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## A glimpse into the Jurassic gastropods of the shallow sea with description of Mid-Jurassic species of Madagascar (Sakaraha) and their relation to species of similar age in Europe and elsewhere

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with 15 plates

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### Abstract

Mid-Jurassic gastropods which lived in shallow water near the shore of the tropical Tethys Ocean at Gondwana and here Madagascar closely resemble those which lived in a similar environment in Eurasia and here Middle Europe. Among them 6 species belong to the Archaeogastropoda and with exception of the Cirridae they are not distinct from still living groups. Cirridae have their embryonic whorl in a concavity formed by the dextral initial whorl of the teleoconch of *Hamusina* GEMMELLARO, 1878 which is represented by *Hamusina* cf. *maxwelli* BANDEL, 1993 that is close to a species from the Jurassic of New Zealand and also resembles *Sororcula costata* HAAS, 1953 from the Late Triassic of Peru. *Guidonia* DE STEFANI, 1880 is preserved with the shell structure. Here an inner nacre layer is connected to an outer crossed lamellar layer, both consisting of aragonite. The shell has similar shape with *Riselloidea perinianus* (ORBIGNY, 1853) from the Jurassic from Germany and France. *Ueckerconulus* sp. is close to species of *Ueckerconulus* GRÜNDEL, 2000 or *Proconulus* COSSMANN, 1918 from Jurassic of Middle Europe. *Eucycloidea madagascariensis* BANDEL, 2010 has a shell structure consisting of an outer complex prismatic layer and central layer of nacre covered by inner prismatic layers. *Eucycloidea* KOKEN, 1897 is related to *Eucycloscala* COSSMANN, 1895 with Triassic to Late Cretaceous species. *Anomphalus* sp. with round outline and smooth surface has a construction of the shell that is partly by nacre within the interior and of crossed lamellar layers on the outer side. It resembles modern *Umbonium* LINKE, 1807 of the family Umboniidae ADAMS & ADAMS, 1854 and also the Anomphalidae WENZ, 1948 based on Devonian and Carboniferous *Anomphalus* MEEK & WORTHEN, 1866, and it has similar Triassic species in St. Cassian Formation. Modern *Umbonium* has the shell of a thick inner layer of nacre and a solid outer layer of spherulitic irregular structure, which differs from the well organized crossed lamellar structure noted in case of the outer layer of *Anomphalus* of the Jurassic of Sakaraha. Thus similarity of modern *Umbonium* with Jurassic *Anomphalus* sp. may be due to convergence rather than being based on actual relation. *Crossostoma* MORRIS & LYCETT, 1851 with *Crossostoma* sp. from Sakaraha has its base ornamented by spiral ribs and resembles the Triassic *Frederikella* as well as modern members of the Liotiinae H. & A. ADAMS, 1854. The six members of the Archaeogastropoda from Sakaraha with

members of the Liotiinae H. & A. ADAMS, 1854. The six members of the Archaeogastropoda from Sakaraha with exception of *Hamusina* could be placed within a taxon uniting living species, and the two species of *Anomphalus* and *Crossostoma* could be interpreted to belong to a group that exists since Devonian times and has become adapted to live in loose sediment. But since trochomorph Archaeogastropoda are represented since Ordovician times and convergent shell shapes have developed over and over again a placement near a modern family makes little sense.

Neritimorpha are few and have decreased in diversity compared to species of that relation from the Triassic. Species of *Neridomus* MORRIS & LYCETT, 1851 and *Oncochilus* ZITTEL, 1882 of the family Neridomidae belong to those Neritoidea and the species from Sakaraha have the internal walls of their shell dissolved and they differ from the living species by ornament of the shell of their plankton living larvae. Similar ornament is present among some members of the Triassic Neritimorpha. Shell composition of *Neridomus* sp. and *Oncochilus* sp. is like that present among living Neritidae.

Caenogastropoda (Taenioglossa) are represented by several groups. Among them Cerithioidea FLEMING, 1822 with *Cryptaulax sakarahensis* BANDEL, 2006 have a larval shell that resembles that of *Argyropeza* MELVILLE & STANDEN, 1901 living in the Pacific and that of the Triassic species of the Ladinulidae BANDEL 1992 with *Ladinula* BANDEL, 1992 and *Ampezzoscala* BANDEL, 1992 from St. Cassian Formation. The Jurassic Procerithiidae/Cryptaulacidae is also common in Europe. *Bigotella* COSSMANN, 1913 resembles *Rhabdocolpus* COSSMANN, 1906 from the Middle Jurassic of France and the Jurassic of New Zealand. A similar larval ornament is noted in case of *Rhynchocerithium* COSSMANN, 1906 from Europe and it is similar to *Juramelanoides madagascariensis* (BANDEL, 2006). *Maoraxis* BANDEL, GRÜNDEL & MAXWELL, 2000 from Jurassic of New Zealand had a development with planktotrophic stage, while *Maoraxis* sp. from Madagascar hatched from its egg as crawling young.

Littorinimorpha are represented by *Hudlestoniella* COSSMANN, 1909, *Palaeorissina* GRÜNDEL, 1999, *Canterburyella* BANDEL et al., 2000, *Mesostrombus* SCHRÖDER, 1995, *Sakarahella* BANDEL, 2006, and *Kalchreuthia* GRÜNDEL & NÜTZEL, 1998. *Hudlestoniella* sp. differs from *Palaeorissina madagascariensis* BANDEL, 2006 especially by the ornament of its larval shell. *Palaeorissina* with type from the Middle Jurassic of northern Germany is closer in shape to the Triassic *Settsassia* BANDEL, 1992 than to the living *Rissoa* DESMAREST, 1814 or *Rissina* ORBIGNY, 1840 and based on the morphology of its protoconch can be placed with Settsassiidae BANDEL, 1992. Among modern representatives of the Rissoidae no species is known in which the larval shell has axial ornament. Canterburyellidae BANDEL, GRÜNDEL & MAXWELL, 2009 resemble modern *Rissoa* regarding the teleoconch but have a protoconch with axial ornament. *Canterburyella pacifica* BANDEL et al., 2000 is from the Jurassic of New Zealand and a very similar species is known from the Valanginian of Poland. *Mesostrombus* SCHRÖDER, 1995 (= *Levipleura* GRÜNDEL & NÜTZEL, 1998) is based on a European Jurassic species and can be applied to describe the species from Madagascar with the larval shell of *Mesostrombus* sp. 1 and *Mesostrombus* sp. 2 differing from each other regarding the size of their larval shell as is the case in *Levipleura blainvillei* from North Germany and from South Germany. *Sakarahella* BANDEL, 2006 of the Sakarahellidae BANDEL, 2006 has a conical protoconch with several whorls and ornament of a ribbon below the suture consisting of short ribs and tubercles. *Kalchreuthia* sp. resembles a species from the Jurassic of Franconia, *Kalchreuthia frankei* (*Pseudomelania frankei* KUHN, 1939) which is one of the most common gastropods in the lower Jurassic of Kalchreuth in southern Germany. It has together with *Mesostrombus* been used by a Jurassic worm to construct *Lanice*-like agglutinated burrows in northern German Jurassic.

“*Opaliopsis*” sp. resembles larval shells as known from the Lower Cretaceous of Poland. *Opaliopsis* sp. is similar to the protoconch of *Tenuiscula* BOURY, 1887 from the Eocene of France and *Ecclesiogyra* DALL, 1892 from the Campanian of Mississippi. The Triassic *Ampezzopleura* BANDEL, 1991 from St. Cassian Formation together with *Protorcula* KITTL, 1894 is member of the Protorculidae BANDEL, 1991. The Zygopleuroidae include predominantly Triassic species and they may represent Ctenoglossa (= Ptenoglossa) of relation to the modern Ianthinoidea GRAY, 1853 (Epitonioidae) and Cerithiopsoidae A. & A. ADAMS, 1853. The ornament of the larval shell resembles that of *Protorcula* and *Ampezzopleura* from the Triassic and this characteristic ornament of its larval shell continued from Triassic through Jurassic time to modern times.

*Dicroloma* GABB, 1868 / *Pietteia* COSSMANN, 1904 / *Undoriptera* GUZHOV, 2014 protoconch consists of three smooth larval whorls and the last fourth is ornamented by axial rib and ends with a spine like projection at the base of the outer lip of the aperture. The development of the larval shell has a first phase of the embryonic shell with simple aperture, a second stage of early larval development with a larval shell with a strong lobe in its outer lip and the last stage with the third whorl when shell diameter increases and the lobe of the outer lip disappears and the pointed siphon appears as well as an umbilical pore. The protoconch has finally 4.5 rounded whorls, and is 1 mm high and 0.8 mm wide and a similar development was noted in case of species of modern *Strombus* LINNÉ, 1758.

Heterostropha - Heteroconchia GRAY, 1840 of the family Mathildidae DALL, 1889 with *Promathildia* ANDREAE, 1887 resembles other Jurassic species of *Teretrina* COSSMANN, 1902, *Turrithilda* SCHRÖDER 1995, *Jurida* GRÜNDEL, 1973. *Bandellina* sp. with small flatly coiled shell resembles living species of the family Vitrinellidae

(= Cornirostridae). Species with similar characters of their shell have been recognized from Devonian onward and *Bandellina* SCHROEDER, 1995 is based on *Bandellina laevis* SCHRÖDER, 1995 from the Valanginian of Poland that is almost identical with *Bandellina* sp with protoconch that has a sinistral mode of coiling which changes from distinctly left coil to plane coil and a rim distinguishes from the teleoconch. The teleoconch is dextral with rounded whorls almost plane spirally coiled, but widened aperture and open umbilicus. Its diameter is less than 1 mm. *Bandellina* sp. closely resembles *Alexogyra* BANDEL, 1996 with Triassic and several similar taxa from the Triassic and Jurassic of Central Europe are known which have been placed into the family Sturaxidae BANDEL, 1996. Members of the Cyndrobullinidae close to the genus *Cyndrobullina* AMMON, 1878 are difficult to classify since the species from Sakaraha is of variable shape. A ramp on its teleoconch whorls may be accompanied by one, two or three spiral lines and the shoulder may form a corner or be rounded. Growth lines are sinuous and may or may not be indistinct or distinct and almost rib-like. Since their appearance in the early Jurassic the *Acteon* - *Retusa* type of shell has changed little with whorls separated by a flattened ramp or deep suture elongate and oval and the protoconch axis forming an angle from 90° to less than about 45° with that of the teleoconch. *Sulcoactaeon* COSSMANN, 1895 with egg-shaped shell with short spire has a large body whorl that is sculptured by spirally arranged grooves and ridges. Its type from the Late Jurassic of France resembles *Sulcoactaeon* sp. from Sakaraha. The ornament of the teleoconch consists of strong, about equally wide spiral ribs which are separated from each other by narrower grooves. The groove next to the suture and below it is wider than the following ones and forms a narrow ramp. *Ceritelopsis* FISCHER, 1961 resembles in shape *Cyndrobullina*, but has a more elongate shell. *Ceritelopsis* sp. from Sakaraha is slender and has ornament of axial folds crossed by three spiral folds, in quite variable arrangement. The spire is almost as high as the body whorl. The first whorl is only partly covered by the first whorl of the teleoconch and about 0.07 mm wide.

## Zusammenfassung

Mitteljurassische Schnecken des flachen Meeres des tropischen Tethys-Ozeans im Bereich Madagaskars ähneln sehr jenen, die gleichzeitig in Eurasien – Mitteleuropa unter ähnlichen ökologischen Bedingungen lebten. Darunter befinden sich im Vorkommen von Sakaraha 6 Arten der Archaeogastropoda, die mit Ausnahme der Cirridae sich nicht wesentlich von heute noch lebenden Arten unterscheiden. Die Cirriden haben eine Embryonalschale die in einer Grube der rechtsgewundenen ersten Windung des Teleoconches liegt, wie bei *Hamusina* GEMMELLARO, 1878. Das ist sowohl bei einer Art des Juras von Neuseeland wie der oberen Trias von Peru der Fall, die beide *Hamusina* sp. aus Sakaraha ähneln. *Guidonia* sp. hat die aragonische Schalenstruktur ihrer Schale gut erhalten, mit einer inneren Perlmuttertschicht verbunden mit einer äußeren Kreuzlamellenschicht. Die Schale ähnelt der von *Riselloidea perinianus* (ORBIGNY, 1853) des mitteleuropäischen Juras. *Ueckerconulus* sp. von Sakaraha ähnelt den Arten der Gattung *Ueckerconulus* GRÜNDEL, 2000 oder *Proconulus* COSSMANN, 1918 des mitteleuropäischen Juras. Die Schale von *Eucycloidea madagascariensis* BANDEL, 2010 ist aus einer äußeren komplex prismatischen Schicht, einer mittleren Perlmuttertschicht und einer inneren prismatischen Schicht zusammengesetzt. *Eucycloidea* KOKEN, 1897 ist mit Arten von *Eucycloscala* COSSMANN, 1895 der Trias wie der späten Kreide vergleichbar. *Anomphalus* sp. von Sakaraha besitzt eine gerundete Gestalt mit glatter Oberfläche und ähnelt der heutigen *Umbonium* LINKE, 1807 der Umboniidae ADAMS & ADAMS, 1854. Allerdings unterscheidet die Schalenstruktur mit Perlmutter innen und Kreuzlamelle außen, während *Umbonium* außen eine prismatische Schalenschicht hat. Ähnliche Gestalt haben Anomphalidae WENZ, 1948 mit devonischen und karbonischen Arten und *Anomphalus* MEEK & WORTHEN, 1866 der triassischen St. Cassian Formation. *Crossostoma* MORRIS & LYCETT, 1851 mit *Crossostoma* sp. von Sakaraha ähnelt der triassischen *Frederikella* wie auch lebenden Arten der Liotiinae H. & A. ADAMS, 1854. Mit Ausnahme von *Hamusina* könnten alle Arten der Archaeogastropoda von Sakaraha in moderne Taxa eingefügt werden. Die beiden Arten von *Anomphalus* und *Crossostoma* könnten der Gruppe zugeordnet werden, die seit dem Devon Lockerböden besiedelten. Trochomorpha unter den Archaeogastropoda haben seit dem Ordovizium konvergente Schalenform und können damit nicht sicher zugeordnet werden.

Die wenig diversen Neritimorpha von Sakaraha zeigen sowohl Anklänge an triassische, wie heutige Arten und sind mit *Neridomus* MORRIS & LYCETT, 1851 und *Oncochilus* ZITTEL, 1882 der Neridomidae vertreten. Beide kleinwüchsigen Neritoidea haben die inneren Schalenwände aufgelöst. Die Arten von Sakaraha hatten eine sich im Plankton entwickelnde Larve mit charakteristischem Schalenornament wie es auch bei einigen Arten Triassischer Neritimorpha vorkommt. Die Schalenstruktur von *Neridomus* sp. und *Oncochilus* sp. ist wie bei rezenten Neritidae mit dünner äußere Kalzit-Lage und dickerer innerer Aragonit-Kreuzlamelle. Ähnliche Arten kommen im Jura Europas vor, sind aber wegen schlechter Schalen-Erhaltung nicht gut vergleichbar.

Caenogastropoda sind mit einigen Taenioglossa ursprünglicher Gruppen sowie Ctenoglossa und frühen Strombimorpha in Sakaraha vertreten. Von den Cerithioidea FLEMING, 1822 hat *Cryptaulax sakarahensis* BANDEL, 2006 eine Larvenschale, die sie sowohl mit pazifischen *Argyropeza* MELVILLE & STANDEN, 1901 wie auch der triassischen Arten der Ladinulidae BANDEL 1992 mit *Ladinula* BANDEL, 1992 und *Ampezzoscala* BANDEL 1992 der St. Cassian Formation in Verbindung bringen lässt. Ganz ähnliche Arten sind im Jura Mitteleuropas reich

vertreten. *Bigotella* COSSMANN, 1913 ähnelt *Rhabdocolpus* COSSMANN, 1906 des Mittleren Jura von Frankreich und von Neuseeland. Ähnliches Ornament der Larvenschale wie bei *Rhynchocerithium* COSSMANN, 1906 von Europa liegt auch bei *Juramelanoides madagascariensis* von Sakaraha vor. *Maoraxis* BANDEL, GRÜNDEL & MAXWELL, 2000 aus dem Jura von Neuseeland hatte eine planktotrophische Larve während *Maoraxis* sp. von Madagaskar kriechend schlüpfte.

Littorinimorpha unter den Taenioglossa sind mit *Hudlestoniella* COSSMANN, 1909, *Palaeorissina* GRÜNDEL, 1999, *Canterburyella* BANDEL et al., 2000, *Mesostrombus* SCHRÖDER, 1995, *Sakarahella* BANDEL, 2006 und *Kalchreuthia* GRÜNDEL & NÜTZEL, 1998 in Sakaraha vertreten. *Hudlestoniella* sp. unterscheidet sich von *Palaeorissina madagascariensis* BANDEL, 2006 vornehmlich durch das Muster der Larvenschale. *Palaeorissina* basiert auf einer mittelljurassischen Art von Nord-Deutschland und ist der triassischen *Settsassia* BANDEL, 1992 ähnlicher als den lebenden Vertretern von *Rissoa* DESMAREST, 1814 und *Rissoina* ORBIGNY, 1840, die sich von den jurassischen Arten hinsichtlich ihrer Larvalen-Schalen-Ornamente unterscheiden. Die Gestalt des Protoconchs stellt sie eher in die Nähe der Settsassiidae BANDEL, 1992. Canterburyellidae BANDEL, GRÜNDEL & MAXWELL, 2009 haben ebenfalls ein larvales Rippenmuster während die ausgewachsene Schale jener einer modernen *Rissoa* ähnelt. *Canterburyella pacifica* BANDEL et al., 2000 aus dem Jura Neuseelands ähnelt Arten wie sie aus dem Valanginium Polens beschrieben wurden. *Mesostrombus* SCHRÖDER, 1995 mit europäischem Typus ähnelt den Arten von Madagaskar, wobei *Mesostrombus* sp. 1 und *Mesostrombus* sp. 2 sich hinsichtlich der Größe ihrer Larvenschale unterscheiden. Sie entsprechen etwas den Varianten von *Levipleura blainvillei* aus Norddeutschland und jenen aus Süddeutschland. *Sakarahella* BANDEL, 2006 der Sakarahellidae BANDEL, 2006 hat ein charakteristisches Muster der Larvenschale mit Spiral-Reifen unter der Suture. *Kalchreuthia* sp. ähnelt der häufigsten Art aus Franken *Kalchreuthia frankei* (*Pseudomelania frankei* KUHN, 1939) und die Art wurde zusammen mit *Mesostrombus* im Jura vom Norddeutschland zum Bau *Lanice*-ähnlicher Wohnröhren genutzt.

“*Opaliopsis*” sp. von Sakaraha ähnelt Larvenschalen wie sie aus der Unterkreide Polens bekannt sind, wie auch aus dem Eozän Frankreichs wie dem Campan von Mississippi. Die triassische *Ampezzopleura* BANDEL, 1991 der St. Cassian Formation wie auch *Protorcula* KITTL, 1894 gehören zu den Protorculidae BANDEL, 1991 und diese sind wohl Ctenoglossa der Verwandtschaft der heutigen Ianthinoidea GRAY, 1853 (Epitoniioidea) und Cerithioidea A. & A. ADAMS, 1853. Das Muster der Larvenschale wie bei *Protorcula* und *Ampezzopleura* der Trias verbindet jurassische Arten mit denen von heute. Die Jugendschale aus Sakaraha die *Dicroloma* GABB, 1868 / *Piettea* COSSMANN, 1904 / *Undoriptera* GUZHOV, 2014 zugeordnet werden kann, hat den Protoconch mit drei glatten larvalen Windungen und eine vierte Windung mit axialen Rippen und einem Mündungsvorsprung. Eine Entwicklung von einfacher Embryonalschale zu Larvenschale mit starkem Mündungsvorsprung und in der letzten Windung mit Siphon ähnelt der Entwicklung die bei Arten der heutigen Gattung *Strombus* LINNÉ, 1758 im Lebensabschnitt der Larve zu beobachten ist.

Heterostropha mit Wechsel im Windungssinn der Schale von links auf rechts während des Endes der Larvenphase sind mit Mathildidae DALL, 1889, Vitrinellidae und einfachen Opisthobranchia in Sakaraha vertreten. Die Art der Gattung *Promathildia* ANDREAE, 1887 ähnelt hierbei anderen jurassischen Arten von *Teretrina* COSSMANN, 1902, *Turrithilda* SCHRÖDER 1995, und *Jurida* GRÜNDEL, 1973 aus Jura und Trias Europas. *Bandellina* sp. mit kleiner flacher Schale ähneln lebenden Vitrinellidae (= Cornirostridae) sowie devonischen Arten und besonders *Bandellina* SCHROEDER, 1995 mit Typus aus dem Valanginium von Polen. *Bandellina* sp. aus Sakaraha hat den flach links gewundenen Protoconch mit verdickter Mündung. Er geht in die flach rechts gewundene adulte Schale über, die sowohl der heutigen Süßwasserschnecke *Gyraulus* als auch der triassischen *Alexogyra* BANDEL, 1996 wie anderen ähnlichen Arten aus Trias und Jura Europas ähnelt und der Family Sturaxidae BANDEL, 1996 zugeordnet werden kann. Allerdings ist die systematische Zuordnung problematisch, da *Gyraulus* auch schon seit Jura existiert und den pulmonaten Stylommatophora zuzuordnen ist.

Cylindrobullinidae mit Gestalt wie *Cylindrobullina* AMMON, 1878 mit triassischem Typus lassen sich nur schwer einer bestimmten Art zuordnen. Auch die Art aus Sakaraha hat eine variable Schalengestalt und mehrere Arten, ja sogar Gattungen aus dem Jura Europas könnten zur Bestimmung herangezogen werden. Die Gruppe ist seit dem Beginn der Trias mit Arten sehr ähnlicher Gestalt vertreten und sie kann auch heute noch bei der ähnlichen *Retusa* innerhalb einer Art variabel sein. *Cylindrobullina* sp. hat den Protoconch links gewunden und dem Teleoconch mit einem fast rechten Winkel aufgesetzt. Die ausgewachsene Schale hat eine apikale Rampe, deren Gestalt und Ornament ebenfalls variabel ausfallen kann. Heute lebende Vertreter mit ähnlicher Schale sind zudem sehr unterschiedlichen Gruppen der Heterostropha zuzuordnen. Bei *Sulcoactaeon* COSSMANN, 1895 ist die Ei-förmige Schale kurz und die erweiterte Endwindung trägt ein Ornament aus spiralig angeordneten Gruben und Rippen. Die Art *Sulcoactaeon* sp. von Sakaraha ähnelt sehr der Typus-Art aus dem oberen Jura Frankreichs und bei ihr ist die Grube unterhalb der Suture ebenfalls breiter als folgende Furchen und es besteht eine schmale apikale Rampe. *Ceritellopsis* FISCHER, 1961 ähnelt hinsichtlich ihrer Schalen-Gestalt *Cylindrobullina*, hat im Falle von *Ceritellopsis* sp. von Sakaraha eine schlankere Gestalt, einen fast im rechts gewundenen adulten Gehäuse verborgenen linksgewundenen Protoconch und spiralige Falten als Ornament. Diverse Individuen sind ebenfalls variabel und gleichen in dieser Hinsicht den europäischen Vertretern der Gattung von verschiedenen Lokalitäten und lebten Übergangsbereich vom Meer zum Süßwasser.

Bei den Heterostropha von Sakaraha ist keine Art dabei, die man nicht mit einem Art-Namen einer europäischen Art etwa gleichen Alters versehen könnte.

## 1 Introduction

Gastropods from the Mid Jurassic of Madagascar are encountered in soft sediments which were deposited in shallow water not far from the margin of the sea. In a general way species composing this fauna resemble gastropods which have been described from similar sediments and similar paleoenvironment and age from Germany. During the Jurassic Germany and Madagascar were close to the margin of the same large tropical Tethys-Ocean but on different sides of it and several thousand kilometers apart. Madagascar with Sakaraha at that time lay on the shore of African Gondwana south of the equator and Germany with Franken especially as described by NÜTZEL & GRÜNDEL (2015) from similar depositional environment had a position near to the Tethys north of the equator. A small fauna from New Zealand of similar age (BANDEL et al., 2000) can be compared as well. The climate in both regions of deposition can have been similar, as were the condition of deposition. Gastropods encountered thus have lived quite far from each other geographically on both sides of the large uniting ocean of the time – the Tethys.

## 2 Geological setting

The locality in which the fossils have been collected lies next to the road from Toliara to Sakaraha only about one km west of the town boundary of Sakaraha and about 100 km from Toliara in the south-west of Madagascar. Near the road two low flat topped hills were cut on their flanks by people during the construction of one of the large graves which are so characteristic for this region of Madagascar. The upper of these hills (closer to Sakaraha) lies above a soft sandstone and it contained the layers that holds the gastropods. They are present in discontinuous intercalations of a few cm in thickness of shell bearing sandy marl in fine silt and carbonate bearing clay-stone (marl). The fossil bearing layers are exposed in the slope of the hill only about 2 m below the flattened hill top. In the shell bearing layers as well as below in the sandstone bed some layers hold pebbles which in part have been utilized by oysters as base for attachment, as found nowadays on beaches within the uppermost intertidal zone in Madagascar. These pebbles do not form conglomeratic beds but only a few are present, as is the case on a sandy beach close to the mouth of a small stream that carries pebbles in its central canal to the sea. They are then carried along by the current and are strewn on the sandy beach. This indicates that the original depositional site had its place in the shallow sea rather close to beach environment.

The shell bearing deposits formed in the Morondava Basin, which is the southern one of the sedimentary basins on the western half of Madagascar. The basins originated when Madagascar was still an integral part of the Gondwana continent and represented the southern portion of the supercontinent Pangea. During Late Paleozoic time a rift valley formed. In it tillites, red beds follow and even a marine limestone of the Permian Sakoa Group (BESAIRIE, 1972) were deposited. After a hiatus of sedimentation, deposition resumed during the Late Permian and Early Triassic and the beds of the Sakamena group formed which were mainly deposited under continental conditions. During the Toarcian of the early Jurassic, around 180 Million years ago, the sea invaded from N to S and reached the Morondava Basin in the late Toarcian (BESAIRIE, 1972). The sea transgressed over eroded faulted blocks between several kilometers to some tens of kilometers wide and limited by NNE - SSW faults (MONTENAT et al., 1996). After the short regressive period during the Aalenian, the first widespread transgression with shallow, open marine deposits in the Morondava Basin is observed during Bajocian times; again followed by a period of continental sedimentation attributed to the Bathonian (LUGER et al., 1994). The partly fluvial sediments of this fan are composed of coarse grains coming from the east into the area of Sakaraha ("série d' Ankazoabo" of BESAIRIE, 1972) and contain layers bearing the gem stones sapphires which have resulted in a "gem rush" that left strong imprints in the character of the town of Sakaraha.

LUGER et al. (1994) recorded near Sakaraha an interval of approximately 70 m attributed to the upper Isalo Group by BESAIRIE (1972) and representing the marine Bajocian in the southern Morondava Basin. This interval "série de Sakaraha" of BESAIRIE (1972) just west of Sakaraha is a marine unit that is overlain by about 350 m of continental sandstone, which constitutes the uppermost part of the Isalo Group ("série d' Ankazoabo"). The continental sediments in turn are overlain by open marine deposits of Early Callovian age as dated by the occurrence of *Macrocephalites* spp. (BESAIRIE, 1972; LUGER et al., 1994). The early Callovian transgression corresponds to the onset of the drift phase between Africa and Madagascar. At this stage Madagascar was still the western portion of a large continent composed of what is now India, Australia and Antarctica as well. The southward drift of Madagascar and the opening of the Mozambique Channel has been determined to have occurred during the Middle Jurassic at about 165 Million years ago (COFFIN & RABINOWITZ, 1987, 1992).

From the Callovian onwards pelagic fauna became more prominent and the type of deposition continued into the Late Jurassic, locally to Valanginian and early Hauterivian deposits. All, Jurassic and Early Cretaceous are unconformably overlain by coarse Aptian sediments (BESAIRIE, 1972, LUGER et al., 1984). In the region just west of Sakaraha Aptian–Albian marine conglomerates and fossil bearing marine beds overlie Late Jurassic marls and clay stones forming a well visible steepening in the escarpment. Above Cenomanian sandstone, Turonian and Campanian marine deposits intercalated with widespread basaltic flows are observed in many parts of the Morondava Basin, as for example the area west of Sakaraha.

### 3 About the gastropods

Jurassic gastropods from Europe have attracted attention of quite a number of people since the times of QUENSTEDT (1852–1884) and have systematically been reevaluated by WENZ (1941) and WENZ & ZILCH (1960). The fauna has attracted especially the attention of GRÜNDEL since 1973 and by this author also jointly with several coauthors up to the times in which this paper has been compiled. Taxonomy of Jurassic species has not become less complicated during this process. Comparison with juvenile stages of Jurassic gastropods from Germany can be carried out with the study of SCHRÖDER (1995) in which many illustrations are presented. In regard to the larger systematic units of the gastropods treated here classification is not resolved in all cases and placement of genera and species will probably change in the future in several cases. The 25 species recognized here from that small locality near Sakaraha represent a rather characteristic spectrum though of soft substrate dwelling gastropods of the Mid-Jurassic time.

Archaeogastropoda with exception of the Cirridae are not distinct from still living groups and 6 species were recognized, but species with slit bearing shells are not included, but were common at the time. Neritimorpha are few and have decreased in diversity compared to species of that relation from the Triassic. But this may be an artifact, since we have very little information in regard to reef living faunas in the Jurassic.

Caenogastropoda of the Jurassic are quite diverse but still without the Neogastropoda and also relatives of *Cypraea*, *Tonna*, *Natica*, *Crepidula* had not developed as yet. One species connects with the Stromboidea and represents a member of the Aporrhaidae. Several of the Caenogastropoda from Sakaraha had relatives in the Triassic and some have still living relation. The taxonomy of the ten recognized species is confusing. Since in the environment of the locality near Sakaraha no sponges were living, Ctenoglossa are represented only by shells of some juvenile individuals.

The Heterostropha (Heterobranchia) are represented by Mathildoidea connecting to the diverse Triassic species and the less diverse modern ones. Species with a small plane shell can be connected with the Paleozoic to the modern marine Valvatoidea. The ancestral Opisthobranchia of the *Acteon-Retusa* type has produced an inflation of names surrounding the genus *Cylindrobullina*.

#### 3.1 Archaeogastropoda

Representatives of the subclass Archaeogastropoda THIELE, 1925, and here the order Vetigastropoda SALVINI-PLAWEN, 1980, the Trochomorpha NAEF, 1911 are represented by a species of the super family Cirroidea COSSMANN, 1916, one of the Eucycloidea KOKEN, 1897 and 4 species of Trochoidea RAFINESQUE, 1815. The diagnosis presented for the Trochoidea by HICKMAN & MCLEAN (1990) regarding the shell is similar to that of the Trochomorpha. Species belonging here usually have a shell without slit, or holes which could serve for water exchange. Usually the diameter of the whorls increases regularly during shell growth and shape of the shell is mostly conical. Often shell base has an umbilicus and the aperture is of rounded outline. Some important characters of species of the Trochoidea regard the anatomy and body construction, as well as presence or absence of a calcified operculum, and the construction and organization of its teeth in the rows of the radula. In fossil shells these characters are usually not preserved. Classification of fossil Archaeogastropoda can thus rely only on features of the shell and on comparison with shell characters found in living species. Species of the living fauna can thus only be used as base to a model of classification in regard to the fossil representatives of the Trochomorpha. Since Archaeogastropoda have only an embryonic shell and no larval shell, the character of the early ontogenetic shell provides fewer data which are useful for taxonomy than present in case in many higher gastropods, which may be provided with a larval shell.

The six members of the Archaeogastropoda from Sakaraha represent species of which one group is nowadays extinct with the characteristic *Hamusina*. Two species could be interpreted to represent members of the Trochoidea (*Guidonia* and *Ueckerconulus*) which have many species in the extant fauna. One species belongs to the Eucycloidea with many species of Mesozoic origin and with a less diverse representation among the living representatives (*Eucycloidea*). Two species could be members of an ancient group of the Anomphalidae (*Anomphalus* and *Crossostoma*) which since Devonian times have become adapted to live in loose sediment.

Trochomorph Archaeogastropoda are represented since Ordovician times with many species often with quite similar shell shapes and genera with convergent shell may have developed over and over again, which makes a placing of fossil species from the Jurassic in any taxonomic group connected to doubts. Within this group of gastropods a larval shell is not available as additional help in placing species into a certain group, as is of use among the Neritimorpha and Caenogastropoda, and lesser extent also the Heterostrophina.

The **Cirroidea** represent trochomorph Archaeogastropoda with the shell coiled to the left (coiled in sinistral mode) and with nacreous inner shell layer. Their protoconch is a plane early portion of the shell. Here a dextral embryonic shell grades into a plane spiral whorl and is later succeeded by a left coiled teleoconch. The aperture may have an uninterrupted outer lip (Cirridae COSSMANN, 1916) or a labial slit (Porcellidae BROILI, 1924) (BANDEL, 1993; FRYDA, 1997; FRYDA & BLODGETT, 1998; BANDEL & FRYDA, 2004). Species belonging to the Cirroidea (= Porcelloidea) lived during much of the Paleozoic and have become extinct by the end of the Cretaceous. Earliest species have been recognized in the Silurian (FRYDA, 1997) and last species lived near the end of the Cretaceous (BANDEL, 1993; KIEL & BANDEL, 2001, 2002).

The family Cirridae or Platyacridae WENZ, 1938 = Hesperocirridae HAAS, 1953 is recognized among Mesozoic species. The embryonic whorl lies in a concavity formed by the dextral initial whorl of the teleoconch which changes into left coiling mode and is ornamented by a dense pattern of axial ribs. Among representatives of the group members of the genus *Hamusina* GEMMELLARO, 1878 have a high conical shell that is without open umbilicus and has flattened whorl flanks with a basal angular peripheral carina as corner. The ornament consists of nodes and spiral threads connected to oblique growth lines. The aperture is angular to rounded (BANDEL, 1993). The genotype is *Turbo berthelothi* ORBIGNY, 1850 from the Late Liassic of France.

Species *Hamusina* cf. *maxwelli* BANDEL, 1993 (Pl. 1/1–2) from the Jurassic of Sakaraha has the shell of conical outline with about 15 ribs seen on the first dextral whorl of the teleoconch. Ribs are only slightly inclined. With 3 whorls the shell measures 1.5 mm in width and is about 1 mm in height. The embryonic shell is largely covered by the following whorl and measures approximately 0.15 mm in width. It is embraced by the succeeding whorl that is coiled in one plane. This first whorl of the teleoconch is rounded and ornamented with axial ribs. Dextral coiling changes into plane and then left handed coiling in the second whorl of the teleoconch and here sides of the whorls become flattened. A corner is developed here between inclined flanks and rounded base. Ribs are transected by fine revolving striation. The base is flattened and the spindle is massive. Outline of the aperture is nearly angular and its orientation is strongly oblique.

**Discussion:** *Hamusina* cf. *maxwelli* closely resembles the species from the Jurassic of New Zealand (BANDEL et al., 2000, pl. 2, figs 1–6). It is unknown to which size the shell of this species actually grew, but the many specimens studied from New Zealand individuals were not larger than 3 mm and composed of 5 whorls only. In comparison to the European members of *Hamusina*, *Hamusina maxwelli* is very small. It resembles *Sororcula costata* HAAS, 1953 from the Late Triassic of Peru, but the latter has an open umbilicus (BANDEL, 1994). The individual from Sakaraha is a part of the formerly conical teleoconch, and represents only the juvenile shell of the individual.

The genus **Guidonia** DE STEFANI, 1880, is represented by *Guidonia* sp. (Pl. 1/3–8). The shell has a low spire and ends in a corner and a second corner lies at the base of the flattened sides. The base is ornamented by spiral ribs and the umbilicus is narrow. The species from the Mid Jurassic of Madagascar documents that shell structure consists of a thick layer of nacre on the inner side of the shell and an outer layer with structure of acicular biocrystals composed of aragonite and arranged in crossed lamellar orientation (Pl. 1/6).

The early teleoconch that succeeds the protoconch is rounded, trochospiral and smooth. The shell is wider than high, broadly *Trochus*-like in shape with wide open umbilicus and apical angle of approximately 100°. The embryonic whorl measures approximately 0.2 mm and is smooth and evenly rounded, ending with a straight margin (Pl. 1/7–8). The juvenile teleoconch is lowly trochospiral with whorls provided by a flattened apical side ending in a corner and it carries several strong spiral ribs on the side. This first lowly coiled rounded whorl of the teleoconch has low spiral ribs which appear on the first whorl. Four spiral ribs have flattened areas between them. Two of the spiral ribs become covered by the succeeding whorl. The uppermost keel-like rib lies next to the suture, the second one is the corner to the inclined side, the third rib represents the corner to the base and lies in the suture and is just covered by the following whorl and the fourth keel-like rib surrounds the conical and wide umbilicus. The interspaces of the spiral ribs are flattened and slightly concave.

22 broad and low axial ribs are on the body whorl and cross the upper two spiral ribs forming nodes at intersection with them. The base is ornamented by 7 spiral ribs. The axial ribs in the large funnel like umbilicus reappear on the upper side of the shell and continue into the open umbilical hole, in which all earlier whorls are visible.

With 4.3 whorls *Guidonia* sp. measures 4.5 mm in width and 3.5 mm in height. Axial ribs appear on the third whorl and the umbilicus is surrounded by a spiral keel. Up to eight whorls may be developed and the shell is mostly wider than high. The stair-case profile shows a comparatively large body whorl and a low or depressed spire. The convex base bears a funnel shaped umbilicus that is encircled by a ridge. The apical and lateral bands of the whorl are more or less concave. The aperture is nearly pentagonal in outline with the inner lip thickened and

forms the inner margin of the umbilicus. Transverse ornamentation consists of growth lines that run obliquely backward.

**Discussion:** *Guidonia* resembles the shell of a juvenile *Cittarium* PHILIPPI, 1847 as lives in the Caribbean Sea (BANDEL & WEDLER, 1987). *Guidonia tricostata* GRÜNDEL, 2000 from the German Jurassic is similar (GRÜNDEL, 2003, pl. 2, figs 5–6). The genus *Guidonia* DI STEFANI, 1880 has the type species *Trochus rotellus* STOLICZKA, 1861 from the Early Jurassic of the Northern Alps (as defined by HAAS, 1953). HAAS (1953) suggested a similarity of *Guidonia* with *Trochonema* SALTER, 1859 from the Ordovician. While the shell of *Trochonema* is unknown in its original composition that of Jurassic *Guidonia* has a structure characteristic to most Vetigastropoda with a thick nacreous layer, as is documented here in case of *Guidonia* sp.

GRÜNDEL (2000, 2003) suggested a place for the genus *Guidonia* among the Nododelphinulinae COX, 1960 of the Turbinidae RAFINESQUE, 1815, while GRÜNDEL (2004) preferred to place it among the Liotiinae ADAMS & ADAMS, 1856. While the first taxon was interpreted to be based on a fossil genus, the second has a type among genera with living representatives. The change in opinion regarding the place of *Guidonia* in the system of the Archaeogastropoda was not explained. A smooth species with the shape of *Guidonia* was suggested to represent *Chartronella* (*Tubertrionella*) GRÜNDEL, 2000 (= *Chartrionella*) from the Mid Jurassic of NE Germany (GRÜNDEL, 2003, pl. 5, figs 9–10) and to be placed in the Paraturbinidae COSSMANN, 1916 as had also been suggested for *Chartrionella* by WENZ (1938, fig. 540). A similar species with smooth but more rounded shell was determined as *Angulataphrus dieteli* GRÜNDEL, 2003 and placed to the subfamily Ataphrinae COSSMANN, 1918 of the Colloniidae (GRÜNDEL, 2007, pl. 3, figs 8–11) which are based on a type species from the Eocene. *Angulataphrus* resembles *Triangaphrus* with the type species *Triangaphrus liassicus* from southern Germany (GRÜNDEL, 2003, pl. 3, figs 7–9, pl. 4, figs 1–2), but the later was assumed to belong to the Helicocryptinae COX, 1960. This later taxon is based on *Heliocryptus* ORBIGNY, 1850 which has the type species in the smooth flatly coiled *Heliocryptus dubius* (BUVIGNIER, 1852) from the late Jurassic of Switzerland. According to WENZ (1938, fig. 808) the type species of *Heliocryptus* is *Helix pusillus* (F.A. ROEMER) from the late Jurassic of France from which KNIGHT et al. (1960, fig. 172, 1a) appear to have copied the illustration. *Triangaphrus* was placed in the Colloniidae, Ataphrinae (GRÜNDEL, 2003, pl. 3, figs 7–9, figs 1–2) and it closely resembles the Late Cretaceous *Ataphrus* documented by DOCKERY (1993), but has the umbilicus open.

NÜTZEL & GRÜNDEL (2015) suggested a place of a gastropod with very similar shell shape to that of *Guidonia* sp. from Madagascar with *Riselloidea* COSSMANN, 1909. The same species with better preserved shell had been documented by SCHULBERT et al. (2009, figs 5, A, B) as *Amphitrochus subduplicatus* (ORBIGNY, 1850) from a clay-pit in Mistelgau of Toarcian age. NÜTZEL & GRÜNDEL, (2015, pl. 5A–F) determined *Trochus perinianus* ORBIGNY, 1853 as *Riselloidea periniana* and illustrated it with specimen found in Buttenheim. This species has a broadly *Trochus*-like shell with 3 whorls is 3.3 mm high and 3.5 mm wide and has step-like shape and ornament of axial ribs and spiral cords which form nodes at crossing. The base has an open umbilicus. They had shells without apical whorls preserved and suggested a resemblance with the type of *Riselloidea periniana* as re-illustrated by FISCHER & WEBER (1997) from the Pliensbachian of France. They illustrated a shell that has neither the protoconch nor the first two whorls of the teleoconch preserved, but the succeeding 1.5 whorls have the ornament very close to that of *Guidonia* sp. from Sakaraha. The argument that they followed BANDEL (2010) in the determination of their species from the lower Jurassic of Buttenheim does not fit, in case the early whorls of their species were like those in *Guidonia* sp. from Sakaraha.

This back and forth of interpretations in regard to the place these fossil Archaeogastropoda may have within the system of the Trochomorpha documents that actually the placement of these fossil species in a system based on the study of living species is difficult, if not impossible. Changing fossil species from one to the other family appears to be a matter of taste. A similar switching of taxonomy without further deeper reasons can be studied quite well when the classification that had been adopted by WENZ (1938) was transformed into that adopted by KNIGHT et al. (1960) in case of the Mesozoic species in question and these changes were carried out mostly without a corresponding change in the amount of available information.

Species *Ueckerconulus* sp. (Pl. 1/9–10) is close to *Ueckerconulus* GRÜNDEL, 2000 or *Proconulus* COSSMANN, 1918 as defined by GRÜNDEL (2000) from Jurassic. The conical shell of *Ueckerconulus* sp. has a flattened apical part and the first whorl of the teleoconch is ornamented by spiral ribs which may have nodes. The spiral ribs may be transected by rounded and weaker axial folds.

**Discussion:** The type species is *Ueckerconulus formosus* GRÜNDEL, 2000 from the Mid-Jurassic of NE Germany. The shell of *Ueckerconulus* is very similar to that of *Proconulus*, with the ornament of the first with more axial elements than the second. There may be only one corner to the base in *Ueckerconulus* GRÜNDEL, 2000 since the former corner lies within the suture. The corner may be just above the suture in *Proconulus* (GRÜNDEL, 2008, figs 3, 10–15) and also *Discotectus* FAVRE, 1913 is very similar (KIEL & BANDEL, 2001, pl. 3, figs 9, 12, 15). Here the groove in the base of the inner lip extends into a larger plate-like extension which is not present in *Proconulus* and *Ueckerconulus*. But such a character of the fully grown shell could not be studied from the juvenile shells present from Sakaraha.



*Ueckerconulus duplicans* BLAKE, 1905–1907 from Germany is similar (GRÜNDEL, 2000, pl. 5, figs 13–17, 18, pl. 6, fig. 1; 2003a, pl. 3, figs 9–10, pl. 4, fig. 1) to *Ueckerconulus monilitectus* (PHILLIPS, 1829) (GRÜNDEL, 2004, pl. 3, fig. 14, pl. 4, figs 1–3) and both are ornamented of spiral ribs consisting of rounded tubercles. KAIM (2004) placed a species with the early whorls ornamented by two strong spiral ribs with *Turcica* ADAMS & ADAMS, 1854 and here especially *Turcica clathrata* (LAHUSEN, 1883) as documented by him (KAIM, 2004, fig. 11B). It has a similar pointed apex with two strongly noded spiral ribs, but the first whorl of the teleoconch with axial ribs. This species comes from the Jurassic of Russia. The juvenile shell of a species determined as *Eucycloscala escheri* (MÜNSTER, 1844) by NÜTZEL & GRÜNDEL (2015, pl. 4, figs A–E) from the Jurassic of Kalchreuth in Franconia would also resemble the species from Sakaraha, but appears to have a larger angle of its spire. But in case of the species from Sakaraha neither determination as *Turcica* or as *Eucycloscala* COSSMANN, 1895 is fitting, since the early ornament of the teleoconch is not with axial ribs, which in case of members of both genera should be present (BANDEL, 2010).

The species *Eucycloidea madagascariensis* BANDEL, 2010 is based only on the first three whorls of the shell, and later stages of shell growth are unknown (Pl. 1/11–12, Pl. 2/1). The protoconch consists of a rounded whorl and measures 0.2 mm. First and second teleoconch whorls are ornamented with strong, rounded axial ribs. The first teleoconch whorl has about 20 such rounded axial ribs with the rounded interspaces covered by fine discontinuous wrinkles. The last whorl that is preserved has some spiral ribs making their appearance.

Shell structure consists of an outer complex prismatic structure that forms the base to the central nacre, which is organized in stacks. Behind the original marginal zone in which the nacre formed it became covered with a prismatic layer (BANDEL, 2010, figs 8 E–I). As is the case in modern species, nacre formed only in a narrow zone near the margin of the growing shell and further inwards nacre is covered by prismatic layers.

**Discussion:** The juvenile shell of *Eucycloidea madagascariensis* closely resembles that of *Eucycloidea verrucosa* GRÜNDEL, 2000, but has a somewhat narrower apical angle and no angle on the second and third whorl of the teleoconch. Early teleoconch whorls have axial ribs and a fine pattern of radial wrinkles and the protoconch is similar in both species. *Eucycloidea* KOKEN, 1897 (family Eucycloscalidae GRÜNDEL, 2007 including all fossil Triassic-Cretaceous species) is related to *Eucycloscala* COSSMANN, 1895 that is based on *Eucycloscala binodosa* (MÜNSTER, 1841) and several species from the same St. Cassian Formation. That connects to *Eucycloscala torulosa* BANDEL, GRÜNDEL & MAXWELL, 2000 and *Eucycloscala praetor* (GOLDFUSS, 1844) from the Jurassic, and *Eucycloscala cretacea* KIEL & BANDEL, 2001 from the Late Cretaceous (BANDEL, 2010).

*Eucycloidea granulata* (HÉBERT & EUDES-DESLONGCHAMPS, 1860) from the Jurassic of North Germany documents the juvenile shell (GRÜNDEL, 2000, pl. 3, figs 10–11) that preserves the change from the axially ribbed rounded early teleoconch to an angular conical shell, as does *Eucycloidea verrucosa* GRÜNDEL, 2000 that has its protoconch succeeded by rounded first whorls of the teleoconch with ornament of strong axial ribs (GRÜNDEL, 2000, pl. 3, figs 12–16). This early ontogenetic shell closely resembles that described by SCHRÖDER (1995, pl. 1, figs 12–14) who documented the central nacre layer as is also noted in case of *Eucycloidea madagascariensis* (BANDEL, 2010, figs 8 E–I).

Members of the *Eucycloscala* relation have a slender shell with keel on the sides of whorls and with a simple inner lip, whereas members of the *Eunemopsis* KITTL, 1891 relation have a ridge on inner lip, and those resembling *Sabrinella* BANDEL, 1993 have a small shell with strongly expressed adult aperture. All three are based on Triassic species as described by BANDEL (1993).

The species *Anomphalus* sp has the shell with round outline and smooth surface (Pl. 2/2–9, Pl. 3/1, 3/3). The umbilicus in fully grown shells is closed by shell deposits and it is open when the shell is not fully grown. Construction of the shell is partly by nacre within the interior and of crossed lamellar layers on the outer side. The sutures are distinct. The embryonic shell has the characteristic shape as in Archaeogastropoda in general.

Shell shape resembles that of modern *Umbonium* LINKE, 1807 of the family Umboniidae ADAMS & ADAMS, 1854 which may well merge with the family Anomphalidae WENZ, 1948 as was suggested by BANDEL (1993). Here the Devonian and Carboniferous *Anomphalus* MEEK & WORTHEN, 1866 is contained as well as *Anomphalus helicoides* (MÜNSTER, 1841) from Triassic St. Cassian Formation (BANDEL, 1993, pl. 5, figs 6–7, pl. 6, figs 1, 3, 4) and *Anomphalus* sp. from Sakaraha. *Anomphalus helicoides* consists of six whorls and is 15 mm wide and 9 mm high. The protoconch is 0.4 mm wide. The first five whorls have the umbilicus open and it is closed in the last whorls. The shell is here constructed of two aragonite layers, the outer of which is of crossed lamellar structure and the inner is nacre with the innermost consisting of irregular prismatic callus deposits.

**Discussion:** The Umboniidae ADAMS & ADAMS 1854 as assembled by WENZ (1938) unite species with lens-like depressed shape and glossy whorl surface sometimes with finely incised spiral lines. The umbilicus is filled by a callus that spreads on much of the base. The family is based on *Umbonium* LINK, 1807 with its type species in the Pacific. THIELE (1931) recognized the radula to have characters of the Trochoidea such as the arrangement of the teeth with five lateral pairs next to the central tooth. HICKMAN & MCLEAN (1990) and HERBERT (1992)

documented that the most important feature in distinguishing member of the Umboniidae is the shape of the central tooth and that of the five pairs of lateral teeth which have a sheet-like base.

Most members of modern Umboniidae are efficient borrowers (HERBERT, 1992) and prefer soft substrate, quite in contrast to most Archaeogastropoda. *Umbonium vestiarius* (LINNÉ, 1758) for example lives in the exit of the Velar Estuary in Tamil Nadu (southern India) and here occurs in huge numbers buried shallowly in sand filtering phytoplankton from outgoing lagoon water. Its radula was checked and fully fits with the data provided by HICKMAN & MCLEAN (1990, fig. 89C, fig. 91) also for shell and radula and mode of life (HICKMAN, 1984, 1985). FRETTER (1975) studied its very special filter feeding mode of life that allows *Umbonium* a life buried shallowly in sand, while most members of the Archaeogastropoda live on hard substrates and feed on organisms they scrape from them with the aid of the teeth of their radula. In case of modern *Umbonium* the shell consists of a thick inner layer of nacre and a solid outer layer of spherulitic irregular structure. This structure of the outer layer differs from the well organized crossed lamellar structure noted in case of *Anomphalus* of the Jurassic fossil bed of Sakaraha. Thus similarity of modern *Umbonium* with Jurassic *Anomphalus* sp. may be due to convergence rather than being based actual relation.

The genus *Crossostoma* MORRIS & LYCETT, 1851 can be recognized with *Crossostoma* sp. from Sakaraha that has its base ornamented by spiral ribs (Pl. 2/10, Pl. 3/2, 3/4–7). The shell of *Crossostoma* sp. is low and conical spiral with rounded whorls. Ornament consists of numerous spiral ribs and furrows. The base is rounded with distinct umbilicus and the circular aperture is inclined. The first whorl has a diameter of approximately 0.2 mm and first whorls are smooth until a diameter of 1.2 mm is reached. The outer layer of the shell has crossed needle structure and the inner consists of a callus cover and nacre forms the central layer (Pl. 3/2).

**Discussion:** *Crossostoma spirata* BANDEL, GRÜNDEL & MAXWELL, 2000 from the Jurassic of New Zealand has a wide conical shell with spiral and axial ornament. The base is flattened and ornament of the early teleoconch differs from that of the later teleoconch. With five whorls the shell *Crossostoma spirata* is 9.5 mm wide and 5.5 mm high. The callus of the inner lip is expanded into the umbilical depression and is of half-moon-shape with a groove. In case of *Crossostoma* sp. from Sakaraha the first whorl of the teleoconch is rounded and ornament of fine spiral ribs begins abruptly on the shell after half a whorl of the teleoconch has succeeded the protoconch. In that regard it resembles *Spiratoconulus* GRÜNDEL, 2000, but the type of the genus, *Spiratoconulus latus* GRÜNDEL, 2000 (pl. 6, figs 13–15) has much higher conical shape as is the case in *Crossostoma* sp.

*Crossostoma* has the type *Delphinula (Crossostoma) pratti* MORRIS & LYCETT, 1951 which was described in detail by GRÜNDEL (1997, pl. 2, figs 5–7, pl. 8, fig 13) and its round shell is similar to that of *Umbonium*. The protoconch has the characteristic of the Archaeogastropoda and the shell is thick, turbinata and depressed. The genus was utilized to create the family Crossostomidae COX, 1960. Here species such as *Crossostoma globulifera* BANDEL, GRÜNDEL & MAXWELL, 2000 and *Crossostoma spirata* BANDEL, GRÜNDEL & MAXWELL, 2000 were described from the Jurassic of New Zealand and *Crossostoma pratti* MORRIS & LYCETT, 1851 is from the Jurassic of England and France.

*Frederikella* BANDEL, 1993 from St. Cassian Formation as documented by BANDEL (1993, pl. 2, figs 2–4) is a lowly trochospiral species with rounded aperture and wide deep umbilicus and ornament of fine spiral lines. This genus based on *Frederikella cancellata* (ZARDINI, 1978) in contrast to *Crossostoma* sp. from the Jurassic of Sakaraha has spiral grooves and ribs appear close to the protoconch. *Crossostoma* sp. (*Frederikella* sp.) is thus close to a Triassic species and can also be set in relation to modern members of the Liotiinae as were documented by HICKMAN & MCLEAN (1990). KAIM (2004, figs 15–16) described Jurassic species determined as *Striatoconulus* and *Crossostoma* suggesting only a status as belonging to an uncertain group of Archaeogastropoda close in shape to some living Trochidae. GRÜNDEL (2007, pl. 5, figs 2–4) found similar shell shape also in *Ataphrus* exemplified in case of *Ataphrus naricopsiformis* GRÜNDEL, 2007 from the Sinemurian of southern Germany, which is rather close to *Crossostoma* sp. from Sakaraha. GRÜNDEL (2008) suggested a relationship of the Proconulidae with the Ataphridae COSSMANN, 1918 as he defined them and suggested that both groups have a rounded apex, with the initial whorls forming a low spire and nearly plane shape, contrasting in regard to this character to members of the Eucyclidae KOKEN, 1897.

### 3.2 Neritimorpha (with the genera *Neridomus* and *Oncochilus*)

The two small representatives of the Neritimorpha GOLIKOV & STAROBOGATOV, 1975 with smooth shells from the Jurassic exposed close to Sakaraha town belong to the Oncochilinae BANDEL, 2007 and Neridomidae BANDEL, 2008 according to the classification adopted by BANDEL (2007, 2008) and both are members of the Neritoidea (Plates 4, 5 and 6). They have an about 0.6 mm wide protoconch of typical globular shape of Neritoidea and the internal walls of the shell have been dissolved. The teleoconch is constructed of a thin outer calcite layer with the color patterns included and most of the shell consists of one thick inner layer with structure of crossed lamellae composed of aragonite (Pl. 4/4–5; Pl. 5/6–8; BANDEL, 1990; 2007, fig. 14, L). In this regard the Jurassic species

resemble *Smaragdina* ISSEL, 1869, *Neritilia* MARTENS, 1879, *Neritina* LAMARCK, 1816 and *Septaria* FERUSSAC, 1807 and differs from *Nerita* LINNÉ, 1758 and *Neritopsis* both of which have a thick outer layer composed of calcite (BOGGILD, 1930). Members of the genus *Neritopsis* GRATELOUP, 1832 live in or near tropical reefs. Their adult shell is strongly ornamented while the embryonic and larval shells of the protoconch are smooth (BANDEL, 2001, 2002, 2007). Inner walls of the shell are not dissolved. Members of the Neritoidea, in contrast, dissolve the walls of the interior of their shell (WENZ, 1938). This character of dissolving the inner walls of the shell has evolved during the Triassic and is present in all living species of the Neritoidea which represent most species of living Neritimorpha. Neritariidae WENZ, 1938 and Neridomidae BANDEL, 2007 have axial ribs on their larval whorls (BANDEL, 2007) and have teeth on the inner side of the inner lip, and an operculum similar to that of *Neritina*. Among Triassic species Neritariinae, Oncochilinae BANDEL, 2007 and Trachynertariinae BANDEL, 2007 are recognized and here *Neritaria mandelslohi* (KLIPSTEIN, 1843) has an operculum that resembles that of modern *Nerita* or *Neritina*, but it is hinged into the shell obviously aided by a tooth or ridge on the inner side of the inner lip (BANDEL, 2008). The larval whorls of *Neritaria* are ornamented with axial and spiral lines which may form small tubercles where crossing each other, contrasting to the larval ornament recognized in case of the two species from Sakaraha.

*Neridomus* sp. and *Oncochilus* sp. of the family Neridomidae belong to those Neritoidea which have the internal walls of their shell dissolved (Pl. 4/7) and thus resemble most modern species regarding the mode of general construction of their shell. Species of extant Neritoidea have veliger larvae which carry a shell with similar shape, but without axial ornament of their larval whorls. Neridomidae are characterized by a round shell that has a smooth surface with simple shape of the inner lip of the aperture.

The genus *Neridomus* MORRIS & LYCETT, 1851 has its type species from the Middle Jurassic with globular shell and a simple smooth aperture (Pl. 4/1–8, Pl. 5/1, 5/5–6, Pl. 6/1, 6/3–6, 6/8; COSSMANN, 1925; BANDEL, 2008, pl. 3, figs 3–4). The inner lip has a callus pad and its edge against the aperture is convex and smooth or wavy. The callus ends before it reaches the base and the margin of the outer lip of the aperture. The outer layer of calcite is very thin and the thick inner aragonite layer consists of crossed lamellar structure with lamellae in one direction arranged according to the aperture. *Neridomus* sp. has a protoconch with almost three convolute whorls and a size of 0.6 mm, and the shape is globular with low axial ribs ornamenting its larval shell (Pl. 6/7–8). The inner walls of the shell become dissolved during shell growth starting during growth of the larval shell. *Neridomus* sp lived in a shallow marine environment probably representing an estuary (BANDEL, 2006).

The protoconch of *Neridomus* sp. from Sakaraha resembles that of *Gnazynium baumilleri* KAIM, 2004 from the Bathonian of Poland with a protoconch that consists of three whorls and has a diameter of almost 0.7 mm (KAIM, 2004, fig. 81). KAIM (2004) suggested that his specimen may represent a relative to the late Cretaceous *Thylacus* resembling that documented by DOCKERY (1993) and BANDEL & RIEDEL (1994), but it more likely is the juvenile shell of a Neritimorpha with protoconch resembling that of *Neridomus*, and comes from the Mid Jurassic of Poland. GRÜNDEL (2001, 2003) described *Neridomus esparcyensis* (COSSMANN, 1885) from the Bathonian of France, northern Germany and Poland with 3–4 mm wide shell consisting of about two whorls and protoconch not detected. It had not been determined whether the interior walls of the shell are dissolved.

**Discussion:** *Neridomus* has a protoconch shaped as in *Nerita*, but contrasting by the ornament of the larval shell. Here axial ribs are present, whereas *Nerita* has fine straight axial lines (BANDEL, 1982). The operculum resembles that of the Neritariidae WENZ, 1938 or Neritiniidae (Pl. 6/4, 6/6). *Neridomus* sp. from Madagascar is quite similar to *Neridomus mais* (BUVIGNIER, 1843) from the Oxfordian of Poland (GRÜNDEL & KAIM, 2006, fig. 11).

*Neridomus* has the genotype *Nerita haemisphaerica* MORRIS & LYCETT, 1851 from the Middle Jurassic of England. HUDDLESTON (1884, pl. 9, figs 4–6; 1894, pl. 28, figs 11–12) described *Neridomus tumidula* (PHILLIPS, 1829) which may be the same species as that considered as type (*Nerita hemisphaerica* ROEMER according to MORRIS & LYCETT, 1851) from the Middle Jurassic of England (WENZ, 1938, fig. 1008). It may also be the same or is a very similar to *Neridomus anglica* COX & ARKELL, 1950. *Neridomus mais* is with a 4.5 mm large shell of greater size than the individuals from Madagascar.

*Oncochilus* sp. has the shell rounded and smooth with the inner lip of the aperture with two characteristic rounded tubercles in its central part (Pl. 5/3–4). The spherical protoconch consists of more than two whorls with ornament of low indistinct axial ribs on the larval whorl. It measures about 0.6 mm in diameter, is round and smooth. The larval whorl covers most of the embryonic whorl (Pl. 5/2, Pl. 6/2). The teleoconch is known only from juvenile shells, and is only up to 1.5 mm in size. The inner lip of the aperture has the characteristic two large tubercles in its middle extending into the semicircular space limited on the other side by a simple rounded outer lip (Pl. 5/3–4). The callus of the inner lip is relatively thin and has only in the base a depression that represents the umbilical groove. The margin of the outer lip continues to limit this basal depression on its outer side. Shell structure is an outer calcite layer and a thick aragonite inner layer of crossed lamellar structure (Pl. 5/7–9).

**Discussion:** *Oncochilus* sp. differs from *Neridomus* sp. in regard to the slightly larger size and smoother shape of the protoconch and especially due to the presence of teeth on the inner lip of the teleoconch. General shape of the shell, ornament of the teleoconch and shell structure is quite similar in both species.

The Neritimorpha with a predominantly Jurassic to Cretaceous occurrence have besides the Neridomidae also the limpet-like Pileolidae BANDEL, GRÜNDEL & MAXWELL, 2000 and the *Nerita*-like representatives of *Otostoma* ARCHIAC, 1859. The rotelliform Deianiridae WENZ, 1938 as was documented by BANDEL & RIEDEL (1994) are exclusively of Cretaceous occurrence. Within the Neritidae, Cretaceous representatives of the modern *Nerita* LINNÉ, 1758 have also been documented (BANDEL & KIEL, 2003). Genera such as *Neritoptyx* OPPENHEIM, 1892 and *Neritoplica* OPPENHEIM, 1892 are seen as intermediating or ancestral to the Neritinae. *Mesoneritina* YEN, 1946 may relate to *Neritina* LAMARCK, 1816 as was assumed by BANDEL (2001) and BANDEL & KIEL (2003) and *Schwardtina* BANDEL & RIEDEL, 1994 may be related to the terrestrial Hydrocenidae TROSCHEL, 1856. Otostomidae BANDEL, 2008 (BANDEL, 2008, pl. 2, figs 13–15) with rounded shell and depressed spire are ornamented by axial ribs above the periphery and spiral and axial elements below it. The shell has a thick outer calcite layer and an inner aragonite layer of crossed-lamellar structure. The protoconch is globular with several whorls and ornamented by straight (orthocline) low axial ribs on its larval whorls. *Otostoma* ARCHIAC, 1859 lived during the Jurassic with type species *Otostoma rugosa* (HOENINGHAUS, 1865) from the Maastrichtian of Europe and Otostomidae are common in Late Cretaceous near-shore deposits of warm seas (SAUL & SQUIRES, 1997; BANDEL & KIEL, 2003). Their calcareous operculum resembles that of *Nerita* and *Neritina*, with a strong projection at the inner side next to the anterior inner lip. The nucleus on the outer side of the operculum is located at the lower side close to the inner margin (JAGT & KIEL, 2007, figs 1–2).

Within the Oncochilinae BANDEL, 2007 a large projection from the callus and a groove on base of the inner lip is noted in case of *Oncochilus* ZITTEL, 1882 with *Oncochilus subovatus* (MÜNSTER, 1841) from St. Cassian Formation and the Jurassic *Oncochilus* sp. from Madagascar have two projections of their inner lip of the aperture (BANDEL, 2007; plate 5, figs 4, 5). *Cassianpisulina* BANDEL, 2007 has only one angular projection into the aperture (BANDEL, 2007, fig. 14 A, B). WENZ (1938–1944, fig. 1010) based the genus *Oncochilus* on *Natica globulosa* KLIPSTEIN, 1843, which is the same as *Natica subovata* MÜNSTER, 1841 (KITTL, 1892) from St. Cassian Formation, Italian Alps. *Oncochilus* was called *Sphaerochilus* COSSMANN, 1898 and COSSMANN (1925) characterized it by a smooth round shell and two teeth on the inner lip. He suggested that species of this genus existed from the Triassic to the Turonian, all with two teeth on their inner lip (see BANDEL, 2007). The shell is smooth with *Nerita*-like shape with simple edge of the inner lip of the aperture. The inner lip carries no teeth or may have one or two teeth (PETHÖ, 1906). The type species, according to WENZ (1938, fig. 1010) is *Natica globulosa* (KLIPSTEIN) from the St. Cassian Formation, but may also be *Oncochilus chromatinus* ZITTEL as was described from the Tithonian of Stramberg.

*Mesoneritina* YEN, 1946 based on *Neritella nebrascensis* MEEK & HAYDEN, 1861 from the early Cretaceous of Nebraska, USA, according to YEN (1946), has a small shell with smooth whorls with irregular zigzag color patterns. The aperture is broadly oval in shape, the outer lip is thin, and the inner lip is nearly flat, well defined, thickened, and smooth, with a blunt and almost straight edge. BANDEL & KIEL (2003, pl. 3, figs 1–6) described *Mesoneritina ajkaensis* from the Ajka Coal Formation in the Csongárd, near Ajka (Bakony Mountains), Hungary. Its aperture has somewhat angular shape with narrow callus pad with a smooth and straight edge on the inner lip, and with a simple outer lip. The small smooth neritid lived within an estuarine environment of a river mouth and coastal swamp (BANDEL & RIEDEL, 1994). *Mesoneritina guimarotensis* BANDEL & KIEL, 2001 differs by having less rapidly expanding whorls and a concave edge of the inner lip. This species from the Late Jurassic of Portugal is globular in shape with small and globular *Neritina*-like shell consisting of the protoconch and about two smooth and well-rounded whorls of the teleoconch. Shells are about 4.5 mm wide and 4 mm high. *Mesoneritina* differs from *Neritina* by its smooth edge of the inner lip, while it bears here small teeth in case of *Neritina* (BANDEL & KIEL, 2003).

### 3.3 Caenogastropoda

Caenogastropoda, are developed with five groups, of which the Cerithimorpha are present with four species, the Littorinimorpha with 8 species with conical more or less ornamented larval shell, the Ampullospiridae with *Plesiotrochus*-like larval shell with raised margin and one species, the Ctenoglossa with one species and one early representative of the Strombimorpha. In this early Jurassic fauna clearly no representatives of the higher Caenogastropoda and the Neogastropoda have lived.

**Cerithimorpha** GOLIKOV & STAROBOGATOV, 1975, belonging to the super family Cerithioidea FLEMING, 1823 among the many species living nowadays in the sea have a plankton-living larva in the original course of their ontogeny (BANDEL, 1982). The transition from the larval shell is connected to a change in growth line pattern from sinuous to more even and a change of ornamental design. Thus several of the families which were distinguished

by their anatomy by HOUBRICK (1988, 1993) can also be recognized by characters of the ornament of their larval shell. BOUCHET & ROCROI (2005) used the term Cerithimorpha in connection to the interpretation of the taxon as was provided by HOUBRICK (1988).

The shell grown before begin of benthic life often consists of several, usually 3 and up to 6 whorls, connected to a small (around 0.1 mm wide) first embryonic whorl. The larva hatching from its egg usually consists of about one whorl that is ornamented by a fine groove and ridge pattern (BANDEL, 1975). The larval shell is provided with an anterior lobe on the outer lip. The pattern of ornament developed on the larval shell is usually characteristic for different larger units (families) (BANDEL, 2006) and most modern families of Cerithioidea can be characterized by their larval shell, in case the species involved has a planktotrophic larval stage in its ontogeny (BANDEL et al., 1997). The adult shell is commonly strongly ornamented, often has a short siphon at the aperture, and construction material of the shell is aragonite calcium-carbonate with composition of the biocrystals as crossed lamellar structure. The dominantly slender elongate teleoconch is usually ornamented by strong axial ribs which are crossed by weaker spiral ribs. It is often connected to a conical protoconch with dominant ornament of the whorls produced by the larva which often carries an ornament of two spiral ribs visible above the suture.

Among the Caenogastropoda of Sakaraha Jurassic four species belong to the Cerithimorpha and are represented by the genus *Cryptaulax* TATE, 1869 (*Procerithium*) with *Cryptaulax sakarahensis* BANDEL, 2006, genus *Juramelanoides* BANDEL, 1991 with *Juramelanoides madagascariensis* (BANDEL, 2006), genus *Maoraxis* BANDEL et al., 2000 and genus *Bigotella* COSSMANN, 1913 with *Bigotella* sp. (BANDEL, 2006, pl. 3, figs 1–7). Its larval shell resembles that of living species of members of the super family, especially that of *Argyropeza* MELVILLE & STANDEN, 1901 (BANDEL, 2006, pl. 3, figs 9–14).

***Cryptaulax*** TATE, 1869 is based on *Cerithium tortile* HÉBERT & EUDES-DESLONGCHAMPS, 1860 from the Mid-Jurassic of France. It was redefined by GRÜNDEL (1999) and he recognized it also from the Middle Jurassic of Germany. Its teleoconch is slender and the protoconch consists of several rounded whorls in which the larval shell is ornamented by two spiral ribs which may be tubercle bearing. The teleoconch is ornamented by axial ribs which may be arranged in an alternating screw-like pattern. The whorls are crossed by two primary spiral ribs. There may be more spiral lines present which form tubercles when crossing axial ribs. In the juvenile shell the base forms an angle with the sides and it is rounded in the adult shell. Commonly three spiral ribs ornament the base. The anterior notch of the aperture is indistinct.

*Cryptaulax sakarahensis* BANDEL, 2006 can also be determined as member of the genus *Procerithium* as well as of *Argyropeza* as has been discussed by BANDEL (2006). *Cryptaulax sakarahensis* has the larval shell composed of a smooth embryonic whorl that ends with the first growth line and is 0.06 mm in diameter (Pl. 7/8). It consists of a little less than one whorl and is ornamented with a very fine groove and ridge pattern. Curving growth lines are the only ornament of the first half of the larval shell, with spiral rows of tubercles appearing with begin of the second larval whorl, here three spiral ridges are present. In the fourth larval whorl only the lower of these spirals remains and forms the upper corner of a lobe in the outer lip of the aperture. The larval shell has its last whorl higher than the earlier whorls and transition to the teleoconch is abrupt (Pl. 7/3–4).

The teleoconch is of variable shape in regard to its ornament (Pl. 7/1–4, 7/6, 7/8). In case Pl. 7/1 ornament is of nodules below an apical ramp and spiral lines only on the base. Pl. 7/2 illustrates a shell with well developed axial ribs and indistinct spiral ribs. Pl. 7/3 with the protoconch seen in Pl. 7/5 illustrates an individual with two well developed spiral keels connecting the less developed axial ribs and forms pointed nodes with them, resembling those seen in the specimen shown in Pl. 7/1. Pl. 7/6 has the teleoconch with a very regular ornament of axial ribs which reflect the former outline of the outer lip of the aperture. Three distinct spiral ribs cross the axial ones on the visible part of the whorls and three more of such spirals are on the base. The illustrated individuals are morphologically interconnected with each other when more shells of the numerous individuals present from the locality and from the same layer are compared. Intermediate ornaments are developed among them. Individuals of *Cryptaulax sakarahensis* are very common and occur within the same narrow faunal layer at Sakaraha. Several of the varieties of this variable species could be described as distinct species, and all studied in detail have the same size and ornament of their larval shell. Preservation is very good and it consists of crossed lamellar structure as in case of *Maoraxis* sp. (Pl. 7/5).

**Discussion:** The larval shell of *Argyropeza* MELVILLE & STANDEN, 1901 (BANDEL, 2006, pl. 3, figs 1–14) as it lives in the Gulf of Aqaba resembles that of *Cryptaulax sakarahensis*. The teleoconch of *Cryptaulax sakarahensis* is as variable in shell shape as are some living species of *Cerithium* BRUGUIERE, 1789 as documented by HOUBRICK (1988, 1993), and as is confirmed by own data assembled from the species of different *Cerithium* living in the shallow water at the Gulf of Aqaba. Among Triassic species from St. Cassian Formation relation to the Procerithiidae/Cryptaulacidae of the Jurassic can be recognized among the Triassic Ladinulidae BANDEL, 1992. Here the conical shell has flattened whorls and in juvenile stage an angular, later a round aperture. Ornament consists of spiral and straight axial ribs. The protoconch is provided with an approximately 0.1 mm wide embryonic shell and an around 0.2 mm high larval shell. That larval shell has a projection of its outer lip and ornament of

spiral lines and rows of tubercles. The Ladinulidae with the name giving *Ladinula* BANDEL, 1992 and with *Ampezzoscala* BANDEL, 1992 have these larval characters developed well (BANDEL, 1992, 1993, 2006).

The genus *Procerithium* COSSMANN, 1902 with the Jurassic type species *Procerithium quinquegranosum* COSSMANN, 1902 from the Hettangian of France was restudied by GRÜNDEL (1997, pl. 5, figs 1–5) and he suggested that its protoconch may have only one spiral rib and adult ornament develops only within the early whorls of the teleoconch. Such larval shells with one spiral only on the larval whorls are documented to occur in case of two species of *Procerithium* from the Mid-Jurassic of Franken (SCHULBERT & NÜTZEL, 2009, figs 10–11). *Cryptaulax* TATE, 1869 and *Procerithium* are very similar to each other, as is also *Frankocerithium* NÜTZEL & GRÜNDEL, 2007. KAIM (2004) interpreted *Procerithium* as synonym of *Cryptaulax* and preferred to place both genera in the family Cerithiidae FERRUSAC, 1822. This taxon is based on a genus with type species of the living fauna. Among still living species *Argyropeza* MELVILLE & STANDEN, 1901 is close to *Procerithium* and the larval shell resemble those known from the Cretaceous (SCHRÖDER, 1995; BANDEL, 1993, 2006; KIEL & BANDEL, 2006; KAIM, 2004). Species from the Jurassic of Germany determined as *Procerithium* by SCHRÖDER (1995, pl. 3, fig. 16) were considered by KAIM (2004) as belonging to *Cryptaulax*, but on the other hand Kaim accepted the genera *Schroederium* KOWALKE, 1998 which is based on an Early Cretaceous species that closely resembles a *Cryptaulax*, and *Shurovites* GUZHOV, 2004 that also has the typical protoconch ornament. GRÜNDEL (2003, pl. 8, fig. 9–12) determined a *Procerithium?* *pupaeformis* (KOCH & DUNKER, 1837) and suggested it place in the Procerithiinae COSSMANN, 1902, while the more slender *Rhabdocolpus muricatum* (SOWERBY, 1825) and the very similar *Cryptaulax echinatus* (V. BUCH, 1831) from the same locality were placed with the Cryptaulacinae GRÜNDEL, 1976. But GRÜNDEL (2007, 2014) rejected a close relation to exist between *Procerithium* and *Cryptaulax* as had been suggested by BANDEL (2006) based on the fact that the type of the first lived during the Hettangian, while that of the second *Cryptaulax protortile* (COX, 1969), (= ?*Cryptaulax tortile*) lived within the Callovian and that the difference between *Procerithium* and *Cryptaulax* as has been discussed by GRÜNDEL (1976, 1997, 1999, and 2007) supposedly can be recognized in the ornament of the teleoconch. But that character, in case of *Cryptaulax sakarahensis* is extremely variable.

The genus *Bigotella* COSSMANN, 1913 is characterized by a slender tower-like shell with cornered whorls (Pl. 7/9). The protoconch consists of approximately 2 whorls which appear to be smooth. The whorls of the teleoconch initially have three, later five or more spiral ribs. Approximately 10 axial ribs are slightly curving ending in the sutures and on the fourth whorl of the teleoconch change into a row of curving ridges separated from spiral lines from a lower row of shorter ridges. The spiral lines cross the axial ribs. The apical row of ridges next to the suture increases in magnitude during shell growth. The base is convex, continuous with the sides and is ornamented by spiral lines. The shape of the ornament and shape of the whorls of the teleoconch change and ribs are in a somewhat screw like orientation on the shell. The aperture has a short anterior notch and the shape of the outer lip is not preserved.

*Bigotella* sp (Pl. 7/9) from Sakaraha could also be placed as species of *Rhabdocolpus* COSSMANN, 1906 or *Paracerithium* COSSMANN, 1902. *Rhabdocolpus* resembles *Bigotella* as documented by GRÜNDEL (2007, pl. 5, figs 3–8 and 17–20). It occurs in the Pliensbachian of France and has similar ornament consisting of coarse axial ribs crossed by finer spiral ribs on its early portion of the teleoconch.

**Discussion:** Even though *Bigotella* is only known by the shape of its teleoconch, and the protoconch is unknown, GRÜNDEL (2007) placed the genus with the Cryptaulacidae. This is so even though he stated that such a place in the system can only be determined when the larval shell is known, as GRÜNDEL (2007) formulated when he criticized the placement of *Procerithium* close to *Cryptaulax*, as was proposed by BANDEL (2006). *Bigotella* resembles the type of *Rhabdocolpus* that is *Melania scalariformis* DESHAYES, 1830–32 from the Middle Jurassic of Bayeux as figured by ETUDES-DESLONGCHAMPS (1842), WENZ (1938, fig. 2103), COSSMANN (1913, pl. 3, figs 101–102). *Rhabdocolpus* can be quite variable in shape (GRÜNDEL, 1999, pl. 2, figs 4–8; 2003, pl. 7, figs 5–8; 2003, pl. 7, figs 5–8). The species connected to *Rhabdocolpus* by BANDEL et al. (2001) from the Jurassic of New Zealand has a protoconch with approximately 4 rounded whorls and ornament by two spiral ribs. It resembles the *Rhabdocolpus* described by GRÜNDEL (1999, pl. 2 and 3; 2003, pl. 7 and 8). A similar larval ornament was noted in case of *Rhynchocerithium* COSSMANN, 1906 by GRÜNDEL (1997) resembling that of *Cryptaulax*.

The genus *Juramelanoides* BANDEL, 1991 is based on *Juramelanoides villersense* (DE LORIO, 1864) originally described as *Cerithium villersense* by LORIO & JACCARD (1865) and again described by BANDEL (1991, pl. 3, figs 2, 7). The slender turreted shell has a sculpture consisting of spiral ribs and the embryonic shell roundish and consisting of less than two whorls. The type species with 3 mm long shell consists of 8 whorls with rounded flanks and well developed sutures. The apical angle is about 22 ° and the base is rounded. The aperture is small and ovate and supplied with an anterior canal in case of *Juramelanoides madagascariensis* (BANDEL, 2006) (Pl. 7/7). The conical protoconch consists of 1.5 rounded whorls which have as only ornament a corner on the last whorl of the embryonic shell. Ornament of the teleoconch in the first whorls changes in regard to that of the later ones in which sculpture of broad axial ribs is overridden by narrow spiral ribs that are swollen into beads on the ribs. The rounded

embryonic whorl measures approximately 0.12 mm in diameter and in contrast to the former interpretation the spiral ornament on the third whorl appears to be crossed by axial ribs and ornament is thus like that on the succeeding teleoconch (Pl. 7/7). The first whorl of the teleoconch is ornamented with two spiral ribs and within the next two whorls around 8 axial ribs appear on each whorl and increase in width with each whorl. In the fifth whorl of the shell an additional spiral rib is added and produces a strong reticulate pattern with the somewhat inclined axial ribs which are arranged to form continuous lines across the shell.

**Discussion:** BANDEL (2006) suggested a subfamily Probittinae to include *Probittium madagascariensis* BANDEL, 2006 from the Jurassic and that the taxon has no living representatives. Here it is transferred into the genus *Juramelanoides* as was described from the transition time of the Jurassic to the Cretaceous in the French Jura (BANDEL, 1991). As indicated by BANDEL (2006), individual shells of this species from Sakaraha are mostly somewhat corroded, which indicates that they have been transported into this environment, while *Cryptaulax sakarahensis* lived right next to the locality at which it was deposited, and thus is usually not corroded. *Juramelanoides villersense* has on its fifth whorl 5 spiral ribs, while in case of *Juramelanoides madagascariensis* there are only three here, and a less well developed one consisting of rounded nodes lies just below the suture, and in addition the axial elements of the species from the French Jura Mountains are less developed. Ontogeny may well have been without a plankton-feeding larva and the species may have lived in coastal environment with water not fully marine, as may also be the case in *Maoraxis* sp. (Pl. 7/10).

*Exelissa* PIETTE, 1860 with type *Cerithium strangulatum* ARCHIAC, 1843 from the Mid-Jurassic of France has a similar ornament but has a pupa-like shell (WENZ, 1938; COSSMANN, 1913; GRÜNDEL, 1997, pl. 4, figs 12–13; 2000, pl. 1, figs 17–19). *Exelissa* has axial and spiral ribs with the axial ribs forming the stronger ornament from the early whorls onward, and their number remains the same on consecutive whorls, as is the case in *Juramelanoides madagascariensis*. *Exelissa binodosa* GRÜNDEL, 1990 from the Mid Jurassic of North Europe has more straight axial ribs and a less variable ornament on the different whorls of the teleoconch. Compared with *Exelissa distans* COSSMANN, 1913 as described by KAIM (2004, fig. 32) from the Late Jurassic of Poland the early ornament of the teleoconch is similar to that of *Juramelanoides madagascariensis*, while later ornament is dominated by spiral ribs. *Exelissa* was suggested to represent a member of the Procerithiidae but its protoconch is still unknown.

The genus *Maoraxis* BANDEL, GRÜNDEL & MAXWELL, 2000 is based on the genus *Maoraxis* from the Jurassic of New Zealand with the type *Maoraxis kieli* BANDEL, GRÜNDEL & MAXWELL, 2000 which regarding teleoconch shape and ornament resembles *Maoraxis* sp. (Pl. 7/10). In case of the species from Madagascar, ontogenetic development was that of a small animal hatching as crawling young, while *Maoraxis kieli* had a planktotrophic veliger with characteristic larval ornament. Different species of one and the same modern genus of the Cerithimorpha may have different embryogenesis, one with yolk-feeding development and hatching with simple shell of the size close to one whorl, and the other related species with the presense of a planktotrophic larva and well developed ornament on the larval shell (BANDEL, 1982). In case of *Maoraxis* this is also assumed to have been the case with the species that lived in the Jurassic of New Zealand having a development with long lasting larval life, while *Maoraxis* sp. from Madagascar that lived during approximately the same time developed without planktonic larval stage and hatched from its egg as crawling young.

*Maoraxis* sp (Pl. 7/10, structure Pl. 7/5) differs from type species of the genus by yolk-feeding development and thus no larval shell and the first whorl measuring 0.2 mm in diameter. The individuals found in Sakaraha have the first whorls of the shell with rounded shape. The first 1.5 whorls appear to have been smooth and almost 0.2 mm wide with a slightly thickened margin of the simple aperture. The first whorl of the teleoconch has a corner towards the suture and here on the next whorl a spiral rib has its place. The whorls of the teleoconch initially have three, later five or more spiral ribs. The numerous axial ribs are straight at first and later curve with their anterior end that does not reach the base. The spiral lines form tubercles where they cross axial ribs. The apical row of tubercles just next to the suture usually increases in magnitude during shell growth. The base is convex, continuous with the sides and is ornamented by 5–7 spiral lines. The aperture has an indistinct anterior notch and the outer lip forms a low rounded anterior projection.

Growth lines change in the onset of the teleoconch from simple to sinuous, reflecting the presense of a sinus in the aperture and thus the presense of a frontal channel of the aperture. On the third whorl of the teleoconch weak axial ribs appear and become more prominent in the following whorls. Their number may decrease or remain about 10 and on later whorl they are distinguished into a strong upper part and the weaker lower portion. The fourth whorl develops a teleoconch ramp below the suture. With the begin of ramp the apical angle increases and the radial ribs are interrupted in the middle of the whorls, forming an upper row of large short ribs and a lower row of nodes, while spiral lines ornament the middle. Ornament consists of about 8 strong axial ribs on each whorl. Since their number does not increase with growth their distance to each other increases. These ribs are oriented in such a way that they form a screw-like pattern on succeeding whorls. Spiral lines cross the axial ribs in more or less equal distance to each other. The base is weakly convex and forms a rounded margin that carries a spiral lira with the side. The base is flattened and smooth.

In ornament and shape of the teleoconch *Maoraxis* sp. resembles *Maoraxis kieli* which in contrast to the species from Sakaraha has a protoconch of 4 whorls with rounded shape and ornament of the larval shell with two spiral ribs crossed by numerous smaller axial ribs (BANDEL et al., 2000, pl. 7, figs 5–11).

**Littorinimorpha** are represented by species which resemble each other somewhat in shape and ornament and due to characters of their protoconch can be placed as member of the genus *Hudlestoniella* COSSMANN, 1909. This genus may represent a member of the Settsassiidae BANDEL, 1982. Also species of *Palaeorissolina* GRÜNDEL, 1999 of the Palaeorissolinidae GRÜNDEL & KOWALKE, 2002, *Canterburyella* BANDEL et al., 2000 of the Canterburyellidae BANDEL, GRÜNDEL & MAXWELL, 2001 can be recognized. *Mesostrombus* SCHRÖDER, 1995 (= *Levipleura* GRÜNDEL & NÜTZEL, 1998) with two species which differ in regard to the size of their larval shell and can be interpreted as members of the Pseudomelaniidae HOERNES, 1884.

Several gastropod species from Sakaraha have a teleoconch with ornament of axial ribs and protoconch that has little or no ornament and they could be included with the Littorinimorpha with the Caenogastropoda. The teleoconch may be rissoiform (like a *Rissoa-Rissoina* among modern gastropods) or slender, and the protoconch may be pointed conical or rounded conical. Both characters can be interpreted by themselves, and utilized to connect the involved species with different groups among recent and fossil taxa. These species can be compared with Jurassic species that have been placed with *Canterburyella*, *Palaeorissolina*, *Mesostrombus* (= *Levipleura*) and *Sakarahella*. Their relation to living species is in doubt. It reflects the problem of detecting relations which may exist between species in which only the shell is known and which have lived a long time ago. Between the fossil gastropods described and interpreted here and the species living now more than 160 Million years have passed. Even when comparing living species with such from the Paleocene for example, maybe some genera can be recognized but species are all different, and species that lived 160 Million years ago can be expected to have changed even much more. Their place within a modern family is usually questionable and their relation to it is usually in doubt and may only rely on more or less good assumptions.

*Hudlestoniella* sp., *Palaeorissolina madagascariensis*, *Canterburyella* sp. and *Sakarahella* resemble each other by having the teleoconch ornamented by ribs. These ribs are straight in case of *Sakarahella* and curving in the three others. Best difference is noted in comparing them by their protoconch. The protoconch of *Palaeorissolina* is of wide conical shape (Pl. 8/2, 8/5), and that of the other three is more elongate-conical. Ornament of *Hudlestoniella* (Pl. 7/12, Pl. 8/1) and *Sakarahella* consists of a ribbon of tubercles below the suture in case of *Canterburyella* and whorls are more rounded in *Hudlestoniella* than in *Sakarahella*.

*Hudlestoniella* sp. (Pl. 7/11–12, Pl. 8/1) closely resembles *Palaeorissolina madagascariensis*, with difference in the ornament of the larval shell of a ridge in case of *Hudlestoniella* and smooth and more rounded larval whorls in *Palaeorissolina*. The difference with *Sakarahella lugeri* is the shape of the protoconch that is higher conical than in the two others and with flattened sides (BANDEL, 2006). *Katosira basistriata* GRÜNDEL, 2007 from the Sinemurian of southern Germany consists of approximately 10 whorls and is more than 8 mm high. Its protoconch of conical shape with 4 smooth whorls and 0.7 mm in size with simple growth lines (GRÜNDEL, 2007, pl. 4, fig. 7a–b). It resembles *Hudlestoniella* sp. regarding general style of ornament, but differs from it by a more slender shell shape and more axial ribs on the whorls of the teleoconch. As in the species from Sakaraha a very fine pattern of spiral lines is here present as well.

The protoconch of *Hudlestoniella* sp. consists of 3.5 whorls and its characteristic difference in regard to the protoconch of other species with similar shape lies in the presence of a low ridge on part of the larval shell. The embryonic whorl measures about 0.1 mm across and has a beaten ornament (Pl. 8/4), and appears smooth when first growth lines are present with beginning of the larval shell. The first larval whorl is provided with a rounded corner on its side, while the second larval whorl is evenly rounded (Pl. 7/12, Pl. 8/1). In one specimen the larval shell ends in a fracture (Pl. 8/1), in another one the rounded basal larval projection of the outer lip is well developed (Pl. 7/12). The larval shell is a little higher than wide and measures about 0.5 mm in height. The end of the protoconch is well developed and growth line pattern of the teleoconch reflects a straight margin of the aperture. About 15 simple rounded axial ribs with broad evenly rounded interspaces are present on each whorl, of which only two are preserved. The aperture is oval and there appears to be an anterior notch.

*Palaeorissolina* sp. (Pl. 8/2–5) from Sakaraha has a protoconch that consists of 3.3 whorls, is as wide as high and with lowly rounded embryonic whorl. Larval whorls are rounded and smooth with growth lines lobed. The lobe of the outer lip of the aperture does not continue onto the teleoconch. Axial ribs on the teleoconch are sinuous and end before reaching the suture. The embryonic whorl measures approximately 0.14 in width and is succeeded by 2 larval whorls without ornament and with evenly rounded shape. The margin of the protoconch to the teleoconch is weakly sinuous and this shell is more than 0.4 mm high and a little less wide. The teleoconch consists of whorls with evenly rounded sides and is ornamented by about 14 rounded axial ribs and there is a fine pattern of spiral lines. The ribs curve and end on the base. The aperture is rounded and provided by a notch. In case of *Palaeorissolina* from Sakaraha curving axial ribs may be present only in the transitional last portion of the larval



shell into the teleoconch. The outer lip has no large projection, but is just sinuous. Larvae of Rissoidae have their embryonic shell usually with spiral lines, and the larval shell is ornamented by spiral lines which may be inclined and rows of tubercles (BANDEL et al., 1997, pl. 1, fig. K).

**Discussion:** *Palaeorissina* from the mid-Jurassic of northern Germany has a shorter shell than is present in *Canterburyella pacifica* but *Palaeorissina acuminata* (SOWERBY, 1818) from the Middle Jurassic of northern Germany is close in teleoconch shape to the species from New Zealand (GRÜNDEL, 1999, pl. 4).

*Palaeorissina* sp. from Sakaraha resembles *Hudlestoniella* sp. regarding shape and ornament of the teleoconch but differs from it in respect to the protoconch which is shorter, with whorls rounder and with smooth surface of the larval whorls. SCHRÖDER (1995, pl. 6, figs 1–4, 8) determined similar species from the lower Jurassic of Germany (Hambühren) and regarded them to belong to unknown species that may belong to the Aporrhaidae. It has a tower like shell shape with the protoconch ornamented by lines composed of tubercles on early whorls of the larval shell.

The genus *Palaeorissina* GRÜNDEL, 1999 is based on *Palaeorissina compacta* GRÜNDEL, 1999 from the Middle Jurassic of northern Germany (GRÜNDEL, 1999, pl. 1, figs 1–4) with broad shell ornamented by curving axial ribs and fine spiral striation and broadly conical protoconch that is smooth with sinuous outer lip. The type species of the genus is closer in shape to the Triassic *Settsassia* than to the living *Rissoa* or *Rissoina* and thus its place within the Rissoidae, Rissoinae as suggested by GRÜNDEL (1999) can be questioned and the Settsassiidae BANDEL, 1992 based on *Settsassia* BANDEL, 1992 from the Triassic are available as well. Their protoconch resemble each other closely (BANDEL, 1992, pl. 12, figs 1–2). GRÜNDEL (1999) suggested that his genus *Palaeorissina*, together with *Hudlestoniella* COSSMANN, 1909, *Bralitzia* GRÜNDEL, 1998, and *Kalchreuthia* GRÜNDEL & NÜTZEL, 1998 can be placed with the family Rissoidae GRAY, 1847 which is based on living species of *Rissoa-Rissoina*. This situation did not change when *Palaeorissina* became the characteristic genus to the Palaeorissinidae GRÜNDEL & KOWALKE, 2002.

KAIM (2004) regarded both genera *Palaeorissina* and *Palaeoceratia* as synonyms to the genus *Bralitzia* GRÜNDEL, 1998 which is based on *Bralitzia foersteri* GRÜNDEL, 1998 from the mid Jurassic of Northern Germany (GRÜNDEL, 1998, pl. 3, figs 7–9; 1999, pl. 4, figs 1–3; 2003, pl. 12, figs 7–9). KAIM (2004) suggested that the protoconch of *Bralitzia* is very similar to that of a recent *Rissoina* with planktotrophic larval stage. But *Rissoina* ORBIGNY, 1840 differs regarding the shape of the first whorl, the presence of projection of the outer lip of the larval shell and the ornament of the embryonic shell with its spiral lines quite distinctly. The outer lip of the larval shell of *Bralitzia* is sinuous with shallow upper lobe and the embryonic shell is smooth. In case of planktotrophic development most of the modern members of the *Rissoa* FREMINVILLE, 1814 and *Rissoina* relation have characteristic embryonic whorls, which bear fine spiral lines (BANDEL et al., 1997 for ref.). Similar protoconch as those of modern Rissoidae GRAY, 1847 are known from the Early Cretaceous onward and are documented in case of *Buvignieria bandeli* KAIM, 2004 from the Valanginian of Poland (KAIM, 2004), and *Buvignieria berwaldi* KIEL, 2005 from the Albien of Madagascar as described by KIEL (2005, figs 5, 9–11) from Mahajanga. The presence of Rissoidae in the Jurassic was suggested by KAIM (2004) with the genera *Bralitzia* and *Buvignieria*, but only the Valanginian *Buvignieria bandeli* has characters of the protoconch such as spiral lines on the embryonic shell which indicate that his species may very well have represented a member of the Rissoidae, which usually have this ornament. The Jurassic species described from both genera have no such ornament, but, if preserved, a groove and ridge pattern on their embryonic shell. Apparently species with the characteristic pattern of the protoconch of the planktonic larva of Rissoidae appear in the geological record at the Late Early Cretaceous of Madagascar (KIEL, 2005) and the middle early Cretaceous of Poland (KAIM, 2004). As alternative it has been suggested by SCHULBERT & NÜTZEL (2013) that *Bralitzia* may represent a member of the Iravadiidae THIELE, 1928 together with *Kalchreuthia*.

The genus *Canterburyella* BANDEL, GRÜNDEL & MAXWELL, 2009 (Pl. 8/6–11) with *Canterburyella pacifica* has its slender shell ornamented by broad axial ribs which in the juvenile teleoconch end at the edge to the rounded margin to the base, in the adult are continuous across the rounded conical base. The shell has a drop-shaped aperture which forms a final varix when fully grown. Ornament consists of about 8 axial ribs with spiral lines crossing. *Canterburyella* sp. from Sakaraha has a conical protoconch that consists of 3.5 whorls and is higher than wide and approximately 0.5 mm high (Pl. 8/6–11). The embryonic whorl is almost smooth with very fine pattern of grooves and ridges and 0.12 mm wide. The first larval whorl has a ridge above the suture, which disappears in the last larval whorl. Short axial ribs below the apical ridge are present as ornament of the larval whorls (Pl. 8/7–8). The aperture of the larval shell has a strong rounded projection of its outer lip. Axial ribs on the teleoconch are rounded and separated from each other by rounded interspaces, and whorl size increases in a regular mode. The teleoconch is slender elongate and consists of whorls which are wider than high. Only the early part of the teleoconch is preserved, and it is unknown whether the ornament of axial ribs of the teleoconch is less well developed in later whorls as is the case in some species of *Bralitzia* as described by GRÜNDEL (1999). *Canterburyella* sp. resembles *Metacerithium* COSSMANN, 1906 with slender shell ornamented by large rounded axial ribs that are crossed over by fine spiral lines (KIEL et al., 2000; KIEL, 2005).

**Discussion:** The family Canterburyellidae BANDEL, GRÜNDEL & MAXWELL, 2009 (Pl. 8/6–11) is characterized as having a teleoconch resembling in shape and ornament that of a *Rissoina* but connected to a protoconch in which the larval shell has weak axial ornament. The aperture of the teleoconch is provided with an anterior notch. The genus *Canterburyella* is based on *Canterburyella pacifica* BANDEL et al., 2000 from the Jurassic of New Zealand (BANDEL et al., 2000, pl. 7, figs 12–16, pl. 8, figs 1, 4). A very similar species from the Valanginian of Poland was documented by SCHRÖDER (1995, pl. 5, figs 18–21 determined as juvenile stage of an undetermined member of the Aporrhaidae. *Canterburyella pacifica* differs from *Rissocerithium nicosiai* CONTI & FISCHER, 1981 by having a shorter siphon notch and otherwise is quite similar also in size. Among modern representative of the Rissoidae no species is known in which the larval shell has axial ornament.

Jurassic *Mesostrombus* has its larval shell with only growth lines on a smooth surface. The conical protoconch of *Mesostrombus blainvillei* consists of about 4–4.5 smooth whorls, is almost 1 mm high and 0.6 mm wide with 0.13–0.14 mm wide first whorl and abrupt change of ornament with begin of the teleoconch. *Mesostrombus* sp. 1 from Sakaraha has a conical protoconch that consists of almost five whorls with apical angle approximately 40°. Its larval whorls are smooth with growth lines reflecting a lobe present on the outer lip of the aperture projection (Pl. 9/1, 9/3, 9/5, 9/7, 9/10). The embryonic whorl is rounded and measures about 0.1 mm in diameter. Its end is recognized by first lines of growth and minute irregularities in the growth lines. Larval whorls increase evenly in height and width and have weakly rounded sides, which are more strongly curved near the suture. A strong projection of the outer lip of the aperture is reflected by the growth lines of the larval whorls and may be preserved at the final whorl of the protoconch, which is approximately 0.7 mm high and less than 0.4 mm wide. Growth line pattern changes strongly with beginning shell of the teleoconch and axial ribs appear of which about 10 are present on each of the preserved whorls. Only juvenile individuals with not more than two whorls of the teleoconch are present. The ribs end at the rounded edge to the base and the aperture has oval shape. The teleoconch consists of marginally flattened whorls with straight axial ribs which end at the corner to the flattened base.

*Mesostrombus* sp. 2 differs regarding the protoconch which is composed of only 4.5 whorls (Pl. 9/2, 9/4, 9/6, 9/8–9). Larval whorls of the protoconch have flat sides and a rounded basal to the deep suture. The apical angle is larger and axial ribs of the teleoconch are more curving. The apical angle is approximately 60°.

**Discussion:** *Mesostrombus blainvillei* (MÜNSTER, 1844) represents a very common species from the Jurassic of Franken in southern Germany. The genus *Mesostrombus* SCHRÖDER, 1995 (= *Levipectura* GRÜNDEL & NÜTZEL, 1998) is based on *Mesostrombus vetustus* as was again described by SCHRÖDER (1995 pl. 6, figs 5–7). HUDDLESTON (1888) and WALTER (1951) also described the species. *Mesostrombus* as presented by SCHRÖDER (1995) on plate 6, figs 5–7 has a well preserved larval shell and juvenile teleoconch, and therefore the identity of his proposed type to *Mesostrombus* is well documented. *Mesostrombus* is thus identical with *Levipectura* GRÜNDEL & NÜTZEL (1998).

*Levipectura* GRÜNDEL & NÜTZEL, 1998 is based on *Melania blainvillei* MÜNSTER, 1844 from the Pliensbachian of Franconia (GRÜNDEL & NÜTZEL, 1998, pl. 3, figs 8–10; Nützel, 1998, pl. 19, figs R–U), while *Mesostrombus vetustus* (PHILLIPS, 1829) is based on *Terebra vetusta* PHILLIPS, 1829 as described by SCHRÖDER (1995, pl. 6, figs 5–10) from rocks of the same age at Hambühren in northern Germany. NÜTZEL & GRÜNDEL (2015) follow GRÜNDEL & NÜTZEL (1998) and suggest that their *Levipectura* may represent a member of the order Ptenoglossa GRAY, 1853 and here the super family Zygopleuroidea WENZ, 1940, family Zygopleuridae WENZ, 1940 and subfamily Ampezzopleurinae NÜTZEL, 1998. Both genera *Zygopleura* KOKEN, 1892 and *Ampezzopleura* are based on species which lived during the Triassic and are from St. Cassian Formation and have larval shells with strong ornament (BANDEL, 1991; NÜTZEL, 1998).

NÜTZEL & GRÜNDEL (2015) suggested that general shell shape of *Mesostrombus/Levipectura* is close to that of *Zygopleura* that has the type species *Zygopleura hybrida* or as suggested by NÜTZEL (1998) the newly defined *Zygopleura hybridissima* NÜTZEL, 1998. Its larval shell has a row of tubercles below the suture as ornament while that of *Mesostrombus (Levipectura)* bears only indistinct growth lines. The smooth protoconch of *Mesostrombus* distinguishes it clearly from *Zygopleura*, but regardless of this difference it was determined as *Zygopleura blainvillei* by NÜTZEL & KIESSLING (1997) as had been suggested by NÜTZEL (1998). Axial ornament of the larval shell is present in all the known species of members of the family Zygopleuridae WENZ, 1938 and this ornament represents a character of the group. NÜTZEL (1998) had suggested that in the subfamily Zygopleurinae WENZ, 1938 there may also be species with smooth larval whorls contrasting to his own diagnosis of the super family Zygopleuroidea and family Zygopleuridae. These are defined by the presence of ornament with axial ribs on their larval shells. Thus NÜTZEL (1998) did not abide to his own definitions when he placed the Jurassic *Levipectura* (= *Mesostrombus*) into the Zygopleuridae, Zygopleurinae.

GRÜNDEL (1999, pl. 6, figs 3–5) illustrated the protoconch of *Levipectura blainvillei* from North Germany and noted that it consists of 4 whorls. *Mesostrombus* sp. 2 from Sakaraha is close to *Levipectura blainvillei* of the specimens described by GRÜNDEL & NÜTZEL (1998, pl. 34, figs 5–7; 2015) from South Germany. *Mesostrombus* sp. 1 from Sakaraha has one larval whorl more and is closer the individuals documented from North Germany.

The Triassic *Settsassia* BANDEL, 1992 from the St. Cassian Formation of the Italian Alps of the Settsassiidae BANDEL, 1992 has a similar protoconch (BANDEL, 1992, pl. 12, figs 1–2; NÜTZEL, 1998, pl. 27, L–R) and also its teleoconch resembles that *Mesostrombus* sp. Genus *Settsassia* and the related *Lacunina* KITTL, 1891 have egg-conical shape and the teleoconch with axial ornament. *Settsassia* is also similar to the Jurassic *Kalchreuthia* as was noted by (GRÜNDEL, 1999) but *Kalchreuthia* has a smoother shell. NÜTZEL (2010) suggested that *Kittliconcha* BONARELLI, 1927 from the Triassic St. Cassian Formation may represent a synonym of *Settsassia* BANDEL, 1992 and to have a small, smooth, *Helix*-like larval shell and smooth early teleoconch whorls, which is actually not the case as documented by BANDEL (1992) and also by NÜTZEL (1998, pl. 27, figs L, M, N, O).

The genus *Sakarahella* BANDEL, 2006 was proposed to characterize a family Sakarahellidae BANDEL, 2006 in which the protoconch is conical and consists of several whorls. Its larval shell has a projection of its outer lip of the aperture and ornament of a ribbon below the suture consisting of short ribs and tubercles. *Sakarahella angulata* BANDEL, 2006 (Pl. 9/11, Pl. 10/1–6) has a conical protoconch with smooth rounded embryonic whorl of about 0.1 mm in diameter succeeded by larval whorls with a spiral ribbon below the suture and tubercles or short inclined lines above the suture. The whorls of the larval shell have flattened sides with rounded edge to the suture. The conical protoconch consists of 4.5 whorls, is 0.7 mm high and 0.45 mm wide. Larval whorls in contrast to the straight growth lines of the embryonic whorl have curving growth lines which reflect the lower lobe on the outer lip of the aperture. This projection of the aperture is largely covered by the succeeding whorls. Above the suture whorls are stronger inclined than on the flank above which is evenly rounded. The strongly sinuous growth lines of the larval shell do not continue onto the teleoconch that is sculptured by slightly convex and rounded axial ribs, of which approximately ten are found on each whorl. The aperture is oval.

The teleoconch is ornamented by straight axial ribs of which 13 are present on the first whorl. Weaker spiral ribs, one on the side and four on the rounded corner to the base. The aperture of the juvenile teleoconch is rounded. Fully grown shells are not known.

**Discussion:** *Sakarahella* with *Sakarahella angulata* had been interpreted as a potential precursor of the Vermetimorpha BANDEL, 2006, and placed in a family Sakarahellidae BANDEL, 2006. It resembles with elongate and basically smooth shell *Kalchreuthia* GRÜNDEL & NÜTZEL, 1998 of the *Pseudomelania* PICTET & CAMPECHE, 1862 and *Brevizyia* GRÜNDEL, 1999 groups. Whorl ornament and shape of the protoconch of *Sakarahella* resembles that of *Azyga faustiankensis* KAIM, 2004. Here also the rounded embryonic whorl tops a barrel shaped larval shell in which the whorls are ornamented with a row of nodes below the suture and have a large median lobe in the outer lip of the aperture (KAIM, 2004, fig. 49). *Katosira flexuosa* (MÜNSTER, 1844) from the Mid-Jurassic of Germany as described by GRÜNDEL (1999, figs 1, 8–10) differs by having one whorl less in the protoconch and a less dense pattern of axial ribs on the teleoconch. The teleoconch resembles that of *Metacerithium* COSSMANN, 1906 with slender shell ornamented by large rounded axial ribs that are crossed over by fine spiral lines (KIEL et al., 2000; KIEL, 2005). A similar protoconch was documented in case of *Zardinistylus betsibokaensi* KIEL, 2005 from the Aptian-Albian of the Mahajanga Basin of Madagascar which has a teleoconch with slender cylindrical shape and rounded axial ribs (KIEL, 2005, figs 4, 2–3). KIEL (2005) suggested that his *Zardinistylus betsibokaensis* closely resembles the Late Triassic *Zardinistylus misurinensis* (ZARDINI, 1978). Sakarahellidae were suggested to connect the Triassic Coelostylinidae COSSMANN, 1909 and here to the genus *Pseudoschwartziella* BANDEL, 2006 which lives in the Indo-Pacific.

A smooth protoconch is present in *Kalchreuthia* GRÜNDEL & NÜTZEL, 1998 with *Kalchreuthia* sp. from Madagascar. This genus is based on *Kalchreuthia frankei* (KUHN, 1936) that is very similar. It did not grow to large size and only approximately 3 mm high when consisting of 7–8 smooth whorls. The shell of *Kalchreuthia frankei* has a high spire and is slender. The protoconch consists of about 3.5 to 4 smooth whorls and is 0.6 mm 0.5 mm wide with the initial whorl 0.14 mm in diameter and is broader than the early teleoconch. The transition from protoconch to teleoconch is abrupt.

*Kalchreuthia* sp. (Pl. 10/7–9, Pl. 11/2–3) closely resembles *Kalchreuthia frankei* and differs only in regard to the protoconch that has half a whorl more and fine lamellar ornament on its larval shell. Here the shell is high and slender with 5 whorls 1.2 mm high. First four whorls are rounded and smooth and belong to the protoconch. Their suture is distinct and growth lines are slightly curving. The base is convex and smooth and its transition to the whorl face is formed by a rounded edge. The protoconch is 0.6 mm wide with the initial whorl 0.08 mm in diameter and included in the flattened apex. The protoconch is broader than the early teleoconch and transition to the teleoconch is abrupt but indistinctly seen only due to growth lines changing from lightly curving to straight. Ornament on the protoconch consists of fine growth lines that are expressed in fine lamellae just below the suture (Pl. 11/2–3).

**Discussion:** *Pseudomelania frankei* by KUHN (1936, pl. 13, fig. 11) had been called *Tournoueria* cf. *frankei* (KUHN) by NÜTZEL & KIESLING (1997, pl. 35, figs 5–7) and was subsequently considered the type species to the genus *Kalchreuthia* GRÜNDEL & NÜTZEL, 1998. Similar species have been placed with the Pseudomelaniidae HOERNES, 1884 by KAIM (2004). *Kalchreuthia frankei* has been described several times, also in SCHUBERT et al.

(2008, figs 5 A, B) from NW Germany, GRÜNDEL & NÜTZEL (1998, pl. 3, figs 2–3), NÜTZEL & GRÜNDEL (2013, pl. 9 J–N, 10, A–E). NÜTZEL & GRÜNDEL (2015, pl. 10, figs H–Q) found *Pseudomelania frankei* KUHN, 1936 to be one of the most common gastropods found at Buttenheim and Kalchreuth in southern Germany. GÜNDEL & NÜTZEL (1998, pl. 3, figs 2–3) placed *Kalchreuthia* with the Iravadiidae because of its flat protoconch apex resembling that found among modern representatives of that family.

WEITSCHAT & GRÜNDEL (2002) found *Kalchreuthia* together with *Mesostrombus* (*Levipleura*) to have been used by a Jurassic worm with *Lanice*-like agglutinated burrow in the Jurassic of northern Germany.

A super-family Pseudomelanoidea HOERNES, 1884 with its family Pseudomelaniidae has been suggested to hold species with slender elongate shell, which in case of the proposed type of *Pseudomelania* have a large size. The type of *Pseudomelania* PICTET & CAMPICHE, 1862 lived in the Early Cretaceous and is much like *Eulima* RISSO, 1826 in shape but in contrast to it very much larger (more than 10 cm high). The Mesozoic Pseudomelaniidae just as the Paleozoic Loxonematoidae initiated speculations. BOUCHET & ROCROI (2005) for example suggested a place for the fossil families Pseudomelaniidae and Trajanellidae PCHELINTSEV, 1951 in a super-family Pseudomelanoidea of the Caenogastropoda next to the Subulitoidea LINDSTRÖM, 1884. This reflects an old tradition in classification but does not help in understanding the phylogeny of elongate gastropods. PONDER (1985) assumed that the Pseudomelaniidae represent the stem group to the Rissoidea and have their origin among species of *Loxonema* PHILLIPS, 1841 which has been documented to not even represent a member of the Caenogastropoda but is a member of the Archaeogastropoda (FRÝDA & BANDEL, 1997).

In case of *Pommerozygia* sp. from Sakaraha (Pl. 10/10–12) the protoconch consists of more than three whorls of dome shape with about 0.5 mm in height and 0.7 mm in width. The embryonic shell is a little less than 0.1 mm in diameter, rounded and smooth. The larval shell has smooth surface with indistinct growth lines that reflect a sinus in the upper part and a lobe in the lower part of the outer lip of the aperture. Transition to the teleoconch is indistinct, and only noted in the change of growth line pattern from sinuous to straight. The aperture is oval and provided with anterior channel. *Pommerozygia* sp. could also be interpreted to represent a member of *Bralitzia* GRÜNDEL, 1998 or *Brevizygia* GRÜNDEL, 1999.

A family Pommerozygiidae GRÜNDEL, 1999 is based on *Pommerozygia* GRÜNDEL, 1998 with short teleoconch with rounded whorls and barrel shaped protoconch. Change to the teleoconch is indistinct but whorls are relatively higher than those of the protoconch. The type species *Pommerozygia ueckeritzensis* GRÜNDEL, 1998 is from the Bathonian of northern Germany and Poland (GRÜNDEL, 1998, pl. 5, figs 1–5; 1999, figs 1/15–16). The embryonic whorl is simple and lies almost flat on the larval shell. KIEL (2005, figs 4, 4–12) placed species from the Early Cretaceous of Madagascar in the Pommerozygiidae with a similar protoconch.

**Discussion:** The shell resembles species placed with *Pseudomelania* PICTET & CAMPICHE, 1862 from the Valanginian of Poland (KAIM, 2004, fig. 78) and from the Jurassic of Poland (KAIM, 2004, fig. 77). *Brevizygia spiralsulcata* BANDEL, GRÜNDEL & MAXWELL, 2001 from the Jurassic of New Zealand has a spiral groove below the suture and a protoconch with *Natica*-like shape and similar dimensions (BANDEL et al., 2001, pl. 8, figs 10–14). Most other species placed with *Brevizygia* have no furrow below the suture on their teleoconch. *Costazygia* GRÜNDEL, 1999 differs from *Brevizygia* by S-shaped curving growth lines. *Oonia pennina* (PARONA, 1892) as described by SZABO (1983) from the Pliensbachian of Hungary is much larger with a shell reaching 30 mm in height. Here a concavity is accompanied by a spiral groove below the suture and fine spiral ornament is distinctly developed.

As was noted by BANDEL et al. (2000), the Pommerozygiidae could be related to the modern Rissoidea and Littorinoidea but also to the Triassic Settsassiidae. KAIM (2004) preferred to place them with the Pseudomelanoidea HOERNES, 1884, a Mesozoic group which was seen as ancestral to the Rissoidea by PONDER (1985).

### **Family Ampullinidae or Ampullospiridae, Ampullospirinae Cox, 1930**

This group has a quite distinct protoconch of the type as is well developed in *Sakarahina lugeri* described by BANDEL (2006).

The genus *Sakarahina* BANDEL, 2006 was suggested to represent a member Ampullinidae COSSMANN, 1919 and close to the Jurassic *Ampullopira* HARRIS, 1897 and the Triassic Falorininae BANDEL, 2006 based on *Falorina* BANDEL, 2006 and the Cretaceous *Metacerithium* COSSMANN, 1906 from Mahajanga on Madagascar.

*Sakarahina lugeri* BANDEL, 2006 has the protoconch with 2.5 rounded whorls which end with a rounded and strongly raised margin of the aperture. The embryonic whorl is smooth and 0.1 mm wide. It is demarcated from the larval shell by a strong increment of growth of straight outline. The larval shell has curving growth lines which reflect the presence of a lobe on the aperture in low position on the outer lip. Very fine pustules cover the surface especially near the suture, but the surface in general appears smooth. The final varix of the aperture curves slightly reflecting the lobe of the outer lip. To it an outer addition may be preserved that enforces the curving shape of the lip. This added thin shell is often broken. The teleoconch is clearly distinguished and begins with ornament of

spiral grooves of which about 20 are present on the first whorl, of which only about 6 remain uncovered when the next whorl is added.

The protoconch consists of well rounded whorls, is about as wide as high and ornamented by very fine pustules. Its margin with the teleoconch is marked by a strongly thickened outer lip (BANDEL, 2006, pl. 10/4–6; Pl. 11/1, 11/4–5). The protoconch of *Sakarahina* resembles that of *Dzikella* KAIM, 2004, while the teleoconch is quite different (KAIM, 2004, fig. 36). *Dzikella trammeri* KAIM, 2004 from the Early Cretaceous of Poland has the protoconch of quite the same size and shape, and also the teleoconch has the same pattern of rounded strong axial ribs and weak spiral lines. The only difference between both species lies in the number of axial ribs on each whorl, which is a little higher in case of the specimen from Poland.

**Discussion:** The living *Plesiotrochus* FISCHER, 1878 has a very similar larval shell to that of the larval shell of *Sakarahina* (BANDEL, 2006, pl. 10, figs 4–6). The larval shell is like that of *Metacerithium ponsi* KIEL & BANDEL, 2000 from the Campanian of northern Spain. The protoconch of *Sakarahina lugeri* BANDEL, 2006 consists of 2.5 rounded whorls which end with a rounded and strongly raised margin. The embryonic whorl is smooth and measures about 0.1 mm in width and end with growth increments. The teleoconch has ornament of spiral grooves of which about 20 are present on the first whorl, of which only about 6 remain uncovered when the next whorl is added.

In the genus *Pictavia* COSSMANN, 1925 shell shape is egg-like with pointed spire connected to a smooth protoconch with the larval shell ending in a finally thickened margin of its aperture (varix). The whorls of the teleoconch have a narrow rim below the suture and the shell is smooth or ornamented by spiral lines of dots. *Pictavia* COSSMANN, 1925 closely resembles *Oonia* GEMMELLARO 1878, but in contrast the later has a narrow ramp below the sutures of the teleoconch whorls. Both have the same character of the protoconch as is also present in *Sakarahina* which has a more elongate shape of its teleoconch, spiral ornament with lines of dots and fine tubercles as ornament of its larval shell. *Pictavia calypso* (ORBIGNY, 1852) from the Callovian of NE Germany has an egg-shaped shell consisting of 6 smooth whorls is approximately 4 mm high and provided with the protoconch consisting of 4 whorls and 0.8 mm high and strong varix at the end of its larval shell (GRÜNDEL, 2001, pl. 3, fig. 17, pl. 4, figs 1–4; 2003, pl. 13, figs 9–10, pl. 14, fig. 1). This species from northern Germany documents the good exchange of species within the Tethys at Jurassic times from northern shelf seas of Laurasia to such of the Gondwana Continent now at Madagascar. The protoconch of *Metacerithium ponsi* KIEL & BANDEL, 2000 is similar in shape. *Dzikella trammeri* KAIM, 2004 described by KAIM (2004, fig. 36) from the Late Valanginian has similar characters of the protoconch, but the teleoconch is elongated and ornamented by axial ribs.

### Ctenoglossa=Ptenoglossa

Members of the Zygopleuroidea and thus the Ctenoglossa are represented by a protoconch of the *Protorcula* type.

“*Opaliopsis*” sp. (Pl. 11/7) of the Nystiellidae CLENCH & TURNER, 1952 as *Opaliopsis* determined by KAIM (2004, fig. 45) and as member of the Protoorculidae by SCHRÖDER (1995, pl. 2, fig. 8) and both from the Lower Cretaceous of Poland. *Opaliopsis (Protorcula)* sp. from Sakaraha is represented by a larval shell connected to a smooth first whorl of the teleoconch. The protoconch was approximately 0.6 mm high with three whorls of the larval shell preserved and the first larval shell and embryonic shell are broken off. Transition to the smooth first whorl of the teleoconch is rapid and without transition in ornament and growth lines, which change from sinuous in the larva shell to straight and simple in the early teleoconch.

**Discussion:** *Opaliopsis* sp. from Sakaraha resembles species placed with *Opaliopsis* THIELE, 1928 as in SCHRÖDER (1995) and KAIM (2004) from the Valanginian of Poland, and DOCKERY (1993) and NÜTZEL (1998) from the Campanian of Mississippi. A similar protoconch has also been noted in *Tenuiscula* BOURY, 1887 from the Eocene of France (BANDEL, 1991, figs 49–50; NÜTZEL, 1998) and *Ecclesiogyra* DALL, 1892 as illustrated by DOCKERY (1993), BANDEL (1991, figs 43–44), and NÜTZEL (1998) from the Campanian of Mississippi.

Species with a protoconch having axially ornamented larval shells characterize *Ampezzopleura* BANDEL, 1991 from Triassic St. Cassian Formation. This genus was placed together with *Protorcula* KITTL, 1894 with similar protoconch but quite distinct teleoconch in the Protoorculidae BANDEL, 1991. The family was created to encompass slender tower-like shells with many whorls and an aperture with short siphon which have a larval shell with projection on the outer lip and curving axial ribs as ornament. The embryonic shell measures about 0.1 mm and the protoconch is slender to around 1 mm in height. The aperture is oval in shape and higher than wide. The protoconch is usually that of a planktotrophic larva with conical shell having more than 4 whorls with axial ornament. *Protorcula* is based on *Turritella subpunctata* MÜNSTER, 1841 from the Triassic St. Cassian Formation with protoconch that consists of 6.5 whorls (ZARDINI, 1985, pl. 4, fig. 18; BANDEL, 1991, figs 24–25, 33; 1993, pl. 9, fig. 5; NÜTZEL, 1998, pl. 27, figs A–E).

Zygopleuridae from the Triassic St. Cassian Formation include no species with totally smooth larval shells contrasting to suggestions of GRÜNDEL (2003). He even placed *Kosmopleura* GRÜNDEL, 2003 based on *Kosmopleura hoelderi* GRÜNDEL, 2003 from the early Jurassic of SW Germany with strong spiral ribs on the protoconch (GRÜNDEL, 2003, pl. 6, figs 1–6) with the Zygopleuridae. But this ornament of the larval shell clearly

excludes *Kosmopleura* from the Zygopleuridae, as originally defined by BANDEL (1991) and in more detail by NÜTZEL (1998). The Zygopleuridae include predominantly Triassic species and they may represent Ctenoglossa (= Ptenoglossa) of relation to the modern Ianthinoidea GRAY, 1853 (Epitonioidae) and Cerithiopsoidae A. & A. ADAMS, 1853. The genus *Opaliopsis* THIELE, 1928 is based on the modern *Scala (Opaliopsis) elatum* THIELE, 1928 from the Indian Ocean off eastern Africa (WENZ, 1938, fig. 2324). This species is characterized by a teleoconch resembling that of *Epitonium* RÖDING, 1798 connected to a protoconch with larval shell having axial ribs. BANDEL (1993, pl. 10, fig. 2) illustrated the protoconch of *Cerithiopsis meeki* from the Coffee Sand Mississippi which has quite the same ornament of the larval shell, resembling that of *Protorcula* and *Ampezzopleura* from the Triassic (BANDEL, 1991, figs 24–32). It appears as though the group with that characteristic ornament of its larval shell continued from Triassic through Jurassic time to modern times.

The **Strombimorpha** can be recognized by shells of juveniles with characteristic protoconch and relation possibly with *Undoriptera* as described by GUZHOV (2014). The character of its protoconch is provided with stages of morphology which are still preserved within the larval development of modern *Strombus* LINNÉ, 1758, *Strombus (Gibberulus) gibberulus* LINNÉ, 1758.

*Dicroloma* / *Pietteia* / *Undoriptera* sp. (Pl. 15/1–10) has a protoconch that consists of trochospiral whorls of which the three larval ones are smooth up to the last fourth which is ornamented by axial rib and ends with a spine like projection of the base of its aperture. The juvenile teleoconch is slender conical with angular whorls ornamented by broad axial rib crossed by narrow spiral ribs. Whorls are angular with inclined shoulder and vertical flanks and the aperture extended into a siphon.

The embryonic whorl measures 0.15 mm in diameter and is smooth and with rounded whorls. The initial cap is marked by some indistinct folds and ornament is not present (Pl. 15/6). Transition to the larval shell is marked by first increments of growth. The larval shell is completed with 3.5 whorls and a diameter of approximately 0.8 mm in width and height. The last quarter of a whorl of the larval shell has strongly curving large ribs which end in a basal rib. The ribs end in the strong narrow projection of the outer lip of the larval shell. In it a ribbon of tubercles ends that is found on the corner of the larval whorls which otherwise are smooth (Pl. 15/8, 15/10). In transition to the teleoconch also axial ribs appear which continue to the base and do not end on the margin of a projection. They continue onto the siphon present on the aperture of the teleoconch.

Ornament of the teleoconch at first resembles that of the last part of the larval shell, but actually ribs which appear on the first part of the teleoconch belong to a portion of shell with which the wide lobe of the larval aperture is closed. The larval projection continues onto the edge of the teleoconch to the base, but the outer lip of the aperture is not connected to a sinus but continues into the siphon, which with the second whorl of the teleoconch is well developed. Axial ribs continue onto it (Pl. 15/3). The first whorl of the teleoconch has almost round sides and is dominated by axial ribs, while on the second teleoconch whorl spiral ribs appear and dominate on the third whorl. Also the upper flank of the whorls forms a ramp and axial ribs are transformed into elongate nodes on the shoulder (Pl. 15/1–3).

**Discussion:** *Undoriptera* GUZHOV, 2014 is based on *Undoriptera tridactylus* GUZHOV, 2014. It has a shell with many whorls, with short protoconch and teleoconch whorls with a carina, with reticular ornamentation on early whorls and prevailing spiral ornamentation on later whorls. A series of tubercles lie on the carina near the middle of the whorl. The adult shell has three processes on the aperture when fully grown (GUZHOV, 2014, pl. 1, fig. 6; pl. 2, figs 1–6) from the Kimmeridgian of Russia at the Volga River. The first one and a half whorls of the teleoconch are convex and covered with reticular ornamentation. The next whorl has a ridge under the median rib and the upper rib becomes weaker and disappears to the fourth whorl.

Regarding shape and ornament the protoconch of *Pietteia subbicarinata* (MÜNSTER, 1853) as documented by KAIM (2004, fig. 56) is similar in shape and dimensions to the species from Sakaraha. This Mid-Jurassic member of the Aporrhaidae of Poland has the larval shell with embryonic whorls of 0.13 mm in size. It is succeeded by a larval shell with 3.7 whorls and transition to the teleoconch is connected to a change in ornament. In difference to the larval shell of the individuals from Sakaraha those from the locality of Lukow in Poland have a less gradational transition of late larval ornament to early ornament of the teleoconch. Also the early teleoconch of *Pietteia subbicarinata* has a less strongly ornamented and ribbed shell. KAIM (2004) also suggested that in case of the protoconch of Aporrhaidae it may not be clearly demarcated from the teleoconch, which cannot be confirmed by *Undoriptera* sp. from Sakaraha. He also noted that in *Pietteia* spiral ribs may change into a keel, and this observation can be confirmed, but he also described that axial ornament appears later, which is not so in the larval shell from Sakaraha. Also a *Pietteia* documented by GRÜNDEL (2003, pl. 11, figs 12–15) from the middle Jurassic of Sengenthal is similar. This larval shell is not well preserved and also its transition to the teleoconch is different from that of *Undoriptera* sp.

BANDEL (2007) documented the larval shell of Alariidae as usually more than 1 mm high with 3.5 to 4 whorls with a wide upper sinus and a lobe that is covered by the succeeding whorl. But ornament may also begin already on the larval whorl and not only on the teleoconch. The larval shell of *Undoriptera* sp. documents that the indistinct

transition to the teleoconch as suggested by KAIM (2004) to the protoconch of Alariidae among the Strombimorpha may also be developed quite distinctly but a little difficult to detect.

Strombimorpha could have initial connections to the Purpurinoidea ZITTEL, 1895 which appeared during the Triassic, while Aporrhaidae GRAY, 1850 can be recognized from the Jurassic onwards (KAIM, 2004; BANDEL, 2007). Here also the Maturifusidae GRÜNDEL, 2001 based *Maturifusus* SZABO, 1983 and the Purpurinidae ZITTEL, 1895 with *Angularia* KOKEN, 1892 may have a similar relation. SCHRÖDER (1995, pl. 4, figs 17–20) described the larval shell of *Maturifusus szabo* SCHRÖDER, 1995 from the mid Jurassic Aalenian of North Germany. It has a large larval shell of approximately 1 mm in size and he noted that it resembles a species that had been described by GRÜNDEL (1977) from the Jurassic of Poland. This *Maturifusus*, which according to KAIM (2004) should be placed with *Astandes* WADE, 1917 which is not accepted here, since the type of *Astandes* lived in the Late Cretaceous Coon Creek fauna and has a large protoconch resembling that of *Undoriptera* sp in general shape and size, but is ornamented differently with spiral ribs.

*Purpurina* ORBIGNY, 1850 with the Jurassic *Purpurina bellona* ORBIGNY, 1850 from the Middle Jurassic of France as type in case of *Purpurina formosa* (EICHWALD, 1868) has a protoconch with more than 1 mm in width and height (KAIM, 2004, fig. 87). It resembles in size and shape the protoconch of *Undoriptera* sp. It differs from it by a more rapid transition from the smooth larval shell to the teleoconch, but in the documented case presented by KAIM (2004) the larval shell appears to have been fractured when the larva had settled to benthic life.

*Angularia* (*Purpurina*) *subpleurotomaria* (MÜNSTER, 1841) has similar protoconch shape but its size is much smaller (0.35 mm) and the margin of its aperture is thickened, and is extended into a long larval hook as well. The ornament of the teleoconch is also dominated by many axial ribs crossed by single spiral one but there are more axial ribs (ZARDINI, 1978, pl. 38; BANDEL, 1993, pl. 14, figs 2, 4; BANDEL, 1994, pl. 5, fig. 17). BANDEL (2007) discussed the history of the Strombimorpha with Alariidae such as *Undoriptera* and *Dicroloma* evolving during the Jurassic. GRÜNDEL (2005) found similar juvenile shells and called them *Ueckeritzella* placing them within the Aporrhaidae and here close to *Dicroloma*, but without knowledge on the shape of the more grown shell. *Ueckeritzella moths* GRÜNDEL, 1998 representing the type to the genus is based on a less than 4 mm high juvenile with the protoconch preserved that resembles *Undoriptera* sp. from Madagascar. The protoconch consists of 3.5 smooth whorls and the last quarter of the larval shell ornamented by curving axial ribs which end in a basal spiral rib. This rib is also the spiral that forms the upper edge of the strong hook that marks outer edge of the margin of the aperture forming the larval outer lip. GRÜNDEL, NÜTZEL & SCHULBERT (2009) in case of *Toarctocera* from the Toarcian of South Germany documented a protoconch that resembles that of *Piettiea* as illustrated by KAIM (2004) and they characterize it as being smooth and 1.5 mm high

The larval shell of *Undoriptera* sp. thus resembles the outer lip of the early veliger shell as found in case of modern *Strombus gibberulus* LINNÉ, 1758, while fully grown larva here have their margin without hook (BANDEL, 2007, pl. 6, figs 1–14). The embryonic shell of *Strombus gibberulus* measures 0.15 mm in diameter and is ornamented. That differs from the embryonic shell of *Undoriptera* sp. that measures 0.12 mm in diameter and is quite smooth (Pl. 15/6). The second whorl of the protoconch of *Strombus gibberulus* has a strong lobe on its outer lip (BANDEL, 2007, pl. 6, figs 10, 12). On the last whorl of the protoconch and when it has reaches a size of about 1 mm the aperture has an evenly rounded outer lip in case of *Strombus*, while in *Dicroloma* the outer lip has the projection and it is only closed by first growth of the teleoconch. Ornament changes from curving ribs on the late larval shell to straight ribs on the teleoconch. Here also spiral ribs appear and increase in number and strength on the teleoconch of which 3.5 whorls were observed in the oldest of the juvenile shell which were encountered.

*Dicroloma* with its two spiral keels on the adult shell may well have had a larva as that of Madagascan Jurassic *Undoriptera* sp. (BANDEL, 2007, fig. 1b). The similarity of the aperture in case of the not fully grown larva of *Strombus gibberulus* to that of the fully grown larva of *Undoriptera* sp. is amazing (Pl. 15/2–3, 15/8–10). Such a strong projection of the outer lip in case of *Strombus gibberulus* disappears during larval life while it forms the aperture of the larva at metamorphosis in case of *Undoriptera* sp. The resemblance even includes the spiral ribbon with ornament that continues into the pointed larval hook in a larval shell with two whorls and a size of 0.8 mm. It is well developed also with three whorls and 0.5 mm in height. With begin of the third whorl the larva of *Strombus* the large lobe of the aperture begins to be filled with shell increments.

The development of the larval shell continues in three distinct stages. The first phase produced the embryonic shell with simple aperture and a size of 0.15 mm in diameter. The second stage of early larval development produces a larval shell with a strong lobe in its outer lip. In the last stage of larval life during construction of the third whorl shell diameter increases and the lobe of the outer lip disappears and the pointed siphon appears as well as an umbilical pore. The protoconch has finally 4.5 rounded whorls, and is 1 mm high and 0.8 mm wide. Similar development was noted in case of *Strombus gibberulus* and *Strombus fasciatus* BORN, 1758 as documented by BANDEL et al. (1997, fig. 18, A–C).

### 3.4 Heterostropha

Within the class Gastropoda CUVIER, 1779 the Heterostropha FISCHER, 1885 (= Heterobranchia) includes the orders Allogastropoda HASZPRUNAR, 1985, Opisthobranchia and Pulmonata. Their shell is characteristic regarding the protoconch which is usually left handed in case a planktotrophic larva produced a larval shell, while the teleoconch is usually dextrally coiled. A change in the direction of coiling occurs at metamorphosis or during larval life. In cases with simplified ontogeny as is the case in gastropods living on land and in fresh water, their ancestors had the characteristic change in the coiling mode. Oldest species with shell characters of Heterostropha can be recognized among more than 300 Million years old gastropods of Devonian age (FRÝDA, 2001; FRYDA & BLODGETT, 2001; BANDEL & HEIDELBERGER, 2002; BANDEL, 2002). Among the Heterostropha a strong push of evolution occurred after the Paleozoic-Mesozoic boundary with several new units of Heterobranchia/Heterostropha appearing after the Permian-Triassic transition and crisis, as has been recognized by BANDEL (2002) and NÜTZEL (2005).

Among the Heterostropha–Heteroconchia GRAY, 1840 the family Mathildidae DALL, 1889 is represented by one characteristic species that is close to the modern *Mathilda* SEMPER, 1865 but due to its smaller protoconch even closer to the Triassic *Promathildia* ANDREAE, 1887 and similar Jurassic species placed with genera such as *Teretrina* COSSMANN, 1902, *Turritilda* SCHRÖDER 1995, *Jurida* GRÜNDEL, 1973. A species with small flatly coiled shell resembles living species of the family Vitrinellidae (= Cornirostridae) and is probably related to *Bandellina* as was described by SCHRÖDER (1995). Difficult to determine to species level are members of the Cylindrobullinidae close to the genus *Cylindrobullina* AMMON, 1878 since the species from Sakaraha is of variable shape and may be placed with several genera and species according to various descriptions of Jurassic gastropods. Among similar species a *Ceritellopsis* FISCHER, 1961 can be recognized and a *Sulcoactaeon* COSSMANN, 1895. The Heterostropha representatives of most taxa which characterize the Jurassic strata in Europe were also found among the members of this small fauna of Madagascar- with one remarkable exception of relatives of *Ebala* LEACH, 1847 (BANDEL, 2005).

The super-family Mathildoidea DALL, 1889 has as core group the family Mathildidae which has well recognizable species from the Cretaceous to the Recent. With the *Promathildia*-relation in the Mathildoidea species included here usually have an elongated shell with several (4 whorls) to many whorls (up to 20) that are usually ornamented with spiral and axial elements (BANDEL, 1996). The protoconch has a sinistral embryonic shell that twists into dextral coiling at the end of the larval shell or still within the final portion of the larval shell. The super-family has been interpreted to unite the families Mathildidae DALL, 1889, Tofanellidae BANDEL, 1994 and Ampezzanildidae BANDEL, 1994, with the last two families based on Triassic type species. GRÜNDEL & NÜTZEL (2013) suggested that species which had been placed with *Promathildia* ANDREAE, 1887 among the Triassic St Cassian gastropods should rather find their place with the genus *Teretrina* COSSMANN 1912 as discussed by SCHRÖDER (1995), but BANDEL (1995) interpreted the genus *Promathildia* ANDREAE, 1887 to be based on *Promathildia subnodosa* (MÜNSTER, 1941) as described by KITTL (1894) and BANDEL (1995) from St. Cassian Formation. Here the protoconch is essentially like that of *Mathilda*. The early whorls of the teleoconch, in contrast, have only one dominant spiral keel that is crossed by minor axial elements. It is accompanied by none to several minor spiral elements. Axial ribs and growth lines may form tubercles and raised ridges where they cross the spiral keels and costae.

In the Mathildidae DALL, 1889 the elongated cone-shaped shell has many whorls which are sculptured by spiral ridges that may be crossed by costae or growth lines. The aperture is nearly circular. The protoconch is sinistral and rests on the dextral teleoconch at a right angle or an angle smaller than 90° between the axis of the larval shell and the axis of the adult shell. This larval shell is low conical with rounded whorls that may show some axial folds on the apical and umbilical sides. Just before the onset of the teleoconch the shell twists into the plane spire before the dextral coiling of the teleoconch begins. In contrast and difference to the larval shell of Promathididae the size of the fully grown shell of the larva measures around or more than 0.5 mm. The onset of the teleoconch is always abrupt and connected with a change in sculpture.

The family is based on the genus *Mathilda* SEMPER, 1865 has the type species *Mathilda quadricarinata* (BROCCHI, 1814) that lives in the sub-littoral rubble down to 30 m depth in the Mediterranean Sea of southern Italy (WENZ, 1937, fig. 1884). The family Mathildidae has species from the Triassic to the Recent, but *Mathilda* according to WENZ (1937) appears in the Cretaceous, which is here considered as plausible due to the size of the protoconch, which is larger in *Mathilda* than in the Jurassic and Triassic species which could be here placed with a family Promathididae with generally smaller larval shell as that in the Mathildidae.

*Mathilda* has the elongated shell 3 to 4 cm in height, but may also be small, has more than 10 whorls, and shows a sculptural pattern consisting of strong spiral costae crossed by fine to coarse radial ribs which are arranged to form a reticulated pattern. The first 5–9 whorls have at least two main spiral keels and additional, secondary ones may be added later. The aperture is of rounded outline, and the margin of the outer lip is distinct. The inner lip is represented by a glazed over surface on the prior whorl. The protoconch is sinistral, forms a low helical coil, and is immersed in the apex of the teleoconch at 90° or less. The embryonic shell may lie free at the apex or may be partly covered by the first whorl of the teleoconch.



A family Promathildidae could be diagnosed as follows: The protoconch is sinistral, measures approximately 0.2 mm in diameter and consists of an embryonic whorl that is largely covered by a smooth larval whorl that is sometimes ornamented by folds. The protoconch has left-handed coiling and is attached to the teleoconch in a more or less inclined position. The first whorl of the teleoconch is sculptured by two spiral ribs which are crossed by smaller axial ribs. The anterior spiral develops into a keel and additional spiral ribs appear on later whorls. Species of *Promathildia* may also be small, may have more than 10 whorls, and sculptural patterns consisting of strong spiral costae crossed by fine to coarse radial ribs, forming a reticulate pattern.

Regarding shell shape and ornament as well as orientation of the larval shell on the apical adult shell species of the Promathildidae come very close to those of some the Mathildidae as they appear with the Cretaceous. A factor uniting all is the reticulate sculptural pattern of usually dominant spiral cords and axial costae that may be of different width. The size of the larval shell lies between 0.2 mm and 0.4 mm in width among *Promathildia* species. Characteristic species are from the Triassic St. Cassian Formation and differ predominantly regarding the protoconch in which *Promathildia decorata* (KLIPSTEIN, 1843) and *Promathildia sculpta* (KITTL, 1894) have ornament of folds on their larval shells (BANDEL, 1995, pl. 4).

***Promathildia* sp.** (*Teretrina* COSSMANN, 1912, *Jurida* GRÜNDEL, 1973) (Pl. 13/1–6) has its elongated slender shell with 2 cm length and seven whorls of the teleoconch and a protoconch of the size of 0.2 mm that lies almost flat on its apex. The embryonic and larval shells are coiled in opposite direction to the teleoconch. Ornament on the first teleoconch consists of two spiral ribs, of which the upper is largest. Fully grown individuals may have had 10 whorls or even more. Its sculptural pattern consists of strong spiral costae crossed by finer radial ribs, forming a reticulated pattern. On the first 3 whorls of the teleoconch two spiral keels are present and later whorls have three spirals, of which first the upper and later the median one is the strongest, the lower smaller and the upper one that appears later the smallest. Distance of spiral ribs differs. The upper one may be weakly developed from the first whorl onwards but more commonly appears on the third whorl of the teleoconch. The last formed whorl has a corner and on the concave whorl side, that becomes partly covered by the following whorl and the additional spiral rib here will lie as a ridge in the suture. The aperture has rounded outline but fully grown individuals were not encountered. The inner lip is represented by a glazed over surface on the prior whorl.

The protoconch is sinistral, forms a low helical coil, and measures only little more than 0.2 mm in diameter and has its umbilicus pointing upwards. It is immersed in the apex of the teleoconch at almost 180°, but its axis of coiling deviates slightly from the axis of coiling of the teleoconch. The embryonic shell is approximately 0.08 mm wide with clear sinistral coiling mode. Its ornament consist of very fine and regular groove and ridge pattern and the margin of its aperture is thickened to form a rim that separates it from the larval shell (Pl. 13/6). This larval shell has only a pattern of simple growth lines, with the first seen on the very last portion of the embryonic shell. Whorls of the larval shell are evenly rounded and almost plane in coiling mode. The shell formed during larval life consists of less than one complete whorl. The first growth lines indicate the process of hatching from the egg and the beginning of life as plankton living larva. At the end of this larval stage the aperture became thickened (Pl. 13/4–5). Begin of teleoconch growth is with strong change in ornament as well as shape of the whorl from plane coiling to high helical coiling.

**Discussion:** Modern species belonging to *Mathilda* have been described by BIELER (1995) and their larval shell, as has been measured for 13 species, is more than 0.4 and up 0.6 mm wide in diameter. Even though general shape of the teleoconch and the orientation of the protoconch of *Mathilda* resembles closely that of the fossil species, which have been included here, the differences in protoconch size is obvious. It is used here to place the fossil species into a different genus, and *Teretrina* has been proposed by COSSMANN (1912). The *Teretrina* cf. *bianor* as documented by SCHRÖDER (1995, pl. 9, figs 5–8) has a much wider shell angle than that in the species here which rather resembles *Mathilda* with more slender shell as documented by SCHRÖDER (1995, pl. 8, figs 1–9) regarding ornament and shape of the teleoconch. The orientation of the protoconch differs in *Promathildia* sp., since it lies less inclined on the apex and also has no folds on its larval shell. According to the classification adopted by GRÜNDEL & NÜTZEL (2013) the mathildid species described here could be a member of *Jurida* GRÜNDEL, 1973 that is based on *Promathildia (Teretrina) concava* WALTER, 1951 from the Mid-Jurassic of Poland. This *Teretrina* COSSMANN, 1912 resembles the now living *Mathilda* and was considered to represent a subgenus to *Promathildia* by WENZ (1936). It was also connected with a Triassic type, *Turritella bolina* MÜNSTER, 1841 Cassian Formation. GRÜNDEL & NÜTZEL (2013, fig. 4 C) stated that actually *Mathilda janeti* COSSMANN, 1885 is the type as documented by them and according to these authors it should be determined as a species of *Clathrobaculus* COSSMANN, 1912.

The Triassic *Promathildia* ANDREAE, 1887 with several similar species which lived in the tropical reef environment of the Late Triassic Tethys Ocean in the area that is now in the Southern Alps has the protoconch that is essentially like that of *Mathilda* but of smaller size (BANDEL, 1995). The early whorls of the teleoconch have only one dominant spiral keel that is crossed by minor axial elements, as is the case in *Promathildia* so from Sakaraha. In case of the Triassic *Promathildia* it is accompanied by none to several minor spiral elements. Axial ribs and growth lines may form tubercles and raised ridges where they cross the spiral keels and costae. As has

been discussed in detail by BANDEL (1995) the type to the genus *Promathildia* is *Fusus subnodosus* MÜNSTER, 1841 as again described by KITTL (1894) under the name *Promathildia subnodosa* and again by BANDEL (1995). The genus is thus based on *Promathildia subnodosa* (MÜNSTER, 1941) as described by KITTL (1894) and again by BANDEL (1995, pl. 1, figs 5–6, pl. 2, figs 1–4, 6–7).

GÜNDEL & NÜTZEL (2013) suggested an inclusion of *Promathildia* in the Mathildidae (here classified as Promathildidae). Based on Jurassic species a number of new types have been suggested according to the number of spiral ribs which appear on the first whorls of the teleoconch. Here *Jurilda* GRÜNDEL, 1973 has two spiral ribs, *Tricarida* GRÜNDEL, 1973 has three such ribs, *Turrithilda* SCHRÖDER, 1995 has four and more spirals. A species called *Teretrina microstriata* SCHRÖDER, 1995 from the Valanginian of Poland has the protoconch with larval shell almost within the plane of the apex and with ornament of axial folds, which contrasts of *Mathilda schmidtii* (WALTER, 1951) as described by SCHRÖDER (1995) from the Jurassic in Poland with similar ornament of the teleoconch. GRÜNDEL (1997, pl. 1–3) noted in case of *Mathilda schmidtii* three spiral ribs on the first whorl of the teleoconch, otherwise it is very close to the species from Sakaraha. The protoconch is similar to that of *Mathilda orthocosta* SCHRÖDER, 1995 from the Valanginian of Poland (SCHRÖDER, 1995, pl. 8, figs 1–5) which has only two spiral ribs on the first whorl of the teleoconch. GRÜNDEL (2003, fig. 3, 1–3) illustrated a very similar species derived from an ice transported erratic boulder of Callovian age as *Promathildia vierowiensis* GRÜNDEL, 2003. Very similar teleoconch morphology is with *Tricarida* sp from Mistelgau as documented by SCHULBERT (2009, fig. 15), and the main difference is the orientation and ornament of the protoconch that is more inclined and has folds on its larval whorls.

Species of *Promathildia* from St. Cassian Formation have one dominant rib as first teleoconch sculpture with one dominant spiral rib, while *Tirolthilda* BANDEL, 1994 has here two almost equal ribs, and *Turrithilda* BANDEL, 1994 has four such ribs (BANDEL, 1995). GRÜNDEL & NÜTZEL (2013) suggested that the richly diversified Mathildoidea of the Triassic as documented by BANDEL (1995) declined in regard to their diversity at the Triassic-Jurassic boundary with only the *Jurilda* relation surviving, which is thus very close in shape to species which were considered to belong to the genus *Promathildia* among the species from St. Cassian. Thus accepting these suggestions, from the point of view regarding the shape of the shell, a distinction of Promathildidae from Mathildidae is only possible by the size of the larval shell, which is larger in the later. Regarding their occurrence in the stratigraphic record gastropods with *Promathildia* – *Mathilda* shaped shells which are older than Early Cretaceous mostly belong to the Promathildidae and those that lives later are representatives of Mathildidae. Among Jurassic species *Tricarilda* often has its heterostrophic protoconch axially wrinkled. That of the *Tricarilda schoberti* from Unterstürmig has the protoconch more inclined than is the case in the species from Madagascar, while the ornament of the teleoconch is similar but the median rib less expressed (NÜTZEL & GRÜNDEL, 2015, pl. 15, figs a–i).

The genotype is *Mathilda (Tricarilda) plana* GRÜNDEL, 1973 from the Middle Jurassic of northern Germany and Poland (GRÜNDEL, 1997, pl. 3). *Erratothilda* GRÜNDEL, 1997 for example is based on *Eucycloidea erratica* GRÜNDEL, 1990 that was renamed and newly described by GRÜNDEL (1997, pl. 7, figs 102–107). Similar species from the Albion of the Mahajanga Basin were described by KIEL (2005), such as *Mathilda bandeli* KIEL, 2005 and *Gymnothilda pagodoidea* KIEL, 2005. *Mathilda campania* KIEL & BANDEL, 2001 from the Tremp Basin in northern Spain is a Cretaceous species of this genus since its larval shell measures 0.65 mm in diameter (KIEL & BANDEL, 2001). Mathildoidea, family Mathildidae is represented in New Zealand by *Tricarida cancellata* BANDEL et al., 2000 that is rather similar to mid European species of this Jurassic genus and close to some species the modern *Mathilda* (BANDEL, GRÜNDEL & MAXWELL, 2000, pl. 9, figs 1–3, 5). It differs from the *Teretrina (Jurilda) madagascariensis* from Madagascar by the ornament of the teleoconch of three almost equal spiral ribs and also by having a larger apical angle. Shape and size of the larval shell is similar, but in case of *Tricarilda cancellata* the larval shell is ornamented by folds.

Order **Allogastropoda** HASZPRUNAR, 1985, super-family Valvatoidea GRAY, 1840 is characterized by species with a small sized *Trochus*-like to discus-shaped shell with a heterostrophic protoconch that coils in sinistral mode around the same axis as the dextral teleoconch. The outline of the aperture is simple. In living species of this taxon the gill and especially the tentacle of the mantle is characteristic (SALVINI-PLAWEN, 1981; RATH, 1988), the osphradium with unique anatomy lies on the left side right besides the mantle opening (HASZPRUNAR, 1985, 1988), and the morphology of the sperm is also characteristic to the super-family (HEALY, 1991). The radula can have seven teeth in a row (taenioglossate) as is the case in freshwater *Valvata* (BANDEL, 1984) and the marine *Cornirostra* PONDER, 1990 (PONDER et al., 1998, fig. 15, 179D, WARÉN et al., 1993). The super-family Valvatoidea has been extended into the past by BANDEL (1991, 1995), SCHRÖDER (1995), HEIDELBERGER & BANDEL (1999). Transition from species living in the sea to such living in fresh water was noted among the Provalvatidae BANDEL, 1991 among Jurassic fossils. Among living species BIELER et al. (1998) described a *Cornirostra floridana*. The genus *Cornirostra* PONDER, 1990 has very similar shell shape as noted in *Vitrinella* C.B. ADAMS, 1850, and BANDEL (2010) suggested that it actually represents a species of the genus *Vitrinella* with the type *Vitrinella helicoidea* C.B. ADAMS, 1850. Here the shell that is about 1 mm wide with its 0.15 mm wide

protoconch with sinistral embryonic whorl. Vitrinellidae BUSH, 1897 are based on *Vitrinella helicoidea* (WENZ, 1938, fig. 1284). PONDER (1990) included *Tomura* in his concept of the Cornirostridae, but Vitrinellidae BUSH, 1897 is the older taxon that also represents the Cornirostridae PONDER, 1990, as was documented by BANDEL (2010). Marine species with similar characters of their shell as those noted among the living ones have been recognized in deposits as old as Devonian (BANDEL & HEIDELBERGER, 2002).

The family that is based on *Vitrinella* has a smooth and rounded shell with open umbilicus very similar to that of the genus *Bandellina* SCHROEDER, 1995 which is based on *Bandellina laevissima* SCHRÖDER, 1995 from the Valanginian of Poland (SCHRÖDER, 1995, pl. 7, figs 9–17). This type of the genus is almost identical with *Bandellina* sp. in shape and characters of the protoconch, but has half a whorl less teleoconch when fully grown (Pl. 13/7–9). The lowly coiled smooth shell is provided with a left-coiled protoconch of more than two whorls and with the larval shell ending in a rim. The teleoconch is low coiled dextral and consists of two. The shell consists of 3.3 whorls of which 1.8 belong to the protoconch. The aperture is round and the protoconch ends in a varix. Its whorls are smooth and change from sinistral coiling into plane spiral coiling in the larval shell and to dextral coiling in transition to the teleoconch. The protoconch is about 0.13 mm wide with a 0.08 mm wide embryonic part. A distinct growth line distinguishes the embryonic whorl from the larval part of the protoconch as does the mode of coiling which changes from distinctly left coil to plane coil and a rim distinguishes from the teleoconch, while in regard to shape of the whorl and ornament no difference is noted. The teleoconch is dextral with rounded whorls almost coiled in a plane, but wide aperture and open umbilicus. Its diameter is less than 1 mm.

**Discussion:** Among the Triassic and Jurassic species with a shell as found among the Cornirostridae and Hyalogyridae of the modern marine fauna the genera *Bandellina* SCHRÖDER, 1995, *Alexogyra* BANDEL, 1996, *Carboninia* BANDEL, 1996, and *Doggerostr* GRÜNDEL, 1998 are available. *Doggerostr riedeli* GRÜNDEL, 1998 as illustrated by GRÜNDEL (1998, pl. 5, figs 55–59) documents a species from the Bathonian of Poland, and differs from *Bandellina* sp. from Sakaraha by having half a whorl less of the teleoconch and the margin of the protoconch distinct, but not thickened. The difference in shell shape between the species of these genera is small and not sufficient to separate genera as has been noted by KAIM (2004). All have a smooth sinistral protoconch with embryonic whorl clearly left in coiling.

*Bandellina* sp. closely resembles *Alexogyra* BANDEL, 1996 but has a more plane upper side of the shell (BANDEL, 1996, fig. 16 a, c, d). Several minute, more or less plane spiral heterostrophic taxa from the Triassic and Jurassic of Central Europe are known (SCHRÖDER, 1995; BANDEL, 1996; GRÜNDEL, 1998; KAIM, 2004), which have been placed into the family Sturaxidae BANDEL, 1996. *Bandellina miniperforata*, originally as *Carboninia*, by GRÜNDEL (1998), was placed in the genus *Bandellina* by KAIM (2004) and *Bandellina riedeli* (GRÜNDEL, 1998), originally as *Doggerostr*, was also placed with the genus *Bandellina* by KAIM 2004. They are lowly coiled and both have been described from the Jurassic of Poland. The difference between the Jurassic *Bandellina riedeli* and the Triassic *Bandellina cassiana* BANDEL, 1996 are minute with the protoconch of the Triassic species consisting of two instead of 1.5 whorls.

*Bandellina* sp. from Sakaraha has a dextral teleoconch, while that of *Schobertinella heterogyra* NÜTZEL & GRÜNDEL, 2015 is almost plane but coiled slightly to the left regarding its embryonic shell. The teleoconch acquires a left coil again- while retaining a plane top. *Schobertinella* NÜTZEL & GRÜNDEL, 2015 was placed in the super-family Omalogyroidea SARS, 1878, family Omalogyridae SARS, 1878 from which only living species are known. The embryonic whorl here is coiled to the left, in the larval shell the shape changes to plane coiling (NÜTZEL & GRÜNDEL, 2015, pl. 18, figs K–M). The succeeding teleoconch has plane coiling mode with a concave and a flat side. *Schobertinella* closely resembles *Gyraulus loryi* COQUAND, 1855 from the Jurassic/Cretaceous transition as was documented by BANDEL (1991, pl. 6, figs 11–20, pl. 7, figs 1–10). Here the upper side, as in living *Gyraulus*, is flat and the lower side has an open umbilicus and is concave, with the protoconch sinistral. Thus the occurrence of *Gyraulus heterogyra* (NÜTZEL & GRÜNDEL, 2015) extends the occurrence of the genus *Gyraulus* further back, than the *Gyraulus loryi* from the Jurassic-Cretaceous boundary of the French Jura and *Planorbis fisheri* ARKELL, 1840 of the Purbeckian of England. Also the name *Anisopsis* HUCKRIEDE, 1967 based on a species that looks like a modern *Gyraulus* from the Weald of northern Germany (HUCKRIEDE, 1967) would have been available for *Schobertinella*.

The *Cylindrobullina* AMMON, 1878 relation represents the potential stem group to the Opisthobranchia and appears in the Triassic. The earliest undoubted members with a *Cylindrobullina*-like shell and the protoconch clearly heterostrophic are from the Early Triassic (PAN et al., 2003; NÜTZEL, 2005). No species of this super-family are known from the Late Paleozoic (see BANDEL, 2002 for references). *Cylindrobullina* has been placed into or near a super-family Acteonoidea ORBIGNY, 1843 since its shell resembles that of living *Acteon* MONTFORT, 1810 but even more some modern species of the family Retusidae THIELE, 1926. Modern *Retusa obtusa* (MONTAGU, 1803) from shallow European seas can have a shell that closely resembles the Triassic and Jurassic *Cylindrobullina*. WENZ & ZILCH (1960) distinguished here only *Sulcoactaeon* Cossmann, 1895 and *Actaeonina* (including *Cylindrobullina*) from Jurassic occurrences. Among shell bearing Cephalaspidea, with *Retusa* –

*Cylindrobullina* like shell shape, anatomically distinct groups are hidden, as was documented by MIKKELSEN (1996, 2002). Acteonidae differ by having spiral ribs.

Cylindrobullinidae have been interpreted by BANDEL (1994) to unite Triassic and Jurassic species with a shell that is egg-shaped in outline with a conical or step-like spire and growth lines as the major sculptural elements. The larval shell is coiled to the left and twists into the teleoconch that is coiled to the right at the very end of its whorls. The small shell of *Cylindrobullina* has its aperture constricted toward the posterior and widened toward the front. The inner lip rests on the slightly bent columella (central axis of coiled shell) and forms a narrow low fold in its frontal portion and a narrow slit on the spindle. The protoconch is a left-handed, with low-spire attached to the teleoconch at an angle of 90° to about 45° (BANDEL, 1994, pl. 1, figs 1–7, 12).

*Cylindrobullina* sp. individuals from Sakaraha (Pl. 14/11, Pl. 15/1–3, 5, 6 and 11) were collected in large number. They were found to be of variable shape and the ramp on their teleoconch whorls may be accompanied by one, sometimes two and rarely three spiral lines. The apical shoulder in some specimen forms a corner, in others it is rounded and a change in the degree of angularity may occur from one whorl to the next. The protoconch is upright and the angle formed with the teleoconch is slightly smaller than 90°. Growth lines on the whorls of the teleoconch are more or less sinuous and their shape may or may be indistinct or distinct and they can be almost rib-like. The protoconch consists of almost two whorls with the last portion of the larval whorl changing from sinistral coiling into the plane spiral to connect with the dextral teleoconch. The embryonic whorl measures approximately 0.1 mm in diameter and the protoconch is about 0.2 mm wide. It is attached to the teleoconch in a way that the embryonic whorl is only partly covered by the first whorl of the teleoconch. The first two whorls of the teleoconch develop a shoulder and in the second or third whorl of the teleoconch the corner may become angular and growth line pattern more pronounced.

**Discussion:** The genus *Cylindrobullina* AMMON, 1878 is the representative of the super-family Cylindrobullinoidea WENZ, 1947 and according to WENZ & ZILCH (1960) has the protoconch coiled to the left with twist into the dextral teleoconch where whorls end. The shell is egg-shaped in outline with a conical or step-like spire and growth lines as the major sculptural elements. The whorls are separated by a flattened ramp or deep suture. The aperture is elongate and oval and the spindle is thickened but bears no folds. The protoconch axis forms an angle from 90° to less than about 45° with that of the teleoconch.

Cylindrobullinidae have been interpreted by BANDEL (1994) to unite Triassic and Jurassic species with a shell that is egg-shaped in outline with a conical or step-like spire and growth lines as the major sculptural elements. The larval shell is coiled to the left and twists into the teleoconch that is coiled to the right at the very end of its whorls. The small shell of *Cylindrobullina* has its aperture constricted toward the posterior and widened toward the front. The inner lip rests on the slightly bent central axis (columella) and forms a narrow low fold in its frontal portion and a narrow slit on the spindle. The protoconch is a left-handed, with low-spire attached to the teleoconch at an angle of 90° to about 45° (BANDEL, 1994, pl. 1, figs 1–7, 12). The genotype is *Tornatella scalaris* MÜNSTER, 1841 from the Late Triassic St. Cassian Formation (KOKEN, 1889; SCHRÖDER, 1995), and not the Jurassic *Tornatella fragilis* DUNKER, 1847 as was suggested by COSSMANN (1895) and was accepted by KAIM (2004). As stated by GRÜNDEL (2010) the Jurassic *Tornatella fragilis* is not known well and its protoconch is not preserved.

*Cylindrobullina* sp. of Sakaraha either represents a whole group of species, but more likely represent a species with rather variable shell among individuals of the same species. The relative height of the spire differs from individual to individual. It is low in case of the individual on Pl. 15/11 and high in case of the specimen on Pl. 15/1. The expression of the ramp and corner on the whorls of the teleoconch differs, as does its ornament by two spiral ribs (Pl. 15/11), to one or indistinct spiral lines or ribs. In cases without a corner the difference to *Cerithellopsis* is minute (Pl. 14/8–9). Ornament may consist of indistinct growth lines (Pl. 15/11) or distinct growth lines to fine ribs which follow growth lines (Pl. 15/5). Growth lines may be simply and evenly curving or have sinuous shape. The ramp of the shoulder may have strongly curving growth lines almost forming a ribbon that consists of curving growth lines (Pl. 15/5).

Compared with species distinguished by GRÜNDEL (1997) from the German Jurassic, *Cylindrobullina* sp. from the Jurassic of Madagascar could interconnect *Cylindrobullina schneideri* GRÜNDEL, 1997 with *Sinuarbullina ansorgi* GRÜNDEL, 1997 as illustrated from the mid-Jurassic of Poland by KAIM (2004, fig. 128A). With the shell a little more slender it would intermediate to *Sinuarbullina gnaszynensis* KAIM, 2004 (KAIM, 2004, fig. 128B). *Sinuarbullina* GRÜNDEL, 1997 represents a slender *Cylindrobullina* with growth lines well visible and rounded ramp. Shells with growth lines more pronounced were classified by GRÜNDEL (1997, pl. 3, figs 4–7) as members *Costactaeon* with the type *Costactaeon schroederi* GRÜNDEL, 1897 and he described from northern Germany 4 species of that genus which would fall into the variations recognized among the individuals of *Cylindrobullina* sp. from Sakaraha. GRÜNDEL & NÜTZEL (1998) noted that differentiation of *Actaeonina* from *Cylindrobullina* is difficult due to variability of the shell shape, but they created several genera to accompany these potential variations. Among early Jurassic species they determined individuals with egg shaped shell as *Actaeonina submoorei* KUHN, 1936, another with more expressed shoulders was determined as *Actaeonina domeria* GRÜNDEL & NÜTZEL, 1998 (pl. 5, figs 2–4). They raised the subspecies *Actaeonina* (*Ovactaeonina* COSSMANN, 1895) of SCHRÖDER (1995) to generic level and describes several species such as *Ovactaeonina franconica* (KUHN, 1935),

*Ovactaeonina sendelbachensis* (KUHN, 1936) and their *Ovactaeonina kalchreuthensis* GRÜNDEL & NÜTZEL, 1998 (pl. 6, and pl. 7). GRÜNDEL (1999) illustrated the later two also from Greifswald and added a new species with very slender shell as *Ovactaeonina pommerana* (pl. 13, figs 3–8 and pl. 14, figs 1–4). All these species have similar teleoconch and were suggested to differ in regard to the shape of their protoconch and its attachment to the teleoconch. They could also be included within the genus *Melampoides* YEN, 1951 as described by BANDEL (1991, pl. 5, figs 4–11), as *Melampoides jurassicus* BANDEL, 1991. Even more new genera were suggested by GRÜNDEL & NÜTZEL (2012) when they created *Domerionina* GRÜNDEL & NÜTZEL, 2012 based on *Actaeonina domeria* formerly determined as *Cylindrobullina domeria* (NÜTZEL & HORNUNG, 2007, pl. 1, fig. 3; GRÜNDEL, 2008, pl. 7, fig. 13; NÜTZEL, 2008, pl. 3, fig. 1; SCHUBERT et al., 2008, figs 5H–I). Based on the shape of growth lines and the presense or absence of a furrow of the inclination of the ramp they distinguished more species of their *Domerionina*. NÜTZEL & KAIM (2014) transferred even the Triassic species *Cylindrobullina pralongiana* BANDEL, 1994 into *Domerionina*, but remarked that it could also be placed with *Sinuarbullina*. *Ovactaeonina* as described by SCHRÖDER (1995) changed name into *Cossmannina* GRÜNDEL & NÜTZEL (1998) and a *Cossmannia kalchreuthensis* (GRÜNDEL & NÜTZEL, 2012) was added that had originally been described as *Ovactaeonina* and NÜTZEL & GRÜNDEL (2015) distinguished species of more or less broad teleoconch and more or less convex whorls.

It is here suggested to interpret all these similar species as members of the genus *Cylindrobullina*. All of them belong within the family Cylindrobullinidae. Very similar shell shape can be noted also among members of the genus *Ptychostylus* SANDBERGER, 1870 that was first described from the German Wealden and extensively by HUCKRIEDE (1967) and again from the same age of the French Jurassic by BANDEL 1991 (pl. 4, figs 18–20, pl. 5, figs 1–3).

The genus ***Sulcoactaeon*** COSSMANN, 1895 defines an egg-shaped shell with short spire and a large body whorl that is sculptured by spirally arranged grooves and ridges and not axial ribs. Whorls are well rounded and separated by a deep suture or a narrow ramp. The umbilical slit is almost closed by callus of the inner lip and the spindle is short. The genotype is *Actaeonina striatosulcatus* ZITTEL & GOUBERT, 1861 from the Late Jurassic of France (GRÜNDEL, 1997).

*Sulcoactaeon* sp. (Pl. 15/4, 15/7–10) from Sakaraha has a smooth protoconch that lies strongly inclined in the apex of the teleoconch, and forms an angle of about 90° between axes of coiling of the larval shell and that of the teleoconch. Before meeting the teleoconch the larval shell has turned from the left handed coiling into dextral coiling. The ornament of the teleoconch consists of strong, about equally wide spiral ribs which are separated from each other by narrower grooves. The groove next to the suture and below it is wider than the following ones and forms a narrow ramp.

The shell with two whorls of the teleoconch measures 1.2 mm in height and about 0.8 mm in width. About 20 broad, somewhat angular ribs separated by more narrow, rounded grooves ornament the body whorl which occupies two thirds of the shell height. On the whorls of the spire approximately 10 ribs remain visible. The spiral ornament is transected by fine, axially arranged growth lines, best visible within the grooves. Here they produce a regularly pitted appearance. The inner lip of the aperture is thickened by callus and raised to cover a slit-like umbilicus. The inner lip is without folds and simple and smooth.

The protoconch consists of almost two whorls and is approximately 0.2 mm wide and high (Pl. 15/7, 15/9, 15/10). Its smooth whorls have left handed coiling and *Natica*-like shape with a wide umbilicus. In the very last portion of the larval shell the twist from the left into the right coil is apparent. The larval shell is well distinguished from the teleoconch by an increment of growth as well as the first spiral sculpture of the teleoconch. The axis of coiling of the protoconch is at about a right angle with the spindle axis of the teleoconch.

**Discussion:** *Sulcoactaeon* may be placed with the super-family Acteonoidea ORBIGNY, 1842 and here Acteonidae with *Acteon*-like shell shapes. The modern Acteonoidea hold the family Acteonidae as described by THOMPSON (1976) and Bullinidae RUDMAN, 1972 with solid shells and the Hydatinidae with thin and reduced shell (BURN & THOMPSON, 1998). *Acteon* MONTFORT, 1810 is based on *Voluta tornatilis* GMELIN, 1788 from the North Sea (see THOMPSON, 1976, fig. 49), has a height of the shell between 3 and 15 mm, its shape is ovate with low to moderately elevated spire. The protoconch is heterostrophic and often partly buried within the teleoconch. About four whorls of the teleoconch are present with the last whorl quite wide and ornamented by narrow spiral grooves and spiral rows of pits. The aperture is large with the anterior end rounded and posterior end constricted and its inner lip with a single plait at its posterior end. *Bullina* FÉRUSAC, 1822 with *Acteon*-like shell has a smooth inner lip.

Acteonoidea have been recognized from the Middle Jurassic (COSSMANN, 1895; SCHRÖDER, 1995; GRÜNDEL, 1997) in a continuous line to the modern species. Among species from the Jurassic of Germany *Sulcoactaeon sendelbachensis* NÜTZEL & GRÜNDEL, 2015 has spiral cords on the whorl face and a larval shell that measures 0.5 mm (NÜTZEL & GRÜNDEL, 2015, text-fig. 4). *Sulcoactaeon pullus* (KOCH & DUNKER, 1837) is described by SCHRÖDER (1995, pl. 11, figs 11–15) differs by having a distinct ramp with furrow. *Bullina (Sulcoactaeon) zealata* BANDEL, GRÜNDEL & MAXWELL, 2000 differs from *Sulcoactaeon* sp. from Sakaraha by having no shoulder below the suture and a slightly wider protoconch that is situated within the teleoconch forming a different angle with it.

*Sulcoactaeon polonicus* KAIM, 2004 from the Mid-Jurassic and *Sulcoactaeon wawalensis* KAIM, 2004 from the Valanginian of Poland have an indistinct ramp on their teleoconch whorls and their spiral ornament consists of narrow furrows and the protoconch has almost the same axis of coiling as the teleoconch (KAIM, 2004).

*Leucotina stolarskii* KAIM, 2004 from the Valanginian of Poland differs very little from the two species from the Jurassic of New Zealand and that of Madagascar (KAIM, 2004, fig. 89). Regarding the morphology of its protoconch it is closer to *Bullina zealata* BANDEL et al., 2000, while the teleoconch resembles that *Sulcoactaeon* sp., but has no recess below the suture. A living species of *Leucotina* from Aqaba resembles *Bullina-Sulcoactaeon* and also the *Leucotina* as determined by KAIM (2004, fig. 89). The transition between protoconch and teleoconch is similar. *Leucotina* is based on a living species of the Pyramidelloidea GRAY, 1840 in which the protoconch does not twist into the dextral shell shape before begin of teleoconch formation, while in *Acteon* and relation this appears to be the case. Therefore KAIM (2004) may be quite correct in regarding his Early Cretaceous species as of the Amathinidae as belonging to the Pyramidelloidea GRAY, 1840. In that case it represents the oldest known pyramidellid species, while more species of this so species- rich group appear only later with the Late Cretaceous (SOHL, 1964; DOCKERY, 1993; BANDEL & DOCKERY, 2005). It can thus not be excluded that *Sulcoactaeon* sp. from the Mid-Jurassic of Madagascar represents an early member of the Pyramidelloidea. With the genus *Heteronerita* GRÜNDEL, 1998 from an erratic boulder of Mecklenburg/North-Germany GRÜNDEL (1998, pl. 6, figs 70–81, pl. 7, figs 82–91) suggested a family Heteroneritidae GRÜNDEL, 1998. Thus Pyramidelloidea may hold Jurassic species with conical *Trochus*-shaped teleoconch with ornament of simple spiral grooves and ridges and simple drop-shaped aperture. As in *Sulcoactaeon* sp. from Madagascar the protoconch is coiled to the left and smooth and sharply delimited from the teleoconch.

The genus *Ceritellopsis* FISCHER, 1961 (= *Consobrinella* HAAS, 1953) includes shells with ovoid-conical shape and turreted spire with pronounced shoulders. Apical whorl faces are flattened and form a corner with the lateral faces. The sculpture consists of broad axial ribs and fine growth lines which run obliquely backward in the apical shoulder. The aperture is of nearly elliptical outline. The inner lip is accompanied by a narrow umbilical niche. The protoconch is coiled left handed and forms an angle between 45° and 90° between its axis of coiling and that of the dextral teleoconch. *Ceritellopsis* resembles in shape *Cylindrobullina*, but has a longer shell. The genus does not occur before mid-Jurassic time and its species were found to be connected to brackish water environment (HUCKRIEDE, 1967; BANDEL, 1991; GRÜNDEL, 1997, 2000).

The slender *Ceritellopsis* sp. from Sakaraha (Pl. 13/10–12, Pl. 14/1–6) has axial folds crossed by three spiral folds, in quite variable arrangement. The spire is almost as high as the body whorl. The protoconch consists of almost two whorls and is about 0.1 mm in diameter. The first whorl is only partly covered by the first whorl of the teleoconch and about 0.07 mm wide. The larval whorl twists at its end from sinistral to dextral coiling. The protoconch with its two whorls is of rounded shape with *Helix*-like coiling and 90° angle with the teleoconch. First two teleoconch whorls have curving growth lines, a narrow rounded shoulder, and ornament of spiral elements appears on the third whorl. The first whorl of the teleoconch is rounded smooth and has no shoulder. The shoulder below the suture appears in the second whorl of the teleoconch and ornament begins in the third whorl. Axial ribs cross the corner of the flattened ramp and become weaker further down on the flattened sides. In the fourth whorl of the teleoconch low spiral ribs appear, one below the corner, one in the middle and a third at the corner to the base. This lower rib is covered by the succeeding whorl. The base is conical and smooth.

**Discussion:** *Ceritellopsis* from the Late Jurassic of North Germany and from the transitional beds from Jurassic to Cretaceous in the Swiss Jura Mountains (BANDEL, 1991, pl. 3, fig. 21, pl. 4, figs 1–5) resembles *Actaeonina-Cylindrobullina*, but the spire is more slender, sutures are less pronounced and the aperture is shorter (HUCKRIEDE, 1967, pls. 18, 19). *Ceritellopsis plicatula* (HUCKRIEDE, 1967) as it occurs in the Weald-deposits of North Germany (Jurassic-Cretaceous transition) resembles the *Ceritellopsis* sp. from the Jurassic of Madagascar, but has different ornament.

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Plate 1

- Fig. 1: *Hamusina* cf. *maxwelli* in dorsal view with three whorls and 1.5 mm in width.
- Fig. 2: *Hamusina* cf. *maxwelli* in side view with begin of the conical shell and shell height of 1.2 mm.
- Fig. 3: *Guidonia* sp. seen from the side with shell width of 1.2 mm.
- Fig. 4: *Guidonia* sp. with shell in basal view, with shell width of 1.3 mm.
- Fig. 5: *Guidonia* sp. seen from the side with the shell of 0.9 mm in width.
- Fig. 6: Detail of Pl. 1/5 of *Guidonia* sp. demonstrating the construction of the shell with thick inner nacre and outer acicular crossed lamellar structure with the shell 0.15 mm thick.
- Fig. 7: Apical view of *Guidonia* sp. with the shell 1.3 mm wide, and the detail in Pl. 1/8.
- Fig. 8: Detail to Pl. 1/7 with the smooth embryonic whorl of 0.2 mm in width.
- Fig. 9: The juvenile shell of *Ueckerconulus* sp. almost 1 mm in height resembles the spire of *Turcia clathrata* as illustrated by KAIM (2004) with nacreous structure.
- Fig. 10: As in Pl. 1/9 another juvenile shell of 0.8 mm in height with smooth embryonic whorl of *Ueckerconulus* sp.
- Fig. 11: Early whorls of *Eucycloidea madagascariensis* with the shell approximately 0.7 mm wide.
- Fig. 12: Protoconch of *Eucycloidea madagascariensis* ends in a rim on the aperture and measures 0.2 mm in diameter.

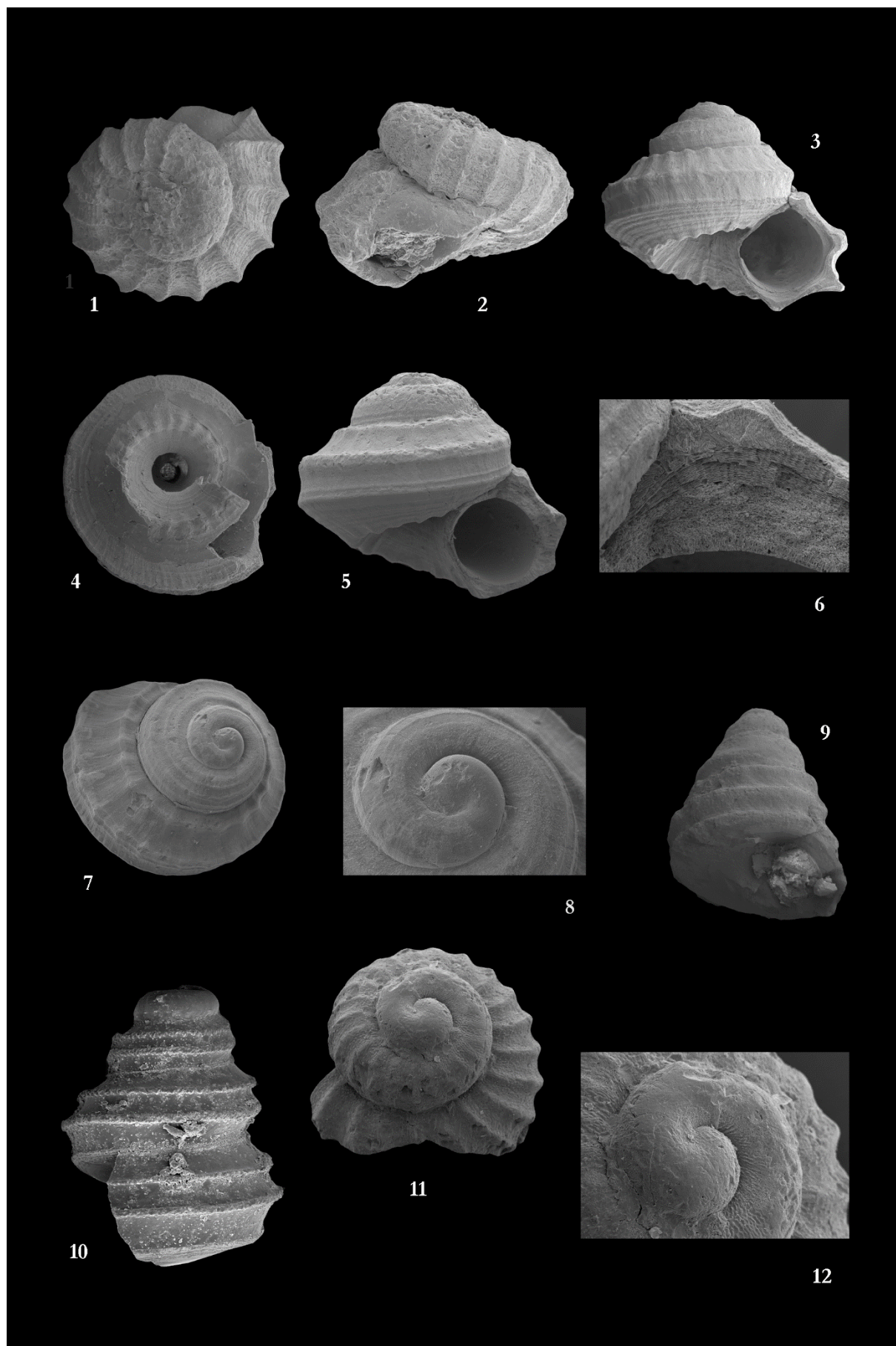


Plate 2

- Fig. 1: Side view of shell on Pl. 1/1 of *Eucycloidea madagascariensis* with shell approximately 0.6 mm high.
- Fig. 2: Embryonic shell of *Anomphalus* sp. of approximately 0.2 mm in diameter.
- Fig. 3: *Anomphalus* sp. with 1 mm wide shell and details of shell structure seen in Pl. 2/9.
- Fig. 4: Crossed lamellar structure in case of *Anomphalus* with the width of each single needle of about 0.2 micron.
- Fig. 5: Intercalated nacre layer of *Anomphalus* sp. in a shell that is approximately 0.3 mm thick. The fractured shell has a shell layer of prismatic type on the interior callus deposits, a central nacreous layer and an outer crossed acicular layer.
- Fig. 6: The shell of *Anomphalus* in apical view and with 1.2 mm in width.
- Fig. 7: *Anomphalus* sp.; 1 mm wide shell which in Pl. 2/9 delivers the structure.
- Fig. 8: Intercalated nacre layer below crossed lamellar layer and above inner prismatic layer in fractured shell of less than 0.2 mm in thickness of *Anomphalus*.
- Fig. 9: Detail to Pl. 2/7 with composition predominantly of spherulite sector marginally connected to crossed lamellar structure.
- Fig. 10: Fractured shell of *Crossostoma* with inner nacre overlain by crossed lamellar structure and underlain by prismatic callus deposits.



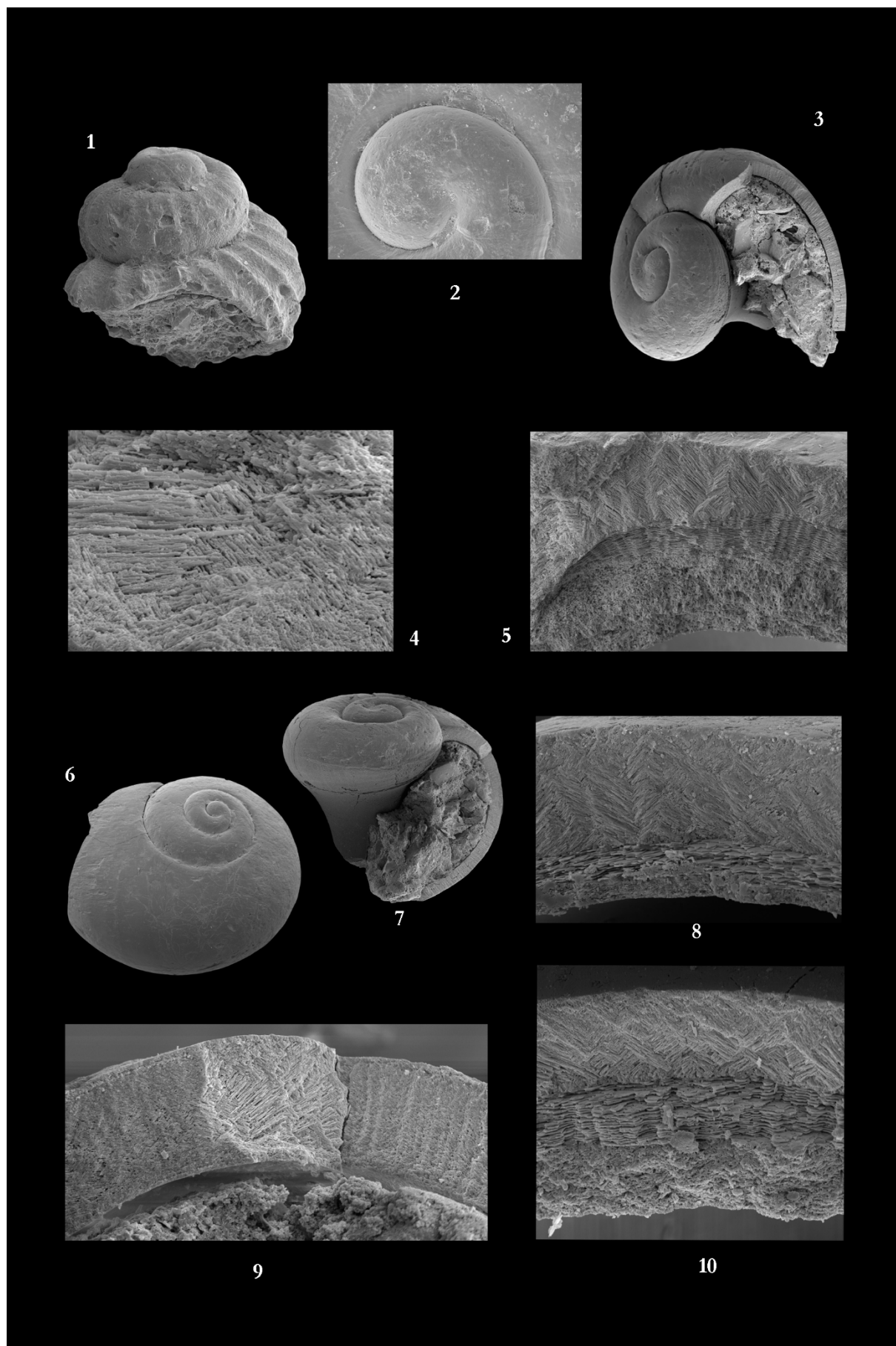
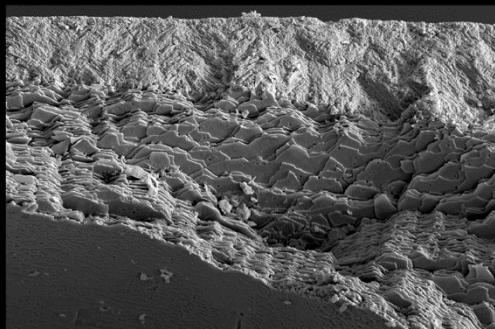
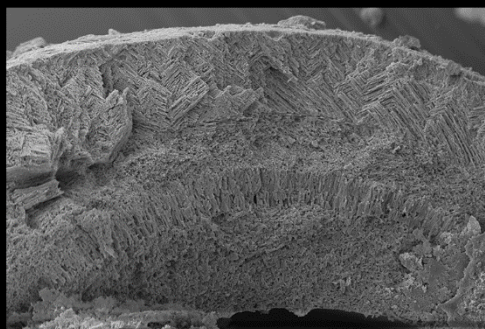


Plate 3

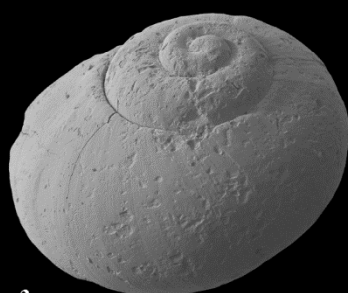
- Fig. 1: Nacre layer fractured to show platelets, each of which is about 0.2 micron wide. Above the nacre the pillars of the spherulite sectors which grade into crossed lamellar structure are developed forming the outer shell layer in *Anomphalus*.
- Fig. 2: *Crossostoma* shell structure.
- Fig. 3: 1.5 mm wide shell of *Anomphalus*.
- Fig. 4: 0.2 mm wide protoconch of *Crossostoma* sp. with its embryonic shell clearly set off from the teleoconch.
- Fig. 5: 1 mm wide shell of *Crossostoma*.
- Fig. 6: 0.8 mm wide shell of *Crossostoma*.
- Fig. 7: 1 mm wide shell of *Crossostoma* in apical view with protoconch, first half whorl of teleoconch smooth and later teleoconch with spiral ornament.



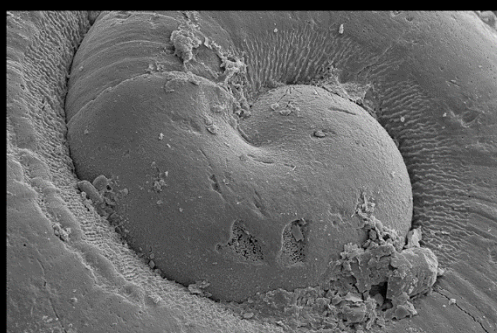
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Plate 4

- Fig. 1: Apertural view of *Neridomus* sp. with the shell almost 1 mm wide. The aperture is half-moon shaped and has a smooth inner and outer lip with basal swell.
- Fig. 2: Apical view of *Neridomus* sp. with 1 mm large shell and detail of protoconch in Pl. 4/6.
- Fig. 3: Half a whorl of the teleoconch of *Neridomus* sp. surrounds the globular larval shell that measures 0.7 mm.
- Fig. 4: Structure of the shell in *Neridomus* sp. with thin outer layer of calcitic material and one continuous crossed lamellar inner layer of aragonite. Shell thickness 0.02 mm.
- Fig. 5: Structure in *Neridomus* with outer calcitic layer that measures approximately 0.05 mm in width and underlain by aragonitic shell in crossed lamellar structure.
- Fig. 6: *Neridomus* detail to Pl. 4/2 with smooth central embryonic shell surrounded by the ornamented larval shell. The embryonic part is smooth and of globular shape with a symmetrical aperture. It measures more than 0.1 mm across. The larval whorls forming a globular shell with 0.4 mm in width have ornament of low axial ribs separated by rounded furrows.
- Fig. 7: Interior of *Neridomus* with all internal whorls dissolved. Shell is 0.7 mm wide.
- Fig. 8: Apical view of *Neridomus* with 1 mm wide shell and transition from 0.7 mm wide larval shell to the teleoconch that is marked by increments of growth. The 2.7 whorls of the larval shell are tightly coiled.

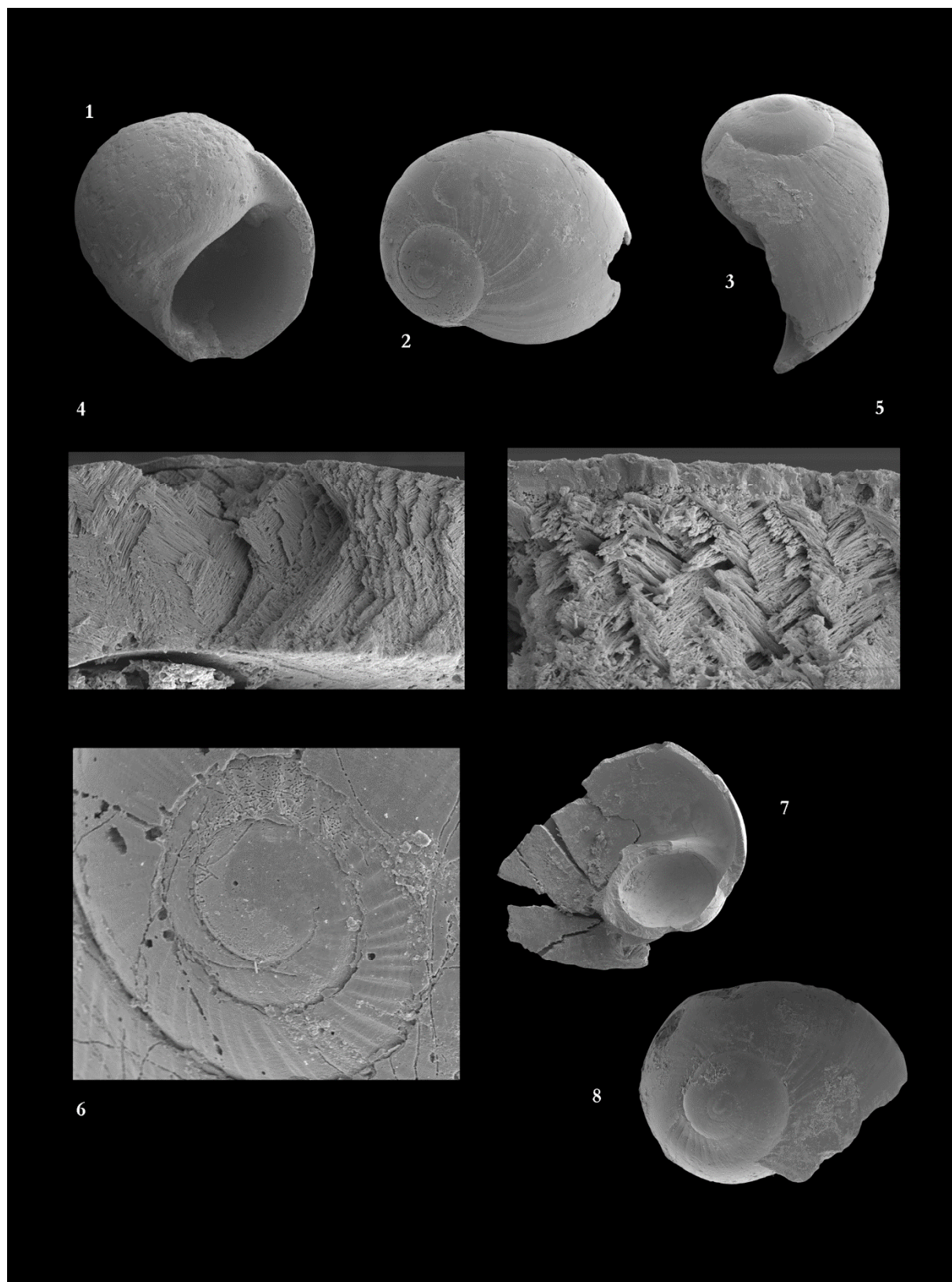


Plate 5

- Fig. 1: Apical view of *Neridomus* sp. with the shell almost 1 mm wide, and the 2.5 larval whorls ornamented by low axial ribs. The early teleoconch was fractured and repaired several time during its growth.
- Fig. 2: Globular larval shell of *Oncochilus* sp. ends with begin of strong growth increments and fractured and repaired shell margins of juvenile. Its ornament consists of low ribs on the two larval whorls which encompass the round embryonic whorl. Shell size is 1.1 mm.
- Fig. 3: *Oncochilus* with the end of the larval shell demarcated by growth increment and the inner lip with two denticles, shell height is 1.2 mm.
- Fig. 4: *Oncochilus* with two denticles on the inner lip and shell height 1.2 mm.
- Fig. 5: Shell of *Neridomus* with large spherical protoconch with ornamented larval shell ending with undulating margin against teleoconch with only increments of growth. The larval shell consist of almost three whorls covering most of the embryonic whorl and measures 0.7 mm across.
- Fig. 6: Shell of *Neridomus* with thin outer calcitic layer covering the crossed lamellar layer and shell thickness 0.06 mm.
- Fig. 7: Shell of *Oncochilus* composed of crossed lamellae composed of aragonite and thin calcitic outer layer and the shell 0.03 mm thick.
- Fig. 8: Shell of *Oncochilus* with outer calcitic layer approximately 3 micron thick and partly detached and exposing well organized crossed lamellar layer below.
- Fig. 9: Surface of the very thin outer layer of juvenile shell with single calcitic crystallites in the begin of the formation of the outer calcite layer.



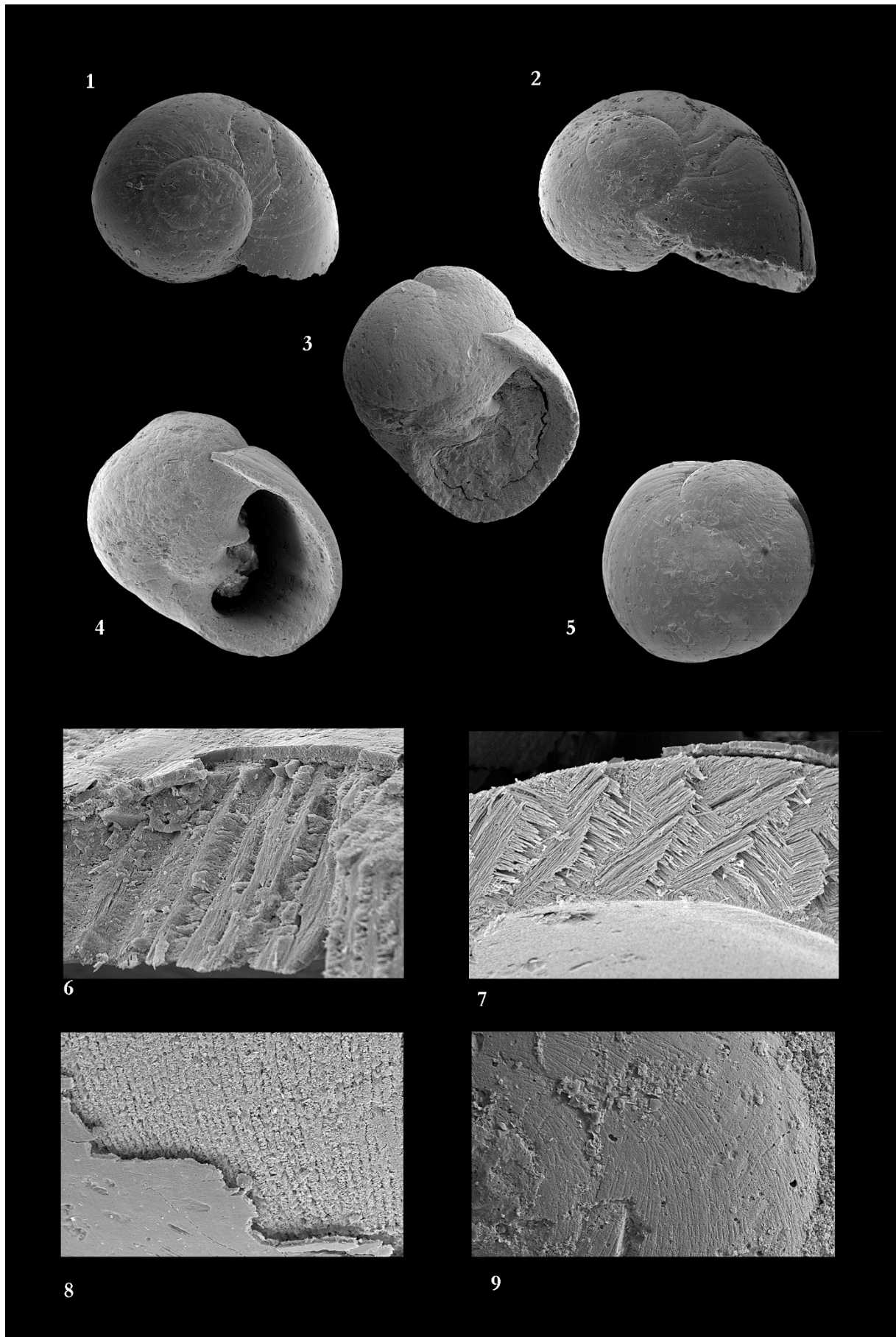


Plate 6

- Fig. 1: *Neridomus* sp. with aperture with smooth inner lip with apical thickening and thin callus cover. The shell is 1.3 mm high.
- Fig. 2: *Oncochilus* sp. with larval shell as in Pl. 6/7.
- Fig. 3: *Neridomus* with detail in Pl. 6/8 with the evenly rounded and axially ornamented larval shell of 0.7 mm in diameter surrounded by teleoconch with thick shell and 1.3 mm in diameter.
- Fig. 4: *Neridomus* with operculum in place and 1.2 mm high shell.
- Fig. 5: *Neridomus* with callus pad in its inner lip and without operculum with smooth inner lip that forms a smooth callus band.
- Fig. 6: *Neridomus* with operculum in place and shell height of 1.2 mm.
- Fig. 7: *Oncochilus* with early ontogenetic shell in which the larval shell is ornamented by low axial ribs and covers most of embryonic and early larval shell, detail to Pl. 6/2.
- Fig. 8: *Neridomus* with larval shell ornamented by fine axial ribs, detail to Pl. 6/3.



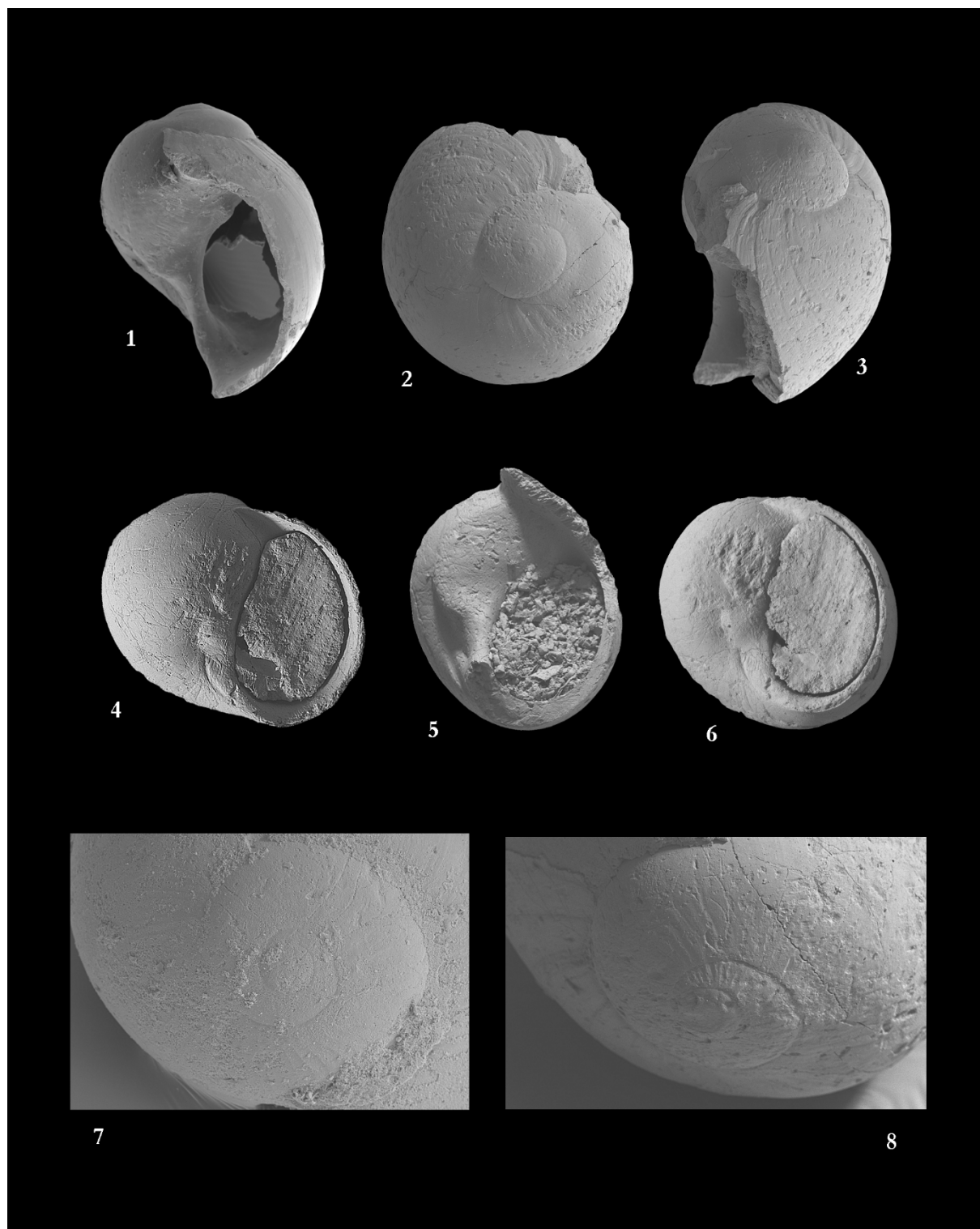


Plate 7

- Fig. 1: *Cryptaulax sakarahensis* with simple ornament of its teleoconch on the shell that is 2 mm long.
- Fig. 2: The shell of *Cryptaulax sakarahensis* is 3 mm long with protoconch complete and ornament predominated by axial ribs.
- Fig. 3: The shell of *Cryptaulax sakarahensis* is approximately 2 mm long with ornament of spiral keels forming tubercles with low axial ribs. Pl. 7/4 is the detail of the protoconch.
- Fig. 4: The protoconch of *Cryptaulax sakarahensis* more than 0.5 mm in height ends with a wide lobe of its aperture.
- Fig. 5: Structure of the shell of *Moaraxis* as in Pl. 7/10, with crossed lamellar aragonite.
- Fig. 6: Ornament of *Cryptaulax sakarahensis* has dominant axial ribs which are crossed by fine spiral ribs and with strong change in ornament from protoconch to teleoconch and 3.3 mm high shell.
- Fig. 7: *Juramelanoides* with 1 mm high shell with rounded protoconch forming the first 1.5 whorls and ornament of the teleoconch by spiral ribs later added also axial ridges.
- Fig. 8: Embryonic shell is 0.06 mm in diameter and ornamented early whorls of larval shell of *Cryptaulax sakarahensis*.
- Fig. 9: *Bigotella* sp. has 2.5 mm high shell and rounded protoconch that consists of approximately two whorls and ornament of the teleoconch by first axial ribs to which later spiral ribs are added.
- Fig. 10: *Maoraxis* has 2 mm long shell and protoconch with one whorl only of 0.2 mm in diameter.
- Fig. 11: *Hudlestoniella* sp. in apical view with the protoconch consisting of 3.5 whorls and the embryonic whorl in detail on Pl. 8/4.
- Fig. 12: *Hudlestoniella* sp. has with juvenile shell of 1 mm in size.

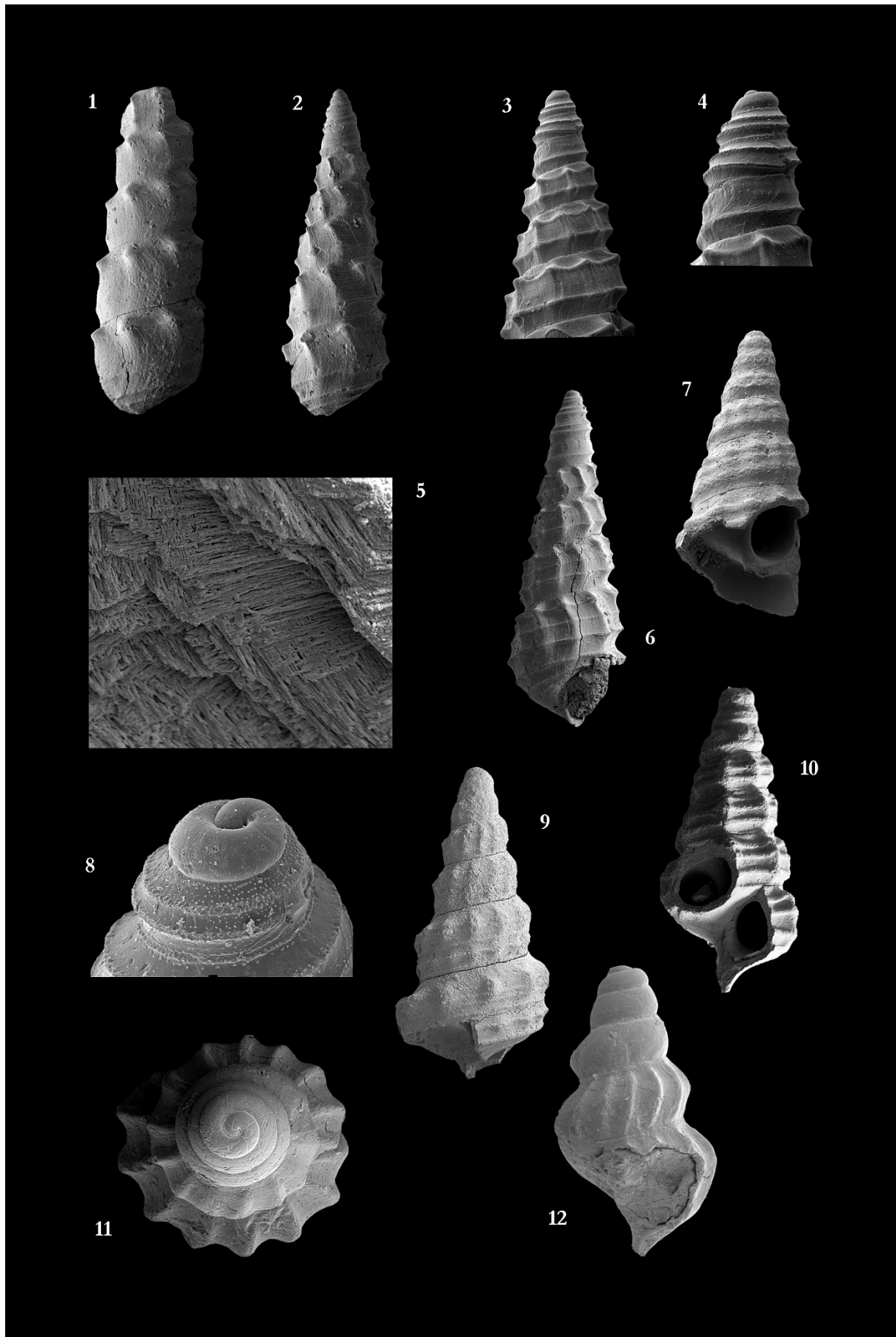


Plate 8

- Fig. 1: *Hudlestoniella* sp. with the larval shell with ornamented ridge above the suture in its first whorl and fractured margin of the aperture in the transition to the teleoconch.
- Fig. 2: *Palaeorissolina* sp. attached to the teleoconch with ornament of very fine spiral line and crossed by axial ribs, shell 1 mm in size.
- Fig. 3: Apical view *Palaeorissolina* sp. has the protoconch consisting of more than 3 whorls and sinuous and thickened margin of the larval shell in transition to the teleoconch.
- Fig. 4: Embryonic ornament of *Hudlestoniella* consists of fine groove and ridge pattern, detail to Pl. 7/11.
- Fig. 5: Juvenile shell of *Palaeorissolina* sp. shows ornament of the teleoconch of curving axial ribs and aperture with smooth columella and notch. Shell is 1.6 mm high.
- Fig. 6: Shell of *Canterburyella* sp. with protoconch as in Pl. 8/7 and the teleoconch ornamented by simple axial ribs.
- Fig. 7: Larval shell of *Canterburyella* sp. has ornament of short axial ribs below the suture and wide rounded projection of the outer lip of the aperture and almost 0.5 mm high larval shell.
- Fig. 8: Apical view of *Canterburyella* sp. with smooth embryonic whorls of and ornament of short axial ribs below the suture on the larval whorls, details in Pls. 8/10, 8/11.
- Fig. 9: The teleoconch of *Canterburyella* sp. has a very regular ornament of rounded axial ribs which are crossed by very fine spiral striae.
- Fig. 10: The embryonic whorl of *Canterburyella* sp. is smooth, 0.12 mm wide and first growth lines come with begin of the larval shell. Detail in Pl. 8/11.
- Fig. 11: Ornament of the embryonic whorl consists of a very fine pattern of grooves and ridges. Detail to Pl. 8/10.

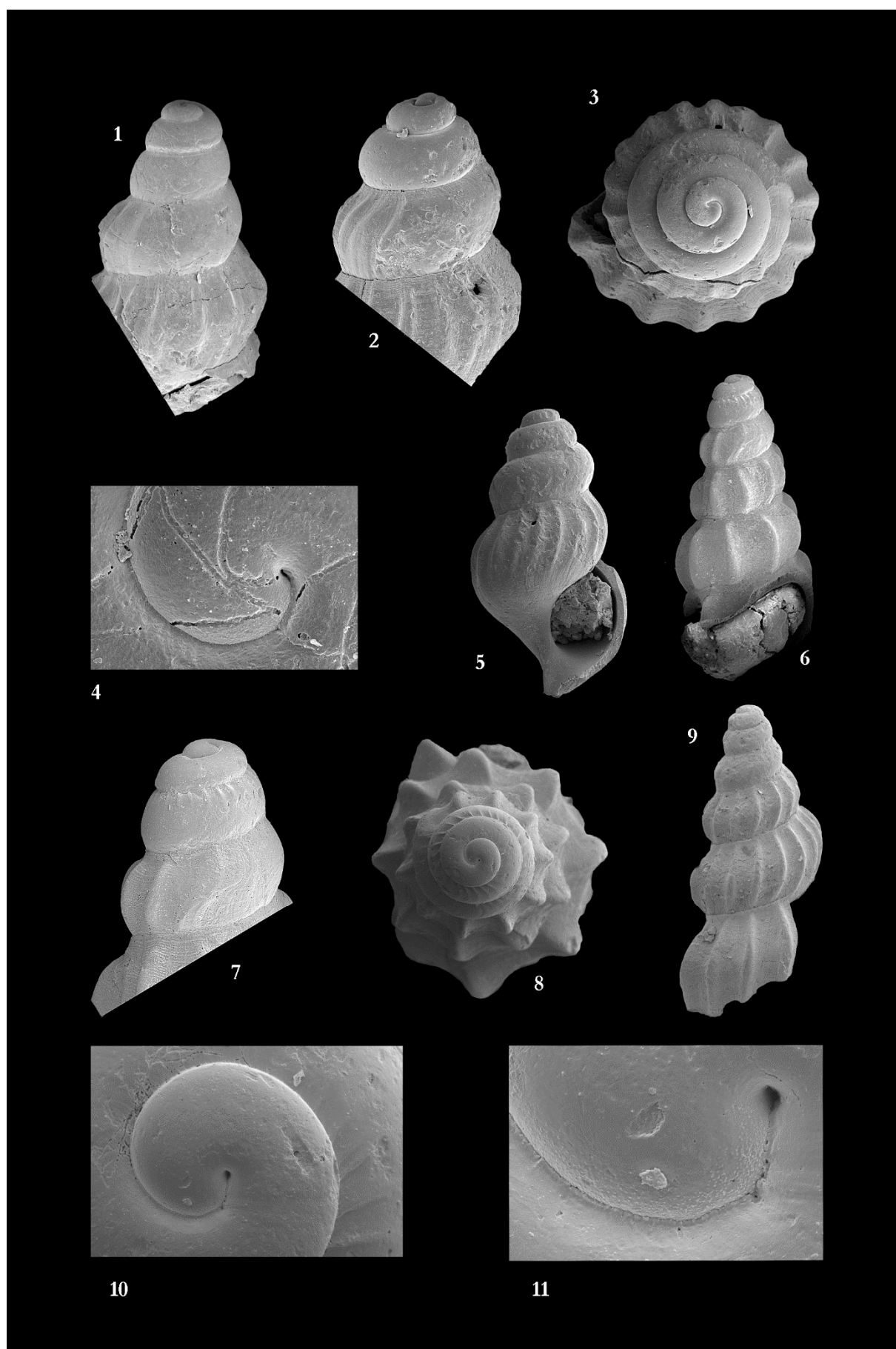


Plate 9

- Fig. 1: Apical view of *Mesostrombus* sp. 1 seen with the apex that displays almost 5 whorls of the protoconch and is 0.7 mm wide and 0.1 mm wide embryonic whorl.
- Fig. 2: *Mesostrombus* sp. 2 has the juvenile shell of 1 mm in height. At transition from the larval shell to the teleoconch has a strong lobe and change in ornament.
- Fig. 3: Transition of the larval shell to the teleoconch in *Mesostrombus* sp. 1 has wide lobe.
- Fig. 4: Apical view of *Mesostrombus* sp. 2 with its apex displaying 4.5 whorls and a 0.12 mm wide embryonic whorl.
- Fig. 5: Protoconch of *Mesostrombus* sp. 1 with its larval shell ending with wide lobe of the aperture, and is 0.7 mm high and consists of 5 whorls.
- Fig. 6: End of larval shell with wide lobe that was fractured during transition of the larval shell of *Mesostrombus* sp. 2 at metamorphosis to benthic life.
- Fig. 7: Apical view of *Mesostrombus* sp.1 shows the 5 whorls of the larval shell. The width of juvenile shell is 0.7 mm.
- Fig. 8: *Mesostrombus* sp. 2 has 4.5 whorls of the protoconch and larval shell is 0.6 mm high.
- Fig. 9: Protoconch of *Mesostrombus* sp. 2 has the larval shell ending with strong lobe of the outer lip of its aperture. The protoconch is 0.6 mm high.
- Fig. 10: Apical view *Mesostrombus* sp. 1 with larval shell seen in Pl. 9/5 and early teleoconch.
- Fig. 11: *Sakarahella angulata* has its larval shell with a ribbon of tubercles above the suture and the shell is 1 mm high.

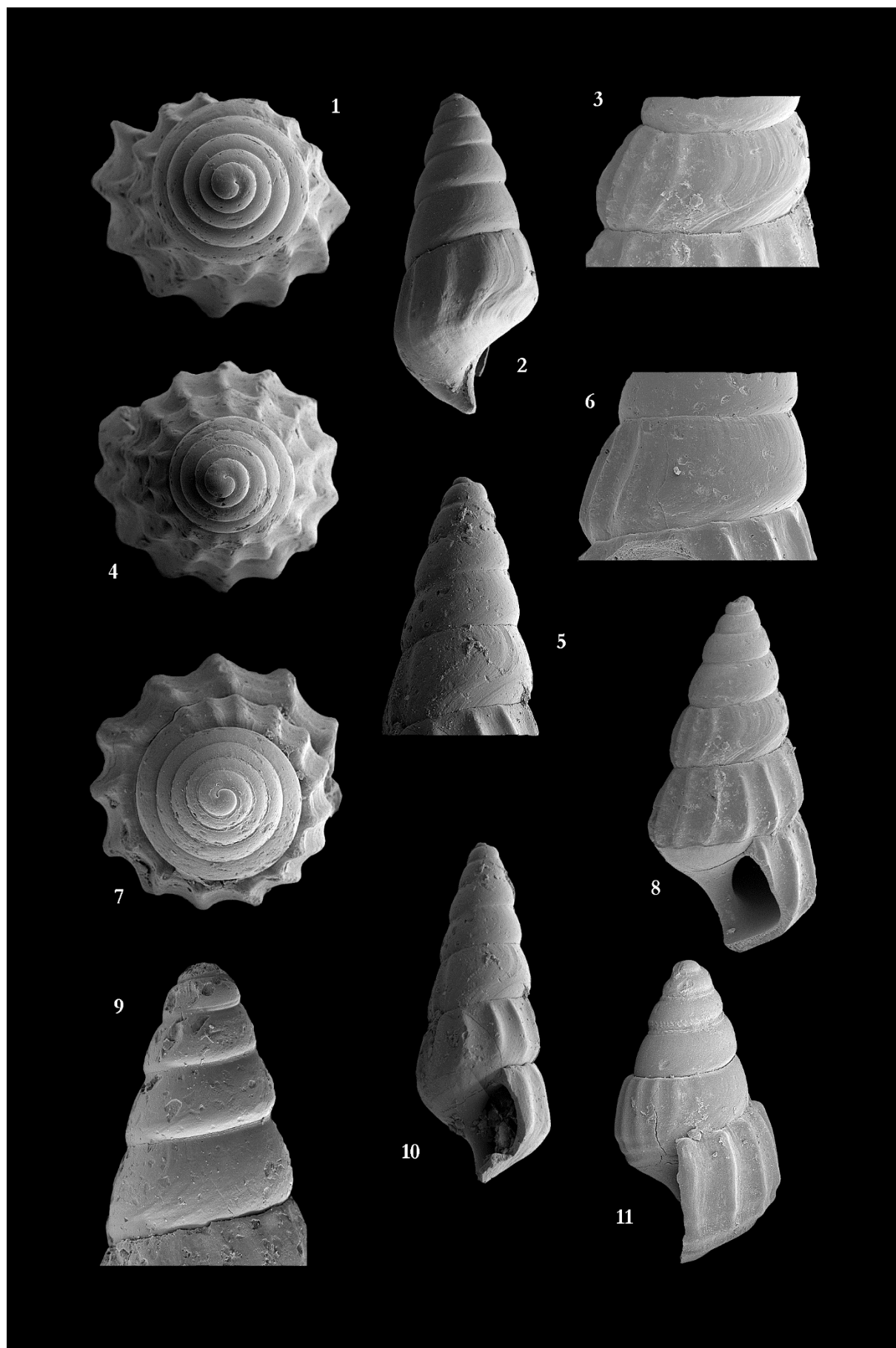


Plate 10

- Fig. 1: The larval shell of *Sakarahella angulata* has ornament and corner above the suture, shell 1 mm high.
- Fig. 2: Apical view of *Sakarahella angulata* with protoconch consisting of 4.5 whorls and change in ornament with onset of the teleoconch.
- Fig. 3: *Sakarahella angulata* has the shell 1.2 mm high. An abrupt change in ornament occurs between larval shell and teleoconch.
- Fig. 4: Detail to Pl. 10/1 of the larval shell of *Sakarahella angulata* with ornamented ribbon and corner above the suture.
- Fig. 5: Embryonic whorl *Sakarahella angulata* with fine groove and ridge ornament and at the begin of the larval shell insertion of an ornamental ridge. The embryonic whorl measures 0.1 mm in diameter.
- Fig. 6: *Sakarahella angulata* with conical protoconch and first teleoconch with more axial ribs than on second whorl (in Pl. 10/3).
- Fig. 7: Juvenile shell of *Kalchreuthia* sp. has the protoconch ending in a wide lobe of the aperture. The following growth lines of teleoconch almost straight. The shell is 1 mm high.
- Fig. 8: Embryonic whorl of *Kalchreuthia* with 0.08 mm in diameter and fine ornament of ridge a groove pattern on the embryonic portion and growth increment with begin of the larval whorl.
- Fig. 9: The juvenile shell of *Kalchreuthia* has a 0.7 mm high shell.
- Fig. 10: Apical view of *Pommerozygia* sp. shows 4.2 whorls and transition to teleoconch with narrow ramp.
- Fig. 11: Juvenile shell of *Pommerozygia* sp. is 0.8 mm high.
- Fig. 12: Apical view of *Pommerozygia* sp. with 0.7 mm wide larval shell consisting of 4 whorls.



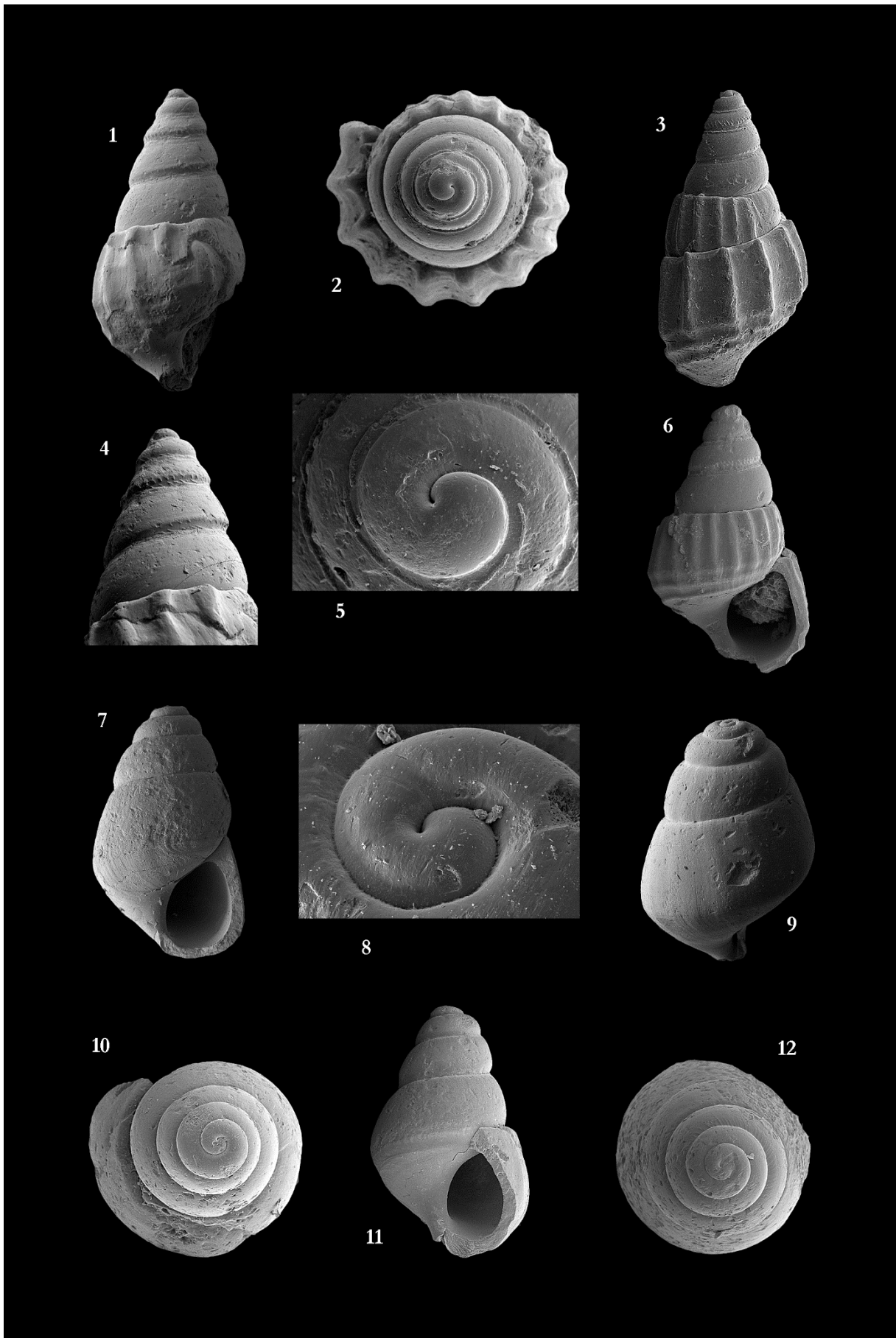


Plate 11

- Fig. 1: *Sakarahina lugeri* in apical view has the embryonic whorl 0.1 mm wide and the larval shell ending in a strongly thickened margin.
- Fig. 2: *Kalchreuthia* has fine lamellar ornament on the larval shell and shell height 1.2 mm.
- Fig. 3: Detail to Pl. 11/2 with the initial whorl 0.1 mm in diameter and fine axial ornament below the suture of the larval shell.
- Fig. 4: Thickened margin of the larval shell of *Sakarahina lugeri* with the strong projection of the basal rim of the end of the protoconch.
- Fig. 5: Shell structure of *Sakarahina lugeri* with well organized crossed lamellar structure.
- Fig. 6: *Sakarahina lugeri*.
- Fig. 7: *Opaliopsis* sp. with *Ampezzopleura*-like ornament of its larval shell and protoconch with strong ribs on the larval shell and 0.6 mm in height.

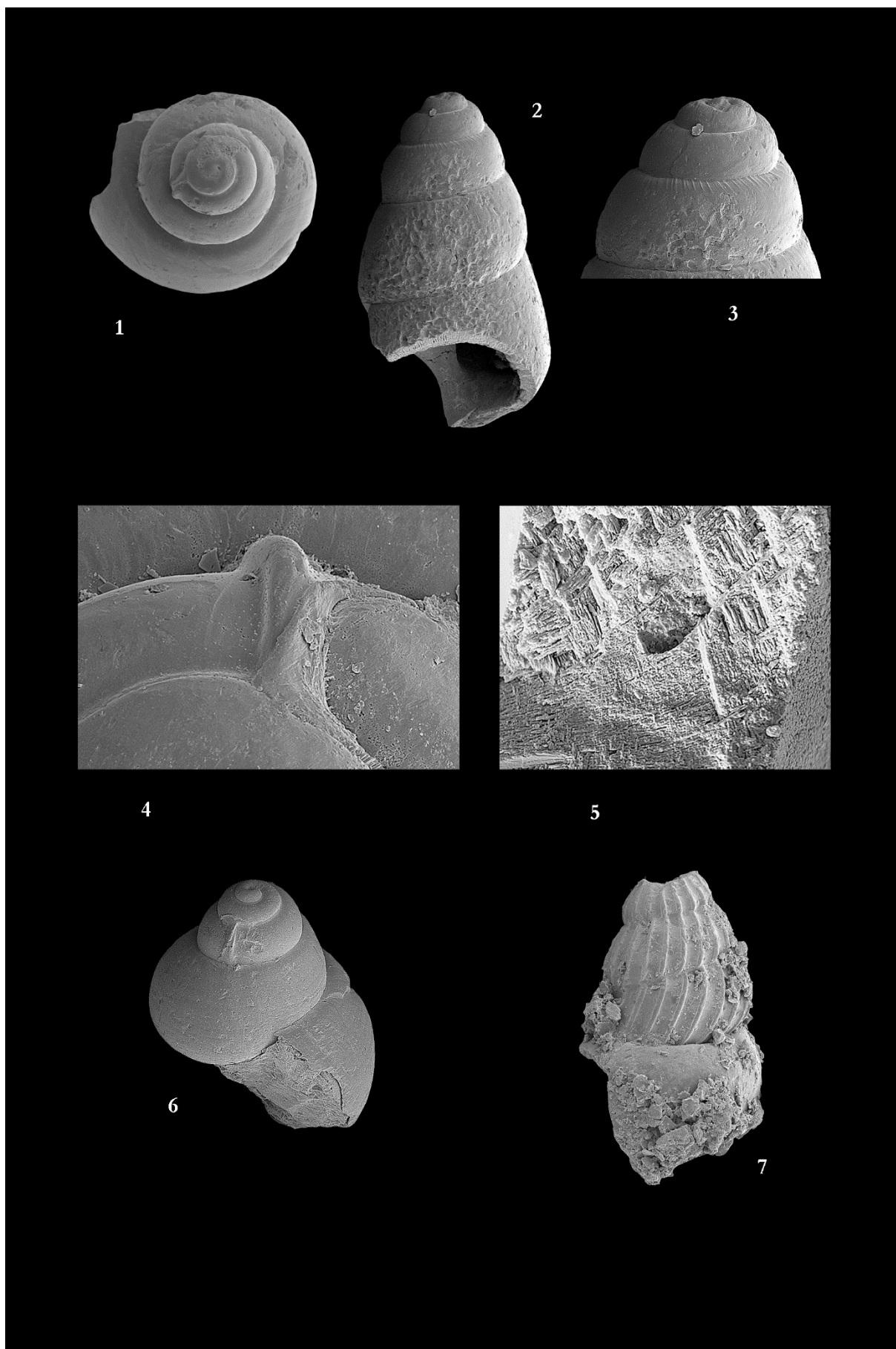


Plate 12

(all pictures of *Dicroloma* sp.)

- Fig. 1: Juvenile shell of *Dicroloma* sp. with 3.5 mm high shell.
- Fig. 2: Transition from the larval shell to the teleoconch on 2 mm high shell is connected to a large hook like projection on the outer lip of the larval shell.
- Fig. 3: The larval shell ends with a pointed apertural projection and change from curving larval ribs to less curving ribs on the teleoconch.
- Fig. 4: Apical view of *Dicroloma* sp. shows almost 4 whorls of the protoconch and shell width 0.8 mm.
- Fig. 5: Apical view of the smooth early larval shell and its ornament consists of 7 curving larval ribs and later more straight ribs on the teleoconch.
- Fig. 6: Apical view with embryonic whorl with wrinkles at its initial part and indistinct first growth lines in transition to the larval shell. Embryonic shell is 0.12 mm wide.
- Fig. 7: Fractured shell of juvenile with crossed lamellar structure developed from prismatic structure on the outer (upper) side and underlain by deposits on the inner shell.
- Fig. 8: The transition from the larval shell to the teleoconch shows the larval apertural projection that ends with begin of teleoconch growth. Shell height about 1.2 mm.
- Fig. 9: Protoconch and early teleoconch on the 1.5 mm high shell.
- Fig. 10: Protoconch and early teleoconch with change from curving ribs on the larval shell to straight ribs on the teleoconch and sculpture ribbon on the larval shell that continues into the larval projection on the aperture.

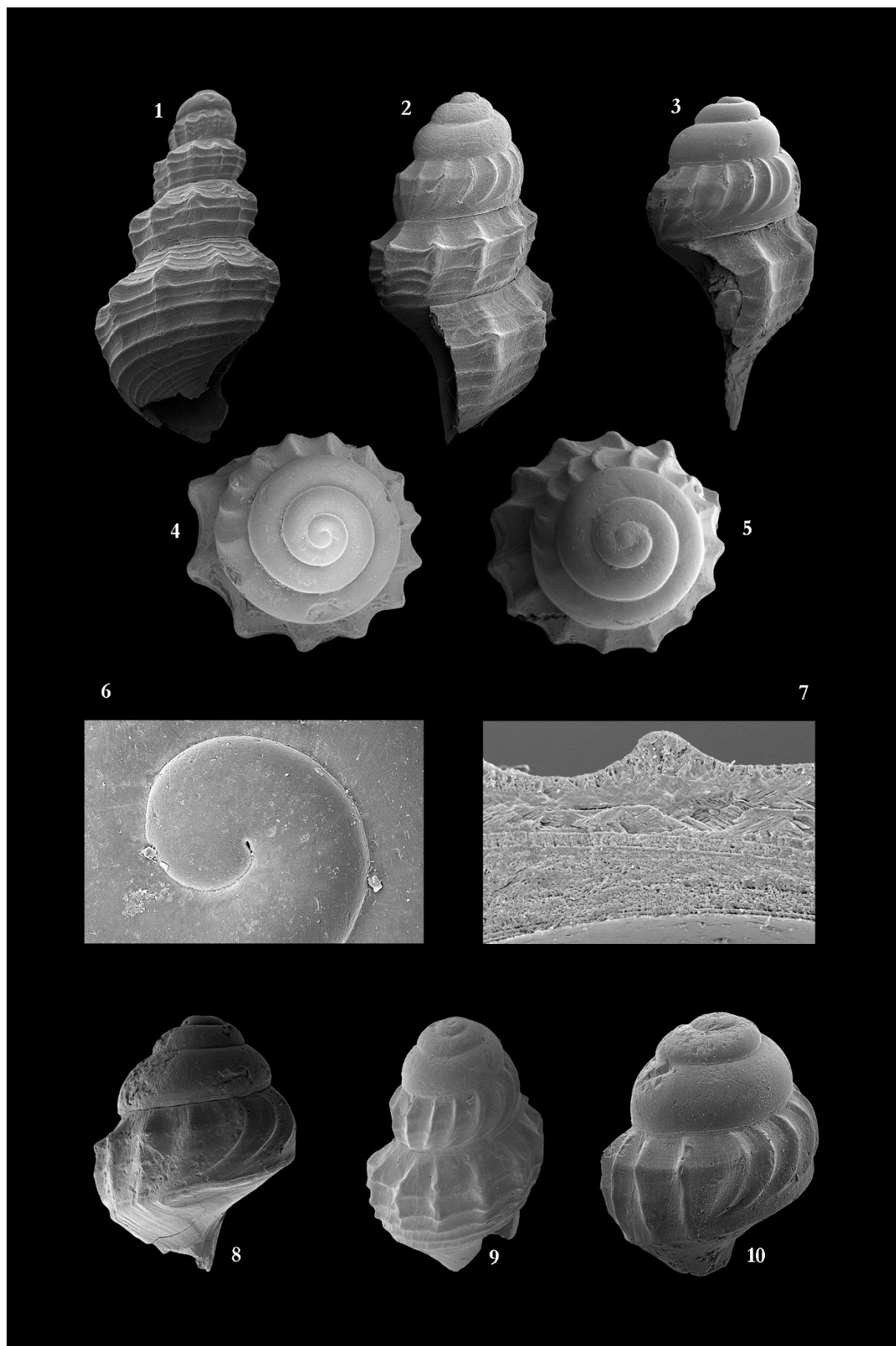


Plate 13

- Fig. 1: 1.6 mm long shell of *Promathildia* sp. from Sakahara has regular ornament of a keel and axial ribs.
- Fig. 2: *Promathildia* sp. (*Teretrina*, *Jurida*) has 1.2 mm high shell.
- Fig. 3: Almost 2 mm long fragment from the teleoconch of *Promathildia-Teretrina* (*Jurida*) sp.
- Fig. 4: Protoconch of *Promathildia* sp. has a 0.2 mm wide protoconch and strong change in shape and ornament in the transition to the teleoconch.
- Fig. 5: Detail to Pl. 13/2 with *Promathildia-Teretrina* – *Jurida* transition form almost plane larval shell to turriiform teleoconch.
- Fig. 6: Detail to Pl. 13/4 of *Promathildia* sp. With the left coiled embryonic shell of 0.08 mm in diameter is included in the almost plane coil of the larval shell. The embryonic shell has a beaten pattern and is distinguished from the larval shell by first growth lines.
- Fig. 7: 1.2 mm wide shell of *Bandellina* sp. has 3.3 whorls of which 1.8 belong to the protoconch.
- Fig. 8: Detail to Pl. 13/9 with the 0.13 mm large protoconch of *Bandellina* sp.
- Fig. 9: Same individual as in Pl. 13/7 of *Bandellina* sp. with the shell less than 1 mm wide.
- Fig. 10: *Cerithellopsis* sp. with almost 1 mm high shell.
- Fig. 11: *Cerithellopsis* sp. with 1.5 mm high shell.
- Fig. 12: *Cerithellopsis* sp. with 1 mm high shell.

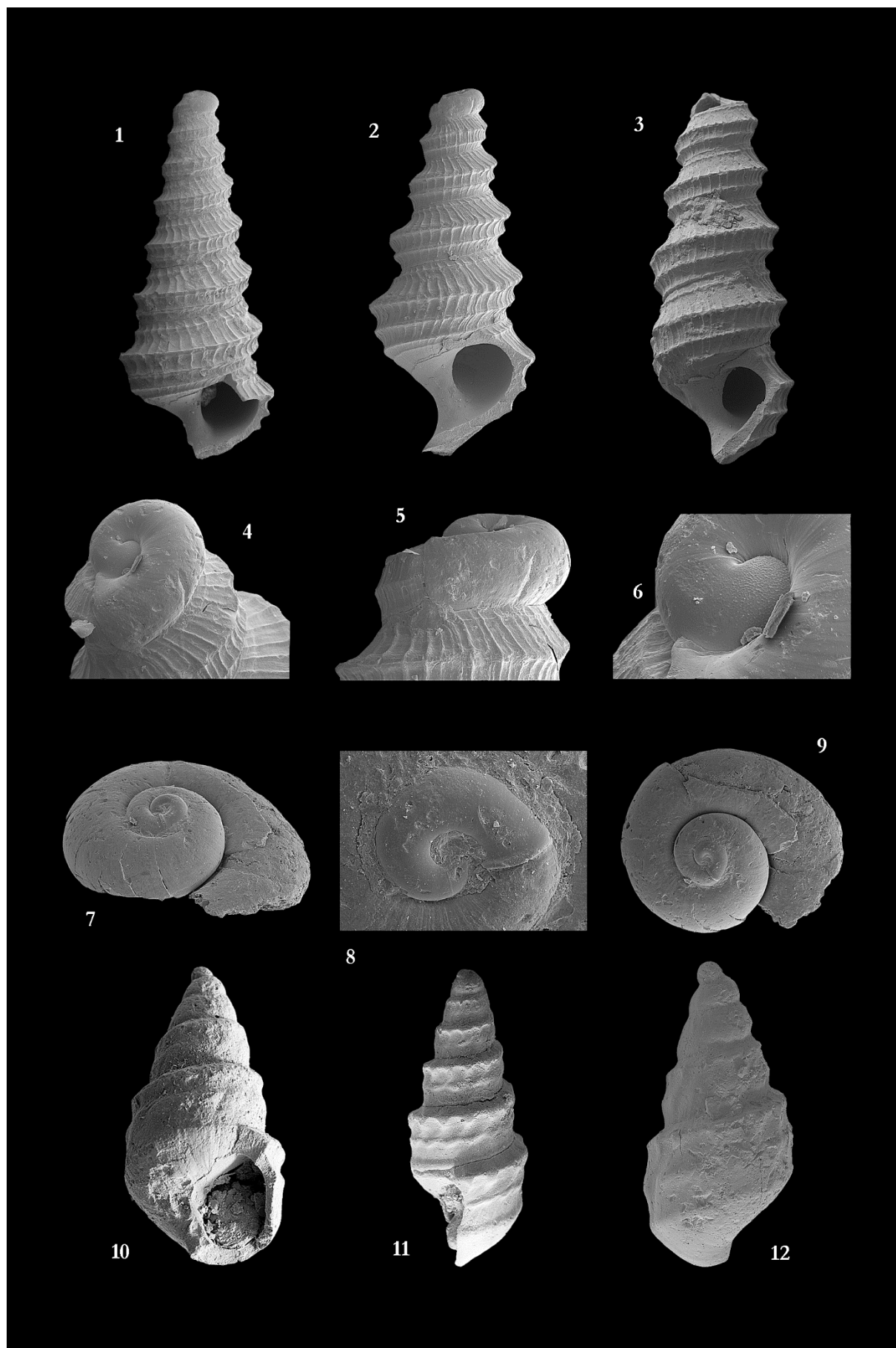


Plate 14

- Fig. 1: 1.5 mm high shell of *Cerithellopsis* sp., with the aperture preserved.
- Fig. 2: 1.8 mm long *Cerithellopsis* with angular shoulders and no ribs.
- Fig. 3: 1.9 mm high shell of *Cerithellopsis* sp. has a corroded shell.
- Fig. 4: *Cerithellopsis* sp. has a 1mm high shell and ornament of sinuous growth lines and groove below the shoulder.
- Fig. 5: Detail to Pl. 13/12 with the protoconch.
- Fig. 6: *Cerithellopsis* sp. shows the detail of the apex of the specimen shown in Pl. 14/2.
- Fig. 7: *Sulcactaeon* sp. detail to Pl. 14/8 with the 0.2mm wide protoconch changing direction of coiling in the transition to the teleoconch.
- Fig. 8: *Sulcactaeon* sp. with 1.2 mm high shell and protoconch in detail of the shell shown in Pl. 14/9.
- Fig. 9: Apical view of *Sulcactaeon* as is seen in Pl. 14/8.
- Fig. 10: Apex of *Sulcactaeon* as detail to Pl. 14/9.
- Fig. 11: *Cylindrobullina* sp. with angular shoulder and almost straight growth lines, shell 1.4 mm high.



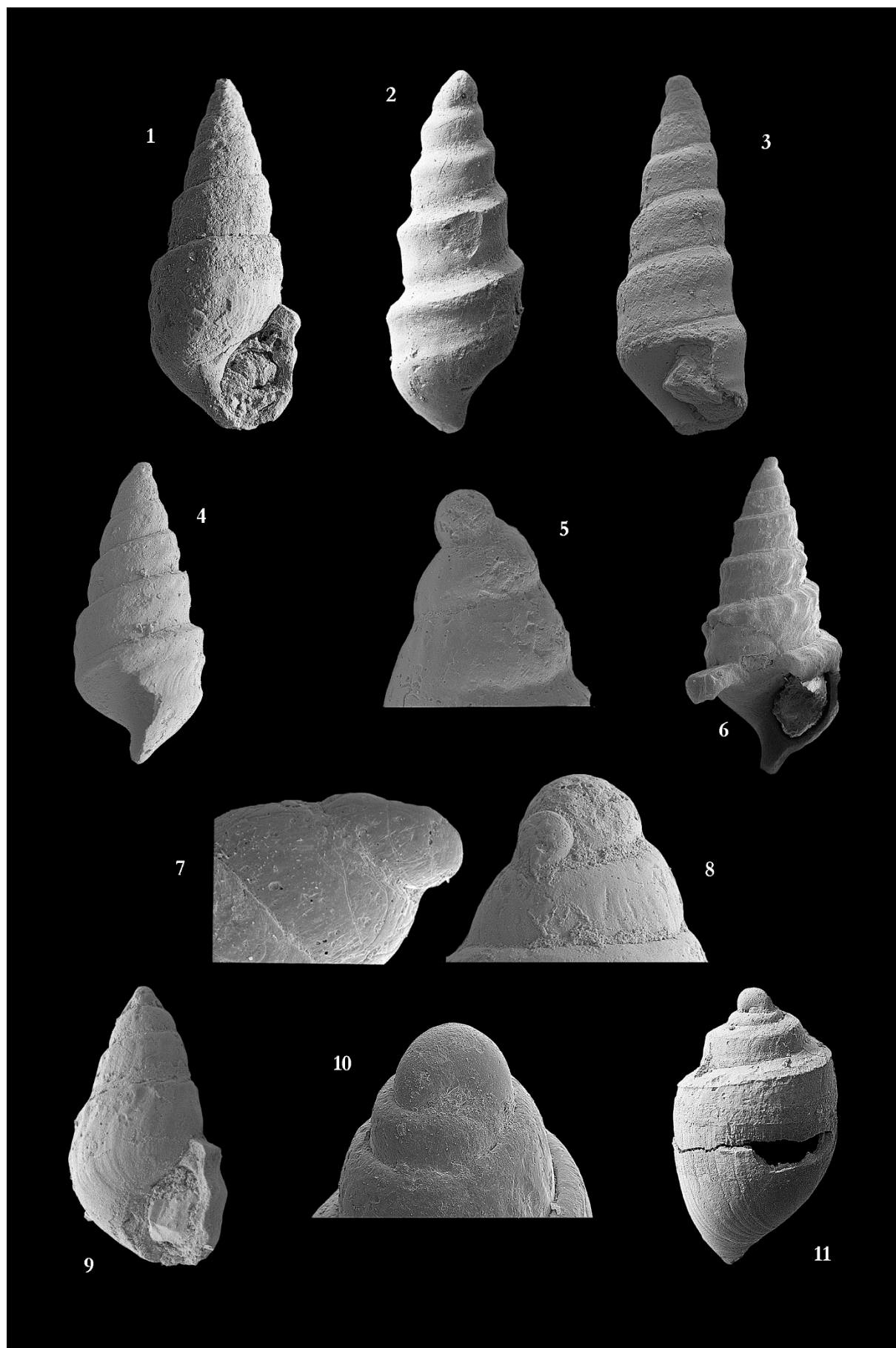
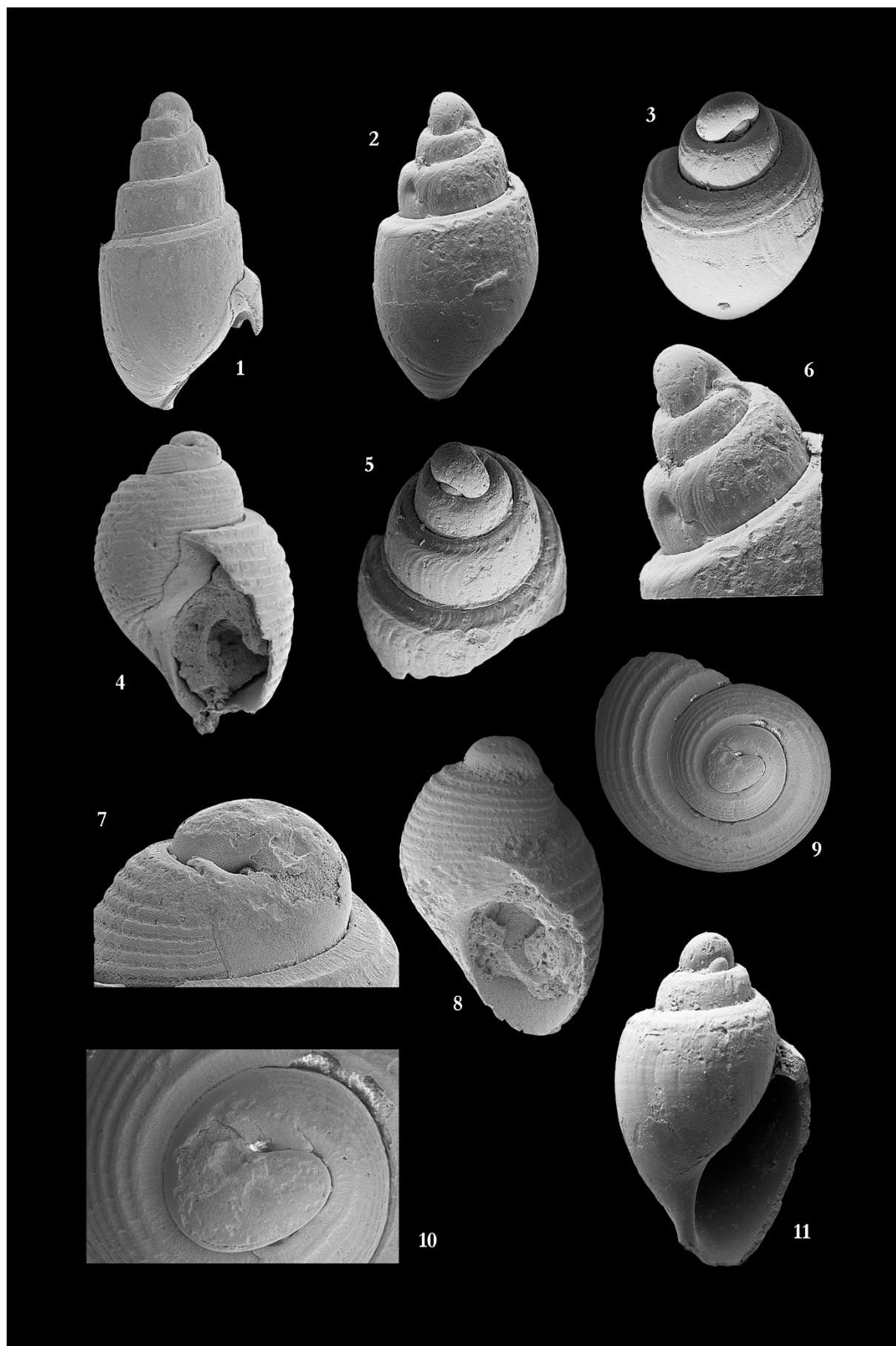


Plate 15

- Fig. 1: *Cylindrobullina* has a 0.2 mm wide protoconch.
- Fig. 2: *Cylindrobullina* shows the 1 mm high shell and evenly curving growth line pattern and apex in Pl. 15/6.
- Fig. 3: *Cylindrobullina* with ridges on the corner resembling rounded ribs and 0.2 mm wide protoconch.
- Fig. 4: *Sulcoactaeon* sp. is with 1.2 mm high shell.
- Fig. 5: *Cylindrobullina* has concave ribbon on the angular shoulder and curving growth lines.
- Fig. 6: *Cylindrobullina* detail to Pl. 15/2.
- Fig. 7: *Sulcoactaeon* sp. detail to Pl. 15/4 with the smooth protoconch of 0.2 mm in width changing to the ribbed teleoconch.
- Fig. 8: Apertural view of *Sulcoactaeon* sp. has a with 1.2 mm high shell.
- Fig. 9: Apical view of *Sulcoactaeon* shows detail in Pl. 15/10.
- Fig. 10: The detail to Pl. 15/9 with the twist from the left coiled protoconch to the right coiled teleoconch and change in ornament from smooth to spiral ribs.
- Fig. 11: *Cylindrobullina* is with simple growth line pattern and 1 mm in height.



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