problematica* and the remaining specimens cannot be assigned to any genus, due to their preservation mode. Therefore, out of existing collection no specimen from Geuser has been discovered, which could serve as neotype of this species. The type locality has partly been filled in the last decades and only strata of UD III are currently still available for re-sampling. In recent time no more loxopteriid material has been collected or is available for this revision.

B6A-35.126 (Pl. 4, Fig. 12) from the Schübelhammer (Franconian Forest, Southeastern Germany), which was collected by Weyer, is selected as neotype of this taxon. It is derived from a locality close to the original outcrop. The originally given stratigraphic level "Clymenienkalk" (Münster, 1840) allows only a broad interpretation as Famennian and the neo-

type is from a level within this time span. Therefore, this loxopteriid shell with fine comarginal and radial ornamentation, which is employed as the neotype, is suitable to finally define this species.

Münster (1842) also described *Cardium problematicum* from the Famennian of Geuser, which was mentioned later by Geinitz (1853). After examining the types of this taxon, BSPG AS VII 1729 is selected as lectotype, because it is the only more or less well preserved and figured specimen (Münster, 1842, pl. 11, fig. 8). This specimen is a loxopteriid shell with fine radial and comarginal ornamentation and, therefore *Cardium problematicum* Münster, 1842 has to be re-assigned to *L. gibbosa*. Münster (1842) stated that this taxon is similar to the *Avicula* species he described 1840 and, to avoid confusion, he assigned it to *Cardium*, although he felt it represents an independent genus. The reasons for erecting this species remain dubious, since he did not describe any morphological differences to other taxa.

Frech (1891) described *L. laevis* as displaying just fine growth lines. This lead to some confusion, because the type specimen (SMF XV/3-2158, Pl. 4, Fig. 14) presents actually fine radial and comarginal lines. SMF XV/3-2158 (Pl. 4, Fig. 14) from the Clymenienkalk of Wildungen is the only one remaining from the type series and is, therefore, holotype by secondary monotypy. Its ornamentation places *L. laevis* Frech in subjective synonymy to *L. gibbosa*.

Avicula laevis Roemer (1850; p. 26, pl. 4, fig. 8) from the Kellwasserkalk of the Harz Mountains is a separate species, which differs distinctly from *L. laevis* Frech. It possesses a smooth shell and a straight long hinge line. Its morphology places it close to the Pteriomorpha and it has no relationships with *Loxopteria*.

Raymond (1907) reported loxopteriid specimens from Montana. He was not sure about their precise assignment and determined them as "*Loxopteria*, near *L. dispar*". Later, Raymond (1909) identified *Loxopteria holzapfeli* for these specimens of uncertain affiliation from Montana. He stated that this taxon is developed such as *L. dispar* but without strong radial undulations. Therefore, due to its fine radial and comarginal ornamentation, this species is a subjective synonym of *Loxopteria gibbosa*.

Schindewolf (1923) erected *Loxopteria radiata*. He felt that this taxon from Gattendorf (Franconian Forest, Southeastern Germany) was close to *L. laevis,* but) interpreted the latter as a species, which is completely missing radial ribs, as described in the comment given by Frech (1891). Therefore, *L. radiata* was established for loxopteriids displaying fine radial and comarginal ornamentation. Thus, *L. radiata* Schindewolf is a subjective synonym of *L. gibbosa* (Münster).

Born (1912) identified a new species, *Kochia* (*Loxopteria*) *losseni* from the Hercynian Mountains. He described it based on a RV, which shows fine radial and comarginal ornamentation and without correlating them with LV´s of known species. As stated above, the range of variation in outline of RV is wide and the slight differences, this species was based on, are not

specific characters of an independent taxon. Therefore, and due to its ornamentation, *L. lossenі* is also re-assigned as a subjective synonym of *L. gibbosa*.

Schmidt (1924) identified specimens, which he designated as *L.* ? *dispar*. He noted (1923) that they are similar to *L. dispar*, but without displaying radial undulations. This description clearly identifies them as *L. gibbosa.*

Kegel (1922) determinated specimens from Nanzenbach (MB.M.4375) and Kirchhofen (MB.M.4374) (both Lahn-Dill Syncline, Southern Rhenish Massif) as *L. laevis* Frech. Examination of these specimens showed that they clearly have to be re-assigned to *L. gibbosa* because they also display the specific fine radial and comarginal ornamentation.

Out of the syntypes of *Cardiola rugosa* Kayser (1873) from the Enkeberg, specimen GZG 490-131 has to be re-assigned to *Loxopteria gibbosa*, because it presents the fine ornamentation of this taxon and is clearly a loxopteriid LV. The remaining syntypes of *C. rugosa* Kayser have to be placed into the lunulacardiids, because they develop the specific notch on the antero-dorsal margin, which is typical for that group (for further discussion see *Elasmatium*)

Occurrence:

UD II-?VI (Tab. 3; Tab. 4).

The youngest occurrence is Schmidt's (1922, 1924) reports of *L. gibbosa* from the “Dasberger Kalk” of the Northeastern Rhenish Massif. These beds are broadly interpreted as UD V/VI. This quote is the only account of the taxon from such young levels, and there is no material supporting it. Therefore, until there is confirmation of actual specimens from the UD V or younger beds, *L. gibbosa* assumed to become extinct after the *annulata* Event in the UD IV-C.

Locality	Region	Reference	Stratigraphic level
Aeketal	Hercynian Mountains	Born, 1912	UD II/III
Beul	Northeastern RM	Lange, 1929	UD IV
Beul	Northeastern RM	Paeckelmann, 1938	UD II/III
Bohlen	Thuringia	Meyer, 1920	UD IV-A
Enkeberg	Northeastern RM	Lange, 1929	UD III
Enkeberg	Northeastern RM	Paeckelmann, 1936a	UD II/III
Eulenspiegel	Northeastern RM	Schmidt, 1924	UD V/VI
Gattendorf	Franconian Forest, Southeastern Germany	Wurm, 1961	UD III-C
Gattendorf	Franconian Forest, Southeastern Germany	Wurm, 1961	UD IV-A
Gattendorf	Franconian Forest, Southeastern Germany	Schindewolf, 1923	UD IV-A
Geuser	Franconian Forest, Southeastern Germany	Münster, 1840	UD II

Hemberg	north of Iserlohn, Northeastern RM	Schmidt, 1924	UD V/VI
Hönnevalley	Northeastern RM	Schmidt, 1924	UD V/VI
Kirchhofen	Lahn Dill Syncline	Kegel, 1922	UD II
Nanzenbach	Lahn Dill Syncline	Kegel, 1922	UD II
Oued Aricha	Southern Meseta	Termier and Termier, 1951	UD II
Oberscheld	Lahn Dill Syncline	Frech, 1891	UD II/III
Reitenberg	Northeastern RM	Becker, 1992	UD IV-A
SW of Hönnevalley	Northeastern RM	Schmidt, 1924	UD V/VI
Three Forks Shale	Montana	Raymond, 1907	UD IV
Three Forks Shale	Montana	Raymond, 1909	UD IV
Wettmarsen	Northeastern RM	Paeckelmann, 1936a	UD II/III
Witoszowa	Swiebodzice Syncline, Poland	Gunia, 1968	UD III-C

Table 3 References quoting the occurrence of *Loxopteria gibbosa*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Aeketal	Clymenien Kalk, Bank 8	Born, 1909	UD III-C	GZG 462-10	
Aeketal	Clymenien Kalk, Bank 8	Born, 1909	UD III-C	GZG 462-9	
Beringhäuser Tunnel	Clymenien Kalk	Denckmann, 1893	UD II/IV	MB.M.2302	
Beul	Oberdevon / IV	Lange, 1922	UD IV	MB.M.222.2	
Beul	Oberdevon / IV	Lange, 1922	UD IV	MB.M.2221.4	
Beul	Oberdevon / IV	Lange, 1922	UD IV	MB.M.2217.3	
Beul	Oberdevon/ Famennian IV	-	UD IV	MB.M.2215.2	
Beul	Prolobites Zone/ Schurf 1/ 2,50m	Paeckelmann, 1931	UD III	MB.M.4368	
Beul	tocl2 annulata-Zone	Haarmann, 1902/3	UD IV-A	MB.M.4367	
Braunau	Clymenien Kalk	Schwalm 1902	UD II/IV	MB.M.4370	
Braunau	tocl b	Denckmann, 1899	UD II/IV	MB.M.4369	
Enkeberg	Oberdevon	Schülcke	UD II/III	MB.M.4356	
Enkeberg	Oberdevon III	Lange, 1922	UD III	MB.M.2217.1	
Enkeberg	Oberdevon III	Lange, 1922	UD III	MB.M.2217.6	
Enkeberg	Oberdevon III	Lange, 1922	UD III	MB.M.2217.8	
Enkeberg	Schicht 11/ Prolobites- Zone	Paeckelmann	UD III	MB.M.4355	
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II-E/F	MB.M.4358	
Enkeberg	Schicht 9/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4354	
Enkeberg	Schicht 9/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4362	
Enkeberg	Schicht 9/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4360	
Enkeberg	tocl	Denckmann	UD II/IV	MB.M.4359	
Enkeberg	v. Koenen Schurf	Denckmann/ Lotz, 1900	UD II/III	MB.M.4361	
Geuser	Clymenien Kalk	Münster	UD II/IV	BSPG	Lectotype C.

				AS VII 1729	problematicum
Hamar Laghdad	UD II C	Becker	UD II-C	B6A-35.125	
Kirchhofen, Weilburg	Kalkschicht, Cypridinenschiefer	Fuchs, 1912	UD II	MB.M.4374	
Mrakib / Maider	Base E	Becker	UD III-C	B6A-35.120	
Mrakib / Maider	D	Becker	UD III-C	B6A-35.123	
Mrakib / Maider	H3	Becker	UD III-C	B6A-35.122	
Mrakib / Maider	N2	Becker	UD III-C	B6A-35.121	
Nanzenbach	to	Kegel, 1927	UD II	MB.M.4375	
Oberscheld	-	Denckmann, 1894	UD II/III	MB.M.4371	
Oberscheld	Oberes Oberdevon	Bolle, 1874	UD II/III	MB.M.4353	
Rich Bon Konrazia	UD III-IV	Becker	UD III-IV	B6A-35.124	
Schübelhammer, Franconian Forest	basis postera-Zone Wagnerbank	Weyer	UD IV-A	B6A-35.126	Neotype A. gibbosa
Schübelhammer, Franconian Forest	basis postera-Zone Wagnerbank	Weyer	UD IV-A	B6A-35.127	
Schübelhammer, Franconian Forest	basis postera-Zone Wagnerbank	Weyer	UD IV-A	B6A-35.128	
Schurf Dasberg	Oberdevon IV, Schicht 34	Paeckelmann	UD IV	MB.M.4372	
Schurf Dasberg	Oberdevon IV, Schicht 34	Paeckelmann	UD IV	MB.M.4373	
Wettmarsen-Hirre	Prolobites-Zone	Paeckelmann, 1931	UD III	MB.M.4364	
Wettmarsen-Hirre	Prolobites-Zone	Paeckelmann, 1931	UD III	MB.M.4365	
Wettmarsen-Hirre	Prolobites-Zone	Paeckelmann, 1931	UD III	MB.M.4366	
Wildungen	Clymenien Kalk	Holzapfel	UD II/IV	SMF XV/3-2158	Lectotype K. laevis
Wildungen	Clymenien Kalk	-	UD II/IV	MB.M.4493	

Table 4 Examined specimens of *Loxopteria gibbosa*.

Loxopteria inflata (Münster, 1840)

Pl. 2 , Figs. 1-3; Pl. 6, Fig. 17

* + 1840 *Avicula inflata* MÜNSTER, p. 53, pl. 11. figs. 5, 5a.
+ v non 1891 *Kochia* (*Loxopteria*) *laevis* FRECH, p. 76, pl. 6, fig. 3.
+ 1901 *Capulus* ? sp. DREVERMANN, p. 42, pl. 14, fig. 11.
1904 *Loxopteria laevis*.- CLARKE, p. 274, pl. 14, fig. 1-7.
+ v 1904 *Loxopteria vasta* CLARKE, p. 275, pl. 13, fig. 18.
1905 *Capulus* ? sp.- DREVERMANN, p. 389.
1923 *Loxopteria laevis*.- SCHINDEWOLF, p. 274.
+ 1923 *Loxopteria Drevermanni* SCHINDEWOLF, p. 286, 287.
v 1923 *Loxopteria laevis*.- PAECKELMANN, p. 71, 72 73, 77, 78.
1924 *Loxopteria laevis*.- SCHMIDT, p. 110, 143, 161.
v 1929 *Loxopteria Drevermanni*.- LANGE, p. 24.
1929 *Sluzka laevis*.- LANGE, p. 29.
1936b *Loxopteria drevermanni*.- PAECKELMANN AND KÜHNE, p. 10.
1961 *Loxopteria drevermanni*.- WURM, p. 120.
1980 *Kochia* (*Loxopteria*) *laevis*.- KAEVER et al., p. 160, pl. 28, fig. 4.
1992 *Loxopteria* cf. *drevermanni*.- BECKER, p. 10.

Lectotype (selected herein): BSPG AS VII 1728.
Type locality: Schübelhammer (Franconian Forest, Southeastern Germany).
Type stratum: "Clymenien Kalk" (Famennian).

Material:
See Tab. 6.

Diagnosis:
Small to medium sized loxopteriid shell.
Ornamentation consisting only of comarginal growth lines.

Description:
As *L. gibbosa* and *L. dispar*, but without any radial ornamentation (Pl. 2, Figs. 1-3).
Ornamentation consisting of irregularly spaced, unequal conentric growth lines, sometimes closer spaced towards ventral margin (Pl. 2, Fig. 1).
Lectotype (BSPG AS VII 1728; Pl. 6, Fig. 17) poorly preserved RV steinkern, with subtle comarginal growth lines, lacking any radial ornamentation. Dorsal margin, umbo and hinge line missing.
Variation of length/height ratio see Fig. 10.
Largest specimen (MB.M.4342): height, 28.1 cm; length, 26.2 cm.
Smallest specimen (MB.M.4352): height, 11.2 cm; length, 10.8 cm.

Discussion:
Münster (1840) identified a new species from Schübelhammer (Franconian Forest, Southeastern Germany), *Avicula inflata*. He stated that at first he thought this taxon belonged to *L. gibbosa*, because they are so similar in morphology. But the lack of any radial ornamentation implicated a separation of both. Out of the two types hosted in the Staatssammlung München, BSPG AS VII 1727 is not identifiable and therefore, BSPG AS VII 1728, which preserves faint ornamentation, is selected as lectotype (Pl. 6, Fig. 17). It is a RV, which displays the morphology of loxopteriids and only subtle comarginal growth lines.
Drevermann (1901) determined a specimen from Langenaubach as *Capulus* ?. Due to its peculiar shape, he suggested that it is a gastropod. Later, Drevermann (1905) corrected this assignment and stated that this specimen probably is a representative of the loxopteriids, but he did not specify this affiliation by any determination.
Frech (1891) described *L. laevis* as displaying only fine growth lines, but this species, based on the holotype (SMF XV/3-2158, Pl. 4, Fig. 14) (see above), presents both fine radial and comarginal ornamentation. Therefore, *L. laevis* is not a junior synonym of *L. inflata* but of *L. gibbosa*.

Subsequent, authors designated their material after Frech´s description and identified specimens with comarginal and no radial ornamentation as *L. laevis* Frech (e.g., Schmidt, 1924, p. 143). Therefore, *L. laevis* material described by Clarke (1904), Paeckelmann (1923), Schmidt (1924), and Kaever et al. (1980) are actually synonyms of *L. inflata* (Münster).
Schindewolf (1923) established *Loxopteria drevermanni* from Gattendorf (Franconian Forest, Southeastern Germany) for loxopteriid without radial ornamentation. Specimens, which lack any radial ornamentation while displaying comarginal growth lines, are representatives of *L. inflata* and, therefore, *L. drevermanni* is a junior synonym of this species.
Furthermore, he determined one LV as *L. laevis* and referred to the figures and description of Clarke (1904). These North American specimens unambiguously belong to *L. inflata*, because they do not present any radial ornamentation (Clarke, 1904) and, therefore, the Schindewolf specimen has to be re-assigned to *L. inflata* as well.
Clarke (1904) identified a new species from Forestville (New York State), *Loxopteria vasta* (NYSM 5327, Pl. 2, Fig. 3). He noted that this large RV, which is the holotype by monotypy, is quite close to *L. laevis*, but the posterior part of the valve is not as distinctly raised upwards as in this taxon. The holotype (NYSM 5327, Pl. 2, Fig. 3) proves, due to its morphology and especially because of its exclusively comarginal ornamentation, distinctly its re-assignment to *L. inflata*.

Occurrence:
UD ?I-J/?VI (Tab. 5; Tab. 6)
The oldest occurrence of *L. inflata* is a specimen from Martenberg, which was derived by Paeckelmann from the "Adorfer Kalk". It remains questionable if this specimen is from the uppermost Frasnian or the basal Famennian. The stratigraphic range of *Loxopteria* would support a first appearance of *L. inflata* in the Famennian after the Kellwasser crisis.
The youngest appearance of this taxon is quoted to be UD V/VI (Schmidt, 1924). Unfortunately, this Schmidt specimen could not be traced in the collection of the Berlin Naturkunde Museum, where the rest of the Schmidt material is located. Therefore, there is no actual material confirming the occurence of *L. inflata* from levels younger than UD IV. Thus, it is assumed herein that this species probably became extinct right after the annulata event (UD IV).

Locality	Region	Reference	Stratigraphic level
Ainghausen	Northeastern RM	Schmidt, 1924	UD V/VI
Albringen	Northeastern RM	Schmidt, 1924	UD V/VI
Balve	Northeastern RM	Kaever et al, 1980	Famennian
Barmen	Western RM	Kaever et al, 1980	Famennian

Beul	Northeastern RM	Kaever et al, 1980	Famennian
Beul	Northeastern RM	Lange, 1929	UD IV-A
Beul	Northeastern RM	Paeckelmann, 1936a	UD II/IV
Beul	Northeastern RM	Schindewolf, 1923	UD IV-A
Bohlen	Saalfeld, Southeastern Germany	Schindewolf, 1923	UD II-IV
Dasberg	Northeastern RM	Schmidt, 1924	UD V/VI
Enkenberg	Northeastern RM	Lange, 1929	UD III-C
Frankenburg	Northeastern RM	Schmidt, 1924	UD V/VI
Gattendorf	Franconian Forest, Southeastern Germany	Wurm, 1961	UD IV-A
Gattendorf	Franconian Forest, Southeastern Germany	Schindewolf, 1923	UD IV
Gowanda Shale, Forestville	Chautauqua County, New York State	Clarke, 1904	UD II-C
Grasberg	Northeastern RM	Paeckelmann, 1924	UD III-C
Kirschhofen/ Weilburg	Northeastern RM	Schmidt, 1924	UD II/III
Reitenberg	Northeastern RM	Becker, 1992	basal UD IV-A
Reitenberg	Northeastern RM	Becker, 1992	middle UD IV-A
Rülsterberg	Northeastern RM	Paeckelmann, 1924	UD III-C
Schübelhammer	Franconian Forest, Southeastern Germany	Münster, 1840	UD II/IV
southwest of Hövel	Northeastern RM	Schmidt, 1924	UD V/VI
Wettmarsen area	Northeastern RM	Paeckelmann, 1924	UD III-C

Table 5 References quoting the occurrence of *Loxopteria inflata*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Beul	*annulata*-Zone/ Schurf 1/ 5.60 m	Paeckelmann, 1931	UD IV-A	MB.M.4348	
Beul	tocl2 *annulata*-Zone	Haarmann, 1902/3	UD IV-A	MB.M.4352	
Beul	*annulata*-Zone/ Schurf 1/ 5.60 m	Paeckelmann, 1931	UD IV-A	MB.M.4349	
Beul	*annulata*-Zone/ Schurf 1/ 5.60 m	Paeckelmann, 1931	UD IV-A	MB.M.4350	
Beul	*annulata*-Zone/ Schurf 1/ 11.40 m	Paeckelmann, 1931	UD IV-A	MB.M.4347	
Beul	Schurf 1/ 7.10 m	Paeckelmann, 1931	UD IV-A	MB.M.4346	
Effenberg	Oberdevon	Henke, 1906	Famennian	MB.M.4345	
Enkeberg	Oberdevon III	Lange, 1922	UD III-C	MB.M.2217.2	
Enkeberg	v. Koenen Schurf	Denckmann/ Lotz, 1900	UD II/III	MB.M.4340	
Eskesberg	Oberes Oberdevon	-	UD II-D/E	MB.M.4351	
Forestville	Gowanda Shale	Clarke	UD II-C	NYSM 5327	Holotype *L. vasta*
Langenaubach	-	Denckmann, 1895	Famennian	MB.M.4341	

Langenaubach	Schalsteinbrekzie/ Block 15	Denckmann	Famennian	MB.M.4342	
Martenberg-Klippe	Adorfer Kalk/ Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4344	
Schübelhammer	Clymenien Kalk	Münster	UD II/IV	BSPG AS VII 1727	
Schübelhammer	Clymenien Kalk	Münster	UD II/IV	BSPG AS VII 1728	Lectotype *L. inflata*
Wildungen	Unterer Clymenien Kalk	Denckmann, 1884	UD II/V	MB.M.4343	

Table 6 Examined specimens of *Loxopteria inflata*.

Loxopteria problematica (MÜNSTER, 1840)
Pl. 2 Figs. 4-13; Pl. 6 Figs. 15-16

* + v 1840 *Avicula ? problematica* MÜNSTER, p. 53, pl. 11, fig. 6.
\+ v 1840 *Avicula semi auriculata* MÜNSTER, p. 51, pl. 10, fig. 1.
\+ v non 1842 *Cardium problematicum* MÜNSTER, p. 119, pl. 11, fig. 8.
\+ ? 1900 *Kochia problematica* BEUSHAUSEN, p. 175.
1907 *Loxopteria* aff. *laevis*.- RAYMOND, p. 118.
\+ 1909 *Loxopteria clarkei* RAYMOND, p. 147, pl. 5, figs. 8-10, 12-17.
1924 *Cardium problematicum*.- SCHMIDT, p. 162.
1912 ? *Avicula problematica*.- BORN, p. 577.

Lectotype (designated herein): BSPG AS VII 1725.
Type locality: Presseck (Franconian Forest, Southeastern Germany).
Type stratum: "Clymenienkalk" (lower Famennian, Nehdenian, UD II).

Material:
See Tab. 8.

Diagnosis:
Small to medium sized loxopteriids shell.
Ornamentation consisting of fine, unequal radial lines, fine comarginal lines, variable number of strong, comarginal rugae underneath umbo. Fine, comarginal ornamentation intersecting radial ribs, partly generating small nodes.
Umbo especially conspicuously set of from shell body of LV and RV.

Description:
As in *L. gibbosa* with several strong comarginal rugae underneath the umbo (Pl. 2, Figs. 6, 10-11).
Valve completely covered by fine radial-comarginal ornamentation (Pl. 2, Fig. 5).

Umbo is separated from the shell body by pronounced groove, emphasizing its the knob-like development (Pl. 2; Figs. 6-7, 10, 13).
Lectotype (BSPG AS VII 1725; Pl. 6, Fig. 16) LV with faint fine comarginal and radial ornamentation and five strong comarginal rugae underneath the umbo. Hinge line and outline not preserved.
Variation of length/height ratio see Fig. 10.
Largest specimen (MB.M.2216): height, 25.6 cm; length, 24.2 cm.
Smallest specimen (B6A-35.96): height, 10.0 cm; length, 9.7 cm.

Discussion:
Münster (1840) described *Avicula* ? *problematica* from Presseck (Franconian Forest, Southeastern Germany). The two types (BSPG AS VII 1725-26) of this species are hosted in the Bayerische Staatssammlung München. BSPG AS VII 1725 (Pl. 6, Fig. 16) corresponds to Münster´s figure (1840, pl. 11, fig. 6) and is selected as the lectotype. Both specimens do not preserve the outline or the umbonal region, but the characteristic ornamentation identifies those specimens clearly as loxopteriids. The development of five to six, additional, strong, comarginal rugae underneath the umbo of the LV is a main feature of both specimens and , therefore, of the species.
Furthermore, Münster (1840) introduced another new species, *Avicula semiauriculata*, also from Presseck. The originals include four specimens BSPG AS VII 1722-24, BSPG AS VII 1727 from Presseck. BSPG AS VII 1723 and BSPG AS VII 1722 cannot be identified at species level since no ornamentation is preserved. BSPG AS VII 1724 does not display any features and is, therefore, indefinable. It is impossible to reconstruct, which of these specimens actually correspond to Münster´s original illustration (1840, pl. 11, fig. 1c). As in other cases, the figure seems to mirror more artistic enthusiasm than reality. The only well preserved specimen is BSPG AS VII 1721 (Pl. 6, Fig. 15) and is selected herein as lectotype of *A. semiauriculata* Münster. It is a RV, which presents strong comarginal ornamentation underneath the beak and fine ornamentation, which comprises radial and comarginal lines. Especially the knob-like development of its umbo is a specific character. This ornamental development is the characteristic feature of *L. problematica*. *A. problematica* is favored over *A. semiauriculata* as valid taxon for this species, because LV´s are more suitable to identify *Loxopteria* species. Therefore, *A. semiauriculata* becomes a subjective synonym of *L. problematica*.
Later, Münster (1842) described *Cardium problematicum* from Geuser (Franconian Forest, Southeastern Germany). The lectotype (BSPG AS VII 1729) of *Cardium problematicum* Münster, 1842, places it in synonymy of *L. gibbosa* (see above).Within the Loxopteria species this taxon is anyways a secondary and invalide homonym of L. problematica (Münster, 1840).
Beushausen (1900) noted in his faunal list of the Clymenienkalk of the Oberharz *Kochia problematica*. There is no discussion or comment concerning the re-assignment of *problem-*

atica to *Kochia*. Also it is ambiguous which of Münster´s species (1840 or 1842) he referred to. Schmidt (1924) listed *Cardium problematicum* from the Franconian Forest (Southeastern Germany), but also without any description it is also dubious, which Münster species his determination is based on.

Raymond (1909) identified a new species from the Three Forks Shale of Montana, *Loxopteria clarkei*. In a prior study, Raymond (1907) described the same taxon as "*Loxopteria*, near *Loxopteria laevis* Frech", because he was not sure about the affiliation of these specimens. This species clearly possesses, apart from the loxopteriid shell development, the characteristic comarginal undulations beneath the beak. Therefore, it is here placed into synonymy of *Loxopteria problematica*.

Born (1912) designated one specimen from the Aeketal as ? *Avicula problematica*. Due to the described ornamentation, it could be assumed to assign it to *L. problematica*. Unfortunately, the specimen has not been traced amongst the Born collection at Göttingen and Born did not figure it. Therefore, its affiliation remains questionable.

Occurrence:

UD II / IV (Tab. 7; Tab. 8)

Locality	Region	Reference	Stratigraphic level
Aeketal	Hercynian Mountains	Born, 1912	UD III-C
Geuser	Franconian Forest, Southeastern Germany	Münster, 1840	UD II
Presseck	Franconian Forest, Southeastern Germany	Münster, 1840	UD II
Three Forks Shale	Montana	Raymond, 1907	UD IV
Three Forks Shale	Montana	Raymond, 1909	UD IV

Table 7 References quoting the occurrence of *Loxopteria problematica*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.90	
Beul	*annulata*-Zone Schurf 1/ 8.70m	Paeckelmann, 1931	UD IV-A	MB.M.4296	
Beul	*annulata*-Zone Schurf 1/ 5.60m	Paeckelmann, 1931	UD IV-A	MB.M.4297	
Beul	*annulata*-Zone Schurf 1/ 5.60m	Paeckelmann, 1931	UD IV-A	MB.M.4298	

Beul	*annulata*-Zone Schurf 1/ 12,75m	Paeckelmann, 1931	UD IV-A	MB.M.4299	
Beul	*annulata*-Zone Schurf 1/ 8.70m	Paeckelmann, 1931	UD IV-A	MB.M.4300	
Beul	*annulata*-Zone Schurf 1/ 5.60m	Paeckelmann, 1931	UD IV-A	MB.M.4301	
Beul	*annulata*-Zone Schurf 1/ 11.40m	Paeckelmann, 1931	UD IV-A	MB.M.4302	
Beul	*annulata*-Zone Schurf 1/ 11.40m	Paeckelmann, 1931	UD IV-A	MB.M.4303	
Beul	*annulata*-Zone Schurf 1/ 12,75m	Paeckelmann, 1931	UD IV-A	MB.M.4304	
Beul	*annulata*-Zone Schurf 1/ 8.70m	Paeckelmann, 1931	UD IV-A	MB.M.4305	
Beul	Enkeberger Kalk	-	UD III/IV	MB.M.4307	
Beul	Prolobites Zone Schurf 1/ 1m	Paeckelmann, 1931	UD III	B6A-35.94	
Beul	Schurf 1, 7,10 m	Paeckelmann, 1931	UD IV	MB.M.4306	
Beul	*annulata*-Zone	Haarmann, 1902/3	UD IV-A	MB.M.4308	
Braunau	tocl	Denckmann, 1898	UD II/III	MB.M.4316	
Dasberg	do IV / Schicht 31	Schindewolf	UD IV	MB.M.4313	
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann, 1931	UD II-E/F	MB.M.4290	
Enkeberg	Unterer Clymenien Kalk/ v. Koenen Schurf	Denckmann, 1893	UD II/III	MB.M.4294	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II/IV	MB.M.4291	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II/IV	MB.M.4292	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II/IV	MB.M.4293	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II/IV	MB.M.4295	
Enkeberg/ Schurf Paeckelmann	Schicht 18	Paeckelmann, 1931	UD II-E/F	MB.M.4289	
Mrakib/Maider	H2	Becker et al., 2002	UD III-C	B6A-35.92	
Mrakib/Maider	N2	Becker et al., 2002	UD IV-A	B6A-35.87	
Mrakib/Maider	N2	Becker et al., 2002	UD IV-A	B6A-35.89	
Mrakib/Maider	TOP I	Becker et al., 2002	UD III-C	B6A-35.88	
Oberscheld	Clymenien Kalk	Lotz, 1901	UD II/III	MB.M.4315	
Oberscheld	Oberes Oberdevon	Bolle, 1874		MB.M.4317	
Presseck	Clymenien Kalk	Münster	UD II	BSPG AS VII 1721	Lectotype *A. semi auriculata*
Presseck	Clymenien Kalk	Münster	UD II	BSPG AS VII 1725	Lectotype *A. problematica*
Presseck	Clymenien Kalk	Münster	UD II	BSPG AS VII 1726	
Schurf Dasberg	Oberdevon IV/ Schicht 34	Paeckelmann	UD IV	MB.M.4314	
Schurf Dasberg	Oberes Oberdevon IV/ Schicht 34	Paeckelmann	UD IV	MB.M.4312	
Tafilalt	UD II-IV, loose	Becker	UD II-IV	B6A-35.93	
Trident Mbr. Logan,	UD IV-A	Becker, 1987	UD IV-A	B6A-35.91	
Trident Mbr. Logan,	UD IV-A	Becker, 1987	UD IV-A	B6A-35.95	

Trident Mbr. Logan,	UD IV-A	Becker, 1987	UD IV-A	B6A-35.96
Weisse Frau/ N-Hang	to2	Paeckelmann, 1924	UD II/III	MB.M.4311
Wettmarsen-Hirre	Prolobites Zone	Paeckelmann, 1931	UD III	MB.M.4309
Wettmarsen-Hirre	Prolobites Zone	Paeckelmann, 1931	UD III	MB.M.4310

Table 8 Examined specimens of *Loxopteria problematica*.

Loxopteria meioklina n. sp.
Pl. 3, Figs. 1-10

Holotype: B6A-35.130.
Type locality: Mrakib / Maider (Morocco).
Type stratum: basal Bed E, UD III-A/B (Famennian).

Etymology: from Greek: meion-less / klino-incline.

Material:
B6A-35.129-132 (collection Becker) from Mrakib/Maider (Tab. 9).

Diagnosis:
Small loxopteriid shell.
Umbo opisthogyrate (Pl. 3, Figs. 4, 10).
Ornamentation consisting of fine comarginal growth lines, subtle radial ribs, sometimes additional irregular and stronger comarginal rugae (Pl. 3, Figs. 1-2).
LV: less inclined posterior than other loxopteriids. Umbo opisthogyrate and blunt; prodissoconch markedly set off from body of the shell (Pl. 3, Figs. 4, 8, 9) .
RV: loxopteriid, sometimes higher convex than other loxopteriids (Pl. 3, Fig. 7).

Description:
LV: trigonal, posterior third of shell less markedly bent downwards and shell less inclined posterior than in other *Loxopteria* species; highest convexity more in centre of valve.
Umbo blunt, strongly convex (e.g., B6A-35.129, Pl. 3, Figs. 2-3; B6A-35.130, Pl. 3, Figs. 8-9), not as far projecting over hinge line as *L. dispar*; prodissoconch anteriorly developing straight edge parallel to the hinge line (e.g., B6A-35.129, Pl. 3, Fig. 4; B6A-35.130, Pl. 3, Fig. 10).
RV: transverse oval, posterior portion of shell subtlely bent upwards (e.g., B6A-35.130, Pl. 3, Fig. 7).

Umbo opisthogyrate, prodissoconch set off from body of shell.
Ornamentation of both valves consisting of fine radial ribs, subtle comarginal growth lines, sometimes stronger comarginal rugae.

Discussion:
Loxopteria meioklina n. sp. is established herein for specimens, which display an opisthogyrate umbo. This development is not shown in any other *Loxopteria* species. The general inequivalve shell morphology, with the lid-shaped RV and the highly convex LV, and the loxopteriid fine comarginal and radial ornamentation of these specimens identify them clearly as a *Loxopteria* species. But the blunt umbo and the edge, which is parallel to the hinge line, are characters, which distinguish this taxon from all other known species and, therefore, allow the embedding of these specimens in a new species.
This taxon could represent a local Moroccan variation of *Loxopteria*, but further studies of this genus will be needed to ascertain the true distribution of this species.

Occurrence:
Loxopteria meioklina is reported from Mrakib/Maider (Morocco). Specimens occur in the UD III-A/B and the UD III-C from this outcrop. Until now these are the only representatives of this species. If the spatial distribution of *L. meioklina* is restricted to Moroccon outcrops, this would be a regional variation of *Loxopteria*.

Collection Number	Height / LV	Length / LV	Inflation / LV
B6A-35.129	8.9 mm	8.5 mm	3.7 mm
B6A-35.130	13.5 mm	13.0 mm	4.0 mm
B6A-35.131	19.8 mm	19.1 mm	6.2 mm
B6A-35.132	14.6 mm	14.5 mm	3.5 mm

Table 9 Measured values of *L. meioklina* specimens.

Loxopteria sp.

Material:
see Tab. 10.

Discussion:
These specimens can unequivocally be placed in the genus *Loxopteria*, but due to the missing ornamentation a determination on species level is impossible.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number
Beul	*annulata*-Zone/ Schurf 1/ 11.40m	Paeckelmann, 1931	UD II/IV	MB.M.4335
Beul	*annulata*-Zone/ Schurf 1/ 5.60m	Paeckelmann, 1931	UD II/IV	MB.M.4334
Beul	*annulata*-Zone	Denckmann, 1900	UD II/IV	MB.M.2290
Beul	Oberdevon / IV	-	UD II/IV	MB.M.2215.1
Beul	Oberdevon / IV	Lange, 1923	UD II/IV	MB.M.2221.1
Biesenberg	-	Denckmann, 1894	UD II	MB.M.4333
Braunau	Unterer Clymenien Kalk	Denckmann, 1884	UD II/V	MB.M.4328
Burg	to4	Paeckelmann, 1924	UD II	MB.M.4336
Enkeberg	-	Denckmann/Lotz, 1900	UD II/III	MB.M.4323
Enkeberg	-	Denckmann/Lotz, 1900	UD II/III	MB.M.4319
Enkeberg	Oberdevon III	Lange, 1922	UD II/III	MB.M.2217.3
Enkeberg	Oberdevon III	Lange, 1922	UD II/III	MB.M.2217.5
Enkeberg	Oberes Oberdevon	Müller, 1882	UD II/III	MB.M.4322
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II/E/F	MB.M.4325
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II/E/F	MB.M.4326
Enkeberg	Schicht 20/ Untere Cheiloceras-Zone	Paeckelmann	UD II-A/E	MB.M.4327
Enkeberg	Schicht 9/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4321
Enkeberg	Schicht 9/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4324
Enkeberg	v. Koenen Schurf	Denckmann/ Lotz, 1900	UD II/III	MB.M.4318
Enkeberg	v. Koenen. Schurf	Denckmann/ Lotz, 1900	UD II/III	MB.M.4320
Eskesberg	Oberes Oberdevon	Grüneberg	UD II-D/E	MB.M.4351
Eskesberg	Unterer Cypridinenschiefer	Grüneberg	UD II-D/E	MB.M.4330
Grube Ypsilanta	Oberdevon Kalk	Lotz, 1901		MB.M.4337
Hauern	Unterer Clymenien Kalk	Denckmann, 1894	UD II/V	MB.M.4329
Hövel	to cl	Denckmann, 1900	UD III	MB.M.4344
Martenberg-Klippe	Adorfer Kalk	Paeckelmann, 1928	Basis UD II	MB.M.4331
Martenberg-Klippe	Adorfer Kalk	Paeckelmann, 1928	Basis UD II	MB.M.4332
Mrakib/Maider	TOP I	Becker et al., 2002	UD III-C	B6A-35.116
Nehden	Mittleres Oberdevon	v. Buch	UD II-C/E	MB.M.2220.3
Oberscheld	Oberdevon	-	UD II/III	MB.M.2214.3

Oberscheld	Oberdevon	-	UD II/III	MB.M.2214.2
Presseck	Clymenien Kalk	Münster	UD II	BSPG AS VII 1723
Presseck	Clymenien Kalk	Münster	UD II	BSPG AS VII 1722
Reitenberg	UD III-C	-	UD III-C	B6A-35.119
Reitenberg	UD III-C	Becker	UD III-C	B6A-35.117
Reitenberg	UD III-C	Becker	UD III-C	B6A-35.118
Schübelhammer	Clymenien Kalk	Münster	UD II/IV	BSPG AS VII 1727
Wettmarsen-Hirre	Prolobites Zone	Paeckelmann, 1931	UDIII	MB.M.4338
Wettmarsen-Hirre	Prolobites Zone	Paeckelmann, 1931	UDIII	MB.M.4339
Ziegelei Nie	Schicht 7 / Lower UD III	Becker	UD III-C	B6A-35.103
Ziegelei Nie	Schicht 7 / Lower UD III	Becker	UD III-C	B6A-35.101
Ziegelei Nie	Schicht 7 / Lower UD III	Becker	UD III-C	B6A-35.111
Ziegelei Nie	Schicht 7 / Lower UD III	Becker	UD III-C	B6A-35.105
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.102
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.112
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.115
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.97
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.108
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.114
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.113
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.106
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.100
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.98
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.104
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.109
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.99
Ziegelei Nie	Schicht 7-9/ Lower UD III	Becker	UD III-C	B6A-35.110
Ziegelei Nie	Schicht 9/ Lower UD III	Becker	UD III-C	B6A-35.107

Table 10 Examined specimens of *Loxopteria* sp.

7.1.4 Elasmatium

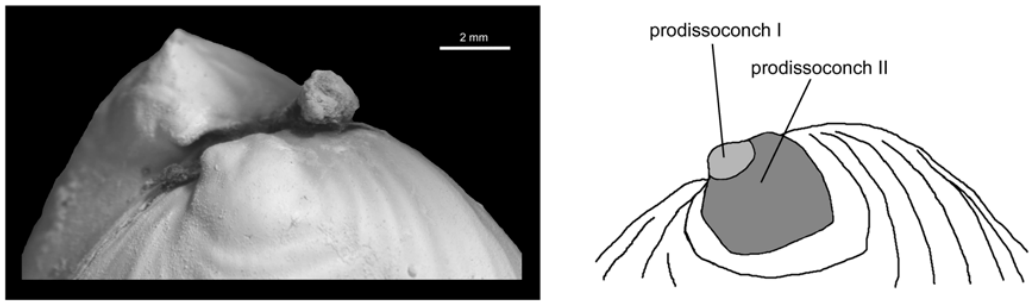


Figure 11 Development of Prodissoconch I/II in *Elasmatium*; (*Elasmatium gowandense* B6A-35.60 from Knoppenbissen Formation, Northern Germany).

Family DUALINIDAE Conrath, 1887
Subfamily LOXOPTERIINAE nov. subfam.
Genus *Elasmatium* Clarke, 1904

Type species: *Elasmatium gowandense* Clarke 1904 (SD Newell and La Rocque, 1969).
Included species: *Elasmatium gowandense* Clarke 1904, *Elasmatium elongata* (Münster, 1840)

Diagnosis (revised):
Strongly inequivalve. Umbo opisthogyrate to orthogyrate.
LV: circular in marginal outline, shell body conical, highly convex. Knob-like umbo. Ornamentation consisting of comarginal growth lines.
RV: lid-shaped valve, strong comarginal rugae developed after knob-like umbo. Comarginal growth lines finer, closer spaced towards ventral margin.

Discussion:
Clarke (1904) designated this genus for disarticulated valves from the Gowanda Shale of New York State. He described these peculiar specimens without having an idea of their affiliation and stated that he included them into the proposed genus *Elasmatium* Clarke. Newell and La Rocque (1969) listed this genus among genera of uncertain assignment, with *Elasmatium gowandense* Clarke as type species.

The study of well preserved articulated specimens, especially from Bergisch Gladbach, (Northeastern Rhenish Massif) clarifies the morphology of LV and RV. The strong inequivalve bauplan and especially the development of the RV, which is similar to the RV of *Loxopteria* Frech prove the re-assignment of *Elasmatium* Clarke to Loxopteriinae nov. subfam. The orientation of the umbo is peculiar in this subfamily. *Elasmatium* is prosogyrate and *Loxopteria* appears to be antigyrate. Therefore, the RV´s of this subfamily are all opisthogyrate, while the LV´s of *Loxopteria* species become, due to the inclination of this valve, prosogyrate. *L. meioklina*, which develops an orthogyrate umbo, could represent a transitional from in this group.

Occurrence:

Elasmatium Clarke occurs all over the Rhenish Massif (Germany), Harz Mountains (Germany) and Franconian Forest (Southeastern Germany) in the UD II/IV. Furthermore, North American localities from Montana and New York State present this taxon from the same stratigraphic levels. Single specimens have been observed from Southeastern Morocco.

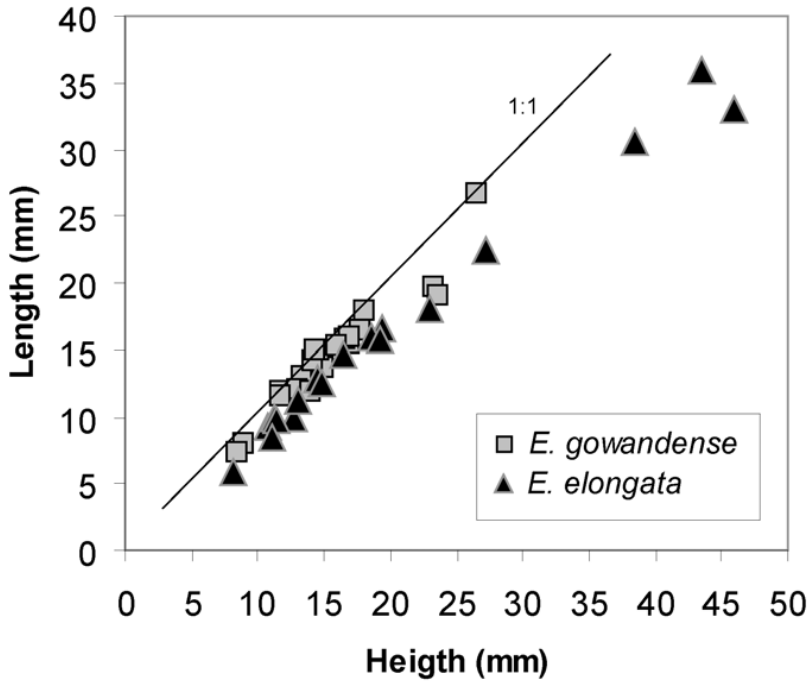


Figure 12 Length/height ratio of *Elasmatium* species showing isometric growth and restricted shape variability.

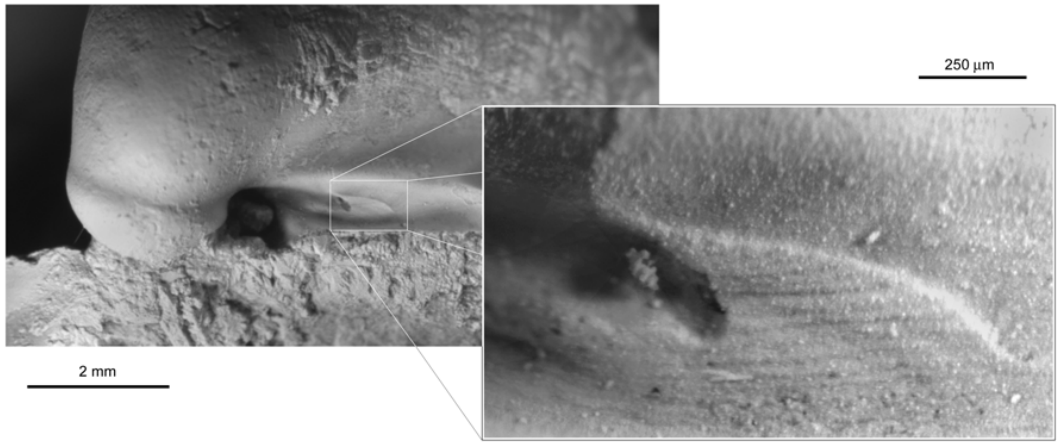


Figure 13 Hinge area and Prodissoconch of *Elasmatium elongata*, with enlarged detail of the anterior portion of the hinge line, showing the faint striae of the lunule region (B6A-35.78 from Nehden).

Elasmatium gowandense Clarke, 1904

Fig. 11; Pl. 5, Figs. 1-12

* + v	1904	*Elasmatium gowandense* CLARKE, p. 294, pl. 12, figs. 21-29.
+ v	1904	*Loxopteria* (*Sluzka*) *corrugata* CLARKE, p. 277, pl. 14, figs. 18-26.
	1923	*Elasmatium gowandense*.- SCHINDEWOLF, p. 275.
	1925	*Elasmatium* cf. *gowandense*.- GRÜNEBERG, p. 83, 55, pl. 3, fig. 12.
	1961	*Elasmatium gowandense*.- WURM, p. 133.
+	1974	*Kochia rugosa* JUX AND KRATH, p. 134, pl. 6, figs. 1-3.
	1990	*Loxopteria corrugata*.- BAIRD AND LASH, p. A34.

Lectotype (designated herein): NYSM 5254.

Type localities: Correll´s Point, Chautauqua Province, Cattaraugus co., New York State.

Type stratum: Gowanda Shale (lower Famennian, Nehdenian, UD II-C).

Material:

see Tab. 12.

Diagnosis:

LV: irregular conical valve, sharp radial ridge subcentral.

Umbo opisthogyrate to orthogyrate.

RV: lid-shaped valve, anterior lateral margin deviating somwhat angularly into ventral margin. Ornamentation parallel to margins, consisting of strong, comarginal rugae, growth lines becoming closely spaced near ventral margin. Umbo opisthogyrate to orthogyrate.

Description:

LV: transverse oval in marginal outline, shell body conical convex, slightly posteriorly inclined (Pl. 5, Figs. 1, 5, 7).

Valve highly inflated, irregular convex, moderately bulging; point of highest inflation more or less in the middle of valve (Pl. 5, Figs. 2, 4, 8, 10).

Prodissoconch I and II, opisthogyrate to orthogyrate (e.g., B6A-35.60, Pl. 5, Fig. 10; B6A-35.70, Pl. 5, Fig. 3; Fig. 11).

Subcentral radial ridge, dividing shell into two disproportional parts. Ridge starting after prodissoconch II from umbo, often with a little, sharp peak in dorsal half of shell (e.g., B6A-35.60, Pl. 5, Fig. 9). Ornamentation consisting of comarginal growth lines (e.g., NYSM 5254, Pl. 5, Fig. 5; NYSM 5246, Pl. 5, Fig. 7).

RV: transverse oval in marginal outline, shell body irregular rectangular. Dorsal portion of valve more or less flat, declining markedly towards margins. Sometimes posterior bit of valve subtle bent upwards. Radial line, separating anterior fourth of the valve from the shell, running towards anterior portion of ventral margin. Along break convexity of shell drawn out, forming edge. Prodissoconch I and II developed, incurved posterior (e.g., Fig. 11; B6A-35.62, Pl. 5, Fig.6; B6A-35.61, Pl. 5, Fig. 12).

Ornamentation consisting of strong comarginal rugae on flat part of valve, finer comarginal growth lines on declining portion of shell (e.g., B6A-35.70, Pl. 5, Fig. 3; B6A-35.60, Pl. 5, Fig. 10).

Pallial line parallel to ventral margin, with small pallial sinus. Pallial line running on both sides up to hinge line. No adductor scars observable (Fig. 9.6).

Hinge line strait to slightly convex, edentulous. Antero-dorsally of umbo lunule-like region with lance-shaped groove.

Transitional forms between *E. gowandense* and *E. rugosa* developing ridge on LV just close to umbo and a less angular RV.

Variation of length/height ratio see Fig. 12.

Largest specimen (NYSM 5254): height, 26.5 cm; length, 26.7 cm.

Smallest specimen (B6A-35.74): height, 8.4 cm; length, 7.3 cm.

Discussion:

Clarke (1904) identified a new species from the Gowanda Shale of New York State, *Elasmatium gowandense*. The syntypes NYSM 5247-53 and NYSM 5246 (Pl. 5, Fig. 7) are all more or less distorted LV´s. NYSM 5254 (Pl. 5, Fig. 5) is selected herein as the lectotype of this species. Clarke (1904) mentioned RV and LV both developing a ridge in the centre of the shell. His misinterpretation of the morphology is result of the lack of articulated specimens. The curve of the umbo is not clearly identifiable in the syntypes, due to their distortion. Therefore, the impression of prosogyrate as well as opisthogyrate beaks probably lead to the

assumption of the presence of LV and RV, although the syntypes are all unequivocally LV´s of this taxon.

Furthermore, Clarke (1904) described a new species based on RV´s from the Gowanda Shale, *Loxopteria* (*Sluzka*) *corrugata* (NYSM 5294-5305). This taxon has to be re-assigned to *Elasmatium gowandense*, because these specimens clearly display the morphology of a RV. Besides the large knob-like umbo, they are characterized by the angular outline, which is generated by the radial ridge located in the anterior portion of the shell. Unfortunatly, the original types have not been restudied herein, and, therefore, no lectotype is selected, but the figures and description given by Clarke (1904) identiefy them unequivocally as *E. gowandense*.

Jux and Krath (1974) described and illustrated well preserved specimens from Koppenbissen Formation (Bergisch Gladbach, Eastern Rhenish Massif) as *Kochia rugosa* Frech. For the first time they described articulated valves. Although they disregarded *Elasmatium* Clarke in their study, they correctly correlated Clarke's *L. corrugata* as RV of these specimens. The marked ridge on the LV and the observation of the corresponding development on the RV places these specimens from the Knoppenbissen Formation clearly into *Elasmatium gowandense*.

Grüneberg (1925) determinated a specimen as *Elasmatium* cf. *gowandense* Clarke. Although it has not been traced in the Grüneberg collection at the Berlin Naturkunde Museum, another specimen (MB.M.4255) and his figures and description confirm the assignment of his material to *E. gowandense*.

Occurrence:

UD II-A / IV (Tab. 11; Tab. 12)

Locality	Region	Reference	Stratigraphic level
Correll´s Point	Chautauqua County, New York State	Clarke,1904	UD II-C
Eskesberg	Elberfeld	Grüneberg, 1925	UD II-D/E
Forestville	Chautauqua County, New York State	Clarke, 1904	UD II-C
Süssengut/Bernstein	Franconian Forest, Southeastern Germany	Wurm, 1961	UD II
Gattendorf	Franconian Forest, Southeastern Germany	Schindewolf, 1923	UD II-A/C
Knoppenbiessener Schichten	Northern RM	Jux and Krath, 1974	UD II-C/E
Nehden	Northeastern RM	Becker, 1993a	UD II-C/E

Table 11 References quoting the occurrence of *Elasmatium gowandense*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
-	-	-	-	MB.M.4419	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.59	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.58	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.61	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.64	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.63	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.67	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.68	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.69	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.70	
Bergisch Gladbach/ Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.71	
Beul	Enkeberger Kalk	Denckmann, 1900	UD II/IV	MB.M.4246	
Beul	Enkeberger Kalk	Denckmann, 1900	UD II/IV	MB.M.4247	
Beul	Enkeberger Kalk	Denckmann, 1900	UD II/IV	MB.M.4248	
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5294	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5295	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5296	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5297	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5298	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5299	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5300	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5301	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 52302	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 52303	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 52304	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 52305	Syntype *L. corrugata*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5246	Paralectotoype *E. gowandense*
Chautauqua Province,	Gowanda Shale	Clarke	UD II-C	NYSM 5247	Paralectotoype

New York					*E. gowandense*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5248	Paralectotoype *E. gowandense*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5249	Paralectotoype *E. gowandense*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5250	Paralectotoype *E. gowandense*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5251	Paralectotoype *E. gowandense*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5252	Paralectotoype *E. gowandense*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5253	Paralectotoype *E. gowandense*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5254	Lectotype *E. gowandense*
Dasberg	do IV / Schicht 33	Paeckelmann	UD IV	MB.M.4254	
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II-E/F	MB.M.4252	
Enkeberg	Schicht 18/ Obere Cheilolceras-Zone	Paeckelmann	UD II-E/F	MB.M.4253	
Eskesberg	Unterer Cypridinenschiefer	Grüneberg	UD II-D/C	MB.M.4255	
Kalkwerk Cox	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.65	
Langenaubach	Schalsteinbrekzie/Block 12	Denckmann	Famennian	MB.M.4249	
Oberscheld	Clymenien Kalk	Lotz, 1902	UD II/III	MB.M.4250	
Schurbusch, east of Nehden	goniatite slate	Becker	UD II-C/E	B6A-35.72	
Schurbusch, east of Nehden	Nehden	Becker, 1993a	UD II-C/E	B6A-35.73	
Schurbusch, east of Nehden	goniatite slate	Becker	UD II-C/E	B6A-35.74	
Schurbusch, east of Nehden	goniatite slate	Becker	UD II-C/E	B6A-35.75	

Table 12 Examined specimens of *Elasmatium gowandense*.

Elasmatium elongata (MÜNSTER, 1840)

Fig. 13; Pl. 4, Figs. 1-9

* + 1840 *Avicula elongata* MÜNSTER, p. 54, pl. 11, fig. 2.
+ v 1891 *Kochia* (*Loxopteria*) *rugosa* FRECH, p.78, pl. 6, figs. 5, 5a.
1900 *Kochia rugosa*.-BEUSHAUSEN, p. 175.
+ v 1904 *Kochia ungula* CLARKE, p. 270, pl. 13, figs. 1-7.
+ v 1904 *Kochia* (*Sluzka*) *intumescentis* CLARKE, p. 276, pl. 14, figs. 8-17.
1905 *Loxopteria* (*Sluzka*) *intumescentis*.- DREVERMANN, p. 389.
1912 *Kochia* (*Loxopteria*) *rugosa*.- BORN, p. 578.
v 1925 *Loxopteria* sp. aff. *laevis*.- GRÜNEBERG, p. 55.
+ v 1925 *Tiariconcha elongata* GRÜNEBERG, p. 55, 92, pl. 2, fig. 11-12.
1993a *Loxopteria rugosa*.- BECKER, p. 47.

Lectotype (designated herein): MB.M.3642.1.
Type locality: Geuser (Franconian Forest, Southeastern Germany).
Type stratum: Famennian (Nehdenian).

Material:
See Tab. 17

Diagnosis:
LV: smooth, regular conical valve, somewhat involute towards the opisthogyrate umbo.
RV: flat, subcircular, lid-shaped valve; umbo opisthogyrate, constant curved; ornamentation consisting of strong comarginal rugae, near ventral margin fine comarginal growth lines.

Description:
LV: Marginal outline subcircular, shell body generally cone-shaped, constant convexity, involute. Umbonal region highly arched. Umbo markedly arched in varying directions over hinge, mostly opisthogyrate, projecting distinctly beyond hinge line (e.g., B6A-35.77, Pl. 4, Figs. 1-4; B6A-35.81, Pl. 4, Figs. 7-8). Distinctly developed prodissoconch II and slightly observable prodissoconch I (Fig. 13).
Ornamentation consisting of fine comarginal growth lines and partly strong comarginal rugae (e.g., NYSM 5283, Pl. 4, Fig. 5; NYSM 5284, Pl. 4, Fig.6).
RV: subcircular lid-shaped shell. Seldom posterior bit of valve slightly bent upwards.
Antero-dorsal margin elevated by a fringe from commissure line. Umbo small, knob-like set off the body of shell, opisthogyrate (e.g., B6A-35.81, Pl. 4, Figs. 7-8; MB.M.788, Pl. 4, Fig. 9). Prodissoconch I-II clearly developed (Fig. 13). Ornamentation consisting of strong comarginal rugae on main part of shell; only fine comarginal growth lines towards ventral margin (e.g., MB.M.788, Pl. 4, Fig. 9).
Pallial line close, parallel to margin running from anterior to posterior hinge line. Small pallial sinus developed. From pallial sinus towards umbo shallow line observable. No adductor scars visible (Figs. 9.1-9.4).
Hinge line straight to slightly convex, edentulous. Anterior of umbo small ridge developed, with fine lines parallel to dorsal margin (Fig. 13).
Variation of length/height ratio see Fig. 12.
Largest specimen (MB.M.2216): height, 46.1 cm; length, 36.0 cm.
Smallest specimen (NYSM): height, 8.2 cm; length, 5.9 cm.

Discussion:
Münster collected MB.M 3642.1-2 from Geuser (Franconian Forest, Southeastern Germany) and present two RV. These specimens were determinated as *Avicula elongata* Münster, 1840

and are the only available Münster specimens of this species. Münster described the RV of *A. elongata* as flat, without radial ornamentation and he stated that the posterior portion of the valve is slightly bent upwards. Münster assigned MB.M 3642.1-2 to *A. elongata* Münster and his original description of this species can be correlated with these specimens. Furthermore, they are from the same locality and horizon as the material described by Münster (1840) and can be regarded as part of the original syntype series. Therefore, MB.M 3642.1 is selected as the lectotype of *Avicula elongata* Münster.

Frech (1891) established the species *Kochia* (*Loxopteria*) *rugosa* for a valve from Oberscheld. MB.M.788 (Pl. 4, Fig. 9) is the holotype by monotypy. He falsely described it as LV, but the examination of well preserved articulated specimens (e.g., Figs. 9.1-9.4; B6A-35.81, Pl. 4, Figs. 7-8) finally clarified the morphology of this inequivalve taxon. Therefore, MB.M.788 (Pl. 4, Fig. 9) can be now determinated as a RV of *E. elongata*. This affiliation is supported by the outline and ornamentation, which clearly identify the taxon as a junior synonym of *E. elongata* Münster.

Grüneberg (1925) identified a new species from Eskesberg, *Tiariconcha elongata*. The lectotype (MB.M.4269), which is selected herein, is the specimen, which is figured and described in his study (1925, pl. 2, figs. 11-12).

He stated that this species is supposed to be equivalve, but he did not examine articulated specimens. Probably this interpretation can be ascribed to the peculiar coiling of the umbo of the LV of *Elasmatium*. These, in some cases, give the impression of being prosogyrate and in other cases of being opisthogyrate. Therefore, without information of the complete morphology, authors interpreted such LV as the LV and RV of the species. MB.M.4269 clearly displays all morphological character of *E. elongata* and the development of the umbo with its markedly prodissoconch supports the re-assignment of *Tiariconcha elongata* Grüneberg to *Elasmatium elongata*.

The genus *Tiariconcha* Frech was originally named *Slava* Barrande. Frech (1891; p. 251) renamed the Upper Silurian genus *Slava* into *Tiariconcha*, because he felt that the Czech term *Slava* was not appropriate. Therefore, the name *Tiariconcha* Frech is a objective synonym of *Slava* Barrande. This Bohemian genus was revised by Kriz (1985). The growth stages I-IV of the Slavidae resemble a little bit the morphology of *E. elongata*, but *Slava* and its type species *Slava bohemica* Barrande, 1881, are completely equivalve and its changes in ornamentation, are not displayed by *Elasmatium* Clarke. Furthermore, the Slavidae do not present a large prodissoconch as in *Elasmatium* Clarke, Therefore, an assignment of *Elasmatium* Clarke and *Slava* Barrande is excluded (for further discussion on Slavidae see Kriz, 1985).

Grüneberg (1925) also described a distorted specimen (MB.M.4272) as *Loxopteria* sp. aff. *laevis* Frech. After re-examining it, this specimen can be identified as LV of *E. elongata*.

Kayser (1873) identified a new species from the Enkeberg, *Cardiola rugosa*. This taxon was later re-assigned to *Tiariconcha* Frech by Beushausen (1895). GZG 490-125-136 are the

original types of Beushausen (1895). Kayser (1873) described material, which was located in the collection of the Berlin Naturkundemuseum, and Beushausen worked on the same specimens, therefore, these specimens are regarded to be the syntypes of *Cardiola rugosa* Kayser. GZG 490-129 is selected herein as its lectotype. It displays, apart from strong comarginal ornamentation, a blunt umbo and a lunulacardiid notch on the antero-dorsal margin. These characters place this species within the Lunulacardiinae. Out of the remaining syntypes, specimen GZG 490-127 has to be re-assigned to *E. elongata*. It is a large LV with comarginal ornamentation presenting the specific cone-shaped *Elasmatium* morphology.

Clarke (1904) described *Kochia ungula* from the Gowanda Shale of New York State. To clearly define the character of *Kochia ungula*, NYSM 5283 (Pl. 4, Fig. 5) is chosen as lectotype. It clearly represents all features of the remaining types and represents best the description of Clarke (1904). The information about the morphology of *E. elongata*, derived from articulated specimens (e.g., B6A-35.81, Pl. 4, Figs. 7-8) shows that Clarke's species actually represents the LV of *E. elongata*. Therefore, *K. ungula* Clarke is regarded as junior subjective synonym. The types series comprises mostly specimens belonging to this taxon, but NYSM 5287 has to be re-assigned to *Loxopteria dispar*, because it is clearly a loxopteriid shell with strong radial undulations. NYSM 5285 (Pl. 13, Fig. 6) cannot be assigned to *E. elongata* without doubt, because due to the distortion of the valve its main portion cannot be observed. Therefore, it cannot be distinguished from *E. gowandense* Clarke. NYSM 5286 (Pl. 13, Fig. 6) certainly does not belong to *E. elongata*. This specimen is a flat valve, oval in outline, with a small, central umbo, and with fine comarginal growth lines. It could belong to the lunulacardiids, but a reliable determination cannot be accomplished, because the hinge region is not observable.

Clarke (1904) erected another species from New York State, *Loxopteria* (*Sluzka*) *intumescentis*. Unfortunatly the original types (NYSM 5313-20) have not been examined in this study, and therefore, no lectotype is selected, but the description (Clarke, 1904) and the figures identify them unequivocally as RV´s of *E. elongata.* Their outline and the comarginal rugae support this affiliation. *Loxopteria* (*Sluzka*) *intumescentis* Clarke is also re-assigned as a subjective synonym to *E. elongata* (Münster).

Occurrence

UD II / IV (Tab. 13, Tab 14)

Locality	Region	Reference	Stratigraphic level
Aeketal	Hercynian Mountains	Born, 1912	UD III-C
Correll´s Point	Chautauqua County, New York State	Clarke, 1904	UD II-C
Eskesberg	Northern RM	Grüneberg, 1925	UD II-E/C
Forestville	Chautauqua County, New York State	Clarke, 1904	UD II-C
Geuser	Franconian Forest, Southeastern Germany	Münster, 1840	UD II
Langenaubach	Lahn Dill Syncline	Drevermann, 1905	UD II/IV
Oberscheld	Lahn Dill Syncline	Frech, 1891	UD II/III

Table 13 References quoting the occurrence of *Elasmatium elongata*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Aeketal	Clymenien Kalk, Bank 8	Born, 1909	UD III-C	GZG 462-8	
Bergisch Gladbach	Knoppenbiessener Schichten	Becker	UD II-C/E	B6A-35.83	
Bergisch Gladbach	Knoppenbiessener Schichten	Becker	UD II-C/E	B6A-35.80	
Bergisch Gladbach	Knoppenbiessener Schichten	Becker	UD II-C/E	B6A-35.81	
Bergisch Gladbach	Knoppenbiessener Schichten	Becker	UD II-C/E	B6A-35.82	
Bergisch Gladbach	Knoppenbiessener Schichten	Becker	UD II-C/E	B6A-35.62	
Bergisch Gladbach	Goniatite slate, II-A	Becker	UD II-A	B6A-35.76	
Bergisch Gladbach	Goniatite slate, II-A	Becker	UD II-A	B6A-35.77	
Bergisch Gladbach	Knoppenbiessener Schichten	Becker	UD II-A	B6A-35.78	
Beul	Schurf 1, 7,10 m	Paeckelmann, 1931	UD III	MB.M.4276	
Beul	*annulata*-Zone	Lotz, Torley	UD IV-A	MB.M.4277	
Braunau		-	UD II	MB.M.4278	
Chautauqua Province, New York	Gowanda Shale	Clark	UD II-C	NYSM 5313	Syntype *L. intumescentis*
Chautauqua Province, New York	Gowanda Shale	Clark	UD II-C	NYSM 5314	Syntype *L. intumescentis*
Chautauqua Province, New York	Gowanda Shale	Clark	UD II-C	NYSM 5315	Syntype *L. intumescentis*
Chautauqua Province, New York	Gowanda Shale	Clark	UD II-C	NYSM 5316	Syntype *L. intumescentis*
Chautauqua Province, New York	Gowanda Shale	Clark	UD II-C	NYSM 5317	Syntype *L. intumescentis*
Chautauqua Province, New York	Gowanda Shale	Clark	UD II-C	NYSM 5318	Syntype *L. intumescentis*
Chautauqua Province,	Gowanda Shale	Clark	UD II-C	NYSM 5319	Syntype *L.*

New York					*intumescentis*
Chautauqua Province, New York	Gowanda Shale	Clark	UD II-C	NYSM 5320	Syntype *L. intumescentis*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5281	Paralectotype *K. ungula*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5282	Paralectotype *K. ungula*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5283	Lectotype *K. ungula*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5285	Paralectotype *K. ungula*
Chautauqua Province, New York	Gowanda Shale	Clarke	UD II-C	NYSM 5286	Paralectotype *K. ungula*
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II-E/C	MB.M.4256	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II-E/C	MB.M.4257	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II-E/C	MB.M.4258	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II-E/C	MB.M.4259	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II-E/C	MB.M.4260	
Enkeberg	Oberdevon II-III	Schindewolf, 1914	UD II/III	MB.M.4261	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II/III	MB.M.4262	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II/III	MB.M.4263	
Enkeberg	Schicht 6/ *annulata*-Zone	Paeckelmann	UD IV-A	MB.M.4264	
Enkeberg	Schicht 9/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4265	
Enkeberg	Schicht 9/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4266	
Enkeberg	Schicht 11/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4267	
Enkeberg	Schicht 9/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4268	
Enkeberg	Schicht 9/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4282	
Enkeberg	v. Koenen Schurf	Denckmann/Lotz, 1900	UD II/III	MB.M.4283	
Enkeberg	Schicht 9/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4285	
Enkeberg	Schicht 11/ Prolobites-Zone	Paeckelmann	UD III	MB.M.4288	
Enkenberg	Oberes Oberdevon	v. Koenen	UD II/IV	490-125-136GZG	
Eskesberg	Unterer Cypridinen-schiefer	Grüneberg	UD II-D/E	MB.M.4269	Lectotype *T. elongata*
Eskesberg	Unterer Cypridinen-schiefer	Grüneberg	UD II-D/E	MB.M.4270	
Eskesberg	Unterer Cypridinen-schiefer	Grüneberg	UD II-D/E	MB.M.4271	
Eskesberg	Unterer Cypridinen-schiefer	Grüneberg	UD II-D/E	MB.M.4272	

Geuser	Clymenien Kalk	Münster	UD II	MB.M.362.1	Lectotype *A. elongata*
Geuser	Clymenien Kalk	Münster	UD II	MB.M.362.2	Paralectotype *A. elongata*
Nehden	Nehdener Schiefer	Denckmann,1900	UD II-C/E	MB.M.4273	
Oberscheld	Clymenien Kalk	Denckmann, 1895	UD II/IV	MB.M.4251	
Oberscheld	Oberdevon	Beyrich, 1837	UD II/IV	MB.M.788	Holotype *K. rugosa*
Oberscheld	Clymenien Kalk, do IV	Paeckelmann	UD IV	MB.M.2288.1	
Oberscheld	Clymenien Kalk	Denckmann, 1895	UD II/III	MB.M.4251	
Oberscheld	-	-	UD II/III	MB.M.4279	
Oberscheld	Oberdevon	Beyrich,1837	UD II/IV	MB.M.788	
Pefferburg/ Grevenbrück	Oberdevon	Henke, 1906	UD II/IV	MB.M.4280	
Trident Mbr. Logan	DM 2	Becker, 1987	UD IV-A	B6A-35.84	
Trident Mbr. Logan	UD IV-A	Becker, 1987	UD IV-A	B6A-35.85	
Wettmarsen-Hirre	Prolobites-Zone	Paeckelmann, 1931	UD III	MB.M.4274	

Table 14 Examined specimens of *Elasmatium elongata*.

7.2 Praecardiids

One of the general problems in the systematics of Paleozoic bivalves is that genus and species names were proposed in studies of local faunas, usually within a single geologic period. This created a vast amount of synonyms for the rather slowly evolving bivalves throughout their stratigraphic range. McAlester (1962a) observed this phenomenon in his study of the Upper Devonian Chemung fauna of New York State, and not much has changed since. On the other hand, it is unlikely that bivalves survived without evolutionary change through the complex sequence of global extinction events and ecological crises, which are known to have affected other marine benthic groups.

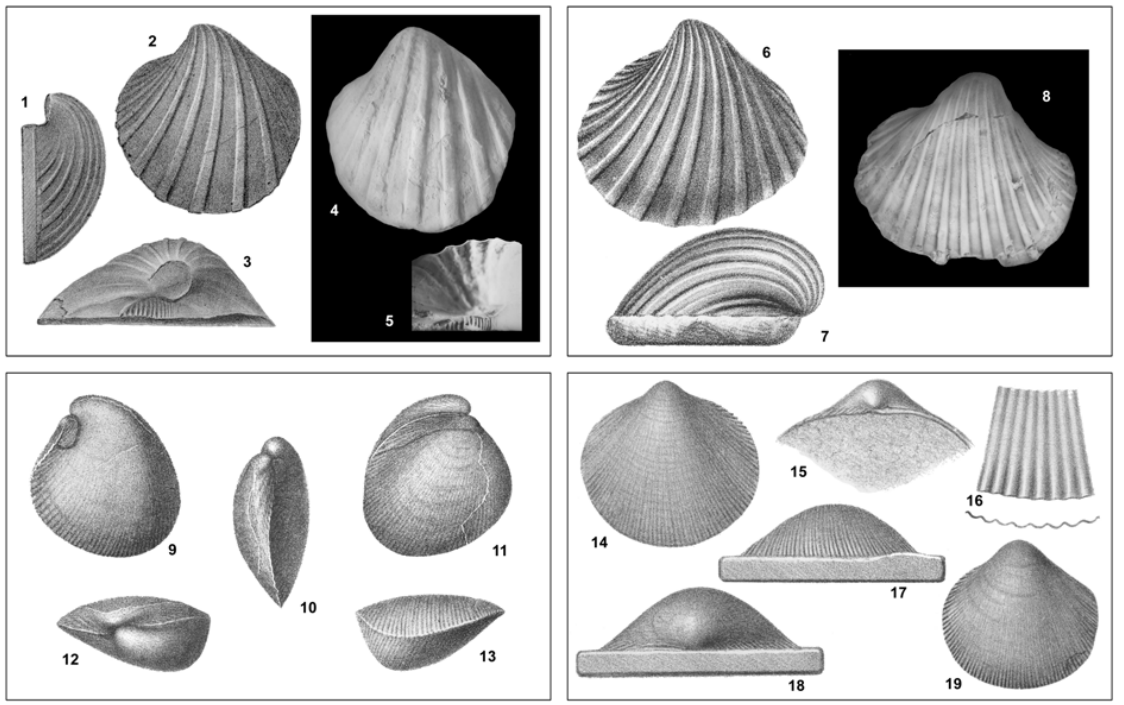


Figure 14 Type species of the Bohemian genera *Praecardium*, *Dualina*, *Paracardium*.

- *Praecardium primulum*: 1-3, original figure of topotype NMP L23344; 4-5, topotype NMP L23344; 6-7, original figure of lectotype NMP L 20361 (Barrande, 1881, Pl. 96, I, Fig. 1-2); 8, topotype NMP L20363.1.
- *Dualina comitans*: 9-13, original figure of lectotype (Barrande, 1881; Pl. 22, Fig. 17-21)
- *Paracardium subharmonicum*: 14-19, original figure of lectotype (Barrande, 1881, Pl. 78, III, 1-6).

7.2.1 *Praecardium*

Class BIVALVIA Linnaeus, 1758
Subclass CRYPTODONTA Neumayr, 1884
Order PRAECARDIOIDA Newell, 1965
Family PRAECARDIIDAE Hörnes, 1884
Genus PRAECARDIUM Barrande, 1881

Type species: *Praecardium primulum* Barrande (SD Ruzicka and Prantl, 1960)

Lectotype of *Praecardium primulum*: NMP L 20361.

Diagnosis:
Original Diagnosis (Barrande, 1881, p. 141):
Shell subcircular, equivalve, slightly inequilateral, moderately inflated. Margins all rounded, but differing in grade. Umbos prosogyrate, projecting markedly above dorsal margin. Below beak a row of vertical riblets developed, varying in shape and number as well as in spacing. Ornamentation consisting of radial ribs, rectangular in cross section with even interspaces, generally broader than the ribs. Rarely, narrow furrows dividing the costae.
Shell covered with thin, narrow, comarginal growth lines.
Musculature and dentition unknown.

Discussion:
Praecardium was defined by Barrande (1881) and occurs in the Upper Silurian Bohemian Facies, where this genus is represented by 45 not yet revised species.
This study claims not a complete review of this Bohemian genus, it just outlines the characters of it, defined by the original diagnosis (Barrande, 1881) and the lectotype of the type species *Praecardium primulum* Barrande, designated subsequently by Ruzicka and Prantl (1960). This summary serves as a basis to re-classify the Upper Devonian taxa, which are the main focus of this study.
(1) The genus has to be clearly defined.
The type species, *P. primulum* Barrande (1881) and its lectotype (1881, pl. 96, figs. I.1-2; Figs. 4.6-7) was subsequently designated by Ruzicka and Prantl (1960). The lectotype NMP L20361 and the topotypes NMP L23344 (Figs. 14.1-5), NMP L20364, NMP L20362, NMP L20363.1 (Fig. 14.8), NMP L20363.2, and NMP L27257 have been located in the National Museum Prague. The type species, the diagnosis (Barrande, 1881), and the lectotype (Figs. 14.6-7) identify characterized *Praecardium* as cardiid in outline, equivalve, slightly inequilateral. Barrande explicitly stated that there are just moderate variations in the development of

the outline. The most important feature, however, is the presence of vertical "riblets" below the beak. These have always been mentioned in later publications and are thus accepted to be an important character of *Praecardium* s. str. This hinge structure, which consists of a various number of small, upright teeth, located underneath the beak. Conrath (1887) examined this type of hinge development in Upper Silurian bivalves. He (1887) figured *P. primulum* displaying a row of little teeth, which start underneath the umbo and proceed on the anterior portion of the hinge line. Neumayr (1891) was of the opinion that these teeth emerged from the prominent radial ornamentation. He felt that the teeth are modified terminations of these radial ribs and support the coherence of the valves. Judging from the figures of Conrath (1887) and the comments of Johnston and Collom (1998) on the probable paleotaxodont dentition of Praecardioidea, it is assumed herein, that these teeth of *Praecardium* is a primitive type hinge, composed of modified, radial ornamentation elements.

(2) Differentiation of *Praecardium* from similar Bohemian genera.

Barrande (1881) stated that the three taxa *Praecardium*, *Paracardium* Barrande (1881), and *Dualina* Barrande (1881) are conditional genera, which are barely distinguishable.

The type species *Dualina comitans* (1881, pl. 22, figs. 17-21; Figs. 14.9-13), identified by Ruzicka and Prantl (1960), characterizes the genus, among other features, by inequivalve shells and places it in the Antipleuridae Neumayr. Therefore, *Dualina* is clearly distinguishable from *Praecardium* and thus it is not a synonym.

Paracardium is characterized by its type species *Paracardium subharmonicum* (Barrande, 1881, pl. 78, III, figs. 1-6; Figs. 14.14-19), subsequently designated by Newell (1969). This assignment did not contribute to stabilise the taxonomic alignment. Already Neumayr (1891) emphasized the close relationships between this taxon and Praecardium, because their similar development of the hinge area as well as the similar ornamentation. The transition between both is blurry and it is impossible to outline true distinguishing features. In Babin´s study (1966) on Paleozoic bivalves from the Armorican Massif (France) he confirmed Barrande´s opinion that the ornamentation of *Paracardium* and *Praecardium* is partly the result of the preservation state. Both authors felt that the spacing of the radial ribs, which is supposed to be distinguishing feature, appears to be closer on steinkerns and wider on the shell. Babin, as well as Barrande, were not able to identify any true distinction between both taxa. Therefore, Babin re-assigned *Paracardium* Barrande (1881) as a synonym of *Praecardium*. Babin´s (1966) revision lacks a proper discussion of both genera, a selection of a type species for *Paracardium*, and he regarded *Praecardium halli* Barrande as type species of *Praecardium*, ignoring the earlier designation of *P. primulum*. However, a complete review of Barrande species, including the entire material from Bohemia, is needed to clarify the true taxonomic relationships between *Paracardium* and *Praecardium*. The current study focuses on Devonian bivalves; a revision of the Silurian supposed praecardiids and related genera is beyond its scope and not relevant for a new generic assignment of the Devonian taxa.

(3) Taxa outside of the Prague basin, which are scrutinized in this study.

Heller (1925) re-studied Upper Silurian specimens from Elbersreuth (Franconian, Southeastern Germany), collected and published by Münster (1840), and re-collected material from the same outcrop. He described a new species, *Praecardium latecostatum*. Specimen BSPG AS VII 1702 is desiganted as the holotype, because other syntypes are missing. It is 14 mm high and 12 mm long, poorly preserved, and displays no observable characteristic features. Heller´s (1925) description of the species provides no information that would clearly identify an independent taxon and his illustration (Heller, 1925, pl. 1, fig. 18) does not really correspond to the actual specimen. He stated that his specimen is strongly inflated, inequilateral and oval in outline and assigned *latecostatum* to *Praecardium*, because he felt that it is close to *Praecardium gallus* Barrande, 1881. However, because of the lack of identifiable characteristics of the specimen, *P. latecostatum* is best regarded as a *nomen dubium*.

Walther (1907) described a new species, *Praecardium angulatum* from the Frasnian of Kirschkau (Eastern Thuringia, Germany). The only specimen, which is the holotype by monotypy, is, as Walther stated, poorly preserved. It is rounded oval in outline and the ornamentation consists of ridges on the radial ribs as well as on the interspaces. These features, especially the ornamentation, exclude *angulatum* unequivocally from *Deltacardium* n. gen. (see below) and *Praecardium*. This kind of ornamentation development has been described for *Regina vola* (Beushausen, 1895). *Regina*, however, is a junior synonym of *Kralovna* Barrande, 1881, from Bohemia (Czech Republic) and the true relationships of the Upper Silurian taxa and the Upper Devonian species, comprising this rib development, are currently unknown. Therefore, *Praecardium angulatum*, which seems be close to Kralovna, cannot be reassigned to any valid taxon with certainty.

The recent overviews of the character of *Praecardium* (Kaever et al., 1980; Amler, 2004) were just compilation of references and did not offer a re-study of this taxon. Type specimens and other material have not been considered. No new information about this taxon has been contributed.

Praecardium potens, mentioned in Carter (1990), refers, in fact, to *Panenka potens* (Hall, 1885) and is, therefore, based on a wrong generic assignment.

Occurrence:

Praecardium is described from the Silurian of Bohemia (Prague Basin, Czech Republic; Barrande, 1881; Ruzicka and Prantl, 1960). Furthermore, this genus is reported from the Upper Silurian of La Meignanne (Massif Armorican; Babin, 1966) and from the Early Pridolian (Upper Silurian) of Sardinia (Italy; Kriz and Serpagli, 1993).

7.2.2 *Deltacardium*

Class BIVALVIA Linnaeus, 1758
Subclass CRYPTODONTA Neumayr, 1884
Order PRAECARDIOIDEA Newell, 1965
Family PRAECARDIIDAE Hörnes, 1884
Genus DELTACARDIUM new genus

Type species: *Cardium* ? *vetustum* Hall, 1843.

Other species: *Praecardium melletes* Clarke, *Cardiola duplicata* Münster, *Praecardium clymeniae* Beushausen.

Diagnosis:
Shell trigonal to subtrigonal, equivalve. Valves highly inequilateral, prosocline; umbos prosogyrate, terminal, situated anterior, projecting more or less over hinge line. Broad, flat radial ribs, oftentimes with groove in the middle; fine, comarginal stria. At posterior margin ribs closer spaced, finer, sometimes rounder, less distinct in outline. Radial ribs almost comarginal on posterior part of shell; on anterior part ribs shorter, perpendicular to commissure; ribs broaden distinctly at margin. Hinge edentulous, ligamental groove faint, narrow, drawn out from beak almost to end of anterior part of dorsal margin. Internal features leave no imprints, even on best preserved moulds.

Etymology:
From the Greek *delta* – alluding to the outline of the valves.

Discussion:
These Upper Devonian species have traditionally been assigned to *Praecardium* Barrande. The first one to assign Upper Devonian species to *Praecardium* was Hall (1883). He felt that there are enough similarities with taxa such as *Praecardium despectum* Barrande, 1881, to support this affiliation. However, *P. despectum* displays an almost orthogyrate umbo, which is just somewhat coiled. The outline of this Silurian species is clearly rostrate. The grade of the ribs in the centre of the valve is almost straight. Therefore, *P. vetustum* and *P. despectum* do not belong to the same genus and it is not certain that *P. despectum* can remain in the revised Silurian *Praecardium* s. str. Already Beushausen (1895) and Clarke (1904) noted that the riblets underneath the beak, which are an important character of typical *Praecardium*, cannot be observed in any Devonian specimens. Apart from the missing riblets, another significant difference between the Upper Silurian and the Upper Devonian species is the outline of the

valves. *Praecardium* is subcircular and slightly inequilateral, whereas deltacardiids are trigonal and distinctively oblique. Especially the gradient of the ribs is different. *Praecardium* shows radial ribs that run from the more or less central beak constantly to the margins. Thus the zone of the greatest shell growth appears to be in the middle of the ventral margin; the valves are almost aklin. Species assigned to *Deltacardium* n. gen. are all markedly prosocline and the maximum shell growth occurs on the posterior part of the valves at the transition from the posterior to the ventral margin. Furthermore, praecardiids are moderately inflated, while the convexity of *Deltacardium* is much higher. In summary, the Upper Devonian taxa bear no resemblance to true *Praecardium*, and because of the lack of any other available Devonian genus, it is necessary to erect *Deltacardium* n. gen. A complete review of the 45 species from Bohemia and of related taxa may provide further information, which allows to relate *Deltacardium* n. gen. to some of the praecardiids group or will reveal a phylogenetic connection between Silurian and Devonian groups. However, at present the new genus is restricted to the Famennian and the large gap in the fossil record between both groups leave the possibility of iterative and homeomorphic developments within the Cryptodonta.

Occurrence:

The oldest occurrence of *Deltacardium* is reported from the Upper Kellwasser beds of Mont Peyroux and Coumiac (Armorican Massif, Southern France; Becker and House, 1994). Furthermore, identified Kriz (2005) this genus from La Serre and Comb d´Izarne from the earliest Frasnian of the same area.

The youngest precisely dated occurrence of *Deltacardium* is UD II-E, after the Condroz event. But there are reports and specimens, which can just broadly be interpreted as appearing in the UD II.

Its currently known geographical distribution extends from New York State (North America), Rhenish Massif (Germany), Franconian (Southeastern Germany), Holy Cross Mountains (Poland) to the Montagne Noire (Southern France), and Tafilalt (Southeastern Morocco). It is likely that further occurrences will be discovered once more attention is paid to bivalves of the pelagic facies.

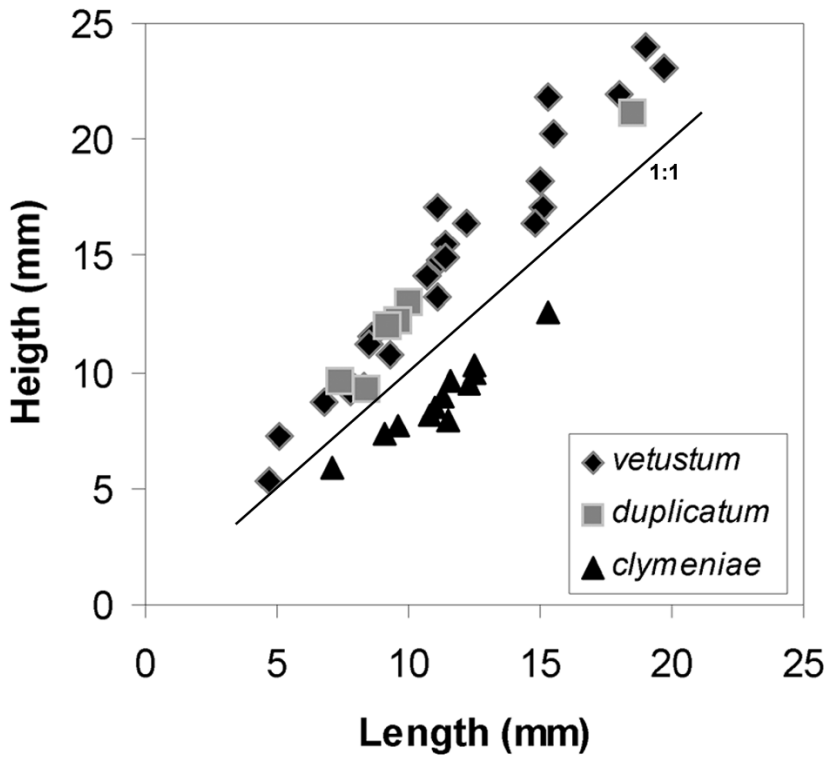


Figure 15 Length/height ratio of *Deltacardium* species showing isometric growth and restricted shape variability.

Deltacardium vetustum (Hall, 1843)
Pl. 6, Figs. 1-14

+	v	e.p.	1840	*Cardiola duplicata* MÜNSTER (partim), p. 68, pl. 13, fig. 20 a-b.
* +	v		1843	*Cardium ? vetustum* HALL, p. 245, pl. 107, fig. 2.
			1882	*Cardiola duplicata*.- HOLZAPFEL, p. 254.
			1873	*Cardiola duplicata*.- KAYSER, p. 639.
+	v		1873	*Cardiola Nehdensis* KAYSER, p. 639, pl. 21, figs. 2-3.
			1877	*Cardiola vetusta*.- MILLER, p. 186.
	v		1885	*Praecardium vetustum*.- HALL, p. 427, pl. 70, figs. 18-20.
			1887	*Cardiola duplicata*.- FRECH, p. 377.
			1887	*Cardiola Nehdensis*.- FRECH, p. 370, 377.
			1896	*Cardiola Nehdensis*.- GÜRICH, p. 98.
	v		1895	*Praecardium vetustum*.- BEUSHAUSEN, p. 301, pl. 31, figs. 6-7.
	v		1904	*Praecardium vetustum*.- CLARKE, p. 306, pl. 11, figs. 11-19.
			1911	*Praecardium vetustum*.- SOBOLEW, p. 36, 37.
			1922	*Praecardium duplicatum*.- SCHMIDT, p. 274.
			1923	*Praecardium duplicatum*.- SCHINDEWOLF, p. 277.
	v		1925	*Praecardium vetustum*.- GRÜNEBERG, p. 55.
	v		1929	*Praecardium duplicatum*.- LANGE, p. 14.
			1931	*Praecardium vetustum*.- MATERN, p. 12.
	v		1936a	*Praecardium vetustum*.- PAECKELMANN and KÜHNE, p. 18.
	v		1936b	*Praecardium duplicatum*.- PAECKELMANN and KÜHNE, p. 26.

1951 *Praecardium vetustum*.- Termier and Termier, p. 65.
1961 *Praecardium vetustum*.- Wurm, p. 133.
1974 *Praecardium vetustum*.- JUX and KRATH, p. 130, fig. b1-b2.
1980 *Praecardium vetustum*.- KAEVER et al., p. 151, pl. 24, fig. 2.
v 1993a *Praecardium vetustum*.- BECKER, p. 80, 81, 88, 115, 121, 122, 128.
2004 *Praecardium* cf. *vetustum*.- AMLER, p. 165.

Holotype (by monotypy): AMNH-F1-42169, from New York.

Type locality: Portage, Chautauqua County, New York.

Type stratum: Gowanda Shale (Upper Devonian II-C, Lower Nehden-Stage, Lower Famennian).

Material:

see Tab. 16.

Diagnosis:

Deltacardiid shell, trigonal, more or less pointed, strongly inflated, umbo distinctly projecting over hinge line. 9-11 radial ribs, faint comarginal growth lines.

Description:

Shell equivalve, strongly inequilateral, prosocline. Variation range of outline restricted, isometric growth (Fig. 1). Umbos prosogyrate, situated anterior, terminal. Long postero-dorsal margin, straight to slightly convex, merging elliptically curved into ventral margin. Anterior margin short, straight to slightly convex, declining abruptly from the beak. Ornamentation consisting of radial costae and fine, comarginal, closely spaced growth lines; comarginal stria not preserved on steinkerns (e.g., B6A-35.22, Pl. 6, Fig. 9; MB.M.4190, Pl. 6, Fig. 13); 9-11 radial ribs, oblong in cross section, evenly distributed. Ribs on steinkerns becoming rounded towards umbo. First and second posterior rib amalgamating, not articulated in outline. Interspaces plain, more or less as wide or wider than the ribs. Costae broadening slightly towards the margins, distinctly at the commissure line (e.g., B6A-35.22, Pl. 6, Fig. 9). Radial ribs appear at early stage of shell growth, interlock at the commissure; number of ribs constant. Ribs of posterior part of shell strongly bifurcate, central and anterior ribs weaker developed. Hinge edentulous, ligamental groove faint, narrow, drawn out from the beak almost to end of anterior part of dorsal margin (e.g., B6A-35.22, Pl. 6, Fig. 9). Internal features not preserved on steinkern. Holotype (AMNH-F1-42169, Pl. 6, Fig. 1) displays comarginal and radial ornamentation in shell preservation. All specimens of Hall collection (AMNH-F1-42169, Pl. 6, Fig. 1, AMNH-F1-42170, Pl. 6, Fig. 2, AMNH-F1-42171) slightly distorted.

Largest specimen (B6A-35.18): height, 19.7 cm; length 23.1 cm.

Smallest specimen (B6A-35.4): height, 4.7 cm; length, 5.3 cm.

Variation of length/height ratio see Fig. 15.

Discussion:

The mode of preservation in *Deltacardium* specimens caused a lot of taxonomic confusion in the past and led to the erection of species that have to be included into *Deltacardium vetustum*. *Cardium* ? *vetustum* was described from the Gowanda Shale (Western New York State) by Hall (1843). Hall (1885) added two topotypes (AMNH-F1-42170, AMNH-F1-42171) to the holotype (AMNH-F1-42169) from the same locality. Beushausen (1895) re-studied and reported *Praecardium vetustum* for the first time from Germany. Hall (1883) was the first to include a Upper Devonian species into the Silurian genus *Praecardium*, and Beushausen (1895) supported this approach by re-assigning further species from the Upper Devonian of Germany to it, e.g., *Cardiola Nehdensis*. This taxon was described by Kayser (1873), who was probably not aware of the North American *Cardium* ? *vetustum*. A lectotype was never chosen for *Cardiola Nehdensis* and the two syntypes are lost. At the Museum für Naturkunde in Berlin, one specimen (MB.M.2228) of the material studied by Kayser (1873) has survived. This specimen, however, did not come from the type locality, but belongs to material collected by Münster at Gattendorf (Franconian, Southeastern Germany) and was originally determined as *Cardiola duplicata* (Münster, 1840). Kayser (1873, p. 638) felt that specimen MB.M.2228 from Gattendorf was close to *Cardiola Nehdensis*, but compared it with a now lost limestone specimen from the Enkeberg (Eastern Rhenish Massif).

Beushausen (1895) was not sure about the affiliation of MB.M.2228 and mentioned another curious taxon, *Lunulacardium inaequicostatum* Münster (1840) in his discussion. This species has been moved earlier to *Conocardium* (d´Orbigny, 1850), but Beushausen (1895) felt it could be close to the praecardiids and especially to MB.M.2228. *L. inaequicostatum* shows affinities with *Prosochasma* Beushausen (1895) because of its drop-shaped outline and the smooth curve of the valve. Yet another specimen figured in a study of Geinitz (1853) and assigned to *L. inaequicostatum* has not much in common with neither this species nor with *Praecardium*. Without restudy it cannot be re-assigned to any taxon. The often discussed Gattendorf specimen can now be clearly re-assigned to *D. vetustum*, due to the information about the range of variation achieved through this study. Since Kayser (1873) designated specimen MB.M.2228 as well as the lost Enkeberg specimen only tentatively to *Cardiola Nehdensis*, it cannot be used as a lectotype. Consequently, a neotype (MB.M.4190, Pl. 6, Figs. 12-14) from the Nehden type locality and from the type horizon (Nehden Shales, Upper Devonian II-B/E) is selected which clearly defines *Cardiola Nehdensis*, and which places the species unequivocally in subjective synonymy of *D. vetustum*.

There was never a clear separation between *P. vetustum* and *Cardiola duplicata* Münster (1840), due to the improper definition of the latter. The character that was used to differentiate both taxa was the bifurcation of the ribs. Already Schindewolf (1923) suggested that this could be an ornamental difference between steinkern and original shell and not a species-level characteristic; the new material supports this. The bifurcate ribs are weaker developed on the

shell of *vetustum*, but they are present. As a consequence of the misinterpretation of the ornamental character, two syntypes of *Cardiola duplicata* (MB.M 2219.1-2) are here reassigned to *D. vetustum*.

Occurrence:

UD ?I/II-E (Tab. 15; Tab. 16)

The oldest specimen, which was examined in this study, is from the Upper Devonian II-B of Col de Puech de la Suque (Montagne Noire, Southern France; Becker, 1993a).

Frech (1887) reported the occurrence this taxon from the Combe de Izarne. This material was quoted to be of Frasnian age, but due to the tectonic situation at Combe d´Izarne (Becker, 1993a), caution is advised concerning the correct age. But other authors also noted the occurences of *D. vetustum* from the Upper Frasnian. Gürich (1896) mentioned it from the cephalopod limestones of Lagow in the Holy Cross Mountains (Poland). The associated goniatites, especially *Maeneceras* and *Paratornoceras*, suggest dating as UD I-F and I-G. Holzapfel (1882) reported this species from the Upper Kellwasser beds of Martenberg (Northeastern Rhenish Massif), and Becker and House, 1994 listed it from the same level of Coumiac (Montagne Noire). Therefore, it can be assumed, although no Frasnian material has been studied herein, *D. vetustum* occurred probably already in the Upper Kellwasser horizon (UD I-L).

Locality	Region	Reference	Stratigraphic level
Aeketal	Hercynian Mountains	Beushausen, 1900	UD II
Barmen	Northern RM	Kaever et al., 1980	UD II
Bensberg	Northern RM	Jux and Krath, 1974	UD II-C/E
Bou Tchrafine	Tafilalt, Morocco	Becker, 1993a	UD II-B/D
Col de Puech de la Suque	Armorican Massif, Montagne Noire, France	Becker, 1993a	UD II-B
Combe d´ Izarne	Armorican Massif, Montagne Noire, France	Becker, 1993a	UD II-B
Combe d´ Izarne	Armorican Massif, Montagne Noire, France	Frech, 1887	UD ?I
Daichet	Southern Meseta	Termier and Termier, 1951	UD II
Dar Kaoua	Tafilalt, Morocco	Becker, 1993a	UD II-B/D
El Gara	Tafilalt, Morocco	Becker, 1993a	UD II-B/D
Enkeberg	Northeastern RM	Beushausen, 1895	UD II/III
Enkeberg	Northeastern RM	Lange, 1929	UD II-A/B
Enkeberg	Northeastern RM Madfeld	Paeckelmann and Kühne, 1936b	UD II-E/F
Enkeberg	Northeastern RM	Kaever et al., 1980	UD II
Eskesberg	Northern RM	Grüneberg, 1925	UD II-D/E

Evertsbusch	Northern RM	Kaever et al., 1980	UD II
Gattendorf	Franconiann Forest, Southeastern Germany	Münster, 1840	UD II
Gattendorf	Francoain Forest, Southeastern Germany	Schindewolf, 1923	UD II-A
Jebel Ihrs	Tafilalt, Morocco	Becker, 1993a	UD II-B/D
Kielce-Sandomierze	Holy Cross Mountains, Poland	Sobolew, 1911	UD III-C
Kielce-Sandomierze	Holy Cross Mountains, Poland	Sobolew, 1911	UD II-C
Lagow	Holy Cross Mountains, Poland	Gürich, 1896	UD ?I/II
Martenberg	Northeastern RM	Holzapfel, 1882	UD I-L
Nehden	Northeastern RM	Kayser, 1873	UD II-C/E
Nehden	Northeastern RM	Beushausen, 1895	UD II-C/E
Nehden	Northeastern RM Alme	Paeckelmann and Kühne, 1936a	UD II-C/E
Nehden	Northeastern RM	Kaever et al., 1980	UD II
Oberscheld	Lahn Dill Syncline	Matern, 1931	UD II-C/E
Oberscheld	Lahn Dill Syncline	Kaever et al., 1980	UD II
Paffrath Syncline	Northern RM	Jux and Krath, 1974	UD II-C/E
Portage	Chautauqua County, New York State	Clarke, 1904	UD II-C
Portage	Chautauqua County, New York State	Hall, 1843	UD II-C
Portage	Chautauqua County, New York State	Hall, 1885	UD II-C
Süssengut/Bernstein	Franconian Forest, Southeastern Germany	Wurm, 1961	UD II

Table 15 References quoting the occurrence of *Deltacardium vetustum*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.17	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.18	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.19	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.20	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.22	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.25	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II-A/F	MB.M.4189	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II-A/F	MB.M.4191	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II-A/F	MB.M.4197	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II-A/F	MB.M.4200	
Col du Puech de la Suque	UD II B	Becker	UD II B	B6A-35.4	
Combe d´ Izarne	UD II C-E	Becker	UD II C-E	B6A-35.1	
Combe d´ Izarne	UD II C-E	Becker	UD II C-E	B6A-35.2.1	

Combe d´ Izarne	UD II C-E	Becker	UD II C-E	B6A-35.2.2	
Combe d´ Izarne	UD II C-E	Becker	UD II C-E	B6A-35.2.3	
Combe d´ Izarne	UD II C-E	Becker	UD II C-E	B6A-35.2.4	
Combe d´ Izarne	UD II C-E	Becker	UD II C-E	B6A-35.2.5	
Combe d´ Izarne	UD II C-E	Becker	UD II C-E	B6A-35.14	
Enkeberg	Schicht 20/ Untere Cheiloceras-Zone	Paeckelmann	UD II-D/E	MB.M.4181	
Enkeberg	Oberdevon	v. Koenen	UD II-D/E	GZG 1258-2	
Enkeberg	Oberdevon	v. Koenen	UD II-D/E	GZG 490-105	
Eskesberg, Elberfeld	Unterer Cypridinen-schiefer	Grüneberg	UD II-D/E	MB.M.4182	
Eskesberg, Elberfeld	Unterer Cypridinen-schiefer	Grüneberg	UD II-D/E	MB.M.4183	
Eskesberg, Elberfeld	Untere Cypridinen-schiefer	Grüneberg	UD II-D/E	MB.M.4202	
Gattendorf	Oberdevon	-	UD II	MB.M.2228	
Gattendorf	Oberdevon	Schneider, 1846	UD II	MB.M.2229.1	
Gattendorf	Oberdevon	Schneider, 1846	UD II	MB.M.2229.2	
Gattendorf	Oberdevon	Schneider, 1846	UD II	MB.M.2230	
Mentaresses	MEN H2	Becker	UD II D/E	B6A-35.12	
Mentaresses	MEN H1	Becker	UD II-D	B6A-35.10	
Mentaresses	MEN H1	Becker	UD II-D	B6A-35.3	
Mentaresses	MEN H1	Becker	UD II-D	B6A-35.11	
Mentaresses	MEN H1	Becker	UD II-D	B6A-35.8	
Mentaresses	MEN H1	Becker	UD II-D	B6A-35.9	
Mentaresses	MEN H1	Becker	UD II-D	B6A-35.5	
Nehden	Nehdener Schiefer	Denckmann, 1900	UD II-C/E	MB.M.4190	Neotype *C. nehdensis*
Nehden	Nehdener Schiefer	Denckmann, 1900	UD II-C/E	MB.M.4198	
Nehden	Nehdener Schiefer	Denckmann, 1900	UD II-C/E	MB.M.4190	
Nehden	Oberdevon	Chelius	UD II-C/E	GZG 1258-4	
Portage, Chautauqua, New York	Gowanda Shale	Hall	UD II-C	AMNH-F1-42169	Holotype *C.* ? *vetustum*
Portage, Chautauqua, New York	Gowanda Shale	Hall	UD II-C	AMNH-F1-42171	
Portage, Chautauqua, New York	Gowanda Shale	Hall	UD II-C	AMNH-F1-42170	

Table 16 Examined specimens of *Deltacardium vetustum*.

Deltacardium duplicatum (Münster, 1840)

Pl. 8, Figs. 6-8

* + v e.p. 1840 *Cardiola duplicata* MÜNSTER p. 68, pl. 13, fig. 20a.
v non 1873 *Cardiola duplicata*.- KAYSER, p. 639, pl. 21, fig. 4.
non 1856 *Cardiola duplicata*.- SANDBERGER and SANDBERGER, p. 271, pl. 28, fig. 7.
v 1895 *Praecardium duplicatum*.- BEUSHAUSEN, p. 303, pl. 31, fig. 4.
v 1904 *Praecardium duplicatum*.- CLARKE, p. 307, pl. 11, fig. 25.
1980 *Praecardium duplicatum*.- KAEVER et al., p. 151, pl. 24, fig. 1.
v 1993a *Praecardium duplicatum*.- BECKER, p. 80, 81.
2005 *Praecardium duplicatum*.- Kriz, p. 88, pl. 1, figs. 1-6.

Lectotype (designated herein): AS VII 366.
Type locality: Gattendorf, Franconian (Southeastern Germany).
Type stratum: Upper Devonian II, Nehden-Stage.

Material:
see Tab. 18.

Diagnosis:
Deltacardiid shell, trigonal to subtrigonal, inflated, umbo projecting over hinge line. 13-15 radial ribs, comarginal growth lines.

Description:
Comparison with *P. vetustum*: valves less pointed in outline, postero-dorsal margin more convex, anterior margin somewhat longer and convex, slightly less inflated. Variation range of outline restricted, isometric growth, same length/height ratio as *P. vetustum* (Fig. 1). 13-15 ribs, markedly in outline. Ribs slightly broader, in shell preservation distinctly bifurcate (e.g., GZG 490-106, Pl. 8, Fig. 7), rib margins developing more or less sharply raised edges on steinkerns (e.g., B6A-35.7, Pl. 8, Fig. 8). Comarginal growth lines, sometimes observable on steinkerns. Interspaces more or less as wide as ribs. Number of amalgamating posterior ribs 3-4. Ligamental area as in *vetustum*. Internal features not preserved on steinkern, edentulous. Lectotype (AS VII 366, Pl. 8, Fig. 6) with shell and internal mould, without insight in dorsal region. Triangular, posterior adductor scar in posterior part of the valve (Kriz, 2005).
Largest specimen (ASVII 366): height, 20.2 cm; length, 25.5 cm.
Smallest specimen (B6A-35.6): height, 6.5 cm; length, 9.3 cm.
Variation of length/height ratio see Fig. 15.

Discussion:
Cardiola duplicata has always been a matter of discussion. The description given by Münster (1840) is ambiguous and likewise is the original type material. Already Kayser (1873) complained in his study about the improper definition of this species. He noted that the original description does not offer a clear definition and he argued that the original figures do not bear much resemblance to the type specimens (MB.M.2229, Pl. 8, Figs. 3-5; MB.M.2219.1-2). Furthermore, he stated that the only common feature of the examined specimens is the dichotomy of the ribs. He figured specimen MB.M.2229 (1873, pl. 21, fig. 4), which he thought to be the only well preserved specimen out of the types. Kayser, however, did not consider another well preserved type (AS VII 366, Pl. 8, Fig. 6), which is housed in the Bayerische Staatssammlung (Munich). In his review of *Praecardium*, Beushausen (1895) suggested to separate MB.M.2229 (Pl. 8, Figs. 3-5) from *P. duplicatum*. Selecting AS VII 366 as the lecto-

type for Deltacardium duplicatum supports Beushausen´s interpretation, because it displays all characteristics of the species. It presents both shell material and the internal mould. The steinkern shows that the radial ribs are rounded, becoming broader towards the margins; no depression can be observed on the costae of the internal mould. The outer shell presents ribs that are rectangular in cross-section and that develop centrally a faint groove. Münster (1840) described this depression on the costae as the main feature of *C. duplicata*, but, in fact, it appears more or less clearly in all deltacardiids. Syntypes MB.M.2219.1-2 are re-assigned to *Deltacardium vetustum*, and MB.M.2229 (Pl. 8, Figs. 3-5) is described as N. Gen. A (see below). Grüneberg (1925) reported *Praecardium vetustum* from Barmen and Eskesberg (Northern Rhenish Massif). Some of these specimens, which are all, like the rest of this collection, distorted, have to be re-assigned to *Deltacardium duplicatum*, because of their higher number of ribs.

Sandberger and Sandberger (1856) assigned one specimen from the Frasnian of Oberscheld (Southern Rhenish Massif) to *Cardiola duplicata*. Kayser (1873) stated in his comparison of *Cardiola Nehdensis* and *C. duplicata* that the almost symmetric, rounded outline of the valve and the radial ribs, which display, besides the main ribs, also small secondary ridges, clearly distinguish the Oberscheld specimen from *C. duplicata*. Beushausen re-studied and described this specimen as a new species, *Cardiola Sandbergeri* (1895, p. 304; p. 334, pl. 36, figs. 8-9), supporting Kayser´s criticism. The type specimen of Sandberger and Sandberger (1856) was untraceable in the collection of the Naturkunde Museum in Wiesbaden. The assignment of s*andbergeri* to *Cardiola* cannot be correct, because the true cardioliids became extinct at the end of the Silurian (Kriz, 1979). The shell outline excludes this species from *Deltacardium* n. gen. The generic affinity of "*C.*" *sandbergeri* is left open until a detailed revision of Devonian "cardioliids" is achieved.

Clarke (1904) described *Praecardium duplicatum* from Johnson's Fall near Strykersville (Chautauqua subprovince, New York State) within the Frasnian/Famennian transition; the precise level, Dunkirk Shale or lower, is not clear. This specimen develops a considerably prominent and bigger umbo than *D. duplicatum*. The radial ribs of the North American specimen are characterized by a deep furrow, which originates sharp edges on the margins of the ribs. The depression on the ribs is as deep as the interspaces. Furthermore, the more or less rounded and symmetric outline of this shell is contradictory to the subtrigonal deltacardiid valve shape. Therefore, the specimen is excluded from *D. duplicata*. Clarke (1904) assumed close affinities with buchioliids, but further conclusions and a re-assignment cannot be made without re-studying the original material and should better be based on new collections.

The alleged synonymy given by Kriz (2005), where he places *D. vetustum* in synonymy with *D. duplicatum*, is obsolete, because this study shows that both species are, clearly distinguishable.

Occurrence:

UD I-L / II (Tab. 17; Tab. 18)

Kriz (2005) reported the oldest occurence of *D. duplicatum* from the earliest Frasnian of Mentaresses and Combe d´Izarne (Armorican Massif, Southern France). Unfortunately, there were no actual specimens, which were studied herein, confirming the first occurrence of this species from the Upper Kellwasser beds (UD I-L). The last appereance of this species cannot be dated precisely, because "Unterer Clymenien Kalk" can only broadly interpreted as UD II.

Locality	Region	Reference	Stratigraphic level
Biesenberg	Northern RM	Kaever et al., 1980	UD II
Combe d´Izarne	Armorican Massif, Montagne Noire, France	Kriz, 2005	UD I-L
Enkeberg	Northeastern RM	Kaever et al., 1980	UD II
La Serre	Armorican Massif, Montagne Noire, France	Kriz, 2005	UD II-A
Mentaresses	Armorican Massif, Montagne Noire, France	Kriz, 2005	UD I-L
Mentaresses	Armorican Massif, Montagne Noire, France	Becker, 1993a	UD II-D
Nehden	Northeastern RM	Kayser, 1873	UD II-C/E
Portage	Chautauqua County, New York State	Clarke, 1904	UD II-C
Various locations	Northeastern RM	Beushausen, 1895	UD II

Table 17 References quoting the occurrence of *Deltacardium duplicatum*.

Locality	Stratigraphic specification on the label	Collection	Strati-graphic level	Collection Number	Types
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.21	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.24	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.23	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II-A/F	MB.M.4203	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II-A/F	MB.M.4194	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II-A/F	MB.M.4196	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II-A/F	MB.M.4199	
Biesenberg	Unterer Clymenien Kalk	Denckmann, 1894	UD II-A/F	MB.M.4192	
Enkeberg	Oberdevon	v. Koenen	UD II-D/E	GZG 490-106	
Eskesberg	Untere Cypridinenschiefer	Grüneberg	UD II-D/E	MB.M.4193	
Gattendorf	Oberdevon	Münster	UD II	BSPG AS VII 366	Lectotype *C. duplicatum*
Gattendorf	Oberdevon	Münster	UD II	MB.M.2227	

Mentaresses	MEN H2	Becker	UD II-D/E	B6A-35.12
Mentaresses	MEN H1	Becker	UD II-D	B6A-35.7
Mentaresses	MEN H1	Becker	UD II-D	B6A-35.13
Mentaresses	MEN H1	Becker	UD II-D	B6A-35.9
Nehden	Oberdevon	Chelius	UD II-C/E	GZG 1258-1
Schurbusch, East of Nehden	Nehden	Becker	UD II-C/E	B6A-35.6
Schurbusch, East of Nehden	Nehden	Becker	UD II-C/E	B6A-35.15

Table 18 Examined specimens of *Deltacardium duplicatum*.

Deltacardium clymeniae (Beushausen, 1895)
Pl. 7, Figs. 1-8; 13

* + v 1895 *Praecardium vetustum* var. *Clymeniae* BEUSHAUSEN, p. 302, pl. 31, fig. 7.
\+ v non 1895 *Cardiola Clymeniae* BEUSHAUSEN, p. 357, pl. 37, fig. 21.
v 1895 *Praecardium* sp.- BEUSHAUSEN, p. 302, pl. 31, fig. 71.
1974 *Praecardium clymeniae*.- JUX and KRATH, p. 130, fig. 5 a1-a3.

Neotype: GZG 490-107 (Beushausen, 1895; collection von Koenen).
Type locality: Enkeberg (Eastern Rhenish Massif).
Type stratum: "Clymenienkalk" (Nehdenian, precise level unknown).

Material:
see Tab. 19

Diagnosis:
Deltacardiid shell, subtrigonal, more or less inflated. 21-24 radial ribs, distinct comarginal growth lines.

Description:
Comparison with *P. vetustum* and *P. duplicatum*: Valves more rounded in outline, ventral margin markedly convex. Postero-dorsal margin elongated, slightly convex. Range variation of outline restricted, growth isometric, length/height ratio higher than in *D. vetustum* (Fig. 1). Umbo less incurved, almost orthogyrate, developing a small ridge in front, observable on steinkerns; 21-24 fine radial ribs, posterior ribs not amalgamating, but more subtle and closer spaced than rest (e.g., B6A-35.35, Pl. 7, Figs. 5-8). Radial ribs in shell preservation strongly bifurcate (GZG 490-107, Pl. 7, Fig. 13), rounded on internal mould (e.g., B6A-35.26, Pl. 7, Figs. 1-4). Distinct, irregular, comarginal striae visible on steinkerns (e.g., B6A-35.35, Pl. 7, Fig. 5) and shell, intersecting radial ribs and interspaces (GZG 490-107, Pl. 7, Fig. 13). Liga-

mental area narrow, parallel to the margin. Edentulous, internal features not preserved on steinkerns. Lectotype (GZG 490-107, Pl. 7, Fig. 13) with shell preservation, dorsal region poorly preserved.
Largest specimen (GZG 490-107): height, 18.9 cm; length, 25.2 cm.
Smallest specimen (B6A-35.27): height, 5.9 cm; length, 7.1 cm.
Variation of length/height ratio see Fig. 15.

Discussion:
Beushausen (1895) described *P. vetustum* var. *Clymeniae* in his commentary of *Praecardium vetustum*. He mentioned two original specimens, which are both from the limestone of the Enkeberg (Rhenish Massif). One of the specimens was previously assigned with a query to *Cardiola Nehdensis*. Kayser (1873), as well as Beushausen (1895), stated that this specimen displays more and closer spaced ribs than all other available taxa. The second type was a poorly preserved specimen, which was housed in the Geowissenschaftliches Zentrum der Universität Göttingen. Unfortunately both specimens are lost. Therefore, in order to stabilise the taxonomy of *D. clymeniae*, a neotype (GZG 490-107, Pl. 7, Fig. 13) from the type locality has been selected. Beushausen (1895) identified this specimen as *Praecardium* sp. and observed, that in contrast to specimen GZG 490-106 (Pl. 8, Fig. 7), which he identified as *P. duplicatum*, the number of ribs is higher. Although the old stratigraphic determination as "Clymenienkalk" (Beushausen, 1895) provides no information about the exact age of the neotype, it is most probable that the lost type and the neotype are contemporaneous, because all were derived from the collection of von Koenen from the Enkeberg type locality (Rhenish Massif). The age of these specimens could represent all levels from the Upper Devonian II to lower V, the total range of this section (Korn and Ziegler, 2002). Re-sampling (Becker, 1993a) did not provide new material and the precise age needs to be inferred from better dated material of other localities. *Cardiola Clymeniae* of Beushausen (1895, p. 357, Pl. 37, Fig. 21) is a separate species, with no relationships with *Deltacardium*, and is not a homonym. Jux and Krath (1974) reported *D. clymeniae* from the Knoppenbissen Formation (Bergisch Gladbach, Rhenish Massif, Germany). This was the first time the species was recognized after its first description.

Occurrence:
UD II-C/E (Tab. 19).
The stratigraphic range of *D. clymeniae* has to be elucidated from the specimens examined in this study; there are no additional literature data. Judging from the past chaotic taxonomic situation, a number of specimens belonging to *D. clymeniae* may have been assigned to other genera (e.g., *Panenka* Barrande, 1881) but such misidentifications cannot be considered here. This species seems to be restricted to localities of the Rhenish Massif.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.26	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.27	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.28	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.29	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.30	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.31	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.32	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.33	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.34	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.35	
Bergisch Gladbach	Knoppenbiessener Schichten	Ebbighausen	UD II-C/E	B6A-35.36	
Enkeberg	Oberdevon	v. Koenen	UD II	GZG 490-107	Neotype *D. clymeniae*
Eskesberg	Unterer Cypridinenschiefer	Grüneberg	UD II-D/E	MB.M.4185	
Eskesberg	Unterer Cypridinenschiefer	Grüneberg	UD II-D/E	MB.M.4186	
Eskesberg	Unterer Cypridinenschiefer	Grüneberg	UD II-D/E	MB.M.4187	
Eskesberg	Unterer Cypridinenschiefer	Grüneberg	UD II-D/E	MB.M.4188	
Nehden	Oberdevon	Chelius	UD II-C/E	GZG 1258-1	
Schurbusch East of Nehden	Nehden	Becker	UD II-C/E	B6A-35.16	
Schurbusch East of Nehden	Nehden	Becker	UD II-C/E	B6A-35.15	

Table 19 Examined specimens of *Deltacardium clymeniae*.

Deltacardium melletes (Clarke, 1904)

* + v 1904 *Praecardium melletes* CLARKE, p. 307, pl. 11, fig. 20.

Holotype (by monotypy).—The specimen illustrated by Clarke (1904) in the New York State Museum, Albany.

Type locality: Forestville, Chautauqua County, New York State.
Type stratum: Sandstone at the top of the Portage Shales (Gowanda Shale, UD II-C)

Diagnosis:
As for *Deltacardium vetustum*, with only 6 radial ribs.

Description:
Valves comprise all features of *D. vetustum*, but with only six radial ribs.
Internal features unknown.
Specimen: height, 6 mm; length, 7,5 mm.

Discussion:
Praecardium melletes Clarke was based on a single shell from near Forestville (Chautauqua County, New York, northeast America). In modern lithostratigraphy (Tesmer, 1967), the specimen probably came from the Gowanda Shale, which is UD II-C (Becker and House, 2000). The specimen closely resembles *D. vetustum* but develops only 6 radial ribs. Clarke (1904) felt that this feature was important enough for erecting a new species, *Praecardium melletes*. *D. vetustum* has never been observed displaying less than 9 ribs, neither in North America nor elsewhere. The North American species, therefore, lies outside the known range of variation of *P. vetustum*. The appearance of all ribs in an early growth stage in *Deltacardium* also suggests that the lower rib number is not an ontogenetic variation in the growth pattern, but a valid character on species level. To obtain further clarification whether this taxon represents a regional variation of *D. vetustum* or a separate species, re-collecting in the type area is necessary. Currently, *P. melletes* is re-assigned to *Deltacardium*. Additional material is required to establish its variability and to stabilize its possible status as a North American species or subspecies.

N. GEN. A. NEW SPECIES A
Pl. 8, Fig. 3-5

* + v e.p. 1840 *Cardiola duplicata* MÜNSTER, p. 68, pl. 12, fig. 21.
v 1873 *Cardiola duplicata*.- KAYSER, p. 639, pl. 21, fig. 4.
v 1895 *Cardiola duplicata*.- BEUSHAUSEN, p. 304.

Material:
Syntype MB.M.2229 of *Cardiola duplicata* MÜNSTER (1840) from Upper Devonian II of Gattendorf (Franconian, Southeastern Germany)

Description:

Shell rounded, somewhat inequilateral. Mostly with shell preservation; subcircular posterior margin from umbo to ventral margin preserved without shell. Postero-dorsal margin short, merging with lateral margin; ventral margin not preserved. Anterior part of dorsal margin amalgamating with lateral margin, not observable. Valve more or less inflated, slightly flattened in centre. Umbo small, prosogyrate, more or less central. Radial ribs coil up in umbo, almost straight towards ventral margin; ribs in anterior part of valve short, in posterior part long. Umbo not projecting far beyond dorsal margin. Ornamentation consisting of more than 19 radial ribs, divided by a distinct groove on each costa, coiled up in umbo. Apart from three conspicuous incisions parallel to antero-dorsal margin, shell without any observable comarginal growth lines

Internal features and dorsal region not preserved.

Specimen: height, 17.3 cm; length, 16.7 cm.

Discussion:

This specimen is one out of the syntype series of *Cardiola duplicata* Münster (1840). Kayser (1873) already separated it from the other syntypes and cited it as an example for the dubious definition of *duplicata*. Beushausen (1895) supported the assumption that there is more than one species hidden in *Cardiola duplicata* and suggested to separate MB.M.2229 as an independent species. It does not display any features of *Deltacardium* n. gen., apart from the bifurcation of the radial ribs. It does not fit in the concept of *Praecardium*, because there is no trace of riblets underneath the beak. The rounded outline of the valve and especially the curved posterior margin distinguishes it from true praecardiids, which are more symmetrical. The radial ribs, which are markedly coiled up in the umbo, definitely separate this specimen from all other Devonian taxa. Until a complete review of pelagic bivalve groups is achieved, MB.M.2229 should not be re-assigned to a newly described genus or species. In order to prevent more taxonomic confusion, the specimen remains currently in open nomenclature.

Occurrence:

The only specimen is from Gattendorf (Southeastern Germany) and can only be assumed to be Upper Devonian II in age; its precise level is ambiguous. Re-collecting has become impossible due to the partial destruction of the outcrop.

"*Praecardium*" *multicostatum* Clarke, 1904
Pl. 7, Figs. 9-12, 14

* + v 1904 *Praecardium multicostatum* CLARKE, p. 308, pl. 11, figs. 21, 22, 24.
1913 *Praecardium* n. sp. aff. *multicostatum*.- PAECKELMANN, p. 256, pl. 6, fig. 2, 2a.
v 1925 *Praecardium* n. sp. aff. *multicostatum*.- GRÜNEBERG, p. 55.
1990 *Praecardium multicostatum*.- BAIRD and LASH, p. A34.

Lectotype (designated herein): NYSM 5493.
Type locality: Walnut Creek, Forestville, New York State.
Type stratum: Gowanda Shale, (UD II-C, Lower Famennian).

Material:
Lectotype, NYSM 5493, from New York;
two more syntypes of the Clarke (1904) collection, NYSM 5490 and NYSM 5491; NYSM 11426 from New York (Tesmer collection);
B6A-35.37-40 from Bergisch Gladbach (von Ebbighausen collection).

Description:
Shell rounded, slightly inequilateral, equivalve. Anteror-dorsally valve somewhat obtuse, posterior slightly elongated. Antero-dorsal margin shorter than posterior part. Umbo central, without observable ornamentation, separated by clear incision from valve on steinkerns as well as on shell (B6A-35.39, Pl. 7, Figs. 9-12; NYSM 5493, Pl. 7, Fig. 14). Shell regularly convex, slightly elevated in the umbonal region. 20-22 radial ribs broad, slightly raised edges, bifurcate. Ribs somewhat broader than interspaces, both flat and regular spaced. Traces of minute comarginal growth lines on shell and steinkern (B6A-35.39, Pl. 7, Figs. 9-12). Lectotype slightly and topotypes markedly distorted, all in shell preservation (NYSM 5493, Pl. 7, Fig. 14; NYSM 5491; NYSM 5490). Probably dimyarian, on pyritic steinkern faint traces of two, more or less equally wide, narrow, slightly elongated adductor scars. No hinge features preserved.
Largest specimen (NYSM 5493): height, 9.7 cm; length, 9.6 cm.
Smallest specimen (B6A-35.39): height, 8.5 cm; length, 8.5 cm.

Discussion:
Clarke (1904) described *Praecardium multicostatum* from Walnut Creek, Forestville (New York State). Four syntype specimens were figured and three of these survived (Clarke, 1904, Pl. 11, figs. 21, 22, 24). All syntypes are more or less distorted and the best preserved (NYSM 5493) is selected as lectotype. Because of the degree of deformation it is not definitely clear, whether the other two syntypes represent the same species or not. Due to the anyway doubtful systematic situation, they are kept together until more details can be established. The some-

what symmetrical outline of the valves and the grade of the ribs exclude "*P.*" *multicostatum* from *Deltacardium* n. gen. These features resemble the valves of Silurian praecardiids, but the relatively inflated, not very prominent umbo distinguishes "*P.*" *multicostatum* from true praecardiids. There are also no riblets displayed underneath the beak as in *Praecardium* s. str. It is highly unlikely that the species can remain in *Praecardium*, but currently there is no alternative genus available. The symmetry of the valves and the grade of the ribs place this taxon closer to the buchioliids, but the ornamentation of "*P.*" *multicostatum*, especially the bifurcation and the incision, which separates the umbo from the rest of the shell, contradicts such affinity (Grimm, 1998). Because of the vast amount of species and genera, which were described earlier and which are not reviewed yet, caution is advised to produce more taxa, which may later turn out to be synonyms. Therefore, "*P.*" *multicostatum* remains conditionally in *Praecardium*, in want of a permanent, valid genus assignment.

Paeckelmann (1913) described a poorly preserved specimen from Hahnenfurt (Northern Rhenish Massif) as *Praecardium* n. sp. aff. *multicostatum*. He noted that it is highly similar to "*P.*" *multicostatum* and that just the development of the bifurcation of the ribs is less distinct. The re-study of Clarke's type specimens showed that the ribs of the syntypes are less markedly bifurcate than originally figured. Therefore, the specimen from the Bergisches Land can be re-assigned to "*P.*" *multicostatum*, as well as a distorted specimen from Eskesberg (MB.M 4188), which was also identified as *Praecardium* n. sp. aff. *multicostatum* in Grüneberg (1925).

Occurrence:

The specimens of the type series from North America probably represent the Gowanda Shale (New York State), as the Hanover Shale, which also crops out in Walnut Creek is closer to Silver Creek on the Lake Erie shoreline. NYSM 11426 from the Gowanda Shale, which was collected near Smiths Mills Station, is UD II-C in age. Furthermore, Baird and Lash (1990) reported one specimen from the Gowanda Member of Corell´s Point, which is, judging from the associated ammonoid fauna, also UD II-C.

The European occurrences of this taxon are from the Lower Famennian of the Wuppertal region (UD II-B/D) and four specimens from the Knoppenbissen Formation (Bergisch Gladbach, Rhenish Massif). The latter fauna is from Upper Devonian II-C/E.

7.3 Lunulacardiids

Lunulacardium Münster, 1840 has always been a genus as a reservoir for somehow peculiar-shaped Paleozoic taxa, which developed some kind of truncated margin or gap. Many questions concerning the actual bauplan of this genus, such as the orientation of the valves, the presence of a gap, and the location and function of the characteristic truncation have never been closely studied or understood. Therefore, and due to the poor state of preservation and improper diagnoses, the lunulacardiids have been subject of much speculation.

Gümbel (1879) listed the Münster species and noted that most of the types were either poorly preserved or not traceable.

Over the years, a lot of assumptions concerning the lunulacardiids were simply adopted without any examination, and discussions were based on false information and wrong assumptions. Symptomatically for these negligence is that in the literature this genus was commonly named *Lunulicardium*, although original spelling was *Lunulacardium* (Münster, 1840).

From the Upper Silurian, 105 species have been placed within this genus:

L. berrans, Barrande, 1881; *L.* ? *aculeatum*, Barrande, 1881; *L. acuminatum*, Barrande, 1881; *L. aliferum*, Barrande, 1881; *L.* alternans, Barrande, 1881; *L. amabile*, Barrande, 1881; *L. ampulum*, Barrande, 1881; *L. analogum*, Barrande, 1881; *L. angulosum*;

L. aspirans, Barrande, 1881; *L. assecla*, Barrande, 1881; *L. binotatum*, Barrande, 1881; *L. Bohemicum*, Barrande, 1881; *L. Branikense*, Barrande, 1881; *L. calvum*, Barrande, 1881; *L. capillosum*, Barrande, 1881; *L. cardiolopsis*, Barrande, 1881; *L. carolinum*, Barrande, 1881; *L. cinctum*; *L. comptma*, Barrande, 1881; *L. concomitans*, Barrande, 1881; *L. confertum*; *L. confortans*, Barrande, 1881; *L. conjugans*, Barrande, 1881; *L. constrictum*, Barrande, 1881; *L. contrarium*, Barrande, 1881; *L. cuneus*, Barrande, 1881; *L. degener*, Barrande, 1881; *L. demissum*, Barrande, 1881; *L. dentiforme*, Barrande, 1881; *L. derelictum*, Barrande, 1881; *L. detersum*, Barrande, 1881; *L. diopsis*, Barrande, 1881

L. dispar, Barrande, 1881; *L. egregium*, Barrande, 1881; *L. emaciatum*, Barrande, 1881

L. evolvens, Barrande, 1881; *L. excellens*, Barrande, 1881; *L. excusum*, Barrande, 1881

L. eximium, Barrande, 1881; *L. expulsum*, Barrande, 1881; *L. extensum*, Barrande, 1881; *L. extraneum*, Barrande, 1881; *L. fasciatum*, Barrande, 1881; *L. firmum*, Barrande, 1881

L. flectens, Barrande, 1881; *L. fortius*, Barrande, 1881; *L. fugitivum*, Barrande, 1881

L. gallus, Barrande, 1881; *L. germanum*, Barrande, 1881; *L. granulosum* , Barrande, 1881; *L. Halli*, Barrande, 1881; *L. humile*, Barrande, 1881; *L. inaequale*, Barrande, 1881; *L.* ? *incertum*, Barrande, 1881; *L. inexpertum*, Barrande, 1881; *L. infaustum*, Barrande, 1881; *L. infirmum*, Barrande, 1881; *L. ingratum*, Barrande, 1881; *L. initians*, Barrande, 1881; *L. jacens*, Barrande, 1881; *L. jucundum*, Barrande, 1881; *L. longiusculum*, Barrande, 1881; *L. macilentum*, Barrande, 1881; *L. majusculum*, Barrande, 1881; *L. marginatum*, Barrande, 1881; *L. miserum*, Barrande, 1881; *L. mixtum*, Barrande, 1881; *L. moderatum*, Barrande, 1881; *L. novellum*, Barrande, 1881; *L. obsoletum*, Barrande, 1881; *L.* ? *obtusum*, Barrande,

1881; *L. omissum*, Barrande, 1881; *L. orphans*, Barrande, 1881;*L. patiens*, Barrande, 1881; *L. paucicosta*, Barrande, 1881; *L. peralatum*, Barrande, 1881; *L. perplectens*, Barrande, 1881; *L. placidum*, Barrande, 1881; *L. primum*, Barrande, 1881; *L.* ? *rebelle*, Barrande, 1881; *L. redux*, Barrande, 1881; *L. remisniscens*, Barrande, 1881; *L. residum*, Barrande, 1881; *L. rostrum*, Barrande, 1881; *L. sejunctum*, Barrande, 1881; *L. selectum*, Barrande, 1881; *L. signatum*, Barrande, 1881; *L. simplex*, Barrande, 1881; *L. simulans*, Barrande, 1881; *L. singulum*, Barrande, 1881; *L. sinuatum*, Barrande, 1881; *L. solum*, Barrande, 1881; *L. spatula*, Barrande, 1881; *L. subalatum*, Barrande, 1881; *L. subjectum*, Barrande, 1881; *L. sulciferum*, Barrande, 1881; *L. tardum*, Barrande, 1881; *L. tegulatum*, Barrande, 1881; *L. tenellum*, Barrande, 1881; *L. transversum*, Barrande, 1881; *L. tumescens*, Barrande, 1881; *L. undulatum*, Barrande, 1881; *L. volitans*, Barrande, 1881 Furhtermore 39 closely related taxa have been described for *Lunulacardium* from the Upper Silurian.

The Devonian of North America produced 22 *Lunulacardium* species: *L. absegmen* Clarke, 1904; *L. accola* Clarke, 1904; *L. acutirostrum* Hall, 1843; *L. beushauseni* Clarke, 1904; *L. clymeniae* Clarke, 1904; *L. enode* Clarke, 1904; *L. curtum* hall; *L. encrinitum* Clarke, 1904; *L. eriense* Clarke, 1904; *L. hemicardioides* Clarke, 1904; *L. finitimum* Clarke, 1904; *L. furcatum* Clarke, 1904; *L. parunculus* Clarke, 1904; *L. libum* Clarke, 1904; *L. marcellense* hall; *L. oratum* Hall, 1843; *L. suppar* Clarke, 1904; *L. pilosum* Clarke, 1904; *L. sodale* Clarke, 1904; *L. velatum* Clarke, 1904; *L. wiscoyense* Clarke, 1904.

From the German Upper Devonian 25 taxa more were identified, which are in the focus this study (see following paragraphs). The re-study of these species and genera provides a basis for further reviews of the Bohemian and North American taxa listed above, which would have been far beyond the scope of this study. Taking into account that bivalves are a rather slowly evolving group, a number of more than 100 species within one genus is more than unlikely, especially for a low-diverse deeper water fauna, such as the one from the Hercynian Facies studied herein. Therefore, the taxa mentioned above, especially the Upper Silurian species will have to be re-assigned to other genera.

In the following systematic review the focus is on the German lunulacardiids.

There are three lunulacardiid genera described from the German Upper Devonian, *Lunulacardium* Münster, *Chaenocardiola* Holzapfel, and *Prosochasma* Beushausen. Holzapfel (1889) separated *Chaenocardiola* from *Lunulacardium* and subsequently Beushausen (1895) identified a third genus amongst the representatives of *Lunulacardium*, *Prosochasma*. Clarke (1904) ranked these and *Pinnopsis* Hall as subgenera of *Lunulacardium*. The latest survey of these taxa (Newell and La Rocque, 1969) placed *Chaenocardiola* into synonymy of *Lunulacardium*, but maintained *Prosochasma* as a subgenus of *Lunulacardium*. No re-study provided a true review of Münster´s *Lunulacardium* or its species.

The orientation of the lunulacardiid shell and, consequently, the orientation of the umbo was always a matter of debate. Münster (1840) and Beushausen (1895) aligned the truncated mar-

gin with the lunule, therefore, anteriorly. Sandberger and Sandberger (1856) and Hall (1843, 1885) suggested that this characteristic section is probably the area. All subsequent authors (e.g., Barrande, 1881; Holzapfel, 1882, 1889) simply followed Münster (1840) and determinated the truncation as lunule, and, therefore located anterior

Clarke (1904) scrutinized the orientation of the shell again. He reported the occurrence of valves that were found spread open, but still connected at the truncated margin (*Lunulacardium encrinitum*, Clarke, 1904, pl. 2, fig. 20). This would suggest that the ligament was somehow located on the truncated margin of the valves and, therefore, posteriorly. However, Clarke (1904) still defined the truncation as anteriorly situated. Later, Nye et al. (1975) described a log and associated lunulacardiids from the Middle Devonian Marcellus Shale of Jamesville, Upstate New York. Next to the log articulated valves were preserved, which were connected on the truncated side of the shells. These specimens and Clarke's observation indicate the development of the ligament at or near the truncation of dorsal margin.

Yancey and Heaney (2000) described a new genus from the Carboniferous Buckhorn Asphalt (Boggy Formation, Middle Pennsylvanian; South-Central Oklahoma, North America), *Buckhornia*. This carboniferous taxon is closely related to *Lunulacardium*, due to the development of a similar prodissoconch, its ornamentation, and, furthermore, its dorsal margin, which is truncated as in the lunulacardiids. Yancey and Heaney (2000) described the preservation of fibrous ligament remains of a juvenile shell. These were located posteriorly and, thus they confirmed the position of the ligament.

These observations are supported by the development of the adductor scars in the lunulacardiid genus *Prosochasma*. Some specimens of this taxon preserve two fused muscle scars on the steinkern (Fig. 19). The larger adductor scar is located posteriorly. In *Prosochasma* it is actually situated next to the truncated margin.

All these details indicate that the truncated margin is located on the posterior portion of the dorsal margin and the truncation represents some kind of ligament bearing area and not the lunule, as the generic name would suggest.

In the course of this study it also appears questionable, wether or not the lunulacardiid shell is truly gaping as commonly accepted. *Lunulacardium* develops, if at all, just a small, posterior slot. The specimens of *L. semistriatum* Münster from Oberscheld present, contrasting to the majority of the material, shell preservation. This material shows that the postero-dorsal portion of the shell is a quite fragile extension of the shell body (e.g., Pl. 9 Figs. 1, 11, 12), which is not observable on steinkerns, which preserve just the main shell body. Therefore, it may be assumed that in taxa, which were described as gaping, this fragile shell part is simply not preserved. Furthermore, the ligament is, as discussed above, located in the portion of the valve, which is supposed to gape. Assuming that there is a distinct opening of the valve, it would be difficult to reconstruct an area of ligamental insertion there. However, for further conclusions new material has to be collected to clarify the actual structure of this part of the shells.

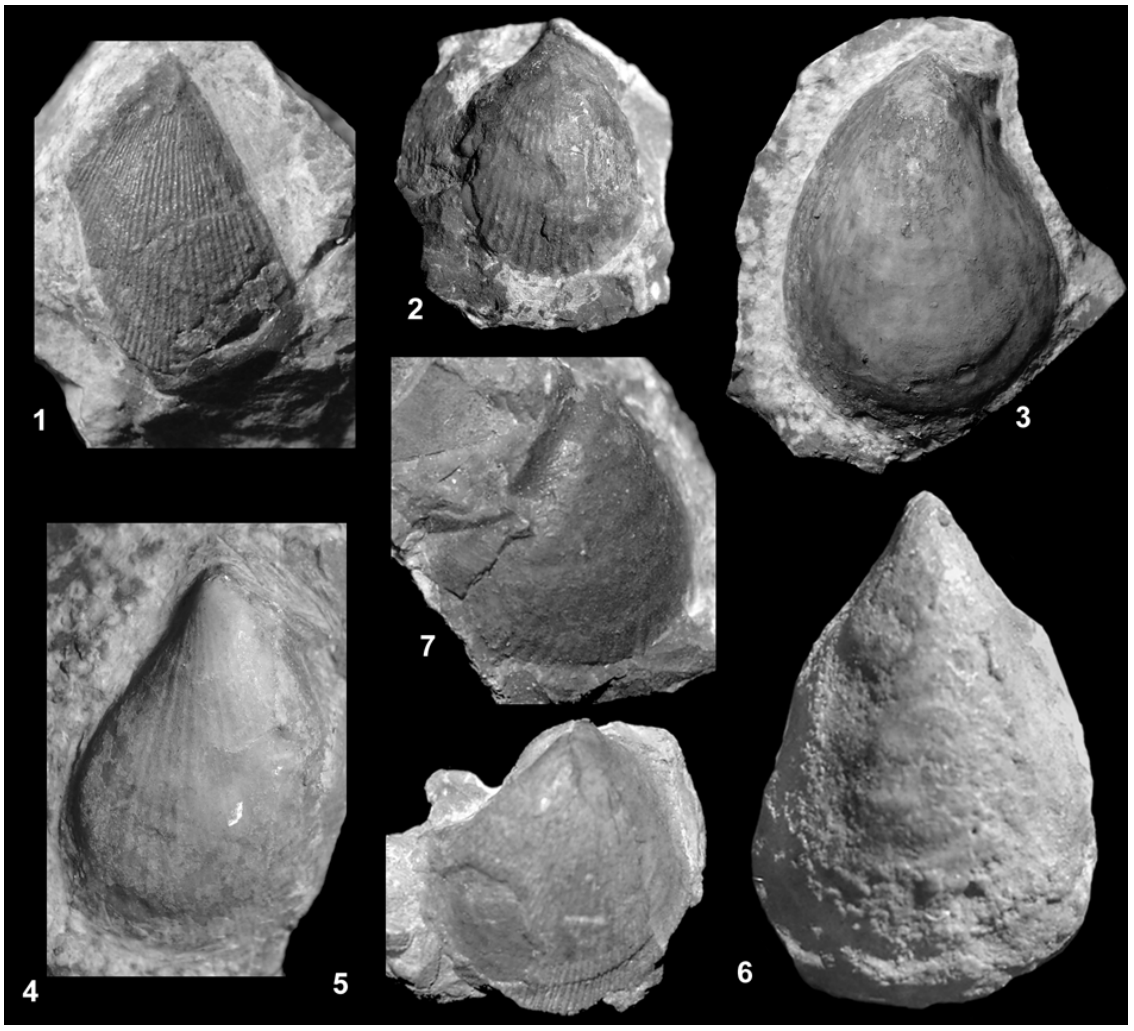


Figure 16 Types of Münster (1840), housed in the Bayerische Staatssammlung, Munich.
1 - *Lunulacardium tetragonum* BSPG AS VII 1736, x 2.0; **2 -** *Lunulacardium excrescens* BSPG AS VII 1735, x 0.75; **3 -** *Lunulacardium ovatum* BSGP AS VII 1737, x 0.5; **4 -** *Lunulacardium partschii* BSPG AS VII 1738, x 1.0; **5 -** *Lunulacardium procrescens* BSPG AS VII 1739, x 1.5; **6 -** *Lunulacardium pyriforme* BSPG AS VII 1733, x 2.0; **7 -** *Lunulacardium canalifer* BSPG AS VII 1734, x 1.5.

7.3.1 *Lunulacardium*

Class BIVALVIA Linnaeus, 1758
Subclass CRYPTODONTA Neumayr, 1884
Order PRAECARDIOIDEA Newell, 1965
Family LUNULACARDIIDAE, Fischer, 1887

Genus *Lunulacardium* Münster, 1840

Type species: *Lunulacardium semistriatum* Münster, 1840 (SD Stoliczka, 1870).

Included Devonian revised species from Germany: *Lunulacardium semistriatum* Münster, 1840, *Lunulacardium excrescens* Münster, 1840.
Further species with uncertain affiliation:
? *L. ovatum*, Münster, 1840; ? *L. partschii*, Münster, 1840; ? *L. procrescens*, Münster, 1840.
(unrevised *Lunulacardium* taxa from North America, and the Upper Silurian of the Prague Basin (Czech Republic) see above).

Diagnosis (revised):
Round to transversely oval in outline, subcircular ventral margin merging regularly into roundly bent anterior and posterior margin. Posterior part of hinge line straight, anteriorly straight to slightly convex.
Small umbo central, opisthogyrate to orthogyrate, often main portion cut off by truncation. Juvenile shell veneriform, turned anticlockwise by 90° compared to orientation of adult shell body, not affected by truncation. Straight to slightly concave truncation posteriorly cutting umbo and dorsal margin. Development, length and angle of truncation variable.
Narrow, elongated groove running parallel to anterior portion of hinge line, developing few parallel corrugations. Truncation creating postero-dorsal edge, its declining portion developing ornamentation of irregular corrugations more or less parallel to upper ridge of carina.
Ornamentation consisting of strong and fine irregular radial ribs, fine comarginal growth lines, strong comarginal rugae. Internal characters unknown.

Discussion:
Münster (1840, p. 58) separated *Lunulacardium* from *Cardium* Münster (1840, p. 58) and noted that the genus includes two subdivisions. But he never mentioned any subgenera and simply described (1840, p. 69) eight *Lunulacardium* species. He described the truncated margin and identified it as a markedly developed lunule, which was the main, eponymous character of this genus.

Beushausen (1895) revised *Lunulacardium* and stated that the valves gape just slightly in the lunule, if at all. Subsequent authors assumed, without explanation, that *Lunulacardium* possesses a distinct gap (e.g., Newell and La Rocque, 1969). Judging from the original description (Münster, 1840), its revision (Beushausen, 1895), and the type specimens examined herein, *Lunulacardium* does not develop a wide gap. It cannot be excluded that it possesses a slight slot at the truncated margin, but due to the state of preservation no final assumption can be made until new material provides more information about this character.

Stoliczka (1870) listed *Lunulacardium semistriatum* as the type species of the genus. He noted that he never examined any material belonging to this group, and described it as higher than long with a deep trench, which cuts one side of the valve. He characterized the ornamentation as consisting of strong radial ribs.

The holotype, by monotypy, of *L. semistriatum* was a damaged specimen, which unfortunately is lost. In his diagnosis he noted that the anterior margin of the specimen is figured disproportionaly long and convex and, therefore, the illustration does not reflect the shape of the actual specimen, due to a misinterpretation by the illustrator. Hence, the types species of *Lunulacardium* is dubious. Nevertheless, this genus is well established, and it is the type genus for the Lunulacardiidae Fischer (1887). Therefore, to obtain stability of the ambiguous group, *Lunulacardium* is maintained by selecting a neotype for its type species and providing a new basis for its diagnosis (see following paragraph).

Münster (1840, p. 70, pl. 12, fig. 18) described *Lunulacardium ovatum* from the Schübelhammer (Franconian Forest, Southeastern Germany). BSGP AS VII 1737 (Fig. 16.3) is the holotype by monotypy. This specimen poorly preserves the external mould of the shell. Interestingly, the postero-dorsal portion of the shell is observable and shows that the valve develops a fragile shell extension beyond the truncated margin (Fig. 16.3). Due to its oval, more or less equilateral outline and its broad radial ribs, *L. ovatum* does not fit the concept of either *Lunulacardium*, *Prosochasma*, or *Chaenocardiola*.

The taxon *Lunulacardium partschii* Münster, 1840 from Schübelhammer (Franconian Forest, Southeastern Germany), with its holotype (BSPG AS VII 1738; Fig. 16.4), appears to be a slender version of *L. ovatum*. Due to their outline and ornamentation, both ? *L. partschii* and ? *L. ovatum* are no members of *Lunulacardium*, and their affiliation to any other valid taxon is dubious. Furthermore, no similar material showing this chimney-shaped extension, which could shed light on their actual bauplan, has been examined. Therefore, at the moment these two species have to be left in open nomenclature.

Another dubious taxon assigned to *Lunulacardium* is *L. procrescens* Münster (1840, p. 70, pl. 12, fig. 19). BSPG AS VII 1739 (Fig. 16.5) from Schübelhammer (Franconian Forest, Southeastern Germany) is the designated as the lectotype, because other syntypes are missing. It is oval in outline with a small central umbo, well developed radial ribs and some comarginal growth lines. This species develops an extension of the shell beyond the concave, truncated

postero-dorsal margin, which is chimney-shaped with a bulging outer edge. The valve seems to gape in this extension. The truncation is one third of the height of the shell's length. *L. procrescens* is probably a representative of the lunulacardiids, but due to the bulk of poorly known taxa included within, its generic assignment remains unknown. In order to avoid more taxonomic confusion and until a complete review of pelagic bivalve groups are achieved, *L. procrescens* also remains currently in open nomenclature.

Hall (1843) identified *Pinnopsis* from Eastern New York State. He subsequently abandoned this genus for *Lunulacardium*, since he felt that both taxa are congeneric. Clarke (1904) re-studied this genus and affirmed its assignment to *Lunulacardium*. Its type species, *Pinnopsis acutirostrum* Hall, 1843, was subsequently designated by Newell and La Rocque (1969). It is subtrigonal in outline with a prominent, acute umbo, and the truncation covers the whole length of the posterior margin. These characters suggest close relationships to the chaenocardiolids, but, unfortunately, the figure of the holotype does not show the dorsal region of the specimen, and the development of the truncation is not precisely described. Therefore, until the holotype of this species is re-studied, its systematic position remains dubious as well as the actual affiliation of *Pinnopsis*.

Kriz (2005) described a new genus from the Montagne Noire, *Metrocardia*. He stated that this taxon is closely related to *Lunulacardium*. He distinguished it from the latter by the lack of a gap and stated that the truncation is not separated from the rest of the shell body by a distinct edge. This review shows that *Lunulacardium* does not develop a wide gap. Further material has to clarify, wether or not members of this genus actually gape.

Furthermore, the development of the edge bordering the truncation appears to be variable. It can range from a pronounced edge to a less distinct carina, and its length also varies. The only true difference between *Lunulacardium* and *Metrocardia* appears to be the slightly prosocline outline of the latter. Therefore, a re-study of *Metrocardia* against the background of the reviewed *Lunulacardium* is necessary to find out, wether or not it is truly an independent genus or another species of *Lunulacardium*.

Occurrence:

Lunulacardium has been described from all over the world, e.g., from the Famennian of Poland (Gunia, 1968), from the Upper Silurian of the Prague Basin (Czech Republic; Barrande, 1881), from the Upper Silurian of the Armorican Massif (Babin, 1966), from the Frasnian and Famennian of France (Frech, 1887; Kriz, 2005), and from the Frasnian and Famennian of North America (Hall, 1843, 1885; Clarke, 1904). These references have to be carefully examined, because it cannot be assumed that all these described taxa are actually *Lunulacardium* species, as revised and re-defined herein.

In this study, its occurrence can only be confirmed from the Eastern Rhenish Massif (Germany) and from the Montagne Noir (France).

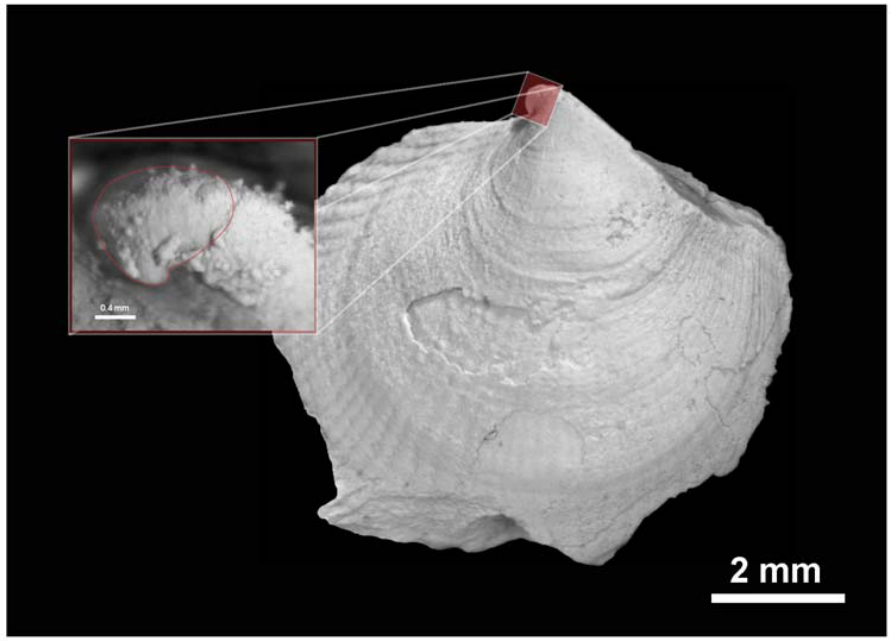


Figure 17 Development of the prodissoconch in *Lunulacardium*, showing the rotation of the veneriform prodissoconch (Neotype of *L. semistriatum*; MB.M.2232.8).

Lunulacardium semistriatum Münster, 1840

Fig. 17; Pl. 9, Figs. 1-12

* +	1840	*Lunulacardium semistriatum* MÜNSTER, p. 69, pl. 13, fig. 9.
	1879	*Lunulacardium semistriatum*.- GÜMBEL, p. 503.
	1870	*Lunulacardium semistriatum*.- STOLICZKA, p. 211.
? +	1856	*Lunulicardium ventricosum* SANDBERGER AND SANDBERGER, p. 269, pl. 28, fig. 6, 6a. [nom. dub.]
v	1895	*Lunulicardium ventricosum*.- BEUSHAUSEN, p. 362, pl. 27, fig. 1-4.

Neotype: MB.M.2232.8.

Type locality: Oberscheld (Eastern Rhenish Massif, Germany).

Type stratum: upper Frasnian, upper Adorfian (UD I-I/J).

Material:

see Tab. 20.

Diagnosis:
As for the genus.

Description:
Transverse to subcircular in outline, slightly wider than high.
Margins subcircular, merging regularly in each other.
Anterior portion of dorsal margin straight, posterior part slightly convex. Shell truncated posteriorly, creating a straight to slightly concave edge. Posterior to the edge valve declining abruptly perpendicular or with more or less acute angle. Declining shell portion deviates in the sagittal plane of the valve into the thin, fragile postero-dorsal portion of shell (e.g., Pl. 9, Figs. 1, 7, 11). Postero-dorsal shell portion carrying faint ornamentation of shell body (Pl. 9, Figs. 10, 11); declining portion of valve developing strong, irregular corrugations, more or less parallel to upper ridge of carina (Pl. 9, Figs. 2, 5). Valves probably slightly gaping.
Hinge line straight to slightly convex, dentition unknown.
Umbo small, central, opisthogyrate, partly cut off by truncation.
Juvenile shell veneriform, completely twisted almost anticlockwise compared to shell body by an 90° angle and not affected by truncation (Fig. 17)
Ornamentation consisting of coarse radial ribs, less distinct on dorsal portion of shell. Fine comarginal growth lines, additional strong comarginal rugae (Pl. 9, Fig. 1, 6).
Pallial line and adductor scars not observable.
Neotype (MB.M.2232.8, Fig. 17) small, with shell preservation. Especially well preserved juvenile shell and dorsal margin. Ventral margin missing, hinge line not observable.

Discussion:
Münster (1840) described a new species from the Schübelhammer (Franconian Forest, Southern Germany), *Lunulacardium semistriatum*. The Münster original type of this species, which was the holotype by monotypy, is lost. It could not be traced in the Münster collection in the Bayerische Staatssammlung, Munich, nor in the Urweltmuseum Bayreuth, and already Gümbel (1879) mentioned that this specimen is lost. The figure given in Münster does not reflect the morphology of the type and the specimens itself was damaged (1840, p. 69).
Therefore, *L. semistriatum* could be treated as nomen dubium. But since it is the type species of *Lunulacardium*, which is a well established genus, and the type genus of the Lunulacardiidae, it seems reasonable to maintain this species, and to the stabilize the whole family. Therefore, a neotype, MB.M.2232.8, collected by Beyrich (1835) at Oberscheld is chosen. MB.M.2232.8 is subcircular in outline, possesses a distict truncation, and a opisthogyrate, central partly cutt off umbo, which characterises *Lunulacardium semistriatum*, and is therefore, suitable as the neotype of it. Unfortunately, there is no bivalve material from the Schübelhammer or other localities from the Franconian Forest available, which could provide

a neotype from the type region. The current outcrop situation (Hartenfels, 2003) does not allow the re-collection of new macrofauna. At the time of Münster, the fauna was collected from weathered limestone wich is not possible anymore. Therefore, a contemporaneous, well preserved specimen from Oberscheld is selected.

Sandberger and Sandberger (1856) identified a new species from the ironstones of the Cypridinenschiefer of Oberscheld, *Lunulicardium ventricosum*. The holotype of this taxon is lost, and, therefore, *L. ventricosum* is considered also a nomen dubium. This Sandberger taxon shows, according to the original illustration and description, striking similarities with *L. semistriatum*. Especially, the subcircular outline with a more or less straight hinge line, which is cut off by the characteristic truncation is a main character of both taxa. Therefore, the material formerly included in *L. ventricosum* can be re-assigned to *L. semistriatum*.

Occurrence:

UD I / II-D (Tab. 20)

The material from the Beyrich Collection is from the Frasnian and represents the oldest occurrence of *L. semistriatum*. The specimen from Col de Puech de la Suech (Montagne Noir, France) is the youngest material examined in this study and can be unequivocally, although of Famennian age, placed within this species.

In the literature, this species has not been quoted after its first description by Münster (1840).

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Bicken	Goniatitenkalk	-	UD I	GZG 1258.10 a	
Bicken	Goniatitenkalk	-	UD I	GZG 1258.10 b	
Col de Puech de la Suque	UD II-A/D	Becker	UD II-A/D	B6A-35.135	
Ense	Unteres Oberdevon	-	UD I	MB.M.4410	
Grube Charlottenzug	? Oberdevon	Denckmann, 1893	UD I	MB.M.4412	
Martenberg	Unteres Oberdevon	Denckmann	UD I-I/L	MB.M.4411	
Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.M.2236.1	
Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.M.2236.2	
Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.M.2236.3	
Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.M.2232.2	
Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.M. 2232.3	
Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.B.2232.4	
Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.M.2232.5	
Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.M.2232.6	
Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.M.2232.7	
Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.M.2232.8	Neotype *L. semistriatum*

Oberscheld	Oberdevon	Beyrich, 1835	UD I	MB.M.214
Oberscheld	Oberdevon, Unteres Frasnium	Beyrich, 1835	lower UD I	MB.M.213 a
Oberscheld	Oberdevon, Unteres Frasnium	Beyrich, 1835	lower UD I	MB.M.213 b
Oberscheld	Oberdevon, Unteres Frasnium	Beyrich, 1835	lower UD I	MB.M.215.1
Oberscheld	Oberdevon, Unteres Frasnium	Beyrich, 1835	lower UD I	MB.M.215.2

Table 20 Examined specimens of *Lunulacardium semistriatum*.

Lunulacardium excrescens Münster, 1840
Fig. 16.2

* + v 1840 *Lunulacardium excrescens* MÜNSTER, p. 70, pl. 13, fig. 12.
\+ 1924 *Chaenocardiola marsica* SCHMIDT, p. 144, pl. 7, fig. 13-14.
1925 *Chaenocardiola marsica*.- PAECKELMANN, p. 70.
1938 *Chaenocardiola marsica*.- PAECKELMANN, p. 25.
1929 *Chaenocardiola marsica*.- LANGE, p. 24.
1980 *Lunulacardium* (*Lunulacardium*) *marsica*.- KAEVER et al., p. 158.

Lectotype (other syntypes missing): BSPG AS VII 1735.
Type locality: Schübelhammer (Franconian Forest, Southeastern Germany).
Type stratum: "Clymenien Kalk" (Famennian).

Material:
Lectotype of *L. excrescens* BSPG AS VII 1735 from Schübelhammer (coll. Münster).

Diagnosis:
As for the genus with valves little higher than long. Ornamentation consisting of fine, closely spaced radial ribs, and few comarginal growth lines.

Description:
Comparison of *L. excrescens* with *L. semistriatum*:
Outline oval; antero-dorsal margin shorter, truncation declines from umbo with acute angle. Radial ribs closer spaced and finer, just few comarginal growth lines. From truncated margin valve declining with sharp edge, postero-dorsal margin convex.
Holotype (BSPG AS VII 1735, Fig. 16.2) steinkern; at truncation small portion of shell preservation; length: 1.3 cm, heigth: 1.4 cm, truncation 1.2 cm.

Discussion:

Münster (1840) described a new taxon from Schübelhammer (Franconian Forest, Southeastern Germany), *Lunulacardium excrescens*. BSPG AS VII 1735 (Fig. 16.2) is the lectotype, because other syntypes are missing. This specimen is closely related to *L. semistriatum* but differs in its finer ornamentation and its more oval outline. This is, until now, the only specimen representing this taxon.

Schmidt (1924) identified *Chaenocardiola marsica* from the Dasberg-Stage of Riemke, Dasberg, Effenberg, Warstein, and Wildungen (all Rhenish Massif). The syntypes of this species could not be traced in the Münster collection in the Bayerische Staatssammlung, Munich, nor in the Urweltmuseum Bayreuth. His description does not reveal any specific characters of this taxon. He gave no explanation justifying the erection of this taxon or for the affiliation to *Chaenocardiola*. Judging from the figures, the ornamentation and the outline, this species is identical with *L. excrescens* and, therefore, it is considered to be a junior synonym.

Occurrence:

UD IV/V

The holotype of this taxon is from the "Clymenien Kalk" of the Schübelhammer. Neither Münster´s (1840) description nor the label of the specimen allows a more precise specification of its age, which can, therefore, only broadly interpreted as UD II/IV. Ddue to the fact that the majority of the macrofauna is from the UD IV-VI at this outcrop, it is likley that this specimen is from the Hembergian-Stage. Schmidt (1924) reported this taxon from the UD V of Reitenberg, Aprike-Riemke, Riemke, Dasberg, Effenberg, Hoevel, Warstein, and Wildungen (all Northeastern Rhenish Massif). Lange (1929) and Paeckelmann (1938) determined a specimen from the *annulata* Zone of Beul by referring to Schmidt´s description. These references have to be treated with caution until the actual Schmidt material can be traced and restudied. Kaever et al. (1980) simply summarized the references above.

7.3.2 *Prosochasma*

Class BIVALVIA Linnaeus, 1758
Subclass CRYPTODONTA Neumayr, 1884
Order PRAECARDIOIDEA Newell, 1965
Family LUNULACARDIIDAE, Fischer, 1887

Genus *Prosochasma* Beushausen, 1895

Type species: *Lunulacardium pyriforme* Münster, 1840 (SD Clarke, 1904).

Included species: *Prosochasma pyriforme* (Münster, 1840), *Prosochasma bickense* (Holzapfel, 1882), *Prosochasma muelleri* (Holzapfel, 1882), *Prosochasma mytiloides* Beushausen, 1895.

Diagnosis (revised):
Valve rounded oval to subtrigonal, more or less equivalve, almost equilateral to slightly inequilateral (Fig. 18).
Shell slightly drawn out antero-ventrally. Sharp, straight to concave edge cutting the postero-dorsal third of shell body. Steinkerns showing valves gaping posterior. Gap framed by fringe almost perpendicular to sagittal plane, usually broader on umbo tapering off towards posterior margin.
Hinge line straight, truncated posteriorly, edentulous.
Umbo small, subcentral, prosogyrate.
Ornamentation consisting of fine comarginal growth lines and/or radial ribs.
Pallial line without pallial sinus, running posteriorly up to gap, anteriorly to umbo. Posterior muscle scar large, rounded, subcentrally fused with round smaller anterior adductor scar.

Discussion:
The type species of *Prosochasma*, which was subsequently designated by Clarke (1904), is *Lunulacardium pyriforme*.
Beushausen (1895) included several species, which were formerly assigned to *Lunulacardium*, in his new genus *Prosochasma*. He felt, due to their orientation and internal morphology, that they had to be separated from *Lunulacardium*.
Beushausen (1895) interpreted the truncated margin as the lunule of the valve and, hence, orientated it incorrectly. Therefore, the prosogyrate umbo sensu Beushausen would be an opisthogyrate beak. As shown in this study, however, this is a misinterpretation because of the true shell orientation *Prosochasma* develops a prosogyrate umbo.

Furthermore, Beushausen felt that the internal features and the soft the bauplan of *Prosochasma*, which he, in fact, did not understand, distinguish it from *Lunulacardium* and *Chaenocardiola*.

Although the characters on which Beushausen (1895) based his genus were dubious and partly false, this revision shows that the morphological group that is characterized by *Prosochasma* can be regognized as a distinctive genus.

Clarke (1904) ranked *Prosochasma* Beushausen as a subgenus of *Lunulacardium* Münster in order to identify species, which are more elongated and display a smoother ornamentation than other lunulacardiids. Babin (1966) and Newell and La Rocque (1969) followed Clarke (1904) in his description of this genus.

Occurrence:

Prosochasma occurs in the Frasnian (UD I) and the lower Famennian (Nehdenian, UD II). Only *P. bickense* appears already in the upper Givetian (Clarke, 1904; Beushausen, 1895).

Additional to the material, which is precisely determinable, Becker (1993a) reported this genus from the Upper Kellwasser horizon of Bine Jebilet (Southeastern Morocco, p. 116), from the top of the Upper Frasnian (UD I-L) just below the Upper Kellwasser horizon of Coumiac (N Cessenon, Montagne Noire, Southern France, p. 99), and from the Uppermost Frasnian of El Atrous (Southern Tafilalt, Morocco; p. 140). Furthermore, Paeckelmann and Kühne (1936b) mentioned it in the comments to the geological map sheet Madfeld from the Kellwasser beds. Grüneberg (1925) noted it from the Frasnian of Barmen. Both Lange (1929) and Paeckelmann (1923) reported *Prosochasma* from the *annulata*-Zone (UD IV-A) of Beul. Further reports of this genus are from Famenian of the Franconian Forest (Schindewolf, 1923), the Frasnian of North America (Clarke, 1904).

Figure 18 Characteristic outlines of *Prosochasma* taxa, showing the actual specimen and the corresponding sketch (partly reconstructed). **1**, *P. pyriforme*; **2**, *P. muelleri*; **3** *P. mytiloides*; **4**, *P. bickense*.

Prosochasma pyriforme (Münster, 1840)

Fig. 16.6, 18.1; Pl. 10, Figs. 8, 10

*	+	v	1840	*Lunulacardium pyriforme* MÜNSTER, p. 69, pl. 13, fig. 10a-b.
?	+		1882	*Lunulacardium cancellatum* HOLZAPFEL, p. 256, pl. 49, fig. 6. [nom. dub.]
	+	v	1882	*Lunulacardium adorfense* HOLZAPFEL, p. 256, pl. 49, fig. 8.
	+	e.p.	1882	*Lunulacardium Muelleri* HOLZAPFEL, p. 256, pl. 49, fig. 7.
		v	1895	*Prosochasma adorfense*.- BEUSHAUSEN, p. 375, pl. 27, fig. 17-18.
		v	1895	*Prosochasma cancellatum*.- BEUSHAUSEN, p. 372, pl. 27, fig. 19-20. [nom. dub.]
			1895	*Lunulicardium pyriforme*.- BEUSHAUSEN, p. 361.
			1979	*Prosochasma adorfense*.- PAECKELMANN, p. 29.
?			1979	*Prosochasma cancellatum*.- PAECKELMANN, p. 29. [nom. dub.]
	+		1924	*Chaenocardiola elongata* SCHMIDT, p. 145, pl. 7, fig. 15.
			1980	*Lunulacardium* (*Prosochasma*) *adorfense*.- KAEVER et al., p. 159, pl. 27, fig. 3.
?			1980	*Lunulacardium* (*Prosochasma*) *cancellatum*.- KAEVER et al., p. 159, pl. 27, fig. 5. [nom. dub.]

Lectotype (other syntypes missing): BSPG AS VII 1733.

Type locality: Schübelhammer (Franconian, Southeastern Germany).

Type stratum: "Clymenienkalk" (Famennian).

Material:
see Tab. 22.

Diagnosis:
As genus with slender subtrigonal valves, less inflated, almost equilateral.
Umbo attenuate, prosogyrate.
Ornamentation consisting of faint comarginal growth lines and subtle radial lines.

Description:
Valves subtrigonal, drop-like in outline (BSPG AS VII 1733, Fig. 18.1).
Anterior and posterior margin straight to slightly convex merging in umbo with acute angle. Ventral margin narrowly rounded. Anterior portion of dorsal margin barely observable, probably immediately declining in the anterior margin. Valves postero-dorsally gaping.
Gap framed by fringe perpendicular to sagittal plane. Truncation aligned with contour of valve (BSPG AS VII 1733, Fig. 18.1; SMFXV/3-2157, Pl. 10, Fig. 8).
Hinge line anteriorly short, posteriorly truncated by section.
Umbo small, prosogyrate.
Ornamentation consisting of faint comarginal growth lines and subtle radial lines (SMFXV/3-2159, Pl. 10, Fig. 10). Ornamentation smooth, on steinkerns sometimes not visible.
Holotype (BSPG AS VII 1733, Fig. 16.6) poorly preserved steinkern; truncation, hinge area, and ornamentation not preserved. Complete outline observable.

Discussion:
Münster (1840) described *Lunulacardium pyriforme* from Schübelhammer (Franconian Forest, Southeastern Germany). Clarke (1904) subsequently designated it as the type species of *Prosochasma*. BSGP AS VII 1733 (Fig. 16.6), which is a poorly preserved steinkern without any traces ornamentation it is the lectotype, because other syntypes are missing.
Holzapfel (1882) identified *Lunulacardium adorfense* based on material from the Martenberg (Northeastern Rhenish Massif) and Beushausen (1895) re-assigned it to *Prosochasma* Beushausen. SMF XV/3-2157 (Pl. 10, Fig. 5) chosen as the lectotype, because other syntypes are missing. Holzapfel (1882) stated that this species is close to *P. pyriforme*, but he noted that *P. adorfense* developed additional fine radial ribs. Although Münster (1840) described *P. pyriforme* as displaying only subtle comarginal growth lines, it is shown herein, that it displayes both fine radial lines and comarginal growth lines (e.g., SMF XV/3-2157, SMF XV/3-2159, Pl. 10, Fig. 10). Therefore, the *L. adorfense* is a subjective junior synonym of *P. pyriforme*.
Holzapfel (1882) identified a second new species from Martenberg, *Lunulacardium cancellatum*. Beushausen (1895) re-assigned it to *Prosochasma*. The syntypes are lost. Neither the

description nor the figure reveal any characteristic differences between *P. cancellatum* and *P. pyriforme*. However, due to the missing holotype, *L. cancellatum* is considered currently to be a nomen dubium.

Schmidt (1924) described *Chaenocardiola elongata* from the Effenberg and Eulenspiegel of the Eastern Rhenish Massif. Unfortunately, the original could not be traced in the Naturkunde Museum Berlin. But his figure (1924, pl. 7, fig. 15) shows clearly that this species developed a truncated posterior margin, which extended around a third of the valve's heights. Therefore, the generic assignment to *Chaenocardiola* is falsely; the truncation of chaenocardiolid taxa takes up the full height of the valves. Schmidt's (1924) brief description of two syntypes lacks comments on the symmetry of *C. elongata*, but according to the figure (1924, pl. 7, fig. 15) the specimens are almost equilateral and display the drop-like outline as in *P. pyriforme*. This affiliation is supported by the ornamentation, which Schmidt described as displaying subtle radial lines and comarginal growth lines. Therefore, *C. elongata* Schmidt is re-assigned to *P. pyriforme* and considered as subjective synonym.

Occurrence:

UD I-L to ? IV (Tab. 21; Tab. 22)

Schmidt (1924) reported the youngest occurrence of *L. pyriforme* from the the UD III/IV of the Effenberg and Eulenspiegel. The actual material of this referrence could not been traced. Due to the dubious taxonomic situation of this group, caution is advised concerning these determinations. The lectotype is from the UD II/IV of the Schübelhammer and cannot be dated precisely.

Locality	Region	Reference	Stratigraphic level
Effenberg	Northeastern RM	Schmidt, 1924	UD III/IV
Eulenspiegel	Northeastern RM	Schmidt, 1924	UD III/IV
Martenberg	Northeastern RM	Kaever et al., 1980	UD I-I/J
Martenberg	Northeastern RM	Paeckelmann, 1979	UD I-I/J
Martenberg	Northeastern RM	Beushausen, 1895	UD I-I/J
Martenberg	Northeastern RM	Holzapfel, 1882	UD I-I/J

Table 21 References quoting the occurrence of *Prosochasma pyriforme*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Martenberg	Unteres Oberdevon	v. Koenen	UD I-I/L	GZG 490-200	
Martenberg	Unteres Oberdevon	Holzapfel	UD I-I/L	SMF XV/3-2159	
Martenberg	Unteres Oberdevon	Holzapfel	UD I-I/L	SMF XV/3-2157	Lectotype *L. adorfense*
Martenberg	Unteres Oberdevon	v. Koenen	UD I-I/L	GZG 1258-5	
Schübelhammer	Clymenien Kalk	Münster	UD II/IV	BSGP AS VII 1733	Lectotype *L. pyriforme*

Table 22 Examined specimens of *Prosochasma pyriforme*.

Prosochasma muelleri (Holzapfel 1882) [nom. corr.]
Fig. 18.2, Fig. 19; Pl. 10, Fig. 5

* + v e.p. 1882 *Lunulacardium mülleri* HOLZAPFEL, p. 256, pl. 49, fig. 5.
+ v 1895 *Prosochasma expansum* BEUSHAUSEN, p. 374, pl. 27, fig. 21.
v 1895 *Prosochasma mülleri*.- BEUSHAUSEN, p. 374, pl. 27, fig. 24-27.
1904 *Lunulicardium mülleri*.- CLARKE, p. 221, 228, pl. 3, fig. 1-2.
1913 *Lunulicardium* aff. *mülleri*.- PAECKELMANN, p. 255.
? + 1923 *Prosochasma lunulonga* SCHINDEWOLF, p. 274.
1931 *Prosochasma mülleri*.- MATERN, p. 124.
1979 *Prosochasma mülleri*.- PAECKELMANN, p. 29.
1992 *Lunulicardium* (*Prosochasma*) *mülleri*.- GRIMM AND ROTHAUSEN, p. 47.

Lectotype (designated herein): SMF XV/3-2154.
Type locality: Martenberg (Northeastern Rhenish Massif, Germany).
Type stratum: upper Frasnian, upper Adorfian (UD I-K/J).

Material:
see Tab. 24.

Diagnosis:
As genus with rounded trigonal valves, somewhat inequilateral.
Umbo small, attenuate, subcentral.
Ornamentation consisting of radial and comarginal lines.

Description:
Valves drop-shaped in outline, slightly inequilateral, more convex than *L. pyriforme*.
Outline dorsally attenuate, slender, trigonal, and ventrally rounded oval in outline (Fig. 18.2).

Antero-dorsal margin short, straight deviating into anterior margin. Antero-dorsally few fine radial ribs parallel to dorsal margin, just faint imprints observable on steinkern (e.g., GZG 490-202). Valves posteriorly gaping.
Gap framed by fringe perpendicular to sagittal plane. Truncation straight to slightly concave, more or less aligned with contour of valve.
Hinge line straight, posteriorly truncated.
Umbo small, attenuate, prosogyrate.
Ornamentation smooth, on steinkerns almost not recognizable.
Two fused adductor scars in anterior portion of valve observable (e.g., SMF XV/3-2154, Fig. 19; Pl. 10, Fig. 5), small anterior one rounded, posterior one large (e.g., GZG 490-204). Pallial line without pallial sinus, running anteriorly up to umbo and posteriorly to truncation (SMF XV/3-2154, Fig. 19; Pl. 10, Fig. 5).
Lectotype (SMF XV/3-2154, Pl. 10, Fig. 5) well preserved steinkern, displaying complete outline, adductor scars, and pallial line. No ornamentation observable. Hinge line not preserved.

Discussion:
Holzapfel (1882) described *Lunulacardium muelleri* based on two specimens from Martenberg (SMF XV/3-2154, SMF XV/3-2159). SMF XV/3-2159 is subequilateral, drop-shaped, and displays faint radial and subtle comarginal ornamentation. These characters identify it as *P. pyriforme*. The other type (SMF XV/3-2154, Pl. 10, Fig. 5), which is a steinkern, is more inequilateral in outline. Due to its characteristic outline and the preservation of the internal features of this taxon, such as the pallial line and adductor scars, SMF XV/3-2154 is selected as the lectotype of *L. muelleri*.
In his description of *L. muelleri* Holzapfel (1882) mentioned the development of a smooth radial and comarginal ornamentation. Although this feature is not preserved on the lectotype, its presence within this species is confirmed by the ornamentation of additional specimens of this taxon.
Beushausen (1895) described *Prosochasma expansum* base on a single valve from Martenberg (Northeastern Rhenish Massif). He based his taxon explicitly on the characteristic inequilateral outline of this specimen. GZG 490-202 (Pl. 10, Fig. 9) is the holotype by monotypy. Comparing it with the lectotype (SMF XV/3-2154) of *P. muelleri*, the outlines of both appear to be just slightly different within the normal range of variation of the latter species. All other characters, such as, e.g., the ornamentation of GZG 490-202 identify this specimen as *P. muelleri*. Therefore, *L. expansum* is a subjective junior synonym of *L. muelleri*.
Paeckelmann (1913) identified some small valves he described as *Lunulicardium* (*Prosochasma*) aff. *muelleri*. The reason for this tentative assignment was the truncated margin, which he felt was higher concave than in *P. muelleri*. This development of the truncation is in

the normal range of variation displayed by this species. Therefore, it is assigned to *P. muelleri*, with certainty.

Schindewolf (1923) described a new taxon from the lower Famennianof Gattendorf (Franconian Forest, Southeastern Germany), *Prosochasma lunulonga*. He gave a short description but no figure. The only characters of this species he mentioned are a long lunule and closely spaced radial ribs. Due to the lack of the holotype, a figure, and the insufficiant description, this taxon cannot be distinguish from other *Prosochasma* species and, therefore, it is considered currently a nomen dubium. Re-sampling of lower Famennian at the Gattendorf type locality is not possible, since the lower part of the section is now covered.

Occurrence:

UD I/II-A (Tab. 23; Tab. 24).

The type material is from the Frasnian of the Martenberg. There, the Lower and Middle Frasnian is incomplete and poorly fossiliferous. Rich macrofauna assamblages start with the basal upper Frasnian (UD I-I/J; see e.g., House and Ziegler, 1977), therefore, most Martenberg specimens are supposed to be this level. The Famennian range is based on a specimen from the Montagne Noire, which is supported by the referrence from Oberscheld (Matern, 1931).

Locality	Region	Reference	Stratigraphic level
“Am Danzert”, Oos	Western RM	Grimm and Rothausen, 1992	UD I-A /I
east of Ellinghausen	Northeastern RM	Paeckelmann, 1913	UD I
Martenberg	Northeastern RM	Beushausen, 1895	UD I-I/J
Martenberg	Northeastern RM	Holzapfel, 1882	UD I-I/J
Martenberg	Northeastern RM	Paeckelmann, 1979	UD I-I/J
Martenberg	Northeastern RM	Paeckelmann, 1979	UD I-I/J
Oberscheld	Lahn Dill Syncline	Matern, 1931	UD I-K
Oberscheld	Lahn Dill Syncline	Matern, 1931	UD II-A

Table 23 References quoting the occurrence of *Prosochasma muelleri*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Martenberg	Unteres Oberdevon	-	UD I-I/J	GZG 490-205	
Martenberg	Unteres Oberdevon	v. Koenen	UD I-I/J	GZG 1258-6	
Martenberg	Unteres Oberdevon	v. Koenen	UD I-I/J	GZG 490-204	
Martenberg	Unteres Oberdevon	v. Koenen	UD I-I/J	GZG 490-203	
Martenberg	Unteres Oberdevon	Holzapfel	UD I-I/J	SMF XV/3-2159	Paralectotype *L. muelleri*
Martenberg	Unteres Oberdevon	Holzapfel	UD I-I/J	SMF XV/3-2154	Lectotype *L. muelleri*
Martenberg	Unteres Oberdevon	v. Koenen	UD I-I/J	GZG 490-202	Holotype *P. expansum*
Oberscheld	Oberdevon	-		GZG 490-202	
Rombachtal, Langenaubach	to	Kegel, 1922	Famennian	MB.M.4378	
Touriére, Cabriére	Oberdevon	Rouville, 1883	UD II	GZG 1258-13	

Table 24 Examined specimens of *Prosochasma muelleri*.

Prosochasma mytiloides Beushausen, 1895

Fig. 18.3; Pl. 10, Figs. 1, 6, 7

* + v 1895 *Prosochasma mytiloides* BEUSHAUSEN, p. 373, pl. 27, fig. 22.
+ v 1895 *Prosochasma abditum* BEUSHAUSEN, p. 371, pl. 28, fig. 13.
1931 *Prosochasma abditum*.- MATERN, p. 124.
1922 *Prosochasma mytiloides*.- SCHMIDT, p. 274.
1923 *Prosochasma* sp. aff. *dilatatae*.- SCHINDEWOLF, p. 285.
1979 *Prosochasma abditum*.- PAECKELMANN, p. 29.
1980 *Lunulacardium* (*Prosochasma*) *abditum*.- KAEVER et al., p. 158, pl. 27, fig. 2.

Lectotype (other syntypes missing): GZG 490-201.
Type locality: Bicken (Lahn-Dill Syncline, Germany).
Type stratum: Upper Kellwasser Limestone (upper Frasnian, Adorfian, UD I-L).

Material:
see Tab. 26.

Diagnosis:
As for the genus with valves narrowly oval, inequilateral, somewhat inflated.
Posterior valve truncated immediately at the umbo, generating straight to concave section. Antero-dorsal margin concave, longer than in *P. muelleri*.
Ornamentation consisting of comarginal growth lines and faint radial lines.

Description:

Valve rounded oval, slightly inequilateral (Fig. 18.3), presenting morphological transition between subtrigonal, attenuate forms and broad oval *L. bickense*.

Ventral margin subcircular, merging regularly into convex anterior margin. Antero-dorsal margin straight to slightly concave, somewhat declining. Anteriorly few radial ribs parallel to hinge line (MB.M.221, Pl. 10, Fig. 7), often incompletely preserved.

Valve posteriorly gaping. Gap framed by slightly concave fringe perpendicular to sagittal plane. Sometimes umbo cut off by truncation.

Hinge line anteriorly straight to slightly concave, posteriorly portion missing.

Umbo prosogyrate, with strongly involute prodissoconch.

Ornamentation consisting of irregular, comarginal growth lines and subtle radial ribs (Pl. 10, Fig. 7).

Subcentral two round fused adductor scars. Anterior muscle scar small, posterior one large. Pallial line without pallial sinus, running from the antero-dorsal margin to the truncation.

Holotype (MB.M.201, Pl. 10, Fig. 6) steinkern with shell remains. Posterior portion of the outline missing. Presenting imprints of radial ribs on the ventral margin. Antero-dorsally shell preserved, with five radial ribs parallel to the hinge line, intersected by fine comarginal growth lines.

Discussion:

Beushausen (1895) described *Prosochasma mytiloides* from the Frasnian of Bicken (Lahn-Dill Syncline). Specimen GZG 490-201 is chosen as the lectotype, due to the lack of other syntypes.

Furthermore, Beushausen (1895) identified *Prosochasma abditum* from the Frasnian of the Martenberg (Northeastern Rhenish Massif). MB.M.221 (Pl. 10, Fig. 7) is the lectotype of this taxon, because other syntypes are missing. Unfortunately, it is lacking the posterior margin and parts of the umbo, therefore, the its actual outline is not completely observable. But the development of the anterior wing-like extension and the ornamentation identifies this specimen as *P. mytiloides*.

Due to the superior state of preservation of GZG 490-201 (Pl. 10, Fig. 6), *P. mytiloides* is favored over *P. abditum* and the latter is placed in subjective synonymy.

Schindewolf (1923) reported a specimen from the Upper Famennian of Gattendorf (Franconian Forest, Germany) as *Prosochasma* sp. aff. *dilatatae*. He stated that this specimen presents a outline similar to *P. bickense* but with a steeper declining posterior margin. Furthermore, he mentioned that the radial ornamentation is stronger developed than in *P. bickense*. This description suggests that the Schindewolf specimens falls in the range of *P. mytiloides*. But the lack of an original or of any illustration does not allow a final identification. With

repect of its much younger age, its affinities cannot be resolved at present, because there is no topotypic material from Gattendorf that allow a classification.

Occurrence:

UD I to UD II (Tab. 25; Tab. 26).

The youngest possible occurrence of *P. mytiloides* is based on "*P.* sp. aff. *dilatatae*" by (Schindewolf, 1923) from Gattendorf (Southeastern Germany). The examined material is exclusively from the Frasnian and the species is probably most common in the Upper Frasnian (starting with UD I-I/J). Schmidt, 1922 reported the occurrence in the lower Famennian of Warstein area but this specimen could not located and, hence, the supposed Famennian range of *P. mytiloides* needs further confirmation.

Locality	Region	Reference	Stratigraphic level
Martenberg	Northeastern RM	Beushausen, 1895	UD I-I/J
Martenberg	Northeastern RM	Kaever et al., 1980	UD I-I/J
Martenberg	Northeastern RM	Paeckelmann, 1979	UD I-I/J
Oberscheld	Lahn Dill Syncline	Matern, 1931	UD I-I/J
Oberscheld	Lahn Dill Syncline	Kaever et al., 1980	UD I-I/J
Warstein area	Northeastern RM	Schmidt, 1922	UD II

Table 25 References quoting the occurrence of *Prosochasma mytiloides*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Bicken	Oberdevon	Krüger	-	MB.M.4376	
Bicken	Unteres Oberdevon	Beushausen	UD I	GZG 490-210	
Bicken	Unteres Oberdevon	Koenen	UD I-L	GZG 490-201	Lectotype *P. mytiloides*
Charlottenzug/ Bredelar	Unteres Oberdevon	Denckmann	UD I	MB.M.4377	
Martenberg	Oberdevon	Müller	UD I-I/J	MB.M.221	Lectotype *P. abditum*

Table 26 Examined specimens of *Prosochasma mytiloides*.

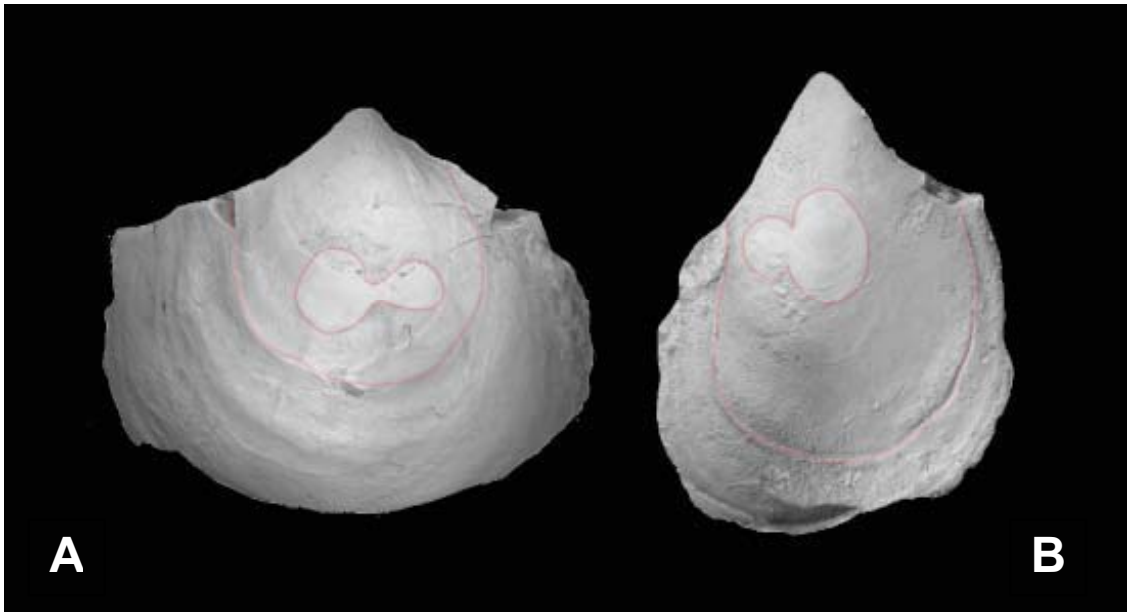


Figure 19 Development of soft tissue attachment areas of *Prosochasma*. adductor scars and pallial line preserved on steinkerns. **A** - *P. bickense* (GZG 490-206), x1.2. **B -** *P. muelleri* (lectotype, SMF XV/3-2154), x3.3.

Prosochasma bickense (Holzapfel, 1882)

Fig. 19, Fig. 18.4; Pl. 10, Figs. 2-4, 11-15

* + v	1882	*Lunulacardium bickense*	HOLZAPFEL, p. 256, pl. 49, fig. 9.
+ v	1882	*Lunulacardium inflatum*	HOLZAPFEL, p. 257, pl. 49, fig. 11.
? +	1882	*Lunulacardium concentricum*	HOLZAPFEL, p. 257, pl. 49, fig. 10. [nom. dub.]
	1887	*Lunulacardium* aff. *bickense*.-	FRECH, p. 377.
+ v	1895	*Prosochasma dilatatum*	BEUSHAUSEN, p. 376, pl. 28, fig. 8-9.
?	1895	*Prosochasma concentricum*.-	BEUSHAUSEN, p. 372, pl. 28, fig. 11. [nom. dub.]
v	1895	*Prosochasma inflatum*.-	BEUSHAUSEN, p. 377, pl. 28, fig. 6-7.
v	1895	*Prosochasma bickense*.-	BEUSHAUSEN, p. 377, pl. 28, fig. 4-5, 10, 12.
	1901b	*Prosochasma bickense*.-	DENCKMANN, p. 40.
	1904	*Lunulicardium inflatum*.-	CLARKE, p. 221, 228.
	1904	*Lunulicardium* (*Prosochasma*) *bickense*.-	CLARKE, p. 240, pl. 3, fig. 3-5, 11.
	1922a	*Chaenocardiola concentrica*.-	HENKE AND SCHMIDT, p. 35.
	1931	*Prosochasma bickense*.-	MATER, p. 124.
	1931	*Prosochasma* cf. *inflata*.-	MATERN, p. 124.
	1979	*Prosochasma dilatatum*.-	PAECKELMANN, p. 29.
?	1979	*Prosochasma concentricum*.-	PAECKELMANN, p. 29. [nom. dub.]
	1979	*Prosochasma inflatum*.-	PAECKELMANN, p. 29.
	1979	*Prosochasma bickense*.-	PAECKELMANN, p. 29.
	1980	*Lunulacardium* (*Prosochasma*) *bickense*.-	KAEVER et al., p. 159, pl. 27, fig. 4.
?	1980	*Lunulacardium* (*Prosochasma*) *concentricum*.-	KAEVER et al., p. 159, pl. 27, fig. 6. [nom. dub.]
	1980	*Lunulacardium* (*Prosochasma*) *dilatatum*.-	KAEVER et al., p. 159, pl. 28, fig. 1.
	1980	*Lunulacardium* (*Prosochasma*) *inflatum*.-	KAEVER et al., p. 159, pl. 28, fig. 2.

Lectotype (other syntypes missing): SMF XV/3-2155.
Type locality: Bicken (Lahn-Dill Syncline, Germany).
Type stratum: Frasnian (UD I).

Material:
see Tab. 28.

Diagnosis:
As for the genus with valves rounded oval, slightly inequilateral, somewhat inflated.
Antero-dorsal margin straight to concave, deviating in anterior margin. Antero-dorsally three to five fine radial ribs, parallel to hinge line.
Ornamentation smooth, consisting of irregular growth lines and faint radial lines.

Description:
Valves broad oval in outline, slightly inequilateral (Fig. 18.4), somewhat inflated.
Subcircular ventral margin merging regularly into less rounded anterior margin. Anteriorly dorsal margin straight to concave, posteriorly truncated. Often umbo is cut off by truncation. Valves gaping posteriorly. Gap framed by slightly concave fringe perpendicular to sagittal plane. Often section set off from body of valves by slight depression. Anteriorly three to four strong radial ribs, mostly preserved as imprints (e.g., MB.M.4384; GZG 490-208, Pl. 10, Fig. 2, 14).
Hinge line straight, edentulous (SMF XV/3-2155, Pl. 10, Fig. 15; MB.M.4388, Pl. 12, Fig. 8, 9).
Umbo small, prosogyrate, with strongly involute prodissoconch (e.g., GZG 490-208, Pl. 10, Fig. 2, 14). Prodissoconch not affected by truncation.
Ornamentation consisting of fine comarginal growth lines, and sometime few irregular, stronger comarginal rugae. Subtle radial lines sometimes observable.
Subcentral two fused adductor scars (Fig. 19). Anterior small , transverse oval muscle scar, posterior one large rounded (GZG 490-207).
Holotype (SMF XV/3-2155, Pl. 10, Fig. 4, 16) well preserved large steinkern. Presenting complete outline, truncation and dorsal margin. Antero-dorsally three small radial ribs and fine comarginal growth lines present; no radial lines observable. Anterior to the truncation slight depression developed. No internal features observable.

Discussion:
Holzapfel (1882) identified a new species from Martenberg (Northeastern Rhenish Massif) and Bicken (Lahn-Dill Syncline), *Lunulacardium bickense*. SMF XV/3-2155 (Pl. 10, Figs. 4, 15) from Bicken is here designated as the lectotype. No other syntypes have been traced.

Furthermore, he (1882) described a second species from Martenberg (Northeastern Rhenish Massif), *Lunulacardium inflatum*. SMF XV/3-2156 (Pl. 10, Figs. 11-12) is the lectotype of this species, because oterh syntypes are missing. Holzapfel (1882) stated that *L. inflatum* is rare and it differs from *L. bickense* by the higher degree of inflation. GZG 490-209 was collected by von Koenen at Martenberg and is an original of Beushausen´s monograph (1895). Both specimens are slightly higher convex than *P. bickense*, but it seems to be within the range of intraspecific variation of *P. bickense*. Therefore, *L. inflatum* is here regarded a subjective synonymy. *P. bickense* is favored over *L. inflatum*, because this species is widely used in the literature and the original material is better preserved.

Holzapfel (1882) identified a third species from the Martenberg, *Lunulacardium concentricum*. According to Beushausen (1895), the holotype was hosted in the collection of Müller in Adorf (Northeastern Rhenish Massif). Unfortunately, this specimen cannot be traced anymore and seems to be lost. Beushausen (1895) re-studied *L. concentricum* and stated that the Holzapfel figure (1882, pl. 49, fig. 10) does not reflect the lack of the posterior margin and, therefore, gives a false impression of the outline of this valve. He assumed that the specimen to be closely related to *P. bickense*. But, due to its poor state of preservation, he was not able to actually re-assign it to *P. bickense*. Henke and Schmidt (1922a) reported *Chaenocardiola concentrica* from the "Adorf Kalk" of Pettmecke, which is probably just falsely quoted. However, due to the missing holotype, *Lunulacardium concentricum* is considered a nomen dubium.

Beushausen (1985) described another species, *Prosochasma dilatatum* from the Frasnian of the Martenberg. He stated that this taxon is closely related to *P. bickense* and *P. inflatum*. According to Beushausen (1895), the difference between *P. dilatatum* and the other two is the broader outline of the valves. Examining the original types of *P. dilatatum* (GZG 490-208, GZG 490-207), this character does not withstand scrutiny. GZG 490-207 is a large valve, which just partly presents the outline of the valve, and GZG 490-208 (Pl. 10, Figs. 2, 14) is definitely a representative of *P. bickense*. The latter is chosen herein as the lectotype of this species and places *P. dilatatum* in subjective synonymy with *P. bickense*.

Interestingly, there are no differences observable that would distinguish the Givetian specimens from the Famennian material.

Occurrence:

MD III to UD I (Tab. 27, Tab. 28).

The oldest occurrence of *P. bickense* is based on a specimen from the Martenberg (Northeastern Rhenish Massif). It is labled as beeing fromt the "Pharciceras Kalk" (MD III). This specimen is the only one from the Givetian, all other material is from the Frasnian (UD I, Tab. 28), therefore, the oldest occurrence has to be treated with caution until there is more Givetian material representing *P. bickense*.

Locality	Region	Reference	Stratigraphic level
Angola area	Eastern New York State	Clarke, 1904	UD I
Combe d´Izarne	Montagne Noire, France	Frech, 1887	UD I
Genesee province	Eastern New York State	Clarke, 1904	UD I
Johnson's falls	Eastern New York State	Clarke, 1904	UD I
Lower Portage falls	Eastern New York State	Clarke, 1904	UD I
Martenberg	Northeastern RM	Beushausen, 1895	UD I
Martenberg	Northeastern RM	Holzapfel, 1882	UD I-I/L
Martenberg	Northeastern RM	Kaever et al., 1980	UD I-I/J
Martenberg	Northeastern RM	Paeckelmann, 1979	UD I-I/J
Oberscheld	Lahn Dill Syncline	Kaever et al., 1980	UD I-I/J
Oberscheld	Lahn Dill Syncline	Matern, 1931	UD I-J/K
Pettmecke	Northeastern RM	Henke and Schmidt, 1922a	UD I
Various localities	Kellerwald, Eastern RM	Denckmann, 1901b	UD I

Table 27 References quoting the occurrence of *Prosochasma bickense*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Bicken	-	Holzapfel	UD I	SMF XV/3-2155	Lectotype *L. bickense*
Bicken	Unteres Oberdevon	Krüger, 1873	UD I	MB.M.4385	
Blauer Bruch	Kellwasser Kalk	Pusch, 1935	UD I-K/L	MB.M.4382	
Braunau	Unteres Oberdevon	v. Koenen	UD I	GZG 490-208	Lectotype *P. dilatatum*
Dillenburg	Oberdevon	Heymann, 1873	UD I	MB.M.4381	
Ense	Unteres Oberdevon	-	UD I	MB.M.4383	
Ense	Unteres Oberdevon	-	UD I	MB.M.4388	
Ense	Unteres Oberdevon	-	UD I	MB.M.4379	
Martenberg	-	Holzapfel	UD I	SMF XV/3-2156	Lectotype *L. inflatum*
Martenberg	Adorfer Kalk	Müller, 1886	UD I	GZG 490-206	
Martenberg	Adorfer Kalk	Müller, 1886	UD I	GZG 490-207	Paralectotype *P. dilatatum*
Martenberg	Intumescens Kalk	Koenen	UD I-E/K	GZG 490-209	
Martenberg	Pharciceras Kalk	-	MD III	MB.M.4386	
Oberscheld	Clymenien Kalk	Lotz, 1901	UD I-I/L	MB.M.4387	
Oued Mzerreb	OM2-W	Becker	UD I-I	B6A-35.133	
Oued Mzerreb	Kellwasser beds	Becker	UD I-I/L	B6A-35.134	
Ooser Wasen	to	Beushausen, 1897	UD I-A/H	MB.M.4380	
Ooser Wasen	to	Beushausen, 1897	UD I-A/H	MB.M.4390	
Wildungen	Intumescens-Zone	Denckmann, 1893	UD I-E/K	MB.M.4384	
Wildungen	Intumescens-Zone	Denckmann, 1893	UD I-E/K	MB.M.4389	

Table 28 Examined specimens of *Prosochasma bickense*.

7.3.3 *Chaenocardiola*

Class BIVALVIA Linnaeus, 1758
Subclass CRYPTODONTA Neumayr, 1884
Order PRAECARDIOIDEA Newell, 1965
Family LUNULACARDIIDAE, Fischer, 1887

Genus *Chaenocardiola* Holzapfel, 1889 [revised by Beushausen, 1895]

Type species: *Cardita haliotoidea* Roemer, 1850 (SD Beushausen, 1895).

Included Devonian species: *Chaenocardiola canalifer* (Münster, 1840); *Chaenocardiola koeneni* Beushausen, 1895; *Chaenocardiola tetragona* (Münster, 1840); *Chaenocardiola denckmanni* Beushausen, 1895; *Chaenocardiola carinata*, Beushausen, 1895.

Diagnosis (revised):
Valve rounded trigonal to oval, equivalve, inequilateral.
Ventral and anterior margin regular rounded.
Posteriorly valves completely truncated, section straight to slightly convex. In front of edge valve slightly depressed. Anterior portion of dorsal margin straight to slightly concave, posterior portion missing, due to truncation. In front of umbo valve somewhat drawn out developing partly distinct wing-like extension, merging abruptly in rounded anterior margin.
Steinkerns gaping posterior, shell probably slightly gaping; gap framed by concave fringe, developed more or less perpendicular or with more or less acute angle to sagittal plane.
Umbo prosogyrate, more or less central.
Hinge line straight, truncated posteriorly somewhat before the umbo, edentulous.
Ornamentation consisting of coarse to fine radial ribs and fine comarginal growth lines.

Discussion:
Holzapfel (1889) separated a new genus from *Lunulacardium* Münster, *Chaenocardiola*. His description is rather confuse. He referred to the carboniferous *Chaenocardia ovata* Meek and Worthen, (1869, p. 170) which develops an anterior wing-like extension with a hiatus. This taxon is eponymous for Holzapfel´s genus. However, *Chaenocardia ovata* has no relationships to the chaenocardiolids. The latter are rounded trigonal in outline and not oval as the Carboniferous taxon. Furthermore, chaenocardiolids develop a straight to slightly concave edge, which extends from the umbo to the middle of the ventral margin and cuts the whole posterior portion of the valve, and they do not present a wing as *Chaenocardia*.

Beushausen (1895) revised *Chaenocardiola* and mentioned that *Chaenocardia ovata* presents more affinities to *Prosochasma* Beushausen than with *Chaenocardiola* Holzapfel. His figure (Beushausen, 1895, p. 361) as well as this study supports this assumption. Furthermore, Beushausen (1895) subsequently designated *Cardita haliotoidea* Roemer as type species of *Chaenocardiola*. Roemer (1850) identified this species from the Carboniferous Posidonia Shale from the Northwestern Hercynian Mountains. This taxon occurs from the Aprathian to the Arnsbergian of the Rhenish Massif and the Namurian A of Belgian, England and Ireland. Re-studies of the Carboniferous representatives of *Chaenocardiola*, including the type species, are given by Yates (1962), Nicolaus (1963), Rathmann and Amler (1992), and Amler (1998, 2006).

The Holzapfel (1889) type (Mdg. AH2006-1; Pl. 11, Fig. 10) of *C. haliotoidea* illustrates the relationships of this carboniferous species and the Devonian taxa, which are re-studied herein. It confirms the assignment of the Upper Devonian species to *Chaenocardiola*, due to its typical posterior margin, which is truncated by the complete height of the valve. Furthermore, the umbo is small, prosogyrate and the antero-dorsal margin slightly concave. All these features and the rounded subtrigonal outline are characters of *Chaenocardiola.*

In the following the emphasize is on the Upper Devonian species, because a re-study of the Carboniferous material would have been beyond the scope of this study.

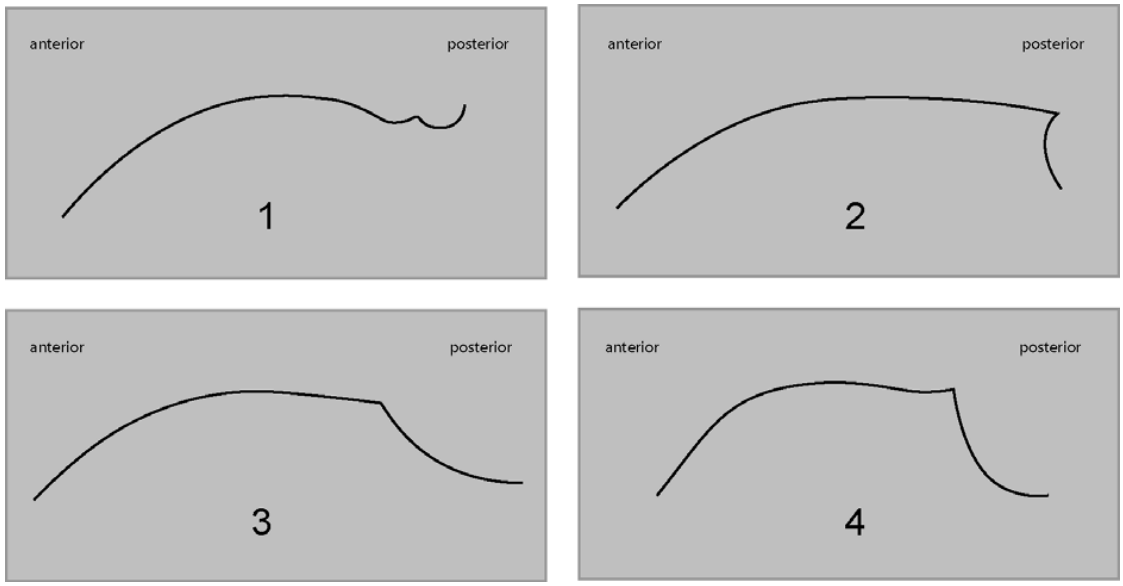


Figure 20 Cross-section through the center of the valve parallel to the hinge line. Showing the development of the truncation and inflation of Upper Devonian chaenocardiolid species. **1**, *C. canalifer*; **2** *C. koeneni*; **3**, *C. tetragona*; **4**, *C. carinata.*

Chaenocardiola tetragona (Münster, 1840)
Figs. 16.1, 20.3, 21.3; Pl. 11, Figs. 10, 12-14; Pl. 12, Figs. 9-10

* + v 1840 *Lunulacardium* ? *tetragonum* MÜNSTER, p. 71, pl. 12, fig. 20.
? + 1895 *Chaenocardiola nassoviensis* BEUSHAUSEN, p. 365, pl. 27, fig. 16. [nom. dub.]
+ v e.p. 1895 *Chaenocardiola carinata* BEUSHAUSEN, p. 367, pl. 28, fig. 2.

Lectotype (other syntypes missing): BSPG AS VII 1736.
Type locality: Geyser (Southeastern Germany).
Type stratum: "Clymenienkalk" (lower Famennian, Nehdenian, UD II).

Material:
see Tab. 29.

Diagnosis:
Characters of genus with attenuate trigonal outline, somewhat inflated.
Antero-dorsal margin merging directly in anterior margin.
Ornamentation consisting of narrow spaced, fine radial ribs.
Internal ornamentation of valve consisting of coarse radial ribs and fine comarginal growth lines.

Description:
Valves acute trigonal in outline (Fig. 21.3).
Ventral margin narrow rounded, merging regularly in somewhat convex anterior margin. From apex of valve directly concavely sloping downward, deviating abruptly in anterior margin (Fig. 21.3).
Valves posteriorly completely truncated; umbo and posterior portion of hinge line cut off by section. Truncation commences immediately, or anteriorly faint depression developed (Fig. 20.3). Posterior to the truncation shell declines concavely, generating a sharp carina. Valve probably posteriorl slightly gaping (MB.M.4388, Pl. 11, Fig. 11).
Umbo small, prosogyrate.
Hinge line straight, edentulous (B6A-135.136, Pl. 12, Fig. 11).
Ornamentation consisting of fine closely spaced radial ribs on outer surface of shell (Pl. 11, Figs, 9-10), on steinkerns broader radial ribs observable (MB.M.220, Pl. 11, Fig. 9); sometimes traces of outer ornamentation faintly observable on internal mould. Ornamentation stronger towards ventral margin; dorsally fine ribs, compact, with only minute interspaces. Irregular, subordinate, fine comarginal growth lines.
No adductor scars or pallial line observed.

Holotype (BSPG AS VII 1736, Fig. 16.4) poorly preserved shell fragment, presenting acute umbo and dorsal portion of truncation. Characteristic fine closely spaced radial ribs well preserved, comarginal growth lines faintly observable (Fig. 16.4).

Discussion

Münster (1840) identified a new species from Geyser (Franconian Forest, Southeastern Germany) as *Lunulacardium* ? *tetragonum*. Specimen BSPG AS VII 1736 (Fig. 16.4) is the elctotype, because other syntypes are missing. The complete anterior margin and parts of the posterior and ventral margin are missing and, therefore, its outline gives the impression of being more or less rectangular, which was probably eponymous for this species. But in comparison with further material and based on the ornamentation it can be clearly asserted that the outline of this specimen was rounded subtrigonal. Especially the development of the ornamentation, which is characteristic for this taxon identifies BSPG AS VII 1736 as a representative of this species (Fig. 16.4). Although the holotype is just poorly preserved, it is the oldest available name for this taxon.

Beushausen (1895) designated a new species, *Chaenocardiola nassoviensis*. This attenuate trigonal valve with markedly radial ornamentation seems, according to the description and figure (Beushausen, 1895, pl. 27, fig. 16) to fit in the concept of *C. tetragona*. However, the types of *C. nassoviensis* are unfortunately lost and, therefore, it is here considered a nomen dubium.

Out of the original material of *C. carinata* Beushausen, three specimens (MB.M.220, Pl. 11, Figs. 12-13; MB.M.4416, Pl. 11, Fig. 14; MB.M.4417) have to be re-assigned to *C. tetragona*, due to their trigonal outline and attenuate umbo.

Occurrence:

MD I-F / UD IV-A (Tab. 29).

The oldest occurrence of *C. tetragona* is from the "Odershäuser Kalk" of Bonzel (Eastern Rhenish Massif), which is of MD I-F to MD II-A age.

The youngest occurrence is from the *annulata* Zone of Beul and Hönnetal (Northeastern Rhenish Massif, Germany), which can be dated as UD IV-A.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Beul	*annulata*-Zone	Denckmann, 1900	UD IV-A	MB.M.4415	
Beul	*annulata*-Zone	Haarmann, 1902/3	UD IV-A	MB.M.4413	
Bonzel	Odershäuser Kalk	Henke, 1906	MD I-F/ MD II-A	MB.M.2281.2	
Bonzel	Odershäuser Kalk	Henke, 1906	MD I-F/ MD II-A	MB.M.2281.3	

Bonzel	Odershäuser Kalk	Henke, 1906	MD I-F/ MD II-A	MB.M.2281.4	
Ense	Mittel Devon, Givetium	Denckmann, 1892	MD II/III	MB.M.220	
Ense	Mittel Devon, Givetium	Denckmann, 1892	MD II/III	MB.M.4417	
Ense	Mittel Devon, Givetium	Denckmann, 1892	MD II/III	MB.M.4416	
Ense	Mittel Devon, Givetium	Denckmann, 1892	MD I-F/ MD II-A	GZG 1258-11	
Geuser	Clymenienkalk	Münster	UD II	BSPG AS VII 1736	Lectotype *L. tetragonum*
Hönnetal	*annulata*-Zone	Schmidt, 1922	UD IV-A	MB.M.4414	
Mentaresses	MR/H1	Becker	UD II-D	B6A-135.136	
Schübelhammer	Clymenienkalk	Münster	UD II/IV	MB.M.2237	

Table 29 Examined specimens of *Chaenocardiola tetragona*.

Chaenocardiola canalifer Münster, 1840 [nom. corr.]
Fig. 16.7, 20.1; Pl. 11, Fig. 7

* + v 1840 *Lunulacardium conalifer* MÜNSTER, p. 70, pl. 13, fig. 11.
\+ v 1882 *Lunulacardium paradoxa* HOLZAPFEL, p. 255, pl. 49, fig. 3-4.
v 1895 *Chaenocardiola paradoxa*.- BEUSHAUSEN, p. 368, pl. 27, fig. 12-15.
1925 *Chaenocardiola* sp. aff. *paradoxa*.- GRÜNEBERG, p. 51, 84, pl. 3, fig. 10.
1979 *Chaenocardiola paradoxa*.- PAECKELMANN, p. 29.

Lectotype (other syntypes missing): BSPG AS VII 1734.
Type locality: Schübelhammer (Franconian, Southeastern Germany).
Type stratum: "Clymenienkalk" (Famennian, UD II/IV).

Material:
see Tab. 30.

Diagnosis:
Characters of the genus with valves rounded subtrigonal to oval in outline, inflated.
Strong groove developed anteriorly to truncation, posterior of it shell concavely bent upwards. Ornamentation consisting of fine, irregular comarginal and radial lines; additional coarser radial ribs developed. Dorsally ornamentation less conspicuous than towards the ventral margin.

Description:
Valves rounded subtrigonal to oval in outline.
Subcircular ventral margin merging regular with less convex anterior margin. Anterior portion of dorsal margin short, slightly concave, declining with rounded transition in anterior margin. Valves regularly inflated (Fig. 20.1).

Posterior portion of dorsal margin and umbo truncated, sometimes no longer identifiable. Section straight to concave, curving slightly anteriorly at umbo generating sometimes S-shaped appearance of truncation. Strong groove located anterior to the truncation edge, posterior to it valve concavely bent upward, generating a gutter-shaped fringe (Fig. 20.1). Valve gaping posteriorly.

Umbo prosogyrate.

Hinge line not observable in the material.

Ornamentation consisting of fine, irregular comarginal and fine radial lines, and strong, widely spaced, comarginal rugae (Pl. 11, Fig. 7). Ornamentation dorsally less conspicuous than towards the ventral margin. Radial ribs with equally broad interspaces, less numerous than in *C. tetragona*.

Holotype (BSPG AS VII 1734, Fig. 16.7) poorly preserved steinkern, presenting the gutter-shaped posterior portion of the valve. Umbo and hinge line not observable, but imprints of radial ornamentation on the ventral margin preserved.

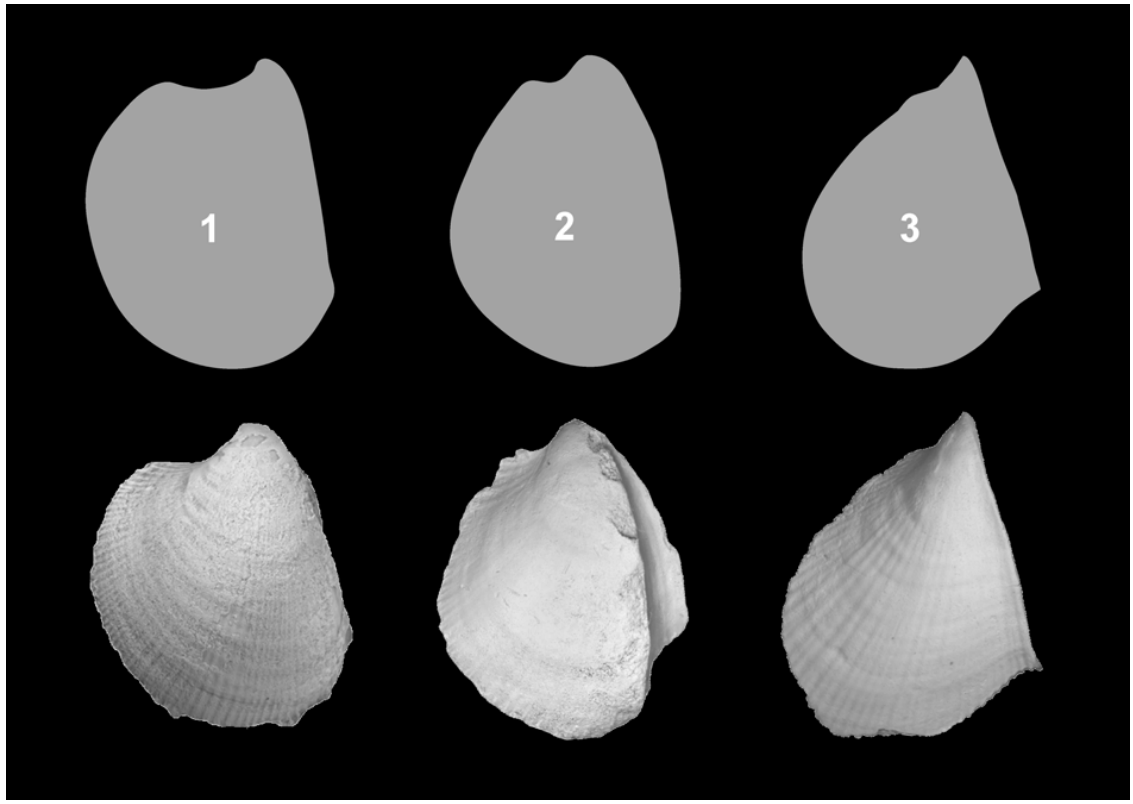


Figure 21 Different outline variations of Upper Devonian *Chaenocardiola* species.
1, *C. koeneni*; **2**, *C. carinata*; **3**, *C. tetragona*.

Discussion:
Münster (1840) described *Lunulacardium canalifer* from the Schübelhammer (Franconian Forest, Southeastern Germany). In the text of the description he misspelled its name, *L. conalifer*. Following his descriptions *L. canalifer* is the valid name for this species. BSPG AS VII 1734 (Fig. 16.7) is the lectotype, due to the lack of other syntypes.
Holzapfel (1882) identified a new species from the Martenberg (Northeastern Rhenish Massif), *Lunulacardium paradoxum*. GZG 490-197 (1882, pl. 6, fig. 4) is the only type that survived and is chosen as the lectotype of this taxon. Although this specimen presents a strong comarginal incision, which generates the impression of a change in ornamentation, it can be ascertained by comparison with additional material, that this is just a break in the shell growth of this single valve. All other features definitely place *L. paradoxum* in subjective synonymy with *C. canalifer*.

Occurrence:
UD I to UD II/IV (Tab. 30).
Grüneberg (1925) described this species from the *Manticoceras*-Stufe, which represents the UD I. Paeckelmann (1979) mentioned it from the UD I-G/L.
The youngest occurrence is the specimen from the Schübelhammer (Southeastern Germany) which cannot be dated precisely (Tab. 30).

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 1258-8	
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-195	
Martenberg	Unteres Oberdevon	v. Koenen	UD I	GZG 1258-7	
Martenberg	Unteres Oberdevon	v. Koenen	UD I	GZG 490-197G	Lectotype *C. paradoxa*
Martenberg	Unteres Oberdevon	v. Koenen	UD I	GZG 490-194	
Schübelhammer	Oberdevon	Münster	UD II/IV	BSPG AS VII 1734	Lectotype *L. canalifer*

Table 30 Examined specimens of *Chaenocardiola canalifer*.

Chaenocardiola carinata Beushausen, 1895
Fig. 21.2, 20.4; Pl. 11, Figs. 1-4, 6

	v	1893	*Lunulicardium carinatum*.- DENCKMANN, p. 13. [nom. nud.]
	v	1893	*Lunulicardium striatulum*.- DENCKMANN, p. 13. [nom. nud.]
* +	v e.p.	1895	*Chaenocardiola carinata* BEUSHAUSEN, p. 367, pl. 27, fig. 1.
+	v	1895	*Chaenocardiola striatula* BEUSHAUSEN, p. 367, pl. 27, fig. 8.
		1895	*Chaenocardiola* cf. *striatula*.- BEUSHAUSEN, p. 368.
		1901b	*Chaenocardiola carinata*.- DENCKMANN, p. 35.
		1901b	*Chaenocardiola striatula*.- DENCKMANN, p. 35.
		1922b	*Chaenocardiola carinata*.- HENKE AND SCHMIDT, p. 21.

Lectotype (designated herein): MB.M.219.
Type locality: Ense (Kellerwald, Eastern Rhenish Massif).
Type stratum: black cephalopod limestone ("Odershäuser Kalk"; upper Eifelian to basalmost Givetian MD I-F/II-A).

Material:
Lectotype of *C. carinata* MB.M.219 from Wildungen (coll. Denckmann);
lectotype of *C. striatula* MB.M.217a from Ense (coll. Denckmann);
paralectotypes of *C. striatula* MB.M.217b and MB.M.217c from Ense (coll. Denckmann);
GZG 1258-12 from Bonzel (coll. Henke).

Diagnosis:
Characters of the genus with rounded trigonal to oval outline, inflated.
Anterior portion of dorsal margin markedly concave.
Groove developed anteriorly to truncation, posterior of it shell declining concavely .
Ornamentation consisting of radial ribs, fine comarginal growth lines.

Description:
Valves rounded subtrigonal to oval in outline (Fig. 21.2), similar to *C. canalifer*.
Subcircular ventral margin merging regular in less convex anterior margin. Anterior portion of dorsal margin longer than in *C. canalifer*, distinct concave, deviating more or less rectangular in anterior margin (Pl. 11, Fig. 1). Valve inflated, oblate in centre (Fig. 20.4).
Posterior portion of dorsal margin and umbo truncated, umbo sometimes observable. Section straight to concave. Groove or depression located anterior to the truncation edge, posterior to it valve declines almost perpendicular, becoming concave towards the margin (Fig. 20.4). Valve gaping posteriorly.
Umbo prosogyrate. Lunule transverse oval to rounded rectangular, underneath bulging dorsal margin (Pl. 11, Fig. 4).
Hinge line straight, edentulous.

Ornamentation consisting of fine, irregular comarginal and radial lines. Ornamentation dorsally less conspicuous than towards the ventral margin. Shell preservation unknown.
Lectotype (MB.M.219, Pl. 11, Figs.1-4) well preserved steinkern. Dorsal margin and hinge line present. Steinkern presenting marked imprints of radial ribs on ventral and anterior margin, center of valve preserved almost completely smooth.

Discussion:
Denckmann collected MB.M.219 (Pl. 11, Figs. 1-4) and MB.M.217a and mentioned them in his publication (1893) as *Lunulacardium striatulum* n. sp. Beushausen and *Lunulacardium striatulum* n. sp. Beushausen, and referred therewith to the species, which Beushausen later published. Thus these quotations are considered here nomina nuda.
Beushausen (1895) established a new species, *Chaenocardiola carinata*, from Wildungen. MB.M.219 (Pl. 11, Figs. 1-4) is chosen as lectotype. Out of four syntypes it is the only one, which can be definitely correlated with the Beushausen figure (1895, pl. 28, fig. 1).
Furthermore, Beushausen (1895) erected a new species from Wildungen, *Chaenocardiola striatula*. MB.M.217a is choosen as the lectotype of this species, because MB.M.217c is neither figured nor well preserved, and MB.M.217b (Pl. 11, Fig. 6) is a plastic cast of MB.M.217a. Due to outline, inflation of the valve, and especially to the development of the carina in front of the truncation, *C. striatula* is here considered a subjective synonym.

Occurrence
MD I-A to MD II-A
Denckmann (1893) reported *C. carinata* from black goniatite limestones from the Kellerwald, which can be dated as topmost Eifelian (MD I-E) to possibly basalmost Givetian (MD II-A).
Later (1901b) he listed this taxon from the "Günteröder Kalk" which is of Eifelian age (MD I-A/E) age, and represent the oldest occurrence oft the species.
The specimens from Ense (Eastern Rhenish Massif) are labeled as Fromelennian, but this cannot beinterpreted in modern stratigraphy since there is no equivalent of the "Belgic Assis de Fromelennes" in the Kellerwald.
The material from the Henke collection by from Bonzel (near Biltstein, Northeastern Rhenish Massif) is from the "Odershäuser Kalk", which can be dated as MD I-F/II-A (Henke and Schmidt, 1922b).

Chaenocardiola denckmanni Beushausen, 1895
Pl. 11, Fig. 5

v	1893	*Lunulicardium denckmanni*.- DENCKMANN, p. 13. [nom. nud.]
* + v	1895	*Chaenocardiola denckmanni* BEUSHAUSEN, p. 366, pl. 27, fig. 9-10.
?	1896	*Chaenocardiola areolata*.- GÜRICH, p. 359, pl. 15, fig. 2.
	1901b	*Chaenocardiola denckmanni*.- DENCKMANN, p. 35.
	1922b	*Chaenocardiola denckmanni*.- HENKE AND SCHMIDT, p. 21.

Lectotype (other sytypes missing): MB.M.218.
Type locality: Ense (Bad Wildungen).
Type stratum: black cephalopod limestone ("Odershäuser Kalk"; upper Eifelian to basalmost Givetian MD I-F/II-A).

Material:
Lectotype of *C. denckmanni* MB.M. 218 from Ense (coll. Denckmann);

Diagnosis:
As *C. carinata* in outline, and umbo development, with coarser radial ribs, some irregular comarginal growth lines. Radial ribs bifurcate on ventral margin.

Discussion:
Denckmann (1893) described a specimen as *Lunulicardium denckmanni* without description, and referred to the monograph, which Beushausen was preparing. His quotation is, therefore, jugded as nomen nudum and Beushausen is the author of the species.
Beushausen (1895) identified this species from Wildungen, *Chaenocardiola denckmanni*. He stated that this species differs from all other species included in *Chaenocardiola* by its markedly coarser radial ornamentation. Specimens MB.M.218 (Pl. 11, Fig. 5) is the only remaining original an, therefore, designated as the lectotype. The ornamentation distinguishes MB.M.218 from all other examined specimens and therefore, this study supports Beushausen´s approach.
Gürich (1900) erected *Chaenocardiola areolata* for one specimen from the lower Famennian of Lagow (Holy Cross Mountains, Poland), which is thus holotype by monotypy,. He described this taxon as being a transitional form between *C. paradoxa* and *C. denckmanni*, due to its ornamentation. Furthermore, he stated that the ornamentation of the truncated margin is the only difference between the German and the Polish form. Judging from the examined material, this distinguishing feature may be a result of preservation, but the large time separating both species is also remarkable The ornamentation of the truncation has not been observed in

the material of C. denckmanni. The actual holotype of *C. areolata* was not available for this study and the dictinction of these species needs further investigation.

Occurrence:

MD I-A / MD II-A

Denckmann (1893) mentioned the occurrence of *C. denckmanni* from black goniatite limestones of Kellerwald which referrs to the Odershauser Formation, representing the Kačák Event interval at the top of the Eifelian.

The material from the Lahn Dill Syncline described by Denckmann (1901b) is of Eifelian age and is therefore, the is the oldest occurence of this taxon.

Henke and Schmidt (1922b) reported this species from the "Odershäuser Kalk", which can be dated as Eifelian and the basalmost of the Givatian (MD I-F/II-A).

Chaenocardiola koeneni Beushausen, 1895

Figs. 21.1, 20.2; Pl. 12, Figs. 1-6, 11-12

* + v	1895	*Chaenocardiola Koeneni*	BEUSHAUSEN, p. 268, pl. 27, fig. 5-7, pl. 28, fig. 3.
	1900	*Chaenocardiola koeneni*.-	BEUSHAUSEN, p. 165.
	1901b	*Chaenocardiola koeneni*.-	DENCKMANN, p. 40.
v	1922a	*Chaenocardiola koeneni*.-	HENKE AND SCHMIDT, p. 35.
	1931	*Chaenocardiola koeneni*.-	MATERN, p. 124.
	1979	*Chaenocardiola koeneni*.-	PAECKELMANN, p. 29.
	1980	*Lunulacardium* (*Lunulacardium*) *koeneni*.-	KAEVER et al., p. 158, pl. 27, fig. 1.
+	2005	*Lunulacardium petrboki*	KRIZ, p. 94, pl. 3, fig. 35-39.

Lectotype (designated herein): GZG 490-186.

Type locality: Bicken (Lahn-Dill Syncline, Germany)

Type stratum: Frasnian (UD I).

Material:

see Tab. 32.

Diagnosis:

Characters of genus with rounded subtrigonal outline, anterior portion of dorsal margin elongated, inflated. Umbo more or less prominent. Anterior to truncation valves oblate, without marked groove.

Ornamentation consisting of various fine radial ribs, and few strong, irregular comarginal growth lines.

Description:

Valves rounded, scalene subtrigonal in outline (Fig. 21.1).

Anterior margin subcircular merging into subcircular ventral margin. Anterior portion of dorsal margin longer than in other chaenocardiolid species, slightly concave, deviating into anterior margin (Pl. 12, Figs. 1-6). Valve regularly inflated (Fig. 20.2).

Posterior portion of dorsal margin truncated, umbo mostly unaffected by section. Truncation straight to slightly concave. Ventral margin merging almost perpendicular into the truncation. Posterior to the section valve declining with an angle of 90° or less, expiring concavely towards the margin (Fig. 20.2). Valves gaping posteriorly.

Umbo prosogyrate, not until very apical portion of valve.

Hinge line straight, edentulous.

Ornamentation consisting of irregular fine radial ribs intersected by minute, irregular comarginal growth lines (Pl. 12, Fig. 11). Closely spaced radial ribs start immediately at umbo, towards ventral margin ribs and interspaces getting broader. Towards truncation ribs getting coarser. Additionally strong widely spaced comarginal growth lines present (Pl. 12, Figs. 1, 4). Sometimes few radial ribs directly anterior to the truncation slightly deflected towards posterior margin (Pl. 12, Fig. 4).

Lectotype (GZG 490-186, Pl. 12, Fig. 5) with shell preservation. Complete outline observable, posterior portion of valve not preserved, with various closely spaced radial ribs and irregular, stronger comarginal growth lines. Hinge line not observable

Discussion:

Beushausen (1895) identified a new species from Bicken (Lahn-Dill Syncline, Germany) as *Chaenocardiola koeneni*. Out of the original types (GZG 490 176-192) GZG 490 186 is chosen to be the lectotype of this species, because its the specimen that shows all characteristic of the species and is well preserved.

Kriz (2005) described a new species from the top Frasnain to basal Famennian of the Montagne Noire (France), *Lunulacardium petrboki*. The figured specimens show all characteristic features of *C. koeneni*, the long antero-dorsal margin, the prominent umbo, and the same ornamentation. They also develop the truncation as in *C. koeneni*. Consequently, *L. petrboki* is considered a subjective junior synonym of *C. koeneni*.

Occurrence:

UD I to UD II-A (Tab. 31; Tab. 32)

Locality	Region	Reference	Stratigraphic level
Bicken	Eastern RM	Kaever et al., 1980	UD I-I/L
Comb de Izarne	Montange Noire, France	Kriz, 2005	UD II-A
Comb de Izarne	Montange Noire, France	Kriz, 2005	UD I-L
Evertsbusch	Northern RM	Kaever et al., 1980	UD II-A
Evertsbusch	Northern RM	Kaever et al., 1980	UD I-J
La Serre	Montange Noire, France	Kriz, 2005	UD I-L
La Serre	Montange Noire, France	Kriz, 2005	UD II-A
Martenberg	Northeastern RM	Kaever et al., 1980	UD I-I/L
Martenberg	Northeastern RM	Kaever et al., 1980	UD II-A
Oberscheld	Lahn Dill Syncline	Kaever et al., 1980	UD I-I/L
Oberscheld	Lahn Dill Syncline	Kaever et al., 1980	UD II-A
Oberscheld	Lahn Dill Syncline	Matern, 1931	UD I-G/J
Pettmecke	Attendorn, Northeastern RM	Henke and Schmidt, 1922a	UD I
Various localities	Hercynian Mountains	Beushausen, 1900	UD I-K/L
Various localities	Kellerwald, Eastern RM	Denckmann, 1901b	UD I-G/J

Table 31 References quoting the occurrence of *Chaenocardiola koeneni*.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number	Types
Bicken	-	Koch	UD I	MB.M.4398	
Bicken	-	Krüger	UD I	MB.M.4401	
Bicken	-	Krüger	UD I	MB.M.4404	
Bicken	-	Krüger	UD I	MB.M.4407	
Bicken	Adorfer Kalk	Koch	UD I	MB.M.4393	
Bicken	Adorfer Kalk	Koch	UD I	MB.M.4403	
Bicken	Adorfer Kalk	Koch.	UD I	MB.M.4400	
Bicken	Adorfer Kalk	Koch.	UD I	MB.M.4394	
Bicken	Unteres Oberdevon	-	UD I	MB.M.4397	
Bicken	Unteres Oberdevon	-	UD I	MB.M.4396	
Bicken	Unteres Oberdevon	Koch.	UD I	MB.M.4399	
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-176	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-177	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-178	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-179	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-180	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-181	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-182	Paralectotype *C. koeneni*

Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-183	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-184	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-185	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-186	Lectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-187	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-188	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-189	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-190	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-191	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 490-192	Paralectotype *C. koeneni*
Bicken	Unteres Oberdevon	v. Koenen	UD I	GZG 1258-8	
Ense	Unteres Oberdevon	-	UD I	MB.M.4408	
Evertsbusch	Kellwasserkalk	Paeckelmann, 1919	UD I-K/L	MB.M.4392	
Gr. Bruch Offenbach	to2	Kegel, 1931	UD II	MB.M.4405	
Gr. Bruch Offenbach	to2	Kegel, 1931	UD II	MB.M.4395	
Hauern	Oberdevon	Denckmann, 1892	UD II	MB.M.4409	
Martenberg	Intumescens Kalk	v. Koenen	UD I-I/L	GZG 1258-7	
Pettmecke	Unteres Oberdevon	Henke, 1906	UD I	MB.M.4406	
Zgl. Winchenbachstr., Barmen	Untere Matagenschichten	Paeckelmann, 1919	UD I-J/K	MB.M.4402	

Table 32 Examined specimens of *Chaenocardiola koeneni*.

7.4 Ontariids

Ontaria is a taxon, which occurs abundantly in the Givetian and Frasnian. It has been reported to occasionally covers whole bedding planes. This taxon has often been quoted to be of Hangenberg-Stage (UD VI) age, and to survive the Devonian/Carboniferous boundary. This assumption was based on two *Ontaria* species established by Schmidt (1924). However, as shown below, these Schmidt taxa do not fit the concept of this genus, and *Ontaria* probably became extinct already before the UD V.
The focus herein is on the specimens, which appear abundantly in the German Middle and Upper Devonian. The actual number of taxa included into *Ontaria* and their relationships to other genera need to be subject of further reviews and is far beyond the scope of this study. Its affiliation to the Praecardioidae has to be scrutinized after its range of variation has been clarified, and more additional information on the morphology has been gathered.

7.4.1 *Ontaria*

Class BIVALVIA Linnaeus, 1758
Subclass CRYPTODONTA Neumayr, 1884
Order PRAECARDIOIDEA Newell, 1965

Genus *Ontaria* Clarke, 1904

Type species: *Ungulina suborbicularia* Hall, 1843 (SD Newell and La Rocque, 1969).

Included species (studied herein): *Ontaria suborbicularis* Hall, *Ontaria concentrica* von Buch.

Diagnosis:
Valves subcircular to transverse oval, equilateral to slightly inequilateral.
Umbo small, central, projecting little over hinge line, orthogyrate to slightly prosogyrate.
Hinge line straight ending posteriorly and anteriorly in three to six small radial ribs.
Ornamentation can comprise of markedly imbricating comarginal rugae, fine comarginal growth lines, and faint radial lines.
Dimyarian, with a large, oval posterior and a smaller irregularly shaped anterior adductor scar. Pallial line showing posteriorly slight indentation, possibly pallial sinus.

Discussion:

Clarke (1904) separated *Ontaria* from the Upper Silurian *Cardiola* Broderip. He based his description on a number of specimens from the Genesee province (Upstate New York).

Ontaria lacks strong radial ribs, which are prominent in *Cardiola*, and the tenuity of their shells also clearly separates the Upper Devonian specimens from the Upper Silurian genus.

The genus *Cardiola* always lacked a proper definition and, therefore, many species and specimens were placed within this group, due to the missing knowledge of the actual concept or other available taxa.

Already Beushausen (1895) hesitated to re-assign the Upper Devonian taxa to *Cardiola* sensu Broderip, but in want of another valid genus and, due to what he felt were transitional morphologies between *Cardiola* and the Upper Devonian taxa, he maintained this genus in the Devonian.

Kriz (1979) finally re-studied the Cardiolidae. Cardiolids are defiened as oval to subcircular in outline, with a prosogyrate umbo, which is markedly projecting above the hinge line. The ornamentation, which consists of strong radial ribs and distinct comarginal growth rugae, is particularly characteristic for this genus. The radial and comarginal elements strongly constrict each other and give the shell surface a "beehive-like" appearance (Kriz, 1979). The cardiolids develop only a posterior adductor scar and preserve some rudimentary pedal muscle scars close to the hinge line. Another feature of the cardiolids is the occurrence of growth bands, which divide the shell comarginally into several portions, which represent growth stages (Kriz, 1979). All these characters, which are assumed to define the cardiolids, are absent in the members of *Ontaria*, which is dimyarian, and develops a small, central umbo. The ornamentation consitis of characteristic comarginal growth lines and rugae, and there are none or only faint radial lines developed.

Schmidt (1924) erected a new species from the Hangenberg beds of the Northeastern Rhenish Massif, *Ontaria centurio*. Furthermore, he re-assigned *Cardium costulatum* Münster from the same level and localities to *Ontaria*. Unfortunately, the Schmidt material has not been traced in the collection of the Berlin Naturkunde Museum. The description (1924; p. 156-157) and figures (1924; pl. 8, figs. 26-31) of these species exclude both from *Ontaria*. Schmidt described both as having radial ribs, but missing comarginal ornamentation. Furthermore, both are highly oval, and *C. costulata* is supposed to be inequivalve. These characters distinctly differ from *Ontaria*, and Schmidt´s reasons for placing these species within this genus remain dubious. A re-assignment of *Ontaria centurio* and *Cardium costulatum* cannot be accomplished herein, due to the amiguous taxonomic situation of the Upper Devonian bivalves. There is no re-studied valid genus yet they would fit in.

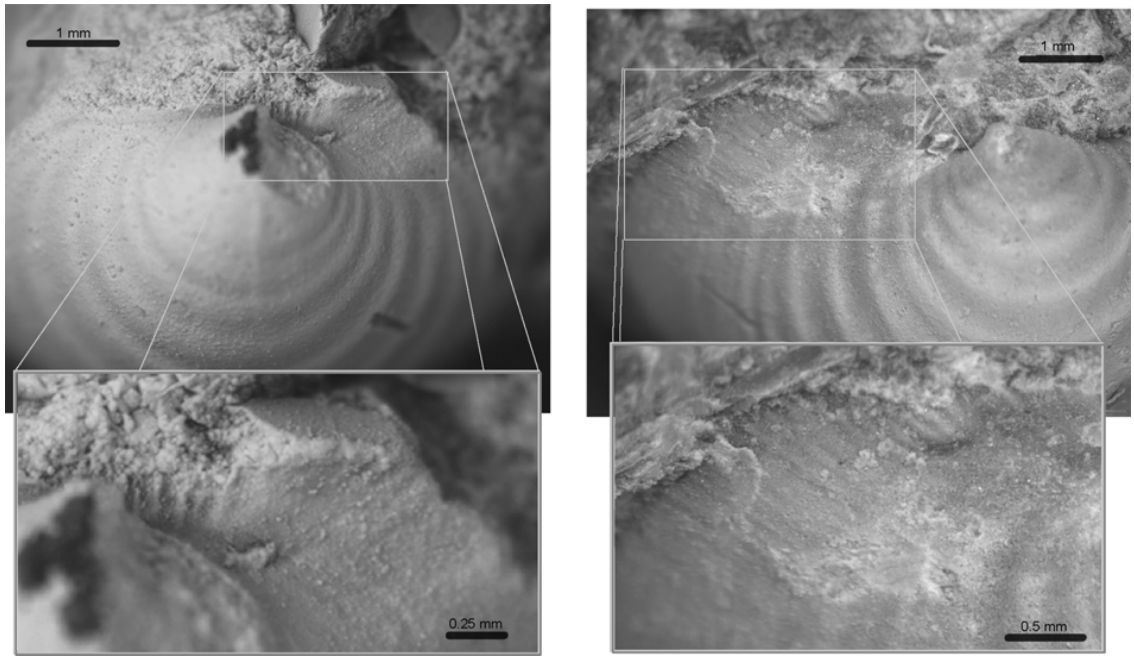


Figure 22 Hinge development of *O. concentrica*; **left**: crenultion of the hinge area and dorsal margin (MB.M.259; paralectotype of *C. subconcentrica*); **right**: transition of fine radial ornamentation from ventral to dorsal margin (MB.M.258; lectotype of *C. subconcentrica*).

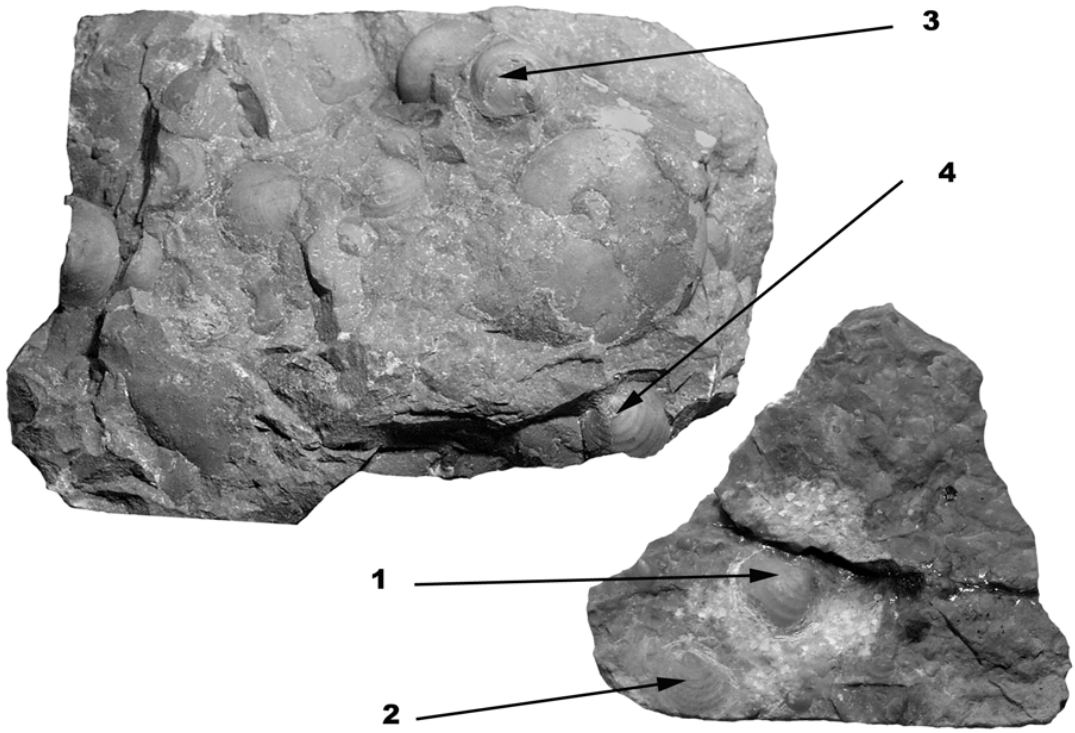


Figure 23 **1**: MB.M.3642.1, neotype of *Avicula elongata*, **2**: MB.M.3642.2; **3**: MB.M.2002.2, paralectotype of *Orbicula concentrica*, **4**: MB.M.2002.1, lectotype of *Orbicula concentrica*.

Ontaria suborbicularis (Hall, 1843)
Fig. 23; Pl. 13; Figs. 8, 10; Pl. 14, Fig. 1, 4-5

* + 1843 *Ungulina suborbicularia* HALL, p. 243, fig. 106.2.
1883 *Cardiomorpha suborbicularis*.- HALL, pl. 63, fig. 9-10.
\+ 1885 *Edmondia* ? *tenuistriata* HALL, p. 393, pl. 63, fig. 9-10.
1904 *Ontaria suborbicularis*.- CLARKE, p. 282, pl. 8, fig. 1-20..

Material:
see Tab. 33.

Diagnosis (after Clarke, 1904):
Shell suborbicular in outline, somewhat inflated.
Umbo is central, minute, slightly incurved. Apical part of the umbo sometimes set off by a low transverse thickening, pronouncing the prodissoconch.
Hinge line straight; area narrow elongated, triangular, not elevated.
Ornamentation consisting of fine comarginal growth lines, getting closely spaces towards the ventral margin; sometimes stronger rugae far apart developed, also covered by the fine ornamentation. Sometimes faint radial lines observable, crenulating the anterior and posterior ventral margin

Description:
Valves subcircular to transversely oval in outline, equilateral to slightly inequilateral, juvenile shell always subcircular, somewhat inflated. Dorsal margin straight, deviating into convex anterior and posterior margin, both regularly merging into subcircular ventral margin (Pl. 14, Figs. 1, 5).
Hinge line straight.
Umbo small, more or less central, slightly prosogyrate.
Ornamentation consisting of fine comarginal growth lines, fine radial lines, and sometimes few, widely spaced comarginal rugae (Pl. 13, Figs. 9, 10; Pl. 14, Figs. 1, 4-5). Comarginal growth lines irregularly spaced, smoothly imbricate; more prominent, and markedly closer spaced towards ventral margin (Pl. 13, Fig. 9). Fine radial lines more or less regular, closely spaced, intersecting the comarginal ornamentation (Pl. 14, Fig. 4). Parallel to dorsal margin posteriorly and anteriorly 3-6 radial ribs, intersecting with comarginal growth lines (Pl. 14, Figs. 1, 5); often anteriorly more ribs than posteriorly. Sometimes if ornamentation poorly preserved, valve smooth only displaying comarginal growth lines (Pl. 13, Fig. 10). Valve surface sometimes uneven, due to irregular growth pattern (Pl. 13, Fig. 10).
Adductor scars dimyarian, pallial line with small indentation posteriorly (Fig. 24).

Discussion:

Hall 1843 established *Ungulina suborbicularis* for a shell from the Portage Group. He (1883) figured another poorly preserved specimen and determined it as *Cardiomorpha suborbicularis*, and 1885 he re-described it as *Edmondia* ? *tenuistriata*. Clarke (1904) re-studied the specimens and concluded that all this material belongs to the first described *Ungulina suborbicularis* and the only difference are faint radial lines on some of the valves. This is not a distinguishing feature, because there are all kinds of transitional forms from valves with slight radial ornamentation to completely sooth ones. Clarke (1904) re-assigned *U. suborbicularis*, subsequently designated as type species by Newell and La Rocque (1969), to his new genus *Ontaria*. Unfortunately, the types neither of the Hall nor of the Clarke collection have been studied herein. Therefore, the diagnosis of *O. suborbicularis* is based on the review of Clarke (1904), the most recent study of this taxon.

Occurrence:

UD I / III (Tab. 33).

Clarke (1904) described *O. suborbicularis* from the lower soft shales of the Naples beds in Yates, Ontario, Livingston, Genesee and Erie counties and from the Styliola limestone on Canadaigua Lake. These occurences represent the Frasnian of Northeastern Upstate New York. Although this taxon has never been mentioned outside North America before, abundant material from Germany has been examined herein. The lack of previous description is probably the result of the ignorance of this species and the ambiguous taxonomic situation. However, *Ontaria suborbicularis* appeared frequently in the Frasnian of the Rhenish Massif. The youngest specimen is from the Beul, collected by Denckmann. The stratigraphic specification as "Enkeberger Kalk" can only broadly interpreted as lower Famennian (UD II/III).

This is supported by specimens from the Beyrich collection, which are just labeled as Upper Devonian. A precise stratigraphic interpretation is not possible, therefore, these specimens may also be of UD II age.

Locality	Stratigraphic specification on the label	Collection	Stratigraphic level	Collection Number
-	-	-	-	MB.M.4428
Berigora Gully	UD I-J3	Becker, 1995	UD I-J	B6A-35.131
Beul	Enkeberger Kalk	Denckmann, 1900	UD II/III	MB.M.4446
Ense bei Wildungen	Unteres Oberdevon	-	UD I	MB.M.4433
Ense bei Wildungen	Unteres Oberdevon	-	UD I	MB.M.4429
Grube Martenberg	Unteres Oberdevon	Denckmann	UD I-I/J	MB.M.4424
Grube Martenberg	Unteres Oberdevon	Denckmann	UD I-I/J	MB.M.4431
Grube Martenberg	Unteres Oberdevon	Denckmann	UD I-I/J	MB.M.4438
Grube Martenberg	Unteres Oberdevon	Denckmann	UD I-J/K	MB.M.4441
Grube Martenberg	Unteres Oberdevon	Denckmann	UD I-J/K	MB.M.4448
Martenberg	Top bed p	Becker	UD I-J	B6A-35.130
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4420
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4421
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4422
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4423
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4425
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4426
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4436
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4430
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4434
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4443
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4442
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4439
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-J/K	MB.M.4450
Oberscheld	-	Lotze, 1901	UD I-I/J	MB.M.4427
Oberscheld	Unteres Oberdevon	Danner	UD I-I/J	MB.M.4437
Oberscheld	Unteres Oberdevon, Goniatitenkalk	Dannenberg	UD I-I/J	MB.M.4440
Oberscheld	Oberdevon	Beyrich, 1835	UD I-I/J	MB.M.2203.1
Oberscheld	Oberdevon	Beyrich, 1835	UD I-I/J	MB.M.2203.2
Oberscheld	Oberdevon	Beyrich, 1835	UD I-I/J	MB.M.2203.3
Oberscheld	Adorfer Kalk / Iγ	Lotz, 1901	UD I-I/J	MB.M.4435
Sessacker	Unteres Oberdevon Goniatitenkalk	Dannenberg	UD I-I/J	MB.M.4432

Table 33 Examined specimens of *Ontaria suborbicularis*.

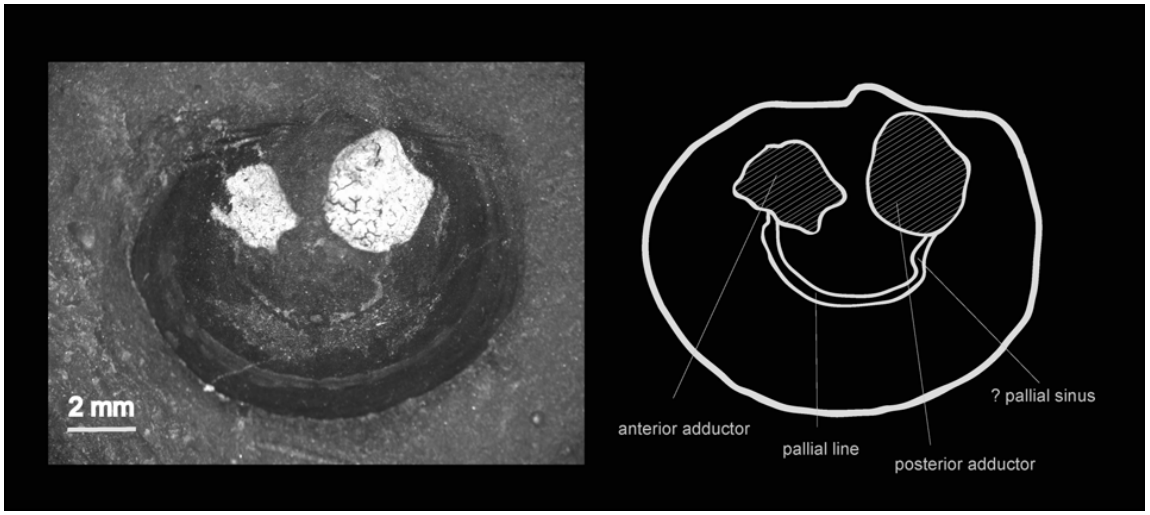


Figure 24 Specimen MB.M.4491 from Bicken: internal mould of *O. suborbicularis* showing phosphatized soft tissue structures.

Ontaria concentrica (von Buch, 1832)

Fig. 22, 23; Pl. 13, Figs. 11, 9, 1-7; Pl. 14, Figs. 2-3, 6-10

* + v	1832	*Orbicula concentrica* VON BUCH, p. 50.
	1846	*Cardiola concentrica*.- KEYSERLING, p.253.
+	1850	*Cardium penctunculoides* ROEMER, p. 26, pl. 4, fig.10.
	1856	*Cardiola concentrica*.- SANDBERGER AND SANDBERGER, p. 273, pl. 29, fig. 1-1.
	1882	*Cardiola concentrica*.- HOLZAPFEL, p. 254.
	1893	*Cardiola* sp. aff. *concentrica*.- DENCKMANN, p. 13, 15.
	1893	*Cardiola concentrica*.- DENCKMANN, p. 15.
+ v	1895	*Cardiola subconcentrica* HOLZAPFEL, p. 228.
	1895	*Cardiola subconcentrica*.- BEUSHAUSEN, p. 353, pl. 37, fig. 13-15.
	1895	*Cardiola concentrica*.- BEUSHAUSEN, p. 355, pl. 37, fig. 16-20.
	1900	*Cardiola* aff. *concentrica*.- BEUSHAUSEN, p. 165.
	1901	*Cardiola concentrica*.- DENCKMANN, p. 35, 40.
	1904	*Ontaria concentrica*.- CLARKE, p. 286, pl. 8, fig. 26.
	1908	*Cardiola subconcentrica*.- TORLEY, p. 41.
	1922a	*Chaenocardiola concentrica*.- HENKE AND Scyhmidt, p. 35.
	1922b	*Cardiola subconcentrica*.- HENKE AND SCHMIDT, p. 21.
	1923	*Ontaria concentrica*.- PAECKELMANN, p. 58.
	1931	*Cardiola subconcentrica*.- MATERN , p. 124.
	1931	*Cardiola concentrica*.- MATERN , p. 124.
	1936b	*Cardiola concentrica*.- PAECKELMANN AND KÜHNE, p. 22, 23.
	1965	*Cardiola concentrica*.- BOTTKE, p. 115, 124.
	1965	*Cardiola concentrica*.- BOTTKE, p. 115, 124.
	1965	*Cardiola subconcentrica*.- BOTTKE, p. 127.
	1968	*Ontaria concentrica*.- GUNIA, p. 183, pl. 10, fig. 23.
	1979	*Cardiola subconcentrica*.- PAECKELMANN, p. 24.
	1979	*Cardiola concentrica*.- PAECKELMANN, p. 19.
	1980	*Cardiola concentrica*.- KAEVER et al., p. 154, pl. 25, fig. 3.
	1993a	*Cardiola concentrica*.- BECKER, p. 52, 78, 124.

Lectotype (designated herein): MB.M.2202.1.
Type locality: Martenberg (Northeastern Rhenish Massif).
Type stratum: "Adorf Kalk" (Frasnian, UD I-I/J).

Material:
see Tab. 35.

Diagnosis (revised):
Valves subcircular to transverse in outline.
Ornamentation consisting of strong, more or less regular comarginal rugae, and faint radial lines; additional fine, irregular, imbricate comarginal growth lines covering whole shell.
Towards ventral margin strong comarginal rugae disappear, fine comarginal lines become more prominent.

Description
Shell subcircular to transversely oval, equilateral to slightly inequilateral, valves somewhat more inflated than *O. suborbicularis*.
Dorsal margin straight, anterior and posterior margin broadly convex merging regularly into subcircular ventral margin.
Umbo small, central, slightly prosogyrate. Prodissoconch sometimes pronounced by corrugation (Pl. 13, Fig. 8).
Hinge line straight, crenulated, generating interlocking indentations below the umbo (Fig. 22; Pl. 13, Fig. 11).
Ornamentation consisting of strong comarginal growth rugae, predominant on the dorsal portion of the shell, disappearing towards the ventral margin (Pl. 13, Fig. 10; Pl. 14, Figs. 8, 6). Complete shell covered by fine, irregular, imbricate comarginal growth lines, bundling towards the ventral margin (Pl. 14, Fig. 8; Pl. 13, Fig. 8). Radial lines irregular closely spaced, covering whole shell (Pl 14, Figs. 8-7), intersecting with comarginal ornamentation, faintly observable on steinkern (Pl. 13, Fig. 2). Parallel to dorsal margin posteriorly and anteriorly 3-6 radial ribs, intersecting with comarginal growth lines (Pl. 14, Figs. 2-3, 10); often anteriorly more ribs than posteriorly.
Lectotype MB.M.2202.1 (Fig. 23; Pl. 13, Fig. 1) subcircular in outline, lacking ventral margin, hinge line and apical portion of umbo. Main portion of the shell presenting smooth steinkern with faint radial lines (Pl. 13, Fig. 2). Postero-dorsal portion of the valve presents shell remains with fine comarginal growth lines, and two radial ribs parallel to the dorsal margin.

Discussion:

In subsequently added comments to his study on goniatites, von Buch (1832) described the abundant occurrence of a subcircular bivalve from the Martenberg (Northeastern Rhenish Massif). He named these specimens as *Orbicula concentrica*. Although he clearly stated that this material represents bivalves, he placed this species into a brachiopod genus, due to its outline, which is similar to the brachiopod genus *Patella* Müller.

The types of von Buch are on a piece of rock, which preserves abundant fossils. There are many bivalve specimens present and, therefore, a well preserved one, which is marginally located, is chosen as lectotype (Pl. 13, Figs. 1-2).

Later, Keyserling (1846) re-assigned the species to *Cardiola*, due to its cardiid outline.

Roemer (1850) described a new species from the Frasnian "Goniatitenkalk" of the Hercynian Mountains (Germany), *Cardium penctunculoides*. The figured specimen (1850; pl. 4, fig. 10) shows all characters of *O. concentrica* and the description of *C. penctunculoides* clearly places it into the concept of this species. Therefore, it is a subjective synonym of *O. concentrica.*

Beushausen (1895) identified a new species from the Kellwasser beds of the Ense area and the "Stringocephalenkalk" of the Martenberg, *Cardiola subconcentrica*. The types (MB.M.258, MB.M.259, MB.M.260) are material of the Denckmann collection from the "Odershäuser Kalk" of the Kellerwald (Eastern Rhenish Massif). This material is, in all probability, the specimens Denckmann (1893) described as *Cardiola* sp. aff. *concentrica*, because his collection was amongst others basis of Beushausen´s monograph, and Denckmann referred 1893 already to bivalve taxa described by Beushausen in 1895. Out of the types, MB.M.258 is chosen as the lectotype of *Cardiola subconcentrica*. This specimen shows, as the remaining types, all characters of *O. concentrica*, and therefore, it is a junior synonym of the latter. Beushausen (1895) himself quoted the development of the hinge line to be the only distinguishing feature of both species. He assumed *O. concentrica* to be edentulous, while *C. subconcentrica* develops interlocking indentations at the dorsal margin. This hinge development was also detected in Upper Silurian taxa (Conrath, 1887) and is interpreted as the ending of radial ornamentation elements, which act as substitute of real hinge teeth. Beushausen´s assumption that *O. concentrica* is actually edentulous could not be proved in the material examined herein. He suggested that *C. subconcentrica* is lacking, contrary to *O. concentrica*, a small area underneath the beak, but the material both types and addinional specimens do not confirm this assumption.

C. subconcentrica var. *irregularis* was described for specimens, which are more inequilateral in outline than *subconcentrica*. As in *subconcentrica* the types of var. *irregularis* cannot be traced and it is as well a nomen dubium. But, due to the herein studied material it can be ascertained that the variation of the outline, which Beushausen described, is within the range of variation of *O. concentrica.*

Occurrence:

MD I-F / UD IV (Tab. 34; Tab. 35)

The oldest specimens are from the black limestones of the uppermost Upper Eifelian of the Kellerwald (MD I-F/II-A). The youngest occurrence are two specimens, one from the Hemberg-Stage, one is from the UD III and one of UD IV age.

Ontaria concentrica is abundant in the Frasnian and seems to get less frequent in the Famennian. Its wide geographical distribution ranges from North America, Rhenish Massif and Hercynian Mountains both of Germany, Holy Cross Mountains, Siberia, the Montagen Noire of Southern France to Tafilalt in Morocco (Tab. 34).

Locality	Region	Reference	Stratigraphic level
-	Hercynian Mountains	Roemer, 1850	UD I
Adorf	Northeastern RM	Trenker, 1867	UD II
Altenau	Hercynian Mountains	Beushausen, 1895	UD I-I/J
Altenau	Hercynian Mountains	Sandberger and Sandberger, 1856	UD II
Beringhäuser Tunnel	Northeastern RM	Becker, 1993a	UD I-I/J
Beul	Northeastern RM	Paeckelmann, 1924	UD I-L
Bicken	Kellerwald, Eastern RM	Beushausen, 1895	UD I
Bicken	Kellerwald, Eastern RM	Holzapfel, 1882	-
Bicken	Eastern RM	Kaever et al., 1980	UD I-G/II
Blauer Bruch/ Wildungen	Kellerwald, Eastern RM	Denckmann, 1901	MD I-F/II-A
Bonzeln	Northeastern RM	Henke and Schmidt, 1922b	MD I-F/II-A
Bou Tchrafine	Tafilalt, Southern Morocco	Becker, 1993a	UD II-D
Burg	Northeastern RM	Bottke, 1965	UD I-J/K
Burg	Northeastern RM	Paeckelmann and Kühne, 1936b	UD I-J/K
Correll´s point	Chautauqua, New York State	Clarke, 1904	UD I
Enkeberg	Northeastern RM	Holzapfel, 1895	-
Enkeberg	Northeastern RM	Paeckelmann and Kühne, 1936b	UD I-J/K
Ense	Kellerwald, Eastern RM	Beushausen, 1895	MD I-F/ II-A
Ense	Kellerwald, Eastern RM	Holzapfel, 1895	MD I-F/II-A
Genesee province	Chautauqua, New York State	Clarke, 1904	UD I
Grube Antonie	Northeastern RM	Bottke, 1965	UD I-I/J
Grube Charlottenzug	Northeastern RM	Paeckelmann and Kühne, 1936b	UD I-I/J
Martenberg	Northeastern RM	Paeckelmann, 1979	MD III
Martenberg	Northeastern RM	Paeckelmann, 1979	UD I-J/K
Martenberg	Northeastern RM	Beushausen, 1895	UD I-I/J
Martenberg	Northeastern RM	Beushausen, 1895	MD II
Martenberg	Northeastern RM	Bottke, 1965	UD I-I/J
Martenberg	Northeastern RM	Von Buch, 1932	UD I-I/J
Martenberg	Northeastern RM	Holzapfel, 1882	UD I-I/J

Martenberg	Northeastern RM	Holzapfel, 1895	UD I-I/J
Martenberg	Northeastern RM	Kaever et al., 1980	UD I-I/J
Mentaresses	Montange Noire, France	Becker, 1993a	UD II-B/C
Oberharz	Hercynian Mountains, Germany	Beushausen, 1895	UD I-K/L
Oberharz	Hercynian Mountains, Germany	Beushausen, 1895	UD I-J/K
Oberscheld	Lahn Dill Syncline	Beushausen, 1895	UD I-I/J
Oberscheld	Lahn Dill Syncline	Trenker, 1867	UD II
Oberscheld	Lahn Dill Syncline	Sandberger and Sandberger, 1856	UD II
Oberscheld	Lahn Dill Syncline	Kaever et al., 1980	UD I-I/J
Pettmecke	Northeastern RM	Henke and Schmidt, 1922b	UD I-I/J
Uchta	Western Siberia	Trenker, 1867	UD I-D/H
Uchta	Western Siberia	Sandberger and Sandberger, 1856	UD I-D/H
Various localities	Kellerwald, Eastern RM	Denckmann, 1901	UD I
Various localities	Kellerwald, Eastern RM	Denckmann, 1893	MD I-F/II-A
Wildungen	Kellerwald, Eastern RM	Beushausen, 1895	UD I
Witoszowa	Holy Cross Mountains, Poland	Gunia, 1968	UD I/II-B

Table 34 References quoting the occurrence of *Ontaria concentrica*.

Locality	Stratigraphic specification on the label	Collection	Strati-graphic level	Collection Number	Types
Adorf	Adorfer Kalk	Gruppe	UD I-J/K	MB.M.4459	
Beul	Adorfer Kalk	Denckmann.,1901	UD I-J/K	MB.M.4455	
Bicken	Unteres Oberdevon	Krüger, 1873	UD I	MB.M.4491	
Dasberg	Oberdevon IV, Schicht 34	Paeckelmann	UD IV	MB.M.4482	
Ense	Odershäuser Kalk	Denckmann	MD I-F/II-A	MB.M.258	Lectotype *C. sub-concentrica*
Ense	Odershäuser Kalk	Denckmann	MD I-F/II-A	MB.M.259	Paralectotype *C. subconcentrica*
Ense	Odershäuser Kalk	Denckmann	MD I-F/II-A	MB.M.260	Paralectotype *C. subconcentrica*
Grube Martenberg	Unteres Oberdevon	Denckmann	UD I-I/J	MB.M.4445	
Grube Martenberg	-	Denckmann	UD I-I/J	MB.M.4454	
Grube Martenberg	-	Denckmann	UD I-I/J	MB.M.4461	
Grube Martenberg	-	Denckmann	UD I-I/J	MB.M.4462	
Grube Martenberg	-	Denckmann	UD I-I/J	MB.M.4465	
Grube Martenberg	-	Denckmann	UD I-I/J	MB.M.4470	
Grube Martenberg	-	Denckmann	UD I-I/J	MB.M.4474	
Grube Martenberg	Unteres Oberdevon	Denckmann	UD I-I/J	MB.M.4476	
Grube Martenberg	Unteres Oberdevon	Denckmann	UD I-I/J	MB.M.4479	
Grube Martenberg	Unteres Oberdevon	Denckmann	UD I-I/J	MB.M.4481	
Grube Martenberg	-	Denckmann	UD I-I/J	MB.M.4483	
Grube Martenberg	-	Denckmann	UD I-I/J	MB.M.4484	
Grube Martenberg	Unteres Oberdevon	Denckmann	UD I-I/J	MB.M.4488	

Königszug, 50m Sohle	Adorfer Kalk	Lotz, 1901	UD I-I/J	MB.M.4447	
Martenberg	Unteres Oberdevon	Denckmann	UD I-I/J	MB.M.4466	
Martenberg	Unteres Oberdevon	Denckmann	UD I-I/J	MB.M.4472	
Martenberg	Oberdevon	Erbenreich	UD I-I/J	MB.M.2201	
Martenberg	Oberdevon	von Buch	UD I-I/J	MB.M.2202.1	Lectotype *O. concentrica*
Martenberg	Oberdevon	von Buch	UD I-I/J	MB.M.2202.2	Paralectotype *O. concentrica*
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4457	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4458	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4453	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4460	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4463	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4464	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4467	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4468	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4469	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4477	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4480	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4487	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4489	
Martenberg-Klippe	Adorfer Kalk / Iγ	Paeckelmann, 1928	UD I-I/J	MB.M.4490	
Messinghäuser Eisenberg	Unteres Oberdevon	-	UD I-I/J	MB.M.4478	
Oberscheld	Roteisenstein	Lotz, 1901/2	MD III	MB.M.4444	
Oberscheld	Clymenien Kalk / Famennium	Lotz, 1901	UD II	MB.M.4449	
Oberscheld	Unteres Oberdevon, Goniatitenkalk	-	UD I-J/K	MB.M.4452	
Oberscheld	Unteres Oberdevon, Goniatitenkalk	Dannenberg	UD I-J/K	MB.M.4456	
Oberscheld	Clymenien Kalk / Famennium	Lotz, 1901	UD II	MB.M.4471	
Oberscheld	-	Lotze, 1901	UD I-I/J	MB.M.4475	
Oberscheld	-	Dannenberg	UD I-I/J	MB.M.4485	
Oberscheld	-	Dannenberg	UD I-I/J	MB.M.4486	
Oberscheld	Goniatitenkalk, Oberdevon	Beyrich, 1835	UD I-I/J	MB.M.2207.1	
Oberscheld	Goniatitenkalk, Oberdevon	Beyrich, 1835	UD I-I/J	MB.M.2207.2	
Oberscheld	Goniatitenkalk, Oberdevon	Beyrich, 1835	UD I-I/J	MB.M.2209.1	
Oberscheld	Goniatitenkalk, Oberdevon	Beyrich, 1835	UD I-I/J	MB.M.2209.2	
Oberscheld	Goniatitenkalk, Oberdevon	Beyrich, 1836	UD I-I/J	MB.M.2204	
Wettmarsen-Hirre	Prolobites Zone	Paeckelmann, 1931	UD III	MB.M.4473	

Table 35 Examined specimens of *Ontaria concentrica*.

8 Stratigraphic distribution

Although first attempts of biozonation based on Devonian bivalves from the Rhenish Facies (Amler, 2004; Sadykov, 1962) confirmed the stratigraphic potential of Devonian bivalves, the stratigraphic distribution of the Upper Devonian pelagic bivalves has been completely neglected in the past. As discussed above (see Chapter 7), one of the major problems is the confused taxonomic situation of these taxa. As a result, names, as used by different authors, often describe various different morphological groups. Therefore, information about the distribution from the literature is often no reliable confirmation of the occurrence of species or genera, and has to be treated with caution. Hence, herein emphasize in the evaluation of the stratigraphic range is on the examined material. Dubious references, which are discussed in the systematics (see Chapter 7), are omitted. Furthermore, it has to be taken into account that the number of individuals representing one species is limited in many cases. This and the lack of any previous data yet prevent final interpretation of the true stratigraphic range.

However, this study presents the first compilation of the stratigraphic distribution of pelagic Upper Devonian bivalve taxa. This data may serve as a basis for a future description of biozones, which could complement the traditional zonations based on e.g., conodonts and ammonoids.

Middle Devonian / Eifelian (MD I)

MD I-A: Entry of *Chaenocardiola carinata*, *Chaenocardiola denckmanni*.

MD I-F: Entry of *Chaenocardiola tetragona*, *Ontaria concentrica*.

Middle Devonian / Givetian (MD II/III)

MD II. Last occurence of *Chaenocardiola denckmanni*, *Chaenocardiola carinata*.

MD III: Entry of *Prosochasma bickense*.

Upper Devonian / Frasnian (UD I)

UD I: Entry of all other *Prosochasma* species *P. pyriforme*, *P. muelleri*, *P. mytiloides, Lunulacardium semistriatum*, *Chaenocardiola canalifer*, *Chaenocardiola koeneni*, and *Ontaria suborbicularis*. Last occurence of *P. bickense*.

Famennian / Nehden-Stage (UD II)

UD II-A: Entry of the characteristic and widely distributed *Loxopteria* species: *L. dispar*, *L. gibbosa*, *L. inflata*, *L. problematica*. Furthermore, entry of *Elasmatium elongata*, *Elasmatium gowandense*. Entry of *Deltacardium vetustum*, *Deltacardium duplicatum*; last occurrence of *Prosochasma muelleri*.

UD II-B: Entry of *Deltacardium clymeniae*.

UD II-D: Last occurence of *Lunulacardium semistriatum*.

UD II-F: Last occurence of the Deltacardiids, *D. vetustum*, *D. duplicatum*, *D. clymeniae*.

UD II-I: Last occurence of, *Chaenocardiola canalifer*, *Chaenocardiola carinata*, *Prosochasma mytiloides*, *Chaenocardiola koeneni*, and *Ontaria concentrica*.

Famennian / Hemberg-Stage (UD III/IV)

UD III-A: Entry of *Loxopteria meioklina*

UD III-C: Last occurence of *Loxopteria meioklina*, and *Ontaria suborbicularis*.

UD IV-C: Last occurence of *Loxopteria problematica, Elasmatium elongata,* and *Elasmatium gowandense*.
Loxopteria dispar, *Loxopteria gibbosa*, and *Loxopteria inflata* became also extinct in the UD IV-C. There are references, which quote younger occurences of these three taxa, but as dicussed in Chapter 7 this is highly unlikely. Therefore, it is assumed that the Loxopteriinae became extinct after the *annulata* Event in the UD IV-C. Last occurence of *Chaenocardiola tetragonum*, which is completly missing in the UD III. *Prosochasma pyriforme* occurs for the last time. *Lunulacardium excrescens* is, according to the current data base restricted to the UD IV.

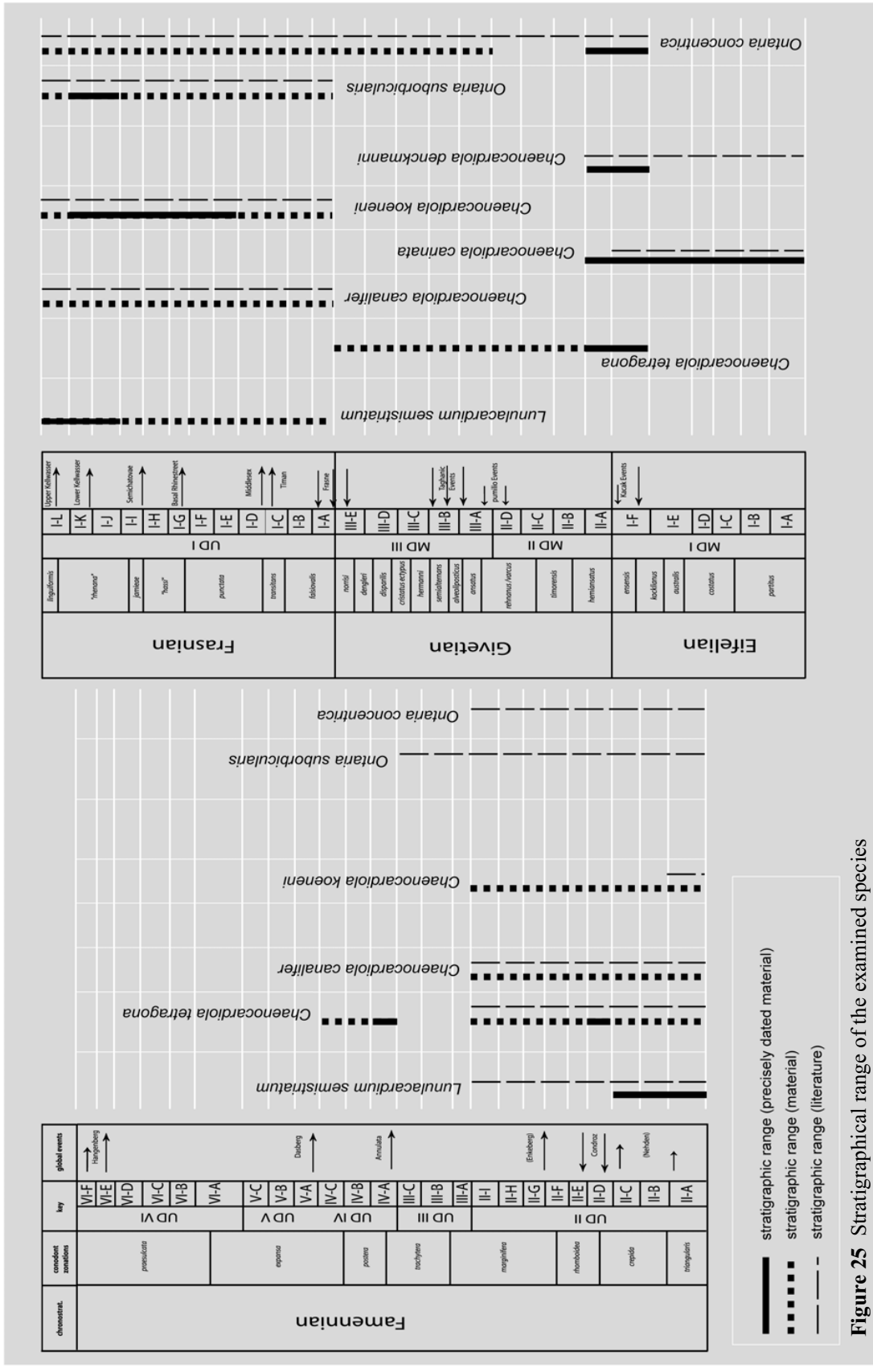


Figure 25 Stratigraphical range of the examined species

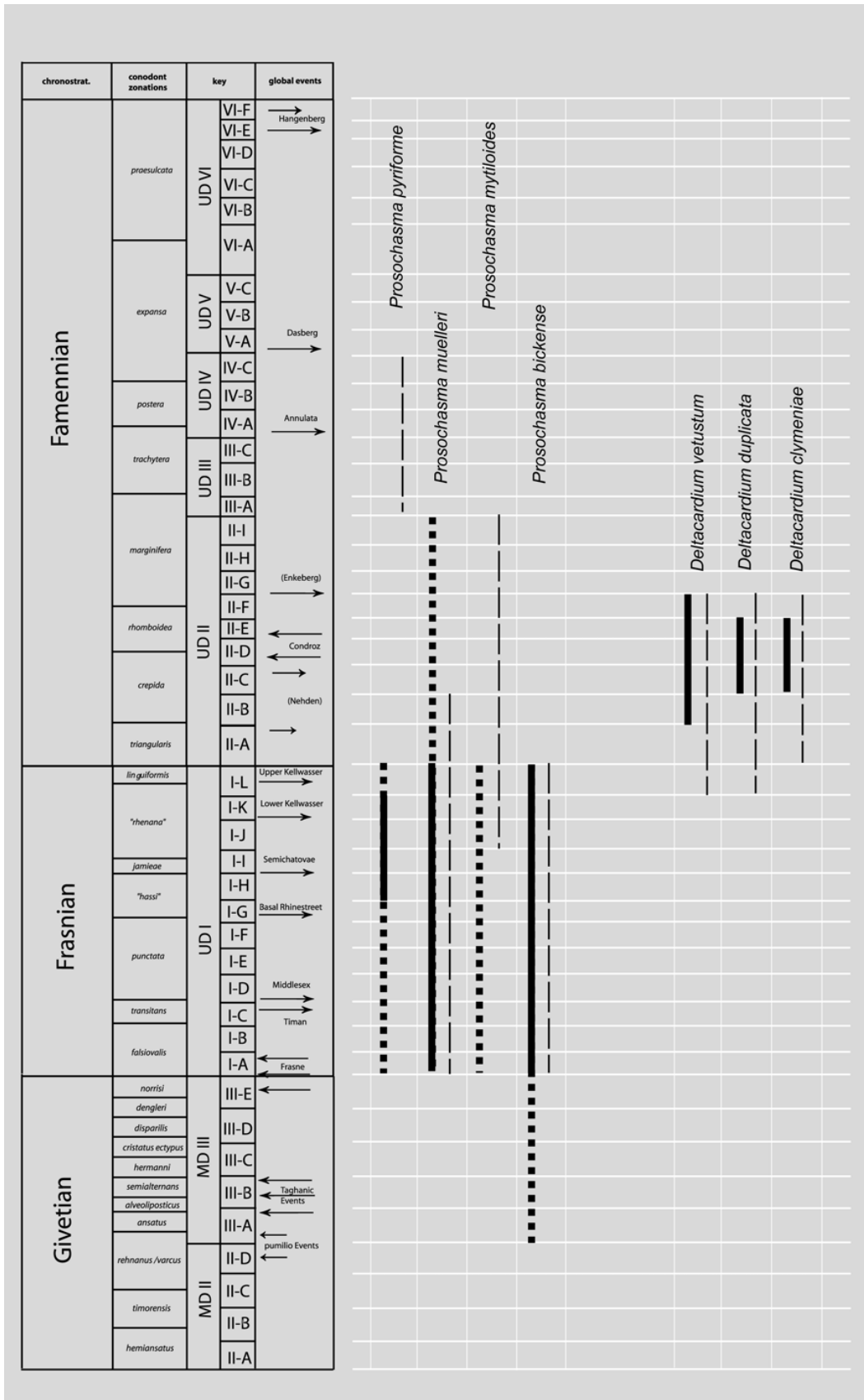


Figure 26 Stratigraphical range of the examined species

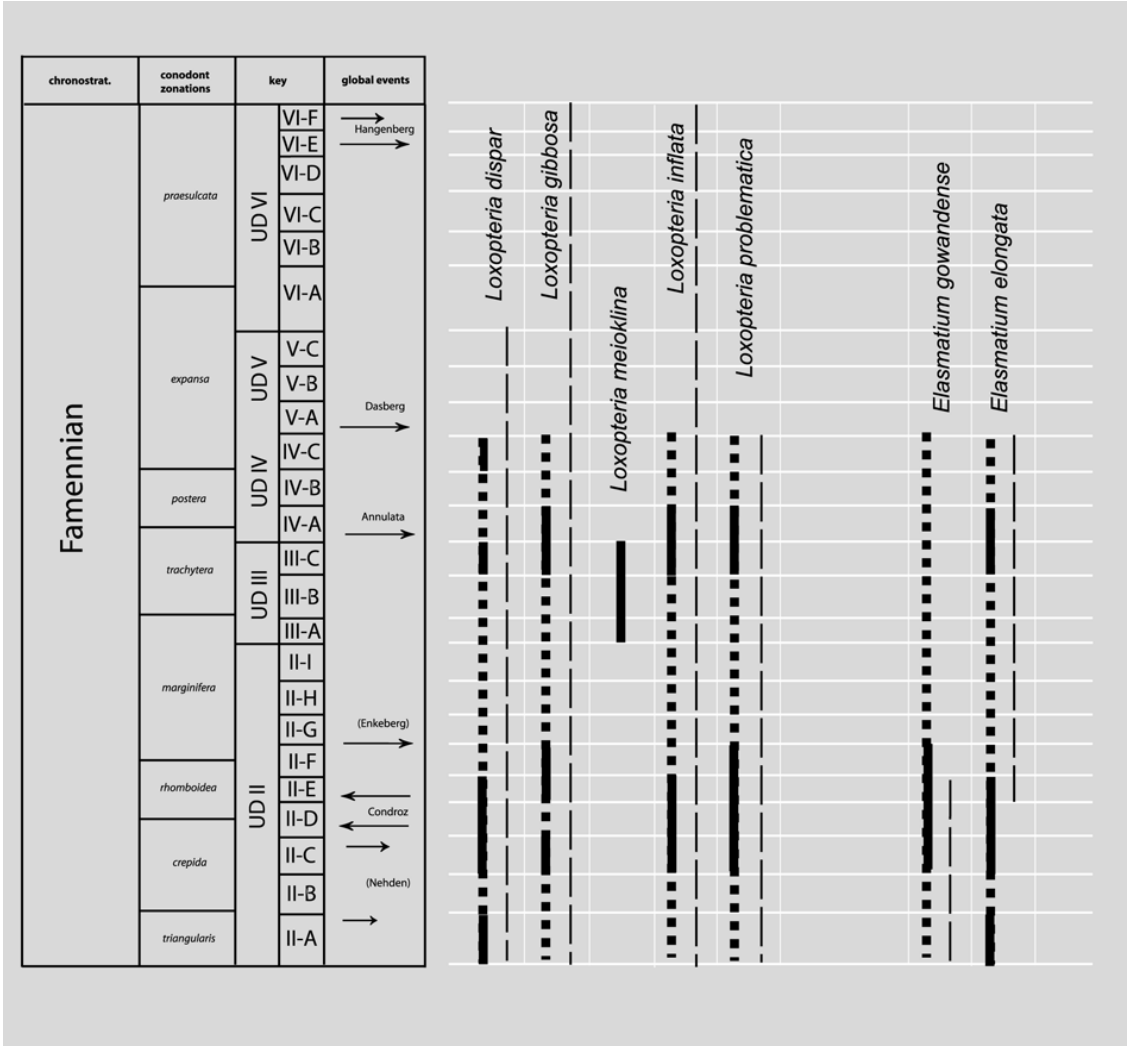


Figure 27 Stratigraphical range of the examined species

In summary, the stratigraphical range of the Upper Devonian pelagic bivalves, as far as known until today, can be resumed as follows:

The deltacardiids are a characteristic taxon of the Nehden-Stage (UD II).
Deltacardium vetustum and *Deltacardium duplicatum* had their first occurence already in the Upper Kellwasser beds (Kriz, 2005, Becker and House, 1994) and were abundant in the Nehden-Stage. *Deltacardium clymeniae*, which probably evolved out of them, appeared later (UD II-A) in the main radiation phase after the Kellwasser crises.

All three species contemporaneously became extinct at the end of the UD II-E, during the regressive Condroz Event (Becker, 1993).

The stratigraphic range of the Loxopteriinae is relatively well defined, because they are a homogenous group that is easily identifiable in the fossil record. Especially, *Loxopteria dispar* is abundant in the fossil record of the Nehden and Hemberg-Stage.
The first appearance of *Loxopteria* (UD II-A) fell in the main radiation phase after the Kellwasser crises at the Frasnian/Famennian boundary. This genus became extinct after the *annulata* Event at the end of the UD IV-C.
The only exception is *Loxopteria meioklina*, which seems to be restricted to the UD III. Furthermore, according to the recent knowledge about this species, it occurred only in Morocco. Therefore, it may be interpreted as a local Moroccan variation of *Loxopteria gibbosa*.
The second genus, which is included in the Loxopteriinae, is *Elasmatium*. It entered the fossil record right after the Kellwasser crises (UD II-A). *Elasmatium elongata* became extinct in the course of the transgressional phase of the *annulata* Event (UD IV-A). *Elasmatium gowandense* is restricted to Nehden-Stage (UD II).

The stratigraphic range of the Lunulacardiinae is not completely represented in the examined material. It is confirmed that, e.g. the chaenocardiolids survived the Devonian/Carboniferous boundary (e.g., *Chaenocardiola haliotoidea*) and became extinct in the Late Mississippian. Herein the focus is on the German taxa from the pelagic Upper Devonian and, therefore, it represents just a part of the stratigraphic distribution of the lunulacardiids.
Lunulacardium semistriatum was abundant in the UD I and one single specimen from the Armorican Massif is from the UD II-A/F. Unfortunately, apart from the holotype of the UD II, no further material of the second *Lunulacardium* species could be examined in this study.
Prosochasma was also abundant in the Upper Frasnian. Few specimens are from the UD II, mostly from the "Clymenienkalk" and its age can only broadly be interpreted as UD II. The references, which quote the occurrence of *Prosochasma* from higher levels, are dubious and their accuracy has to be confirmed (see Chapter 7). However, judging from the examined material, it can be assumed that *Prosochasma* is an Upper Frasnian taxon, which became extinct right after the Kellwasser crises.
The only exception is *Prosochasma bickense*. It already occurred in the Givetian and, therefore, is the oldest species in this genus. Hence, it may be suggested that *P. bickense* is the predecessor of the other *Prosochasma* species, which would, thus, have evolved from it. However, *P. bickense* became also extinct at the top of the Frasnian.

The *Chaenocardiola* species comprise the oldest species in this study. As stated above, the data are not representative for this genus. However, the examined chaenocardiolid species

first appear in the Upper Eifelian (MD I-F). *C. denckmanni* and *C. carinata* has not been observed beyond the basalemost Givetian. *C. koeneni*, and *C. canalifer* seem to restricted to the Frasnian, although *C. canalifer* occurres with one single specimen in the Famennian, but further material is needed to clariefy the its actual range of it. Only specimens of *C. tetragonum* have been found in the *annulata* beds (UD IV-A).
Further studies have to examine more material from the Famennian, in order to complete the stratigraphic range of this genus. The chaenocardiolids seem to be absent or, at least, not as prominent in the Middle Famennian, as they are in the Givetian and Frasnian, and later in the uppermost Famennian and Lower Carboniferous.

The stratigraphic range of *Ontaria* cannot be interpreted yet, due to the insufficiant knowledge of the whole group, especially concerning the North American fauna. Herein, it can be summarized that *Ontaria concentrica*, which is one of the most abundant bivalve taxa in the Frasnian, first occurred in the uppermost Eifelian. Later, in the Frasnian, *Ontaria suborbicularis*, which is a smooth variation of former, entered the fauna. Therefore, it is obvious, that *O. suborbicularis* emerged from *O. concentrica*. The studied material confirms that both became extinct on the Frasnian/Famennian boundary. References quoting these taxa from the Nehden-Stage, and *O. suborbicularis* even from the Hemberg-Stage could not be comfirmed by the examined material.

9 Paleoecological interpretation

In the following chapter, possible modes of life, which are interpreted based on the available information from the morphologies of the revised taxa, are introduced.

Due to the widespread occurrence of the bivalve taxa in hypoxic shales, marls and limestones, they had to be adapted to eutrophic and low-oxygen environmental conditions.

Inhabiting this deeper water environment of the Hercynian Facies confronted the bivalves with two major problems (1) to dwell on soft, muddy substrats and (2) to cope with dysoxic and /or anoxic conditions.

The predominance of rather small valves in this bivalve fauna can be ascribed to both.

Soft sediment species stay generally small in order to maximize surface-volume ratios and thus, gain more support of the substrate per unit of animal weight (Stanley, 1970). Small size associated with a large surface may have enabled them to inhabit dysoxic environments, because, as many invertebrates with an open blood system, bivalves can support their oxygen uptake by adsorption (Oschmann, 1994). Furthermore, as observed in Recent bivalve taxa, they are capable of coping with oxygen-poor or even temporally anoxic conditions for time spans of over a month (De Zwaan, 1991).

The life cycle of the Upper Devonian taxa could provide another way of adapting to periods of anoxia. The planktonic larvae would have served not only as distribution mechanism but also as resort in oxygenated realm of the water column during hostile anoxic periods. There are Recent taxa that prolong their planktonic larval phase to more than half a year (De Zwaan, 1991). In the Upper Devonian this could have enabled them to escape phases of oxygen depletion. Furthermore, Recent bivalve species can delay settlement long after their metamorphosis, until they detected a hospitable settling habitat (Pechenik et al., 1990; Oschmann, 1994). Such a postponement could explain the evident break in shell growth after the juvenile stage, which can be observed in many Upper Devonian taxa (e.g., loxopteriids, lunulacardiids).

The spatial occurrence of masses of tiny, juvenile shells (Becker, 1993) may be interpreted as the result of failed benthic colonization either due to the soupy substrate or to anoxic conditions (Röhl et al. 2001).

In the following the possible life mode is reconstructed by summarizing indications from the bauplan, the facies, and other evidences from the fossil record.

This is the first compilation of paleoecological data of Upper Devonian pelagic bivalves. Due to the restricted number of specimens in some species and the often poor state of preservation, in some cases there is only little information available. Therefore, the discussion of the mode of life is based on higher classification level.

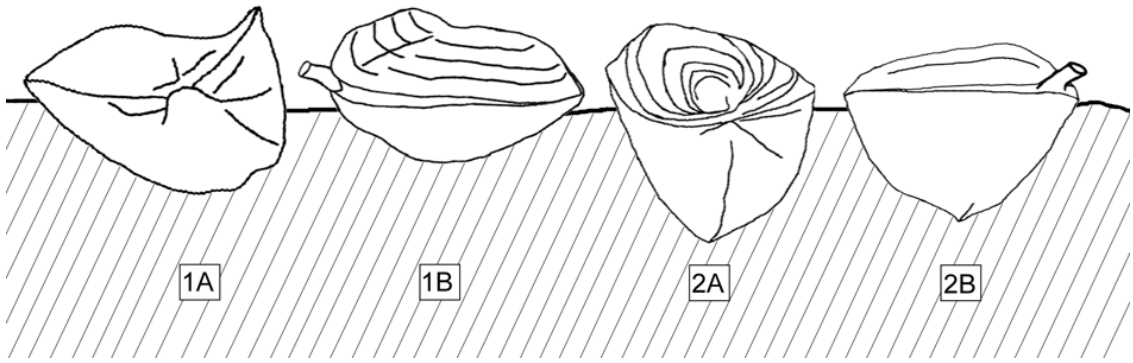


Figure 28 Assumed life position of the loxopteriids.

Loxopteriids: The most striking character of the loxopteriids is their strongly inequivalve morphology. This evolved so far that left and right valves of an individual specimens do not resemble each other anymore, and the characteristic bilateral symmetry of the Bivalvia got lost.

Similar shell morphologies have been observed in Mesozoic taxa, such as e.g., gryphaeiids. The life position of these taxa has been described to be pleurothetic. The shells resting with their sagittal plane more or less parallel to the substrate (Stanley, 1970; Newell and Boyd, 1970). One of the valves is highly convex and laid on or partly in the sediment. The other valve is smaller and lid-shaped, and is positioned "on top" of the larger valve.

Due to the similar bauplan of the loxopteriids, an analogue life position may be assumed. The large, highly convex left valve is, therefore, supposed to be resting on the substrate and is overlaid by the small, lid-shaped right valve. The left valve was probably somewhat sunk into the soft sediment and stabilized, therefore, the animal (Fig. 28).

Further information on the life habit of these bivalves has been provided by the information from the soft-body development of the loxopteriids (Chapter 7.1).

The pallial sinus proves the development of a small siphon and, therefore, it is substantiated that they were suspension feeders. Due to the soft, soupy sediment they inhabited the siphon probably enabled them to filtrate clean water from a slightly elevated position (Fig. 28).

Another feature of their soft-body bauplan is the lack of any true adductor muscles, which may be explained by the low agitated water they lived. Due to these calm conditions, the loxopteriids did not need strong muscles to keep their valves closed. It may be suggested that the exceptionally broad pallial line may have taken over the function of the adductors by providing. Another indication for a life in low agitated water is the lack of true hinge teeth, which would also stabilizes bivalves in high-energetic conditions.

It is assumed herein that the loxopteriids were epibenthic suspension feeders.

Deltacardiids: Apart from the shell symmetry of the deltacardiids there is, unfortunately, no further evidence, which would substantiate an interpretation of their life habits.
Due to the convexity of the shells, the lack of a strong foot, and a pallial sinus, it is unlikely that the deltacardiids were burrowers. The trigonal shell shape suggests that they laid with their long axis in some angle to the substrate to elevate the posterior portion of the shell (Stanley, 1970). There are no indications of a byssus or siphon. The suggestion that these species have been burrowing suspension feeders (Kriz, 2005) was based on the assumption that this group displays a broadly elliptical to subcircular outline. However, the deltacardiids are, in fact, markedly trigonal to subtrigonal. Therefore, the paleoecological presumption of Kriz (2005) may apply for the true praecardiids, but not for *Deltacardium*.
Therefore, the deltacardiids are assumed to be epibenthic suspension feeders.

Ontariids: The ontariids examined in this study provide only little information that would shed light on their mode of life. The lack of data for this group is demonstrated by only one specimen, preserving details of the soft-body bauplan. But there are some details that contradict certain life styles. Ontariids lack a pronoumced pallial sinus and a strong foot. This excludes an adaption to a deep burrowing life position, because a foot would be needed to burrow and a siphon is necessary to survive within the sediment. The only basis for an interpretation would be the comparision with similar-shaped bivalve taxa, the Buchiolinae could serve as analogon concerning the outline of the valve and the convexity. According to Grimm (1998), these taxa were probably shallow infaunal to semiinfaunal, chemoautotroph or mixotroph. Perhaps the *Ontaria* taxa lived in a similar way, but there are no true evidence that would comfirm this yet.

Lunulacardiids: The probably most striking characters of the unulacardiids are the peculiar truncation and the gapping in the majority of the taxa. The function of the posteriorly truncated margin, which is also gaping appears to be curious (see also Chapter 7.3).
One explanation may be that the lunulacardiids protruded a byssus through this opening, to attach themselves closely onto objects on the substrate or floating in the water column (Fig. 30). This would be supported by the observation of an ammonoid shell, which is occupied by *Prosochasma bickense* (Fig. 29). Driftwood with attached lunulacardiid valves has been reported by Nye et al. (1975) and could also be examined in this study (Pl. 12, Fig. 13).
Another indication for this byssal mode of life is the outline of the lunulacardiid valves. The truncated margin generates a more or less straight edge. This may have enabled them to rest with this "contact surface" closer on the object than with a convex margin (Fig. 30).

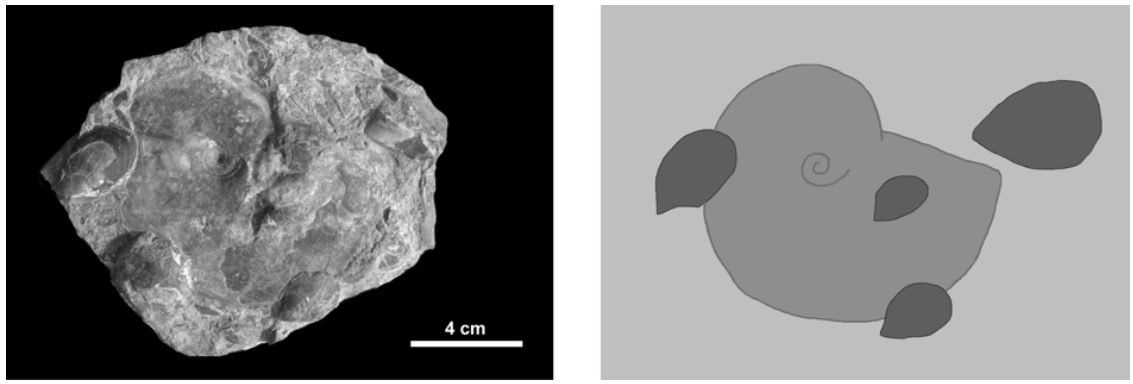


Figure 29 *Belocaeras tenuistriatum* with attached *Prosochasma bickense* (B6A-35.132).

The lunulacardiids lack a pallial sinus and, hence a longer siphon. This indicates, that they were not burrowed in the sediment or lived in a position, where they needed to elevate their inhalation-organ from the soft substrate. Assuming that they were attached onto an object, which was laying on the sediment surface, they would be raised from the substrate. In this position, they could open their posteriorly articulated valves with the subcentral fusing adductors.

It has to be mentioned that, principally, the byssus of bivalves is located anteriorly. The gap of the lunulacardiid shell is, as shown previously (Chapter 7.3), posteriorly. Therefore, assuming the mode of life, as disscussed above, applies for the lunulacardiids, this would be highly exceptional compared to the standard bauplan of bivalves. But considering the evidences from the fossil record, and taking into account that the Cryptodonta seems to be an unusual bivalve group, anyway, this may be a possible explanation for their shell morphology.

Hence, the question arises wether the lunulacardiids dwelled on "benthic island" (Kauffman, 1981), formed by objects on the substrate, or floated pseudoplanktonicly on swimming habitats (Seilacher, 1982). Recent bivalves float attached to the brown algae *Saragassum*, which covers large areas, or colonize even anthropogenic debris (Barnes, 2002). From the *Posidonia* Shale ammonoid shells and driftwood are reported as swimming habitats for bivalves (Seilacher, 1982, 1990). But the floating time of ammonoid shells and the observed small logs have probably never exceeded a few months, and the attached bivalves were significantly older than that. Therefore, it is likely that these objects acted as "benthic island" (Kauffman, 1981) on the soupy substrate. Although it cannot be excluded that the lunulacardiids floated for some time, they probably lived most of their life epibenthic.

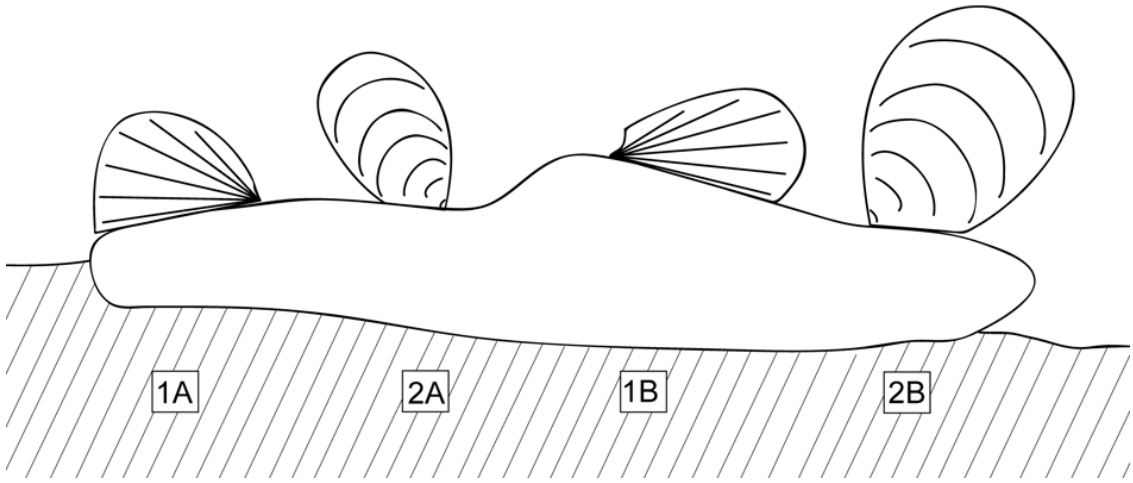


Figure 30 Assumed life position of chaenocardiolids (1A, 1B) and lunulacardiids (2A, 2B).

Another explanation for this gap may be an endosymbiosis with chemoautotrophic bacteria, as Seilacher (1990) proposed for some fossil bivalve taxa. This has been observed, especially in Recent genera, which live in the surrounding of deep-sea vents such as, e.g., *Calyptogena* (Little and Vrijenhoek, 2003). They house sulfuricant bacteria in their gills, which oxydize H_2S (Seilacher, 1990). Although this symbiosis is commonly not observable in the shell morphology, it could be assumed that the gap of lunulacardiid valves could serve as entrance for H_2S-rich water, drawn from the underlying substrate. Especially the occurrence of chimney-shaped shell extensions (Chapter 7.3) could allude to a tube for an H_2S-pump (Seilacher, 1990). But this would not explain valves found attached to objects and, thus, living distantly from the H_2S source. However, this chemosymbiotic life habit is impossible in dysaerobic environments, because oxygen in the bottom water would exclude free H_2S, as well as temporally oxygenating episodes (Oschmann, 1994). Therefore, this mode of life did probably not apply to the lunulacardiids.

It is assumed herein that the lunulacardiids were facultative pseudoplanktonic or endobenthic suspension feeders.

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Plate 1

Figs. 1-4, *Loxopteria dispar*, B6A-35.54, Bergisch Gladbach, steinkern, x3.

Figs. 5-8, *Loxopteria dispar*, MB.M.789, Oberscheld, steinkern, x3.

Figs. 9-12, *Loxopteria dispar*, B6A-35.41, Bergisch Gladbach, steinkern, x3.

Fig. 13, *Loxopteria dispar*, B6A-35.57, Nehden, RV, steinkern, x2.

Fig. 14, *Loxopteria dispar*, MB.M.2222.1, Nehden, RV, steinkern, x3.

Fig. 15, *Loxopteria dispar*, MB.M.4243, Oberscheld, RV, shell preservation, x2.

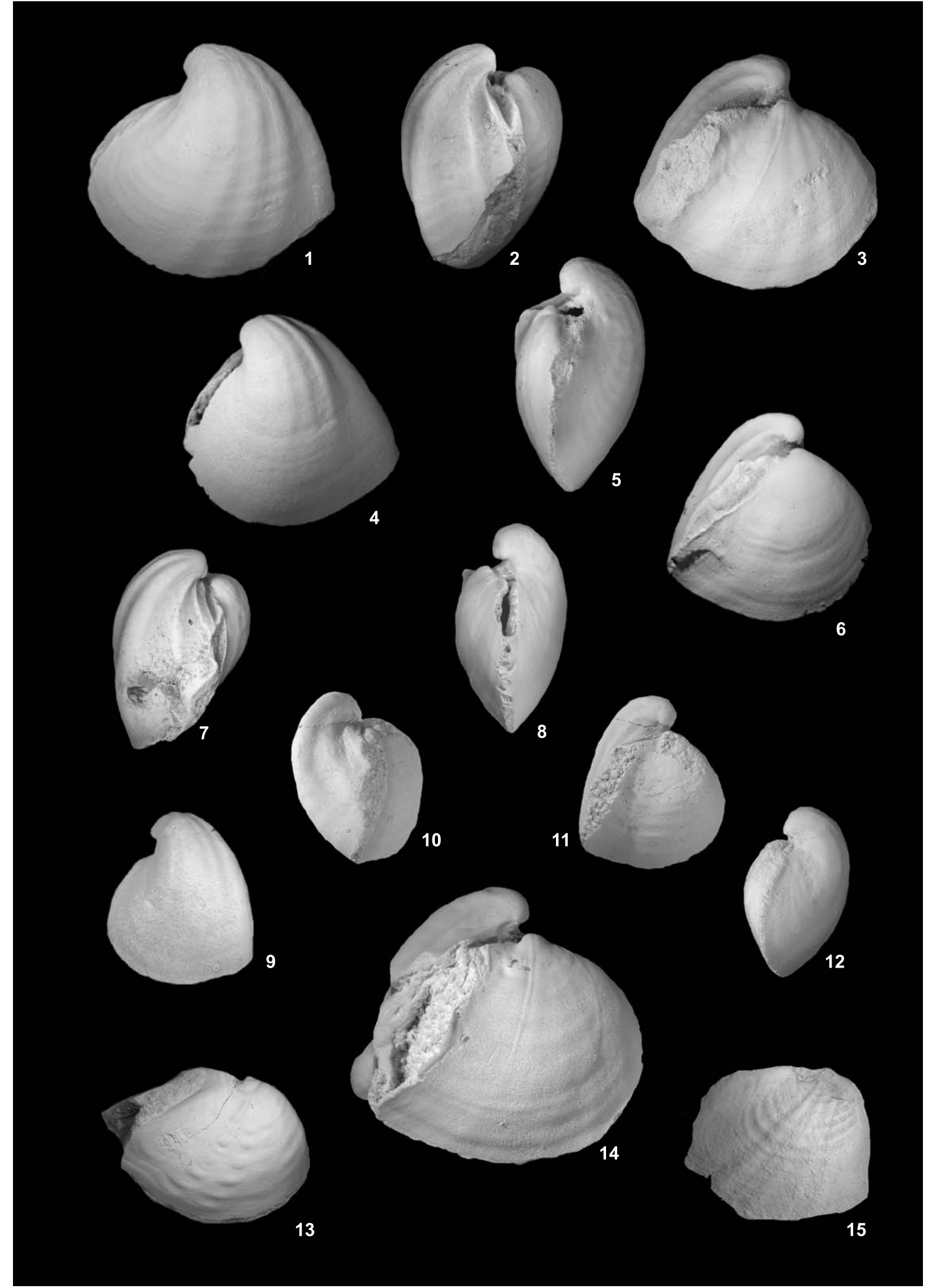
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Plate 2

Figs. 1-2, *Loxopteria inflata*, MB.M.4342, Langenaubach, LV, shell preservation, x2.

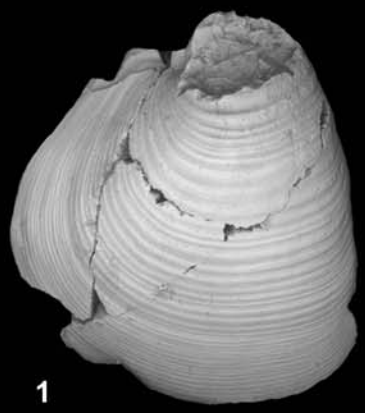
Fig. 3, *Loxopteria inflata*, NYSM 5327 (holotype *Loxopteria vasta*), Forestville, RV, shell preservation, x2.

Figs. 4-5, *Loxopteria problematica,* MB.M.4317, Oberscheld, LV, x3.

Fig. 6, *Loxopteria problematica,* B6A-35.133, Oberscheld, RV, shell preservation, x1.5.

Fig. 7, *Loxopteria problematica*, MB.M.4290, Enkeberg, RV, partly shell preservation, x1.5.

Figs. 8-11, *Loxopteria problematica*, B6A-35.92, Mrakib/Maider, steinkern, x4.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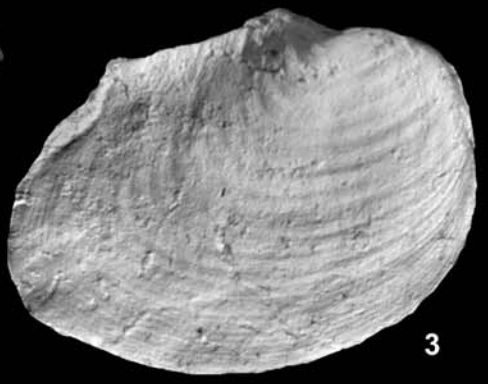
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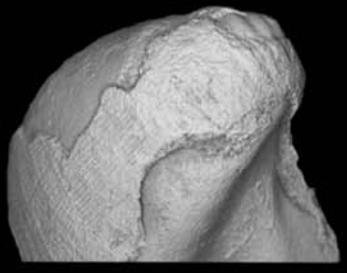
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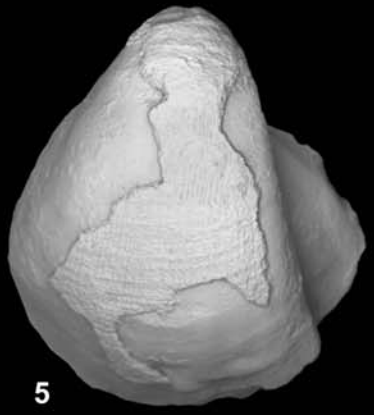
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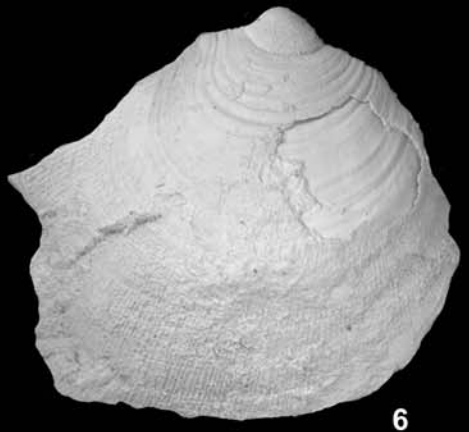
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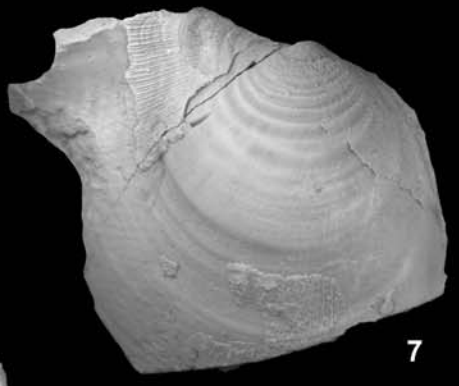
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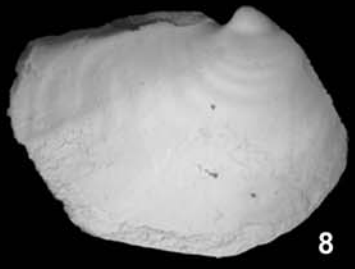
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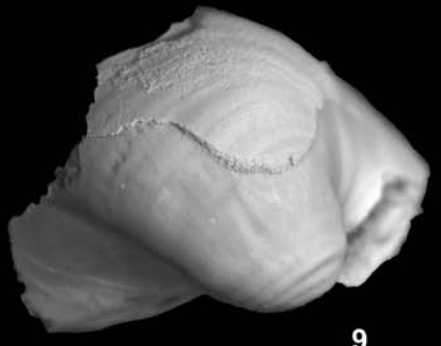
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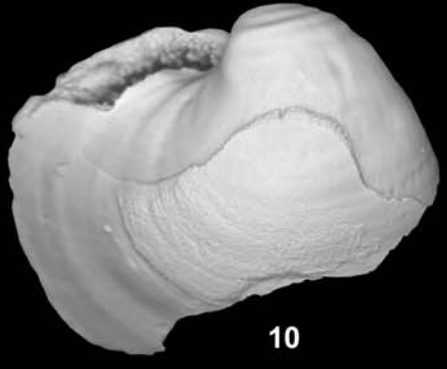
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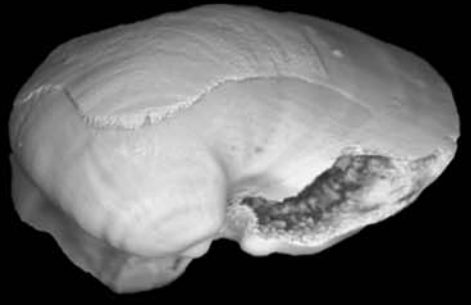
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Plate 3

Figs. 1-5, *Loxopteria meioklina*, B6A-35.129 (topotype *Loxopteria meioklina*), Mrakib/Maider, steinkern, x5.

Figs. 6-10, *Loxopteria meioklina*, B6A-35.130 (holotype *Loxopteria meioklina)*, Mrakib/Maider, steinkern, x4.

Fig. 11, *Loxopteria dispar*, MB.M.2220.1, Nehden, shell preservation, detail ornamentation, centre LV.

Fig. 12, *Loxopteria dispar*, MB.M.2220.1, Nehden, shell preservation, posterior third LV, x3.

Figs. 13-14, *Loxopteria dispar*, MB.M.2220.1, Nehden, shell preservation, detail ornamentation, posterior third LV.

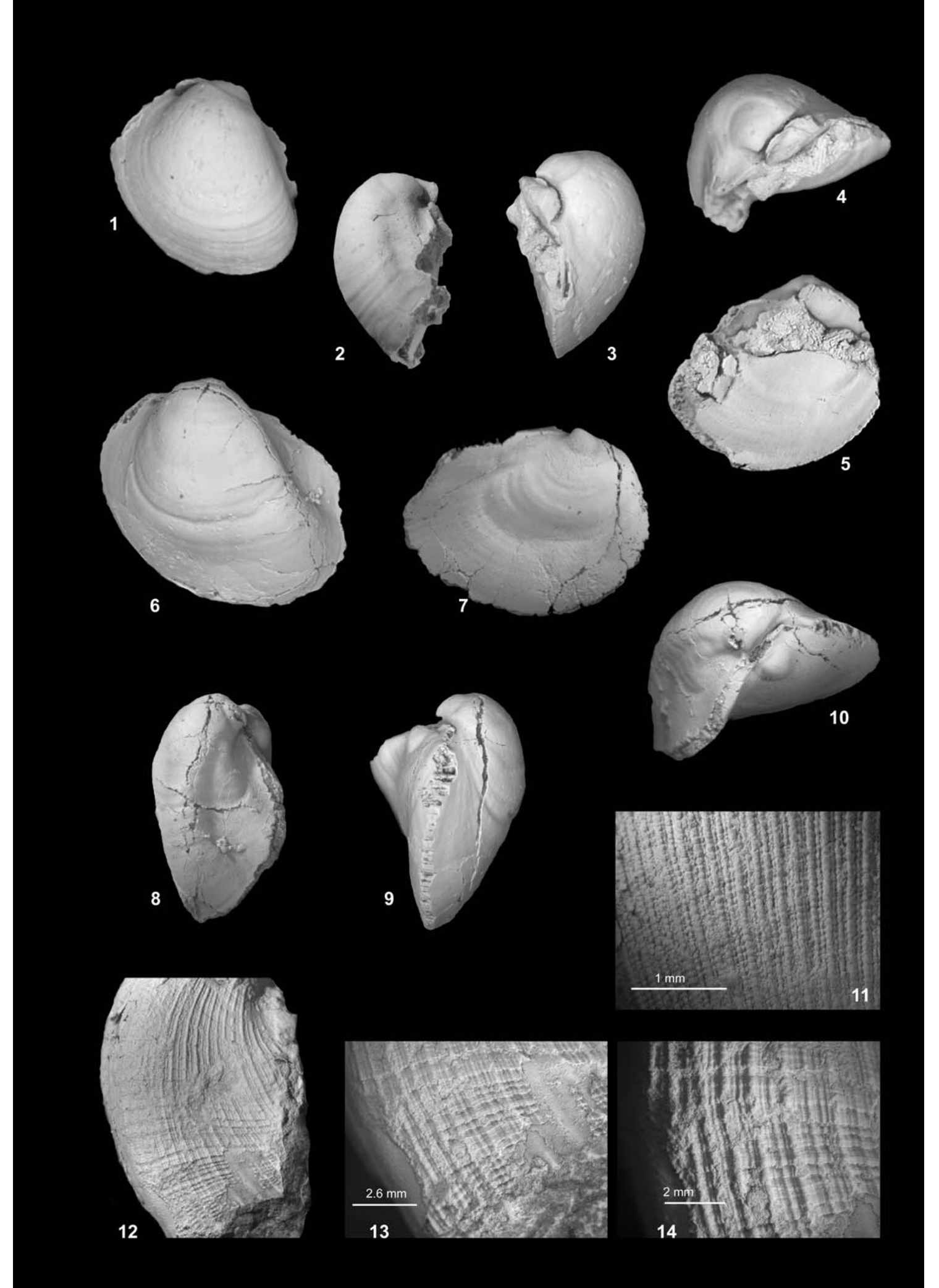
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Plate 4

Figs. 1-4,	*Elasmatium elongata*, B6A-35.77, Nehden, steinkern, x3.
Figs. 5-6,	*Elasmatium elongata*, B6A-35.81, Bergisch Gladbach, steinkern, x4.
Fig. 7,	*Elasmatium elongata*, NYSM 5284, Correll´s Point/Forestville, LV, shell preservation, x4.
Fig. 8,	*Elasmatium elongata*, NYSM 5283, Correll´s Point/Forestville, LV, shell preservation, x4.
Fig. 9-10,	*Loxopteria gibbosa*, B6A-35.120, Mrakib/Maider, steinkern, x3.
Fig. 11,	*Loxopteria gibbosa*, SMF XV/3-2158 (holotype *Kochia laevis*), Wildungen, RV, partly shell preservation, x5.
Fig. 12,	*Loxopteria gibbosa*, MB.M.4493, Wildungen, RV, shell preservation, x3.7.
Fig. 13,	*Elasmatium elongata*, MB.M.788 (holotype *Kochia rugosa*), Oberscheld, RV, partly shell preservation, x2.5.


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Plate 5

Figs. 1-4, *Elasmatium gowandense*, B6A-35.70, Bergisch Gladbach, steinkern, x3.

Fig. 5, *Elasmatium gowandense*, NYSM 5254, Correll´s Point/Forestville, LV, x2.

Fig. 6, *Elasmatium gowandense*, B6A-35.62, Bergisch Gladbach, RV, x4.

Figs. 7-10, *Elasmatium* gowandense, B6A-35.60, Bergisch Gladbach, steinkern, x3.

Fig. 11, *Elasmatium gowandense*, B6A-35.61, Bergisch Gladbach, RV, x4.

Fig. 12, *Elasmatium gowandense*, NYSM 5246, Correll´s Point/Forestville, LV, x3.


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Plate 6

Fig.1, *Deltacardium vetustum* AMNH-F1-42169 (holotype *Cardium vetustum*), RV, Gowanda Shale, x4.

Fig. 2, *Deltacardium vetustum*, AMNH-F1-42170, LV, Gowanda Shale, x2.6.

Fig. 3, *Deltacardium vetustum*, GZG 1258-2, Enkeberg, RV, x5.

Figs. 4-5, *Deltacardium vetustum*, MB.M.4205, Enkeberg, LV, x6.

Figs. 6-8, *Deltacardium vetustum*, MB.M.4198, Nehden, steinkern, x3.

Figs. 9-11, *Deltacardium vetustum,* B6A-35.22, Bergisch Gladbach, steinkern, x3.

Figs. 12-14, *Deltacardium vetustum*, MB.M.4190 (neotype *Cardiola Nehdensis*), Nehden, steinkern, x4.

Fig. 15, *Loxopteria problematica*, BSPG AS VII 1721 (lectotype *Avicula semiauriculata*), Presseck, LV, composition mould, x2.2.

Fig. 16, *Loxopteria problematica*, BSPG AS VII 1725(lectotype *Avicula* ? *problematica*), Presseck, LV, composition mould, x3.

Fig. 17, *Loxopteria inflata*, BSPG AS VII 1728, (lectotype *Avicula inflata*), Schübelhammer, LV, composition mould, x2.6.

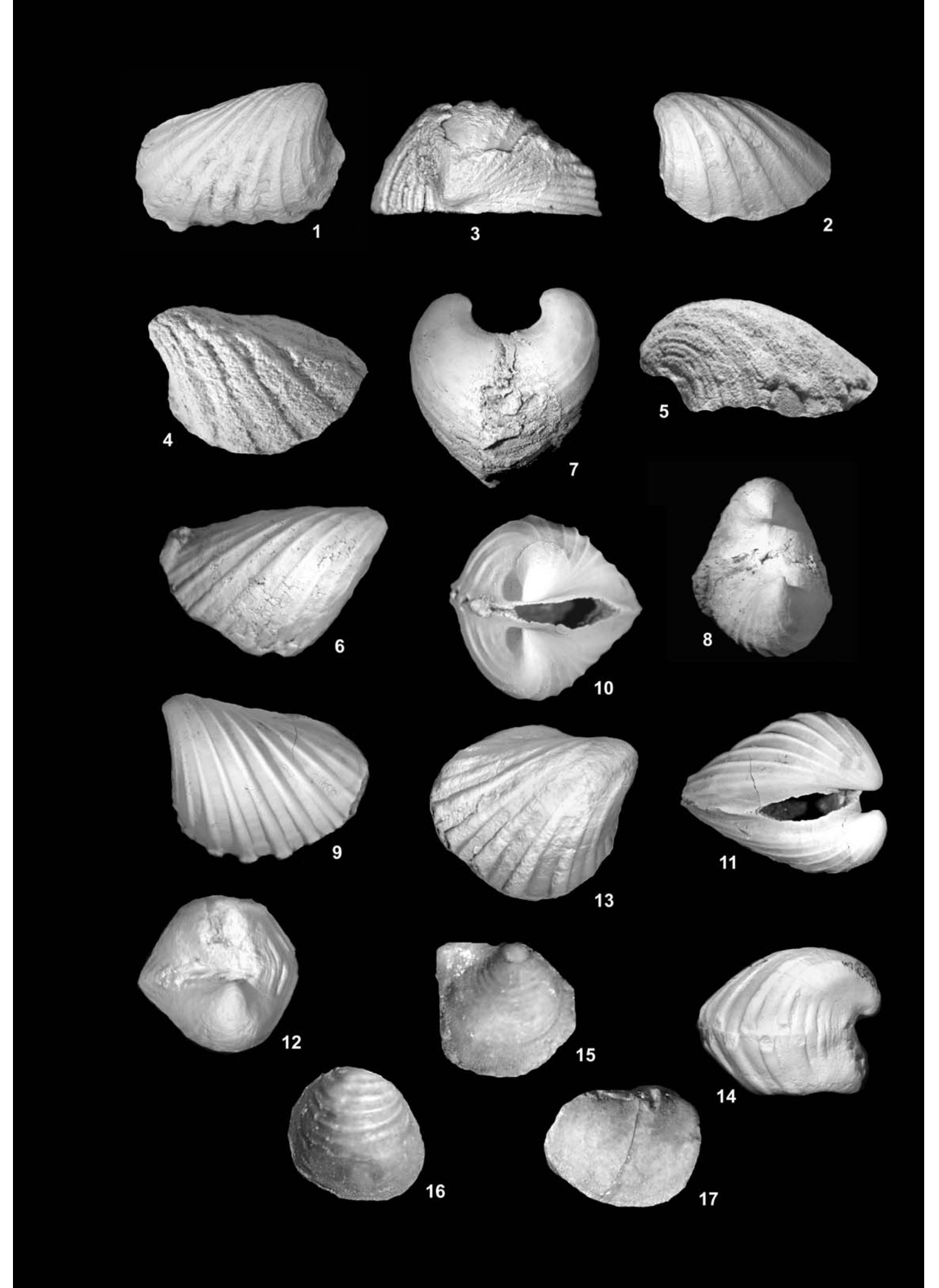
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Plate 7

Figs. 1-4, *Deltacardium clymeniae*, B6A-35.26, Bergisch Gladbach, steinkern, x3.2.

Figs. 5-8, *Deltacardium clymeniae*, B6A-35.35, Bergisch Gladbach, steinkern, x3.7.

Figs. 9-12, "*Praecardium*" *multicostatum*, B6A-35.39, Bergisch Gladbach, steinkern, x5.6.

Fig. 13, *Deltacardium clymeniae*, GZG 490-106 (neotype *Praecardium clymeniae*), Enkeberg, RV, x2.

Fig. 14, "*Praecardium*" *multicostatum*, NYSM 5493 (lectotype *Praecardium multicostatum*), Gowanda Shale, RV, x4.5.

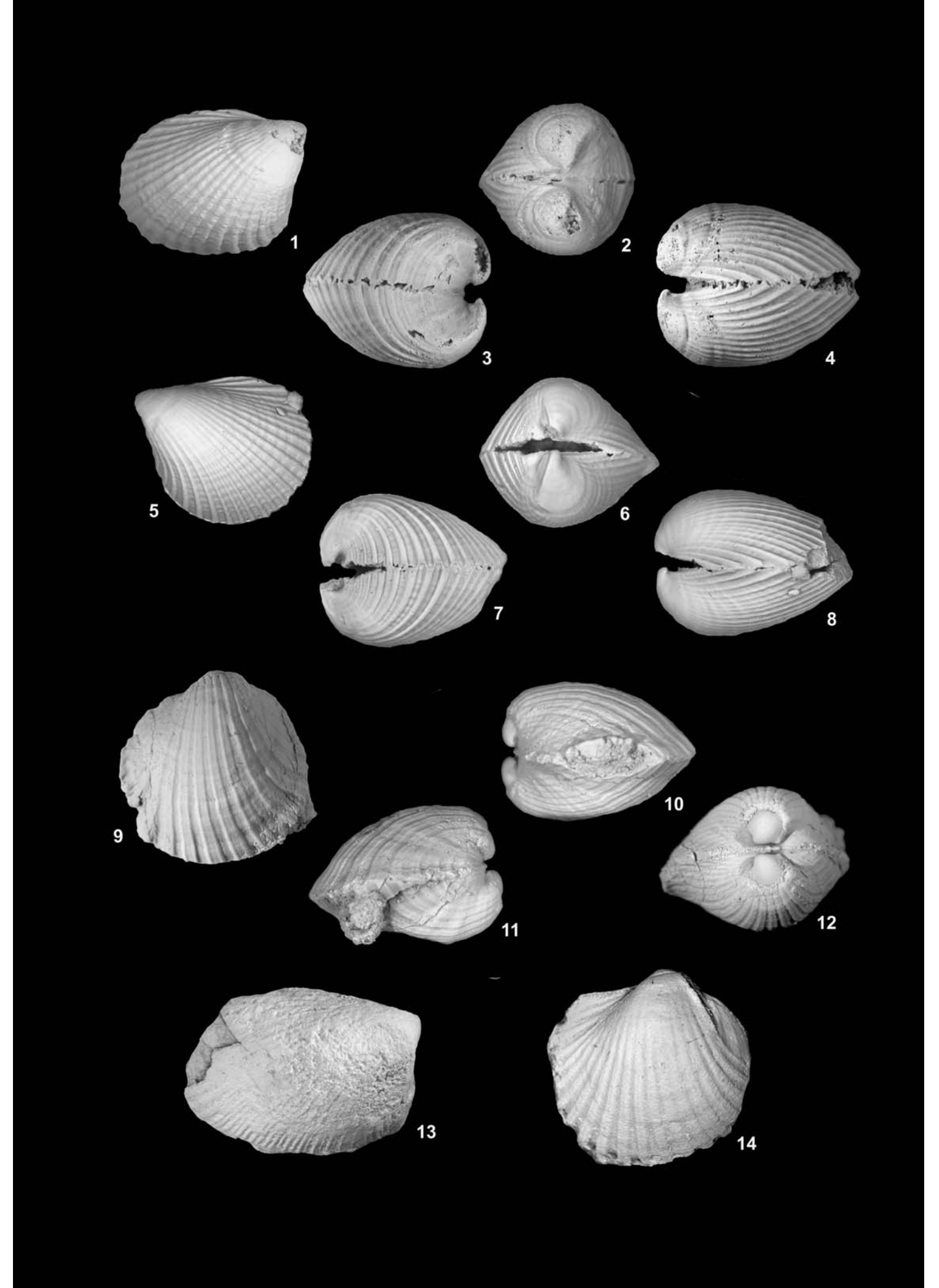
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Plate 8

Figs. 1-2, *Loxopteria problematica,* MB.M.4295, Enkeberg, LV, steinkern, x3.

Fig. 3, *Loxopteria gibbosa*, B6A-35.126 (neotype *Avicula gibbosa*), Schübelhammer, LV, x4.

Fig. 4, *Loxopteria dispar*, NWS 240 (holotype *Avicula dispar*), Oberscheld, LV, shell preservation, x3.

Fig. 5, *Loxopteria dispar*, MB.M.2220.2, Nehden, LV, shell preservation, x3.

Fig. 6, *Loxopteria dispar*, MB.M.2220.2, Nehden, LV, shell preservation, posterior third valve, x4.

Fig. 7, *Loxopteria dispar*, MB.M.2222.2, Nehden, steinkern, hinge line, x3.

Fig. 8, *Loxopteria dispar*, MB.M.2222.1, Nehden, steinkern, hinge line, x2.

Figs. 9-11, N. gen. A n. sp., right valve, Gattendorf, MB.M.2229.

Fig. 12, *Deltacardium duplicatum*; BSPG AS VII 366 (lectotype *Cardiola duplicata*), RV, Gattendorf, x2.

Fig. 13, *Deltacardium duplicatum*, GZG 490-107, RV, Enkeberg, x2.

Fig. 14, mould, *Deltacardium duplicatum*, B6A-35.35.7, Mentaresses, RV, internal x2.3.

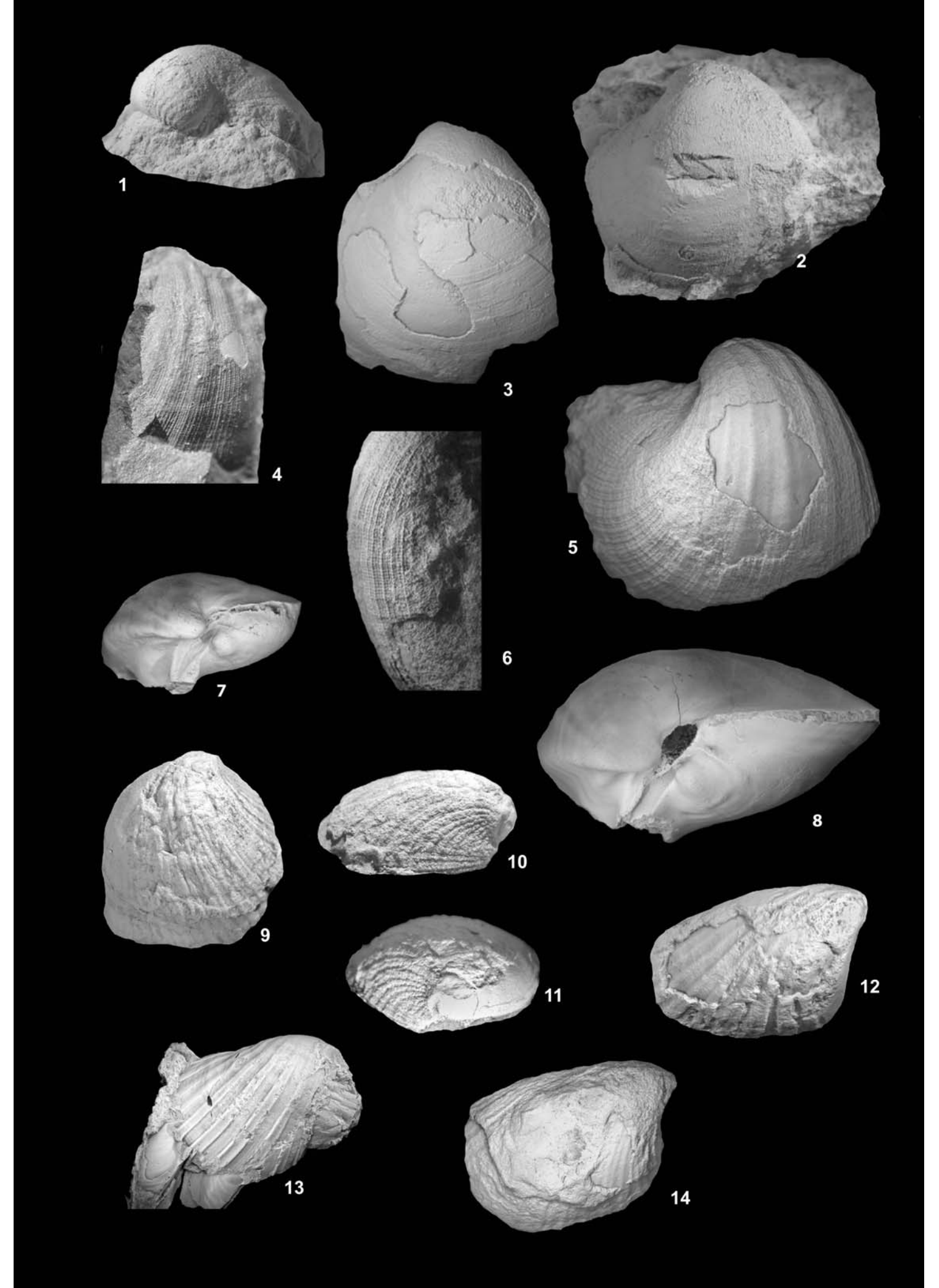
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Plate 9

Fig. 1, *Lunulacardium semistriatum*, MB.M.215, Oberscheld, LV, shell preservation, x5.7.

Figs. 2-3, *Lunulacardium semistriatum*, MBM.215, Oberscheld, LV, shell preservation, dorsal margin, x4.4.

Fig. 4, *Lunulacardium semistriatum*, MBM.215, Oberscheld, LV, shell preservation, posterior margin, x4.4.

Fig. 5, *Lunulacardium semistriatum*, MB.M.2232.8 (neotype *Lunulacardium semistriatum*), Oberscheld, LV, shell preservation, dorsal margin, x11.

Fig. 6, *Lunulacardium semistriatum*, MB.M.2232.8 (neotype *Lunulacardium semistriatum*) Oberscheld, LV, shell preservation, x7.1.

Fig. 7, *Lunulacardium semistriatum*, MB.M.2232.6 (neotype *Lunulacardium semistriatum*), Oberscheld, LV, shell preservation, x2.2.

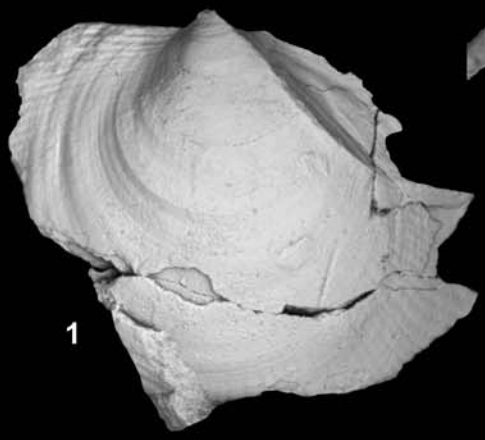
Fig. 8, *Lunulacardium semistriatum*, MB.M.2236.4, Oberscheld, LV, shell preservation, x5.

Fig. 9, *Lunulacardium semistriatum*, MBM 2232.7, Oberscheld, RV, shell preservation, x5.5.

Fig. 10, *Lunulacardium semistriatum*, MBM 213, Oberscheld, LV, shell preservation, x3.3.

Fig. 11, *Lunulacardium semistriatum*, MBM 213, Oberscheld, LV, shell preservation, posterior margin, x3.8.

Fig. 12, *Lunulacardium semistriatum*, MBM 213, Oberscheld, LV, shell preservation, dorsal margin, x4.8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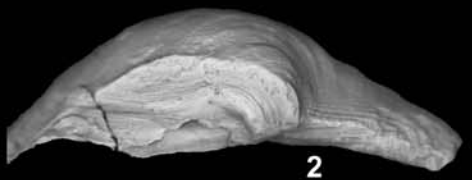
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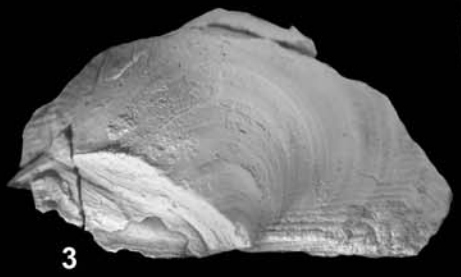
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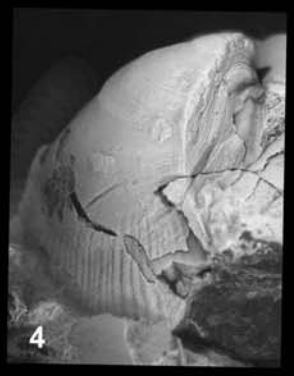
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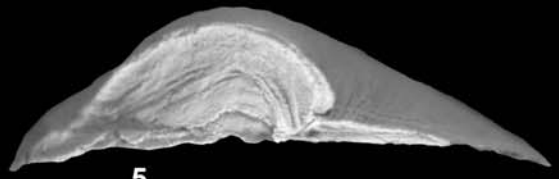
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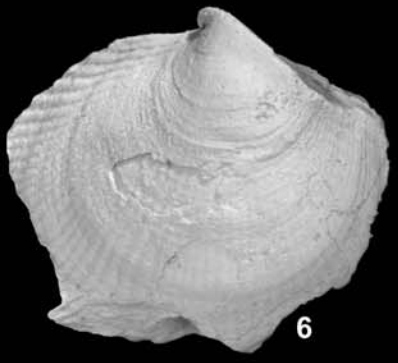
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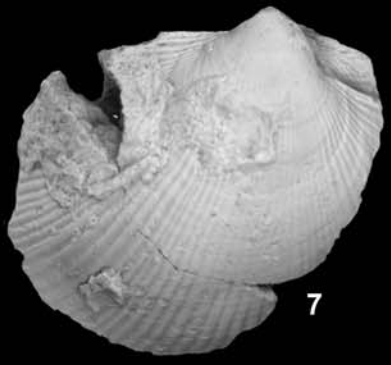
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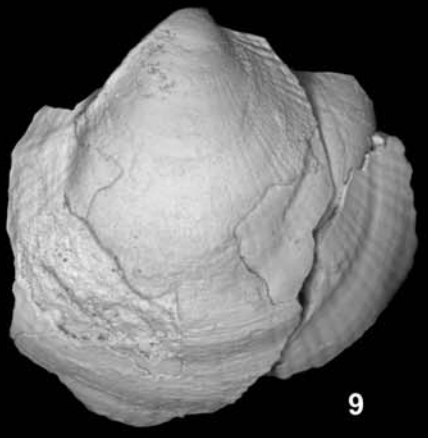
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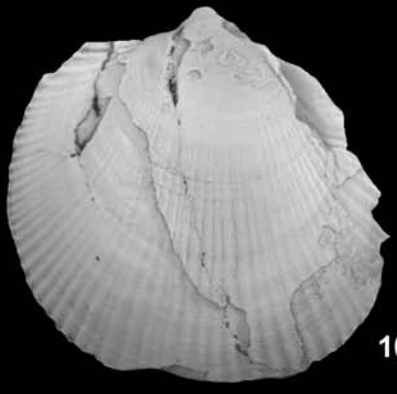
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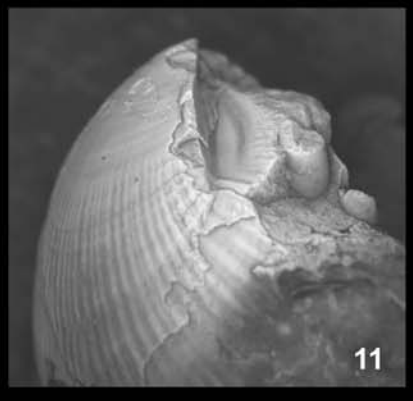
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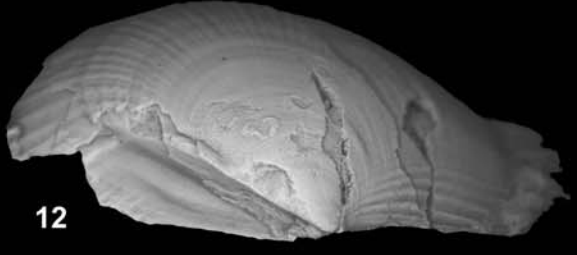
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Plate 10

Fig. 1, *Prosochasma mytiloides*, GZG 490-210, Bicken, LV, steinkern with little shell remains, x2.5.

Fig. 2, *Prosochasma bickense*, GZG 490-208 (lectotype *Prosochasma dilatatum*), Braunau, RV steinkern, x2.

Fig. 3, *Prosochasma bickense*, GZG 490-206, Martenberg, RV, steinkern, x1.5.

Fig. 4, *Prosochasma bickense*, SMF XV/3-2155 (holotype *Lunulacardium bickense*), Bicken, LV, steinkern, x1.5.

Fig. 5, *Prosochasma mülleri*, SMF XV/3-2154 (lectotype *Lunulacardium mülleri*), Martenberg, RV, steinkern, x2.5.

Fig. 6, *Prosochasma mytiloides*, GZG 490-201 (holotype *Prosochasma mytiloides*), Bicken, RV, steinkern, x2.5.

Fig, 7, *Prosochasma mytiloides*, MB.M.221 (holotype *Prosochasma abditum*), Martenberg, RV, steinkern with shell remain anterior dorsally, x2.

Fig. 8, *Prosochasma pyriforme*, SMF XV/3-2157 (holotype *Lunulacardium adorfense*), Martenberg, LV, steinkern, x2.5.

Fig. 9, *Prosochasma mülleri*, GZG 490-202 (holotype *Prosochasma expansa*), Martenberg, LV, steinkern with shell remains, x2.

Fig. 10, *Prosochasma pyriforme*, SMF XV/3-2159, Martenberg, RV, steinkern, x2.

Fig. 11, *Prosochasma bickense*, SMF XV/3-2156 (holotype *Lunulacardium inflatum*), Martenberg, RV, steinkern, x2.

Fig. 12, *Prosochasma bickense*, SMF XV/3-2156 (holotype *Lunulacardium inflatum*), Martenberg, RV, steinkern, dorsal margin, x2.5.

Fig. 13, *Prosochasma bickense*, GZG 490-206, Martenberg, RV, steinkern, dorsal margin, x1.5.

Fig. 14, *Prosochasma bickense*, GZG 490-208 (lectotype *Prosochasma dilatatum*), Braunau, RV steinkern, dorsal margin, x8.

Fig. 15, *Prosochasma bickense*, SMF XV/3-2155 (holotype *Lunulacardium bickense*), Bicken, LV, steinkern, dorsal margin, x1.5.

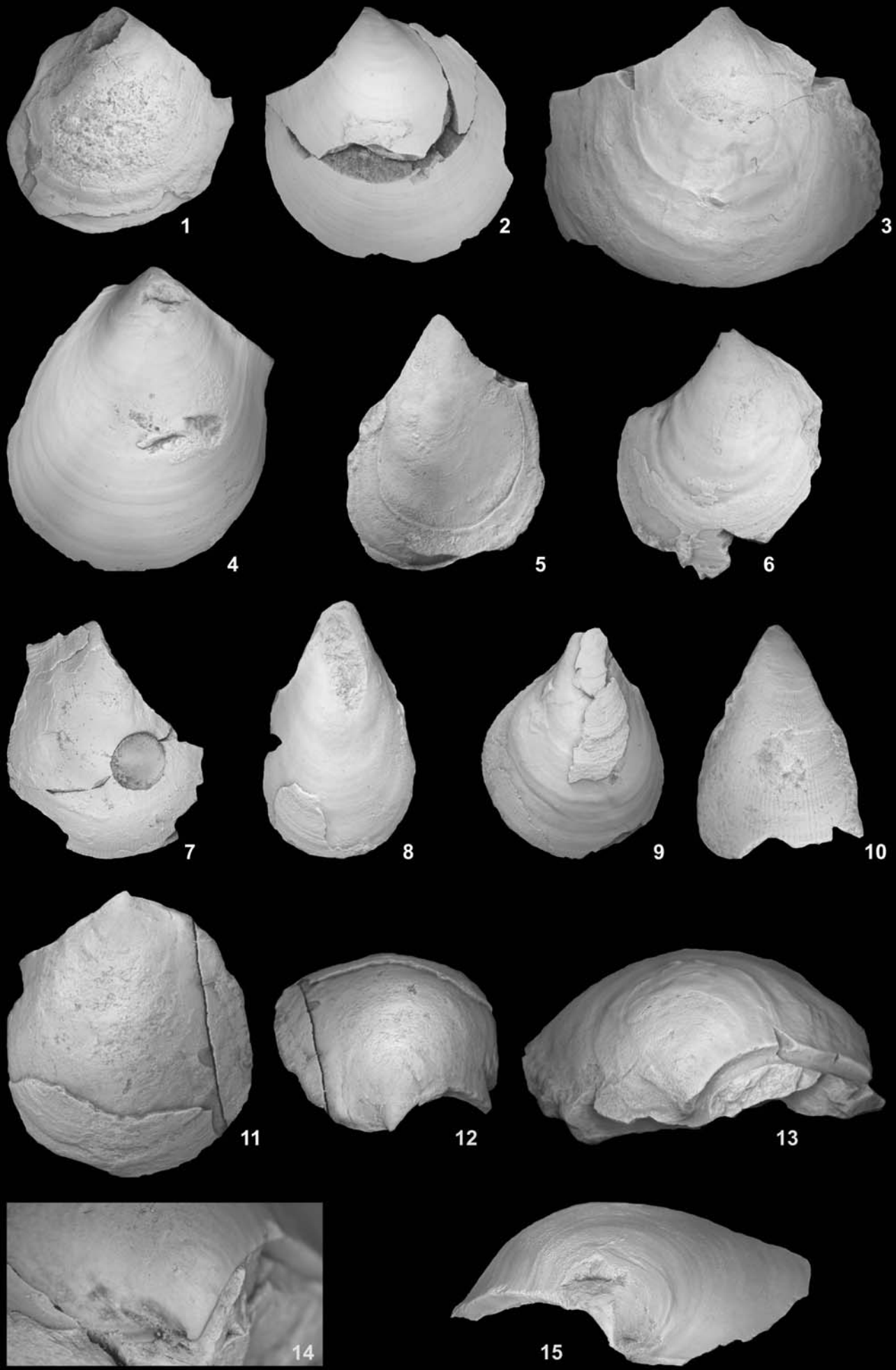
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Plate 11

Fig. 1, *Chaenocardiola carinata*, MB.M.219 (lectotype *Chaenocardiola carinata*), Ense, LV, steinkern, x3.

Fig. 2, *Chaenocardiola carinata*, MB.M.219 (lectotype *Chaenocardiola carinata*), Ense, LV, steinkern, detail anterior margin, x3.5.

Fig. 3, *Chaenocardiola carinata*, MB.M.219 (lectotype *Chaenocardiola carinata*), Ense, LV, steinkern, posterior margin, x3.

Fig. 4, *Chaenocardiola carinata*, MB.M.219 (lectotype *Chaenocardiola carinata*), Ense, LV, steinkern, dorsal margin, x3.

Fig. 5, *Chaenocardiola denckmanni*, MB.M.218 (holotype *Chaenocardiola denckmanni*), Wildungen, LV, steinkern, x3.4.

Fig. 6, *Chaenocardiola carinata*, MB.M.217b, Wildungen, plastic cast, LV, x3.5.

Fig. 7, *Chaenocardiola conalifer*, GZG 490-195, Bicken, LV, composition mould, x5.

Fig. 8, *Chaenocardiola tetragona* MB.M.2237, Schübelhammer, LV, steinkern with shell remains at the umbo, x4.7.

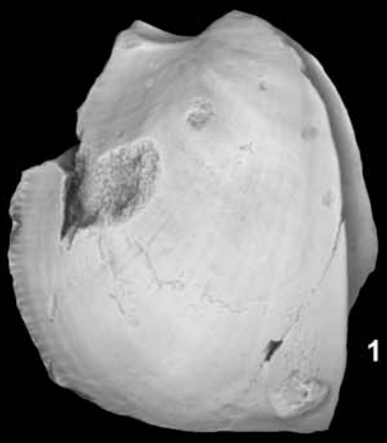
Fig. 9, *Chaenocardiola tetragona*, MB.M.4415, Beul, RV, shell preservation, x5.5.

Fig. 10, *Chaenocardiola haliotoidea*, Mbg.AH2006-1, LV, shell preservation, x3.6

Fig. 11, *Chaenocardiola tetragona*, MB.M220, Ense, RV, composition mould, x2.7.

Fig. 12, *Chaenocardiola tetragona*, MB.M220, Ense, RV, composition mould, posterior margin, x2.7.

Fig. 13, *Chaenocardiola tetragona*, MB.M.4416, Ense, RV, composition mould, x4.2.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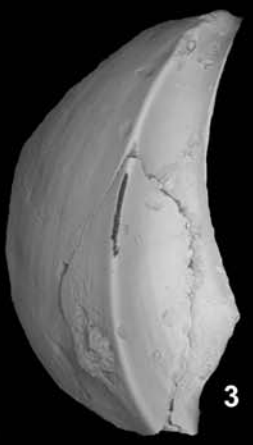
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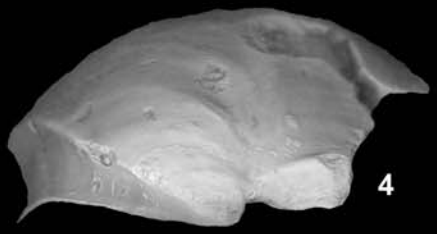
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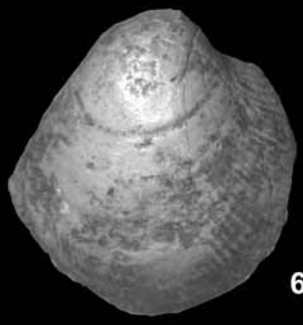
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Plate 12

Fig. 1, *Chaenocardiola koeneni*, GZG 490-189 (*Chaenocardiola*), Bicken, LV, composition mould, x3.1.

Fig. 2, *Chaenocardiola koeneni*, GZG 490-176 (paralectotype *Chaenocardiola koeneni*), Bicken, RV, composition mould, x1.9.

Fig. 3, *Chaenocardiola koeneni*, GZG 490-188 (paralectotype *Chaenocardiola koeneni*), Bicken, RV, composition mould, x2.9.

Fig. 4, *Chaenocardiola koeneni*, GZG 490-191 (paralectotype *Chaenocardiola koeneni*), Bicken, LV, composition mould, x2.5.

Fig. 5, *Chaenocardiola koeneni*, GZG 490-186 (lectotype *Chaenocardiola koeneni*), Bicken, LV, composition mould, x 2.5.

Fig. 6, *Chaenocardiola koeneni*, GZG 490-177 (paralectotype *Chaenocardiola koeneni*), Bicken, LV composition mould, x2.6.

Fig. 7, *Chaenocardiola tetragona*, B6A-35.136, Mentaresses, LV, steinkern, x4.8.

Fig. 8, *Prosochasma bickense*, MB.M.4388, Wildungen, RV, steinkern, dorsal margin, x4.

Fig. 9, *Prosochasma bickense*, MB.M.4388, Wildungen, RV, steinkern, detail umbo, x5.

Fig. 10, *Chaenocardiola koeneni*, GZG 490-195, Bicken, LV, composition mould, x 5.1.

Fig. 11, *Chaenocardiola tetragona*, B6A-35.136, Mentaresses, steinkern, dorsal margin, x7.5.

Fig. 12, *Chaenocardiola koeneni*, GZG 490-195, Bicken, LV, composition mould, detail the ornamentation anterior the truncation.

Figs. 13, *Prosochasma bickense*, B6A-24.134, Oued Mezerreb, RV, steinkern, x0.9.

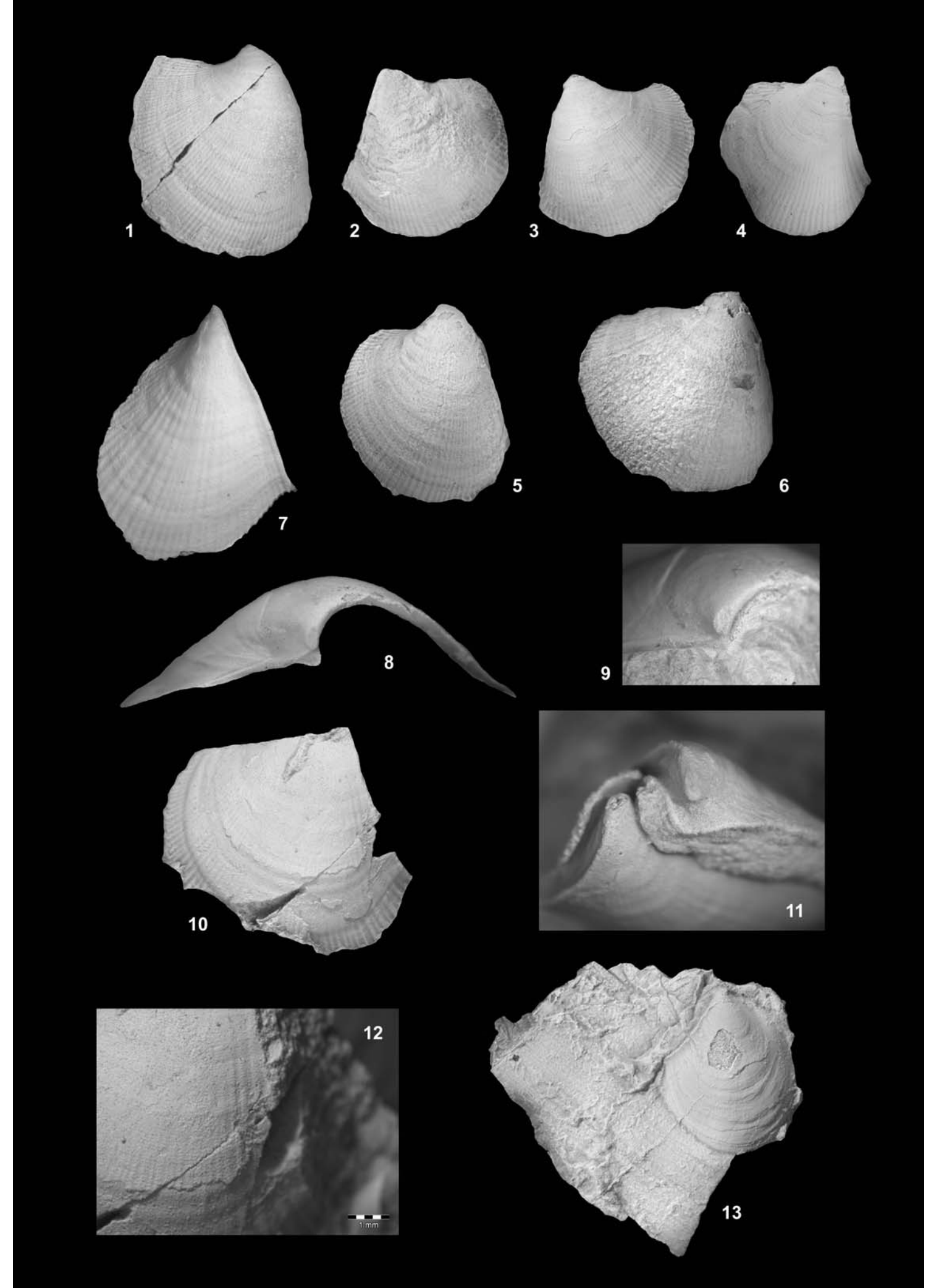
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Plate 13

Fig. 1, *Ontaria concentrica*, MB.M.2202.1 (lectotype *Orbicula concentrica*), LV, steinkern with shell remains, Martenberg, x4.8.

Fig. 2, *Ontaria concentrica*, MB.M.2202.1 (lectotype *Orbicula concentrica*), Martenberg, LV, detail ornamentation, x6.2.

Fig. 3, *Ontaria concentrica*, MB.M. 259 (paralectotype *Cardiola subconcentrica*),Wildungen, RV steinkern, x8.

Fig. 4, *Ontaria concentrica*, MB.M.258 (lectotype *Cardiola subconcentrica*) Wildungen, LV, composition mould, x4.7.

Fig. 5, *Ontaria concentrica*, MB.M. 258 (lectotype *Cardiola subconcentrica*), Wildungen, LV, composition mould, x4.6.

Fig. 6, *Ontaria concentrica*, MB.M. 2207.2, Oberscheld, RV, shell preservation, x3.2.

Fig. 7, *Ontaria concentrica*, MB.M. 2202.2 (paralectotype *Orbicula concentrica*), Martenberg, RV, steinkern with shell remains, x4.

Fig. 8, *Ontaria suborbicularis*, MB.M.2203.1, Oberscheld, RV, shell preservation, x3.6.

Fig. 9, *Ontaria concentrica*, MB.M. 2204, Oberscheld, LV, shell preservation, x4.4.

Fig. 10, *Ontaria suborbicularis*, MB.M.4427, Oberscheld, LV, shell preservation, x3.9.

Fig. 11, *Ontaria concentrica*, B6A-35.129, Oued Mzerreb, steinkern, dorsal margin, x12.2.


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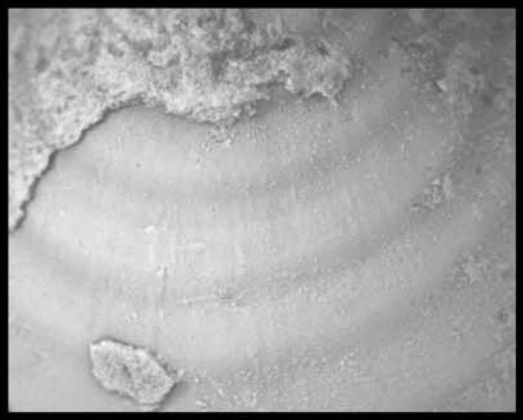
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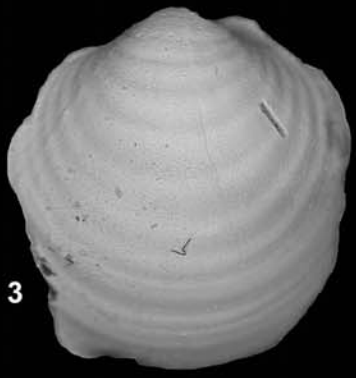
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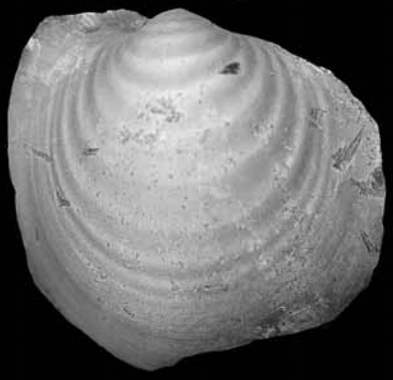
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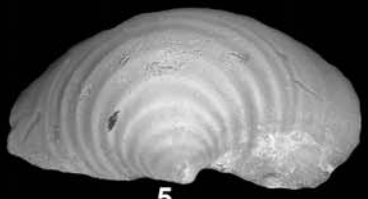
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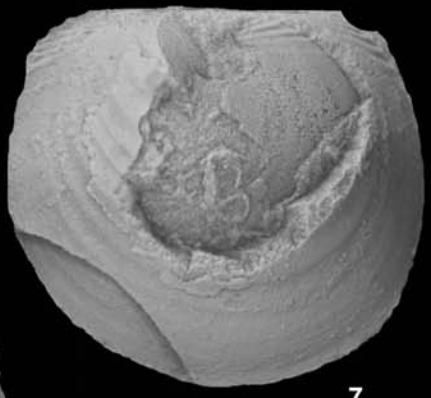
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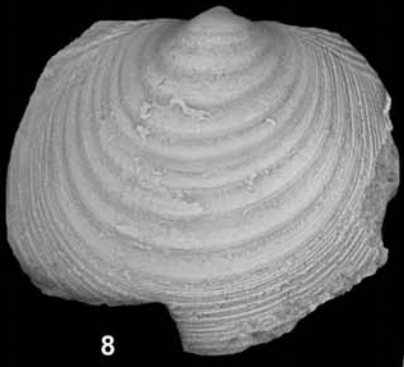
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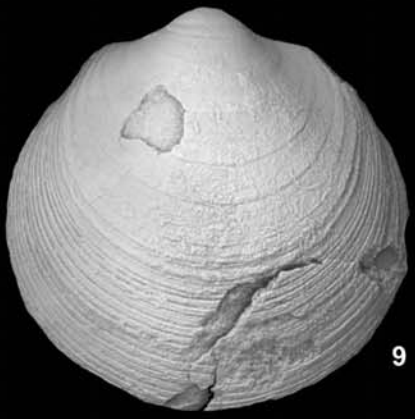
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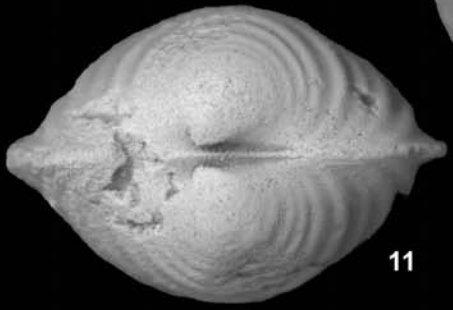
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Plate 14

Fig. 1, *Ontaria suborbicularis*, B6A-35.131, Berigorn Valley Canning Basin, RV, shell preservation, x4.

Fig. 2, *Ontaria concentrica*, MB.M.4444.1, Oberscheld, RV, composition mould, x5.9.

Fig. 3, *Ontaria concentrica*, MB.M.4444.1, Oberscheld, detail radial ribs at dorsal margin, x10.5.

Fig. 4, *Ontaria suborbicularis*, MB.M.4435, Oberscheld, x5.6.

Fig. 5, *Ontaria suborbicularis*, MB.M.4435, Oberscheld, LV shell preservation, x4.3.

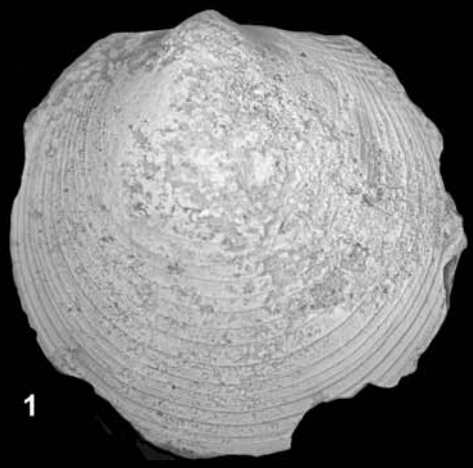
Fig. 6, *Ontaria concentrica*, MB.M.4444.2, Oberscheld, RV, steinkern with shell remains, x4.3.

Fig. 7, *Ontaria concentrica*, MB.M.4444.2, Oberscheld, detail ornamentation at ventral margin, x6.5.

Fig. 8, *Ontaria concentrica* MB.M.2209.3, RV, detail ornamentation x8.5.

Fig. 9, *Ontaria concentrica*, MB.M. 2207.2, Oberscheld, RV, shell preservation, x4.9.

Fig. 10, *Ontaria concentrica*, MB.M. 2207.2, Oberscheld, RV, shell preservation, x3.2.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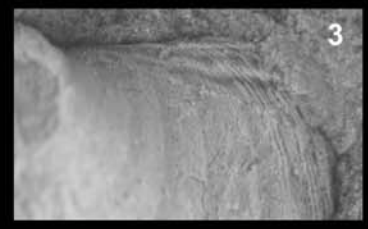
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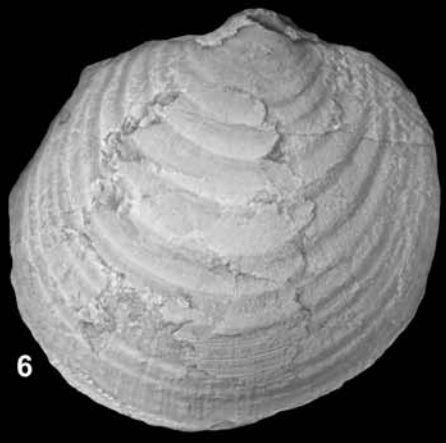
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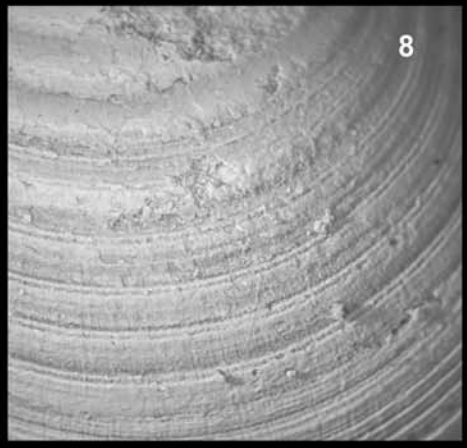
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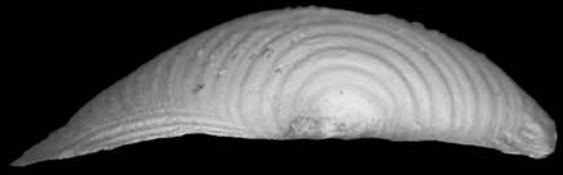
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