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Evolution and classification of Mesozoic mathildoid gastropods

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About 150 Mesozoic (mostly Early and Middle Jurassic) species of the heterobranch superfamily Mathildoidea are classified into four families and 27 genera. Most taxa are assigned to the families Mathildidae, Gordenellidae, and Tofanellidae while the Triassic family Anoptychiidae holds only a single genus and is restricted to the Late Triassic. *Mathilda janeti* is designated as type species for the genus *Promathildia*. Earlier designations are invalid because they refer to species which were not originally included in the genus *Promathildia*. As a consequence, *Promathildia* is transferred from Mathildidae to Gordenellidae. The generic assignment of numerous mathildoid species is changed. The suggested classification represents an arrangement which is based on shell characters; it is not based on a cladistic phylogenetic analysis. However, a great number of fossil taxa can only be classified based on shell characters. A high mathildoid diversity has been recognized from the Late Triassic Cassian Formation. Many of these taxa are unknown from the Jurassic and probably became extinct during the end-Triassic mass extinction event. However, at least five genera (probably eight) survived the end-Triassic mass extinction event. *Tricarilda*, *Jurilda*, and *Promathildia* are rather conservative, long ranging groups of high Jurassic species diversity. They probably gave rise to the modern Mathildidae. One new genus is described: *Angulathilda* gen. nov.

Key words: Gastropoda, Heterobranchia, Mathildoidea, classification, Triassic, Jurassic, end-Triassic mass extinction event.

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Introduction

The present paper reviews and discusses Mesozoic and especially Jurassic genera and families of the heterobranch gastropod superfamily Mathildoidea. Mathildoidea form a marine group of basal Heterobranchia. The family Mathildidae is usually included in the superfamily Architectonicoidea but also used as superfamily Mathildoidea (Bandel 1995; Bouchet et al. 2005). The modern Mathildidae are of moderate diversity with about 130 nominal species (Bieler 1995). They occur in shallow to deep water and feed on cnidarians (Haszprunar 1985; Healy 1998). There are few studies on the anatomy of this group (Haszprunar 1985) and there are no molecular studies so far. In modern biota, Mathildoidea are relatively rare (Healy 1998). However, Mathildoidea can be common in Mesozoic samples. The undoubted fossil history of Mathildoidea goes back to the Late Triassic (e.g., Kittl 1894; Bandel 1995). The superfamily is especially abundant in Early and Middle Jurassic deposits (e.g., Schröder 1995;

Gründel 1997; Kaim 2004). Thus, according to the current state of knowledge, the family Mathildidae was apparently more diverse and abundant in the Mesozoic than today.

Although there is a certain variation in shell morphology of the Mathildidae and closely related families, the group is in general rather conservative in shell morphology. A great number of fossil species have been placed in the genera *Mathilda* and *Promathildia* so that these genera became dustbin taxa. In the last 15 years, several new genera have been proposed for Jurassic and Triassic mathildoids based on characters such as the onset and number of spiral ribs and the orientation of the protoconch or the presence of micro-ornaments. The biological meaning of these characters has been questioned by some authors (e.g., Bieler 1995; Kaim 2004). However, the alternative would be to place >100 Jurassic species in the genus *Mathilda*, a capitulation in terms of phylogeny and taxonomy. Encompassing anatomical and molecular studies of modern representatives of the group are still lacking. Until such studies are published, we consider statements that certain shell char-

acters are useless as pure allegations. However, we admit that the present classification of fossil Mathildoidea represents an arrangement, which is not based on a cladistic phylogenetic analysis. In the absence of a clear phylogenetic framework, the here suggested arrangement is nevertheless justified.

The present work focuses on the type species of Jurassic mathildoid genera. Each genus will be discussed according to its morphological characters and its temporal occurrence. Moreover, we will try to assign the described Jurassic mathildoid species to the appropriate genera whenever possible.

A large number of Jurassic mathildoid species have been placed in the genus *Promathildia* Andreae, 1887. As will be shown below, the traditional designation of the type species of this genus is invalid. A new type species is designated here and this changes the concept of the genus *Promathildia* considerably.

Systematic palaeontology

Superfamily Mathildoidea Dall, 1889

Families included.—Mathildidae, Gordenellidae, Tofanellidae, Ampezzanildidae, and Trachoecidae; the assignment of Anoptychiidae to Mathildoidea is questionable because the protoconch of the type species of *Anoptychia* is unknown. According to the current state of knowledge, all are extinct except Mathildidae and Tofanellidae (the latter only if the modern *Graphis* is really a member of this largely Triassic–Jurassic group). The following classification of Mathildoidea is used herein:

Family Mathildidae Dall, 1889

- Genus *Mathilda* Semper, 1865
- Genus *Tangarilda* Gründel, 2010
- Genus *Jurilda* Gründel, 1973
- Genus *Tricarilda* Gründel, 1973

Group of *Turritella binaria*

- Genus *Gymnothilda* Schröder, 1995
- Genus *Bathraspira* Cossmann, 1906
- Genus *Carinathilda* Gründel, 1997
- Genus *Angulathilda* nov.
- Genus *Erratothilda* Gründel, 1997

?Family Anoptychiidae Bandel, 1995

- Genus *Anoptychia* Koken, 1892

Family Gordenellidae Gründel, 2000

- Genus *Promathildia* Andreae, 1887
- Genus *Gordenella* Gründel, 1990
- New genus to be described by Nützel and Gründel
- Genus *Turritelloidea* Walther, 1951
- Genus *Camponella* Bandel, 1995
- Genus *Proacirsa* Cossmann, 1912
- Genus *Schafbergia* Gatto and Monari, 2010

Family Tofanellidae Bandel, 1995

- Genus *Tofanella* Bandel, 1995
- Genus *Cristalloella* Bandel, 1995
- Subgenus *Cristalloella* (*Cristalloella*) Bandel, 1995

- Subgenus *Cristalloella* (*Wonwalica*) Schröder, 1995
- Genus *Graphis* Jeffreys, 1867 (synonym: *Rofanella* Gründel, 1998)
- Genus *Neodonaldina* Bandel, 1996
- Genus *Usedomella* Gründel, 1998
- Genus *Camponaxis* Bandel, 1995
- Genus *Urlocella* Gründel, 1998
- Genus *Conusella* Gründel, 1999a
- Genus *Reinbergia* Gründel, 2007b

Emended diagnosis.—The majority of Mathildoidea have slender, high-spired shells and are of moderate to small size. The protoconch is heterostrophic. It consists of 1.5 to 3 sinistrally coiled whorls which are smooth in most species but may have axial ribs in some. The shell axis of the protoconch may be 90° (transaxial) to 180° (coaxial) to the axis of the teleoconch (see Schröder 1995 for terminology). The teleoconch ornament consists principally of several spiral ribs crossed by numerous axial ribs. Intersections between spiral and axial ribs may or may not be nodular. The teleoconch whorls are commonly angulated or keeled at one of the spiral ribs. Micro-ornaments occur in some genera. Some forms show a pronounced ontogenetic change of the teleoconch ornament including a changing position of the spiral ribs or a complete reduction of the ornament.

Family Mathildidae Dall, 1889

Remarks.—The family Mathildidae is based on the modern genus *Mathilda* that has a Pliocene type species. Numerous Triassic to Recent species and several genera are assigned to this family. However, there is no report from the Palaeozoic. Mathildidae are most diverse in the Jurassic and are represented by a large number of species. The principal morphology of the group is rather conservative but various character combinations occur. Few characters seem to be suitable to recognize genera so that the systematics of the Mathildidae is difficult. The number of spiral ribs on the whorl face of the early teleoconch, immediately after the protoconch (primary spiral ribs) seems to be a useful character for a classification on the genus-level. In Mathildidae, there are 2, 3, 4 and sometimes more primary spiral ribs. The spiral rib directly at the suture is here not regarded as a primary spiral rib.

Gründel (1973) used the number of primary spiral ribs for a subdivision in genera and subgenera: *Jurilda* (later *Promathildia*) with two primary spiral ribs, *Tricarilda* with three primary spiral ribs and *Turritelloidea* (later *Turritilda* respectively *Mathilda*) with four and more primary spiral ribs. Other authors considered this subdivision as artificial (e.g., Bieler 1995; Kaim 2004). Kaim (2004) treated *Tricarilda*- and *Turritilda*-species (3 and more primary spiral ribs) under the genus name *Mathilda*. However, those with two primary spiral ribs were assigned to *Promathildia* although this character was generally not considered valid by him. Bieler (1995) investigated Recent mathildids and concluded that it is unclear whether the character complex of spiral rib pattern is suitable to recognize monophyletic genera and that anatomical studies

(and one may now also say molecular studies) are needed to test whether this pattern give a phylogenetic signal. These doubts may be justified but the need for a subdivision of the large number of fossil mathildids remains. For Jurassic mathildids the number of primary spiral ribs seems a readily available character which in combination with other characters facilitates a subdivision in genera. However, we are aware that this procedure is artificial to some degree. This problem is typical for highly diverse fossil groups which have notoriously conservative shell morphology.

Additional characters which may be used for a taxonomic subdivision are shell shape (e.g., unusually broad and strongly keeled shells) and the presence of a micro-ornament consisting of numerous fine spiral ribs. This micro-ornament seems not to be strictly diagnostic on the genus level; it is for instance weakly developed in some species of *Jurilda* and *Tricarilda* but is characteristic for the genera *Carinathilda*, *Angulathilda*, and *Erratothilda*.

As outlined below, the diagnosis of *Promathildia* is changed because of the new designation of a type species. For those Jurassic mathildids with two primary spiral ribs (*Promathildia* sensu Gründel 1997 and Kaim 2004), the name *Jurilda* Gründel, 1973 is available. *Tricarilda* Gründel, 1973 can be used for species with three primary spiral ribs. *Mathilda* Semper, 1865 (with modern type species) is used for species with four and more primary spiral ribs.

Genus *Mathilda* Semper, 1865

Fig. 1A.

Type species: Turbo quadricarinatus Brocchi, 1814; subsequent designation by Boury 1883; Pliocene, Italy.

Included Jurassic species: Turritilla angulata Gründel, 1997, Callovian; *Mathilda makowskii* Kaim, 2004, Bathonian–Callovian; ?*Mathilda podlasiensis* Kaim, 2004, Callovian; *Mathilda pseudopalina* Gründel, 2007b, Aalenian; ?*Promathilda reticulata* Jamničenko, 1987 including subspecies, Aalenian to Bajocian.

Remarks.—We include Jurassic species with four or more primary spiral ribs in *Mathilda* with the exception of *Erratothilda*-species which have a broad shell and strongly keeled whorls. Moreover, most *Erratothilda* species have a coaxial protoconch and a distinct micro-ornament and differ from *Mathilda* in these respects. We leave the question whether the Jurassic species which have been assigned to *Mathilda* are really congeneric with the Pliocene type species open although we consider it unlikely. Gründel (1976) re-described the type species *Mathilda quadricarinata* and reported the presence of four primary spiral ribs. In contrast, Bandel (1995: 39) mentioned in his key to Triassic Mathildoidea that *Mathilda* is characterized by two primary spiral ribs. However, he obviously did not refer to the type species. Most of the modern species assigned *Mathilda* by Bieler (1995) have four or more primary spiral ribs; however, some have only three.

Walther (1951) introduced the generic name *Turritelloidea* for species which are here assigned to *Mathilda*. Schröder (1995) replaced *Turritelloidea* by *Turritilla* because he assumed that the ending “-oidea” can only be used in names of

superfamilies—this replacement is of course invalid. The type species of *Turritelloidea* (*Turritella opalina* Quenstedt, 1852) is a representative of the Gordenellidae and differs considerably from Jurassic *Mathilda*-species (Gründel 2005b).

Stratigraphic and geographic range.—The earliest *Mathilda* is known from the Toarcian; similar species have been reported from the Late Cretaceous (e.g., *Mathilda hexalira* Dockery, 1993); Germany, Poland, Russia, ?USA, Ukraine.

Genus *Tangarilda* Gründel, 2010

Fig. 1B.

Type species: Melania turritella Dunker, 1846 (= *Cerithium subturritella* Orbigny, 1850 nom. nov.), original designation; Hettangian, Germany.

Included species: Cerithium subturritella d’Orbigny, 1850, Hettangian; *Tangarilda* sp. sensu Gründel 2010, Hettangian.

Emended diagnosis.—A genus of the Mathildidae with three primary spiral ribs. The middle and sometimes also the abapical spiral rib are stronger than the others (whorls octagonal in transverse section). The growth lines are asymmetrically opisthocyrt with the backmost point between the adapical and the middle spiral rib. The lowermost part of the growth lines is strongly opisthocline. Secondary spiral ribs may be developed.

Stratigraphic and geographic range.—Hettangian (and Sinemurian?); Germany.

Genus *Jurilda* Gründel, 1973

Fig. 1C.

Type species: Mathilda (Jurilda) crasova Gründel, 1973 (= subjective junior synonym of *Promathilda (Teretrina) concava* Walther, 1951); original designation: Bajocian to Bathonian, Poland.

Included Jurassic species: The genus is present with numerous Jurassic species. Some examples are: *Promathildia angularis lineata* Jamničenko, 1987, Toarcian–Aalenian; *Mathilda wonwalensis* Schröder, 1995, Valanginian; *Promathildia conoidea* Gründel, 1997, Bajocian; *Promathildia naricata* Gründel, 1997, Bathonian–Callovian; *Promathildia pommerana* Gründel, 1997, late Bathonian–early Callovian.

Emended diagnosis.—Shell slender to moderately broad; protoconch transaxial to almost coaxial, smooth or with radial folds; teleoconch with two primary spiral ribs; abapical rib may be strong, keel-like; few secondary spiral ribs can occur; spiral ribs intersected by strengthened growth lines; intersections are not or only slightly nodular; strengthened growth lines prosocline, straight to weakly prosoclyrt between adapical suture and abapical spiral rib and nearly orthocline from the abapical spiral rib to the abapical suture; backmost point of growth lines on abapical primary spiral rib; faint micro-ornament of spiral striae present in some species; base more or less convex; aperture oval, rounded, sometimes (always?) with anterior siphonal canal.

Stratigraphic and geographic range.—Possible Triassic representatives of *Jurilda* are still doubtful and may belong to the genus *Teretrina* Cossmann, 1912 (AN and JG personal observations). The type species, *Turritella bolina* Münster, 1841, from the Late Triassic Cassian Formation has growth lines

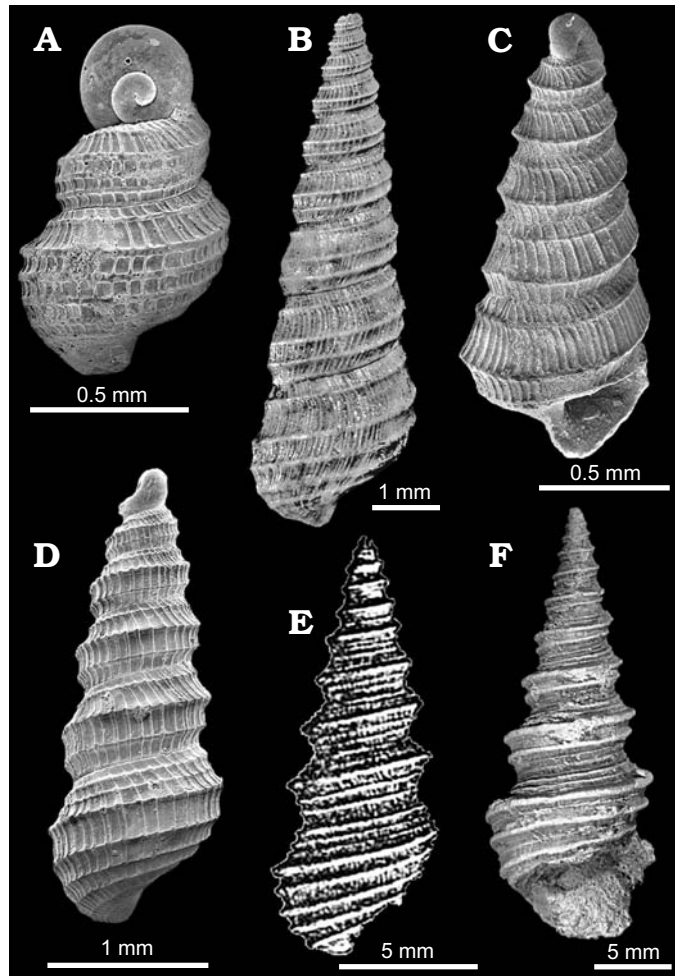


Fig. 1. Type species and examples for Jurassic genera of the family Mathildidae. **A.** *Mathilda angulata* (Gründel, 1997), erratic boulder from Hohendorf near Wolgast 3/96/3, Germany, Callovian; from Gründel (1997: pl. 5: 73). **B.** *Tangarilda subturritella* (d'Orbigny, 1850), Kanonenberg near Halberstadt, Germany, Hettangian; from Gründel (2010: pl. 3: 3). **C.** *Jurilda concava* (Walther, 1951), borehole Klęby (formerly Klemmen) 1/37, Poland, Bathonian; from Gründel (1997: pl. 1: 1). **D.** *Tricarilda plana* (Gründel, 1973), bore Klęby (formerly Klemmen) 1/37, Poland, Callovian; from Gründel (1997: pl. 3: 41). **E, F.** The group of *Turritella binaria* (*Jurilda* or *Tricarilda*). These species were also originally included in *Promathildia*; see also Fig. 4. **E.** *Alaria clathrata* Terquem and Jourdy, 1871, Les Clapes, Bathonian; from Terquem and Jourdy (1871: pl. 4: 7). **F.** *Turritella binaria* Hébert and Eudes-Deslongchamps, 1860, La Motte Bourbon, early Callovian, Bayerische Staatssammlung für Paläontologie BSPG 2012 I 22.

which are distinctly opisthocyrt between the adapical suture and the abapical spiral rib, i.e., their cenit is situated above the abapical primary spiral rib. However, other species which have been described as *Promathildia* species by Bandel (1995) have a course of the growth lines including axial ornaments similar to that of the Jurassic species. The first certain members of *Jurilda* are of Hettangian age. For instance Chapuis and Dewalque (1854), Terquem and Piette (1868), and Piette (1855) reported species which according to their descriptions and illustrations should be classified to *Jurilda*. *Jurilda* is at least present until the Early Cretaceous (Schröder

1995; Kaim 2004). The last occurrence of the genus is unclear. The genus is known from Germany, Poland, Italy, Ukraine.

Genus *Tricarilda* Gründel, 1973

Fig. 1D.

Type species: *Mathilda (Tricarilda) plana* Gründel, 1973, original designation; Callovian; north-western Poland.

Included Jurassic species: The genus is present with numerous Jurassic species. Some examples are: *Tricarilda krumbeki* (Kuhn, 1935), Aalenian; *Tricarilda tareka* Gründel, 1997, Bajocian, ?Bathonian; *Tricarilda toddi* Gründel, Kaim, Nützel, and Little, 2011, Pliensbachian; *Tricarilda striatissima* Gründel, 1999b, Bathonian–Callovian; *Bathraspira* sp. sensu Kollmann 1982, Early Cretaceous; *Tricarilda* sp. sensu Gründel 2003b, Early Sinemurian; *Mathilda schmidti* (Walther, 1951) sensu Kaim (2004), Bajocian–Early Cretaceous(?); *Tricarilda* sp. sensu Gründel 2007c, late Sinemurian.

Emended diagnosis.—Similar to *Jurilda* but the teleoconch immediately with three primary spiral ribs; middle one is strongest, and can be keel-like; additional secondary spiral ribs may lack or are abundant; micro-ornament of spiral striae either absent or weak.

Stratigraphic and geographic range.—The oldest certain member is *Tricarilda* sp. from the early Sinemurian as reported by Gründel (2003a). Possible Hettangian species which probably belong to the *Jurilda*–*Tricarilda*-group are uncertain because their early ontogeny is insufficiently known. The last certain occurrence of *Tricarilda* is Early Cretaceous (*Mathilda schmidti* (Walther, 1951) sensu Kaim 2004, *Bathraspira* sp. sensu Kollmann 1982). However, it is not clear when the genus became extinct. The genus is known from Germany, England, France, Italy, Poland, Russia, Ukraine, New Zealand.

Genus uncertain

“*Turritella*” *binaria* Hébert and Eudes-Deslongchamps, 1860

Fig. 1E, F.

Similar species: *Alaria clathrata* Terquem and Jourdy, 1871, Bathonian; ?*Carinathilda*? sp. sensu Kaim 2004, late Bajocian.

Description.—Shell moderately slender, large; ornament dominated by strong spiral ribs; axial ornament consist of reinforced growth lines only; whorls are keeled at a spiral rib; base convex, not demarcated from whorl face, ornamented with some spiral ribs; protoconch and early teleoconch unknown.

Remarks.—It is unclear whether the “*Turritella*” *binaria*-group belongs to *Jurilda* or *Tricarilda* because the early whorls are unknown. Cossmann (1912) assigned it to the genus *Teretrina*. However, the Triassic type species has another growth line pattern which is opisthocyrt above the keel and it lacks a subsutural spiral rib. *Mathilda binaria* (Hébert and Eudes-Deslongchamps) sensu Andreae (1887) represents another species and belongs to the genus *Angulathilda* gen. nov. *Turritella binaria* and *Alaria clathrata* were originally included in the genus *Promathildia* when this genus was introduced (see below).

Stratigraphic and geographic range.—Late Bajocian?, Bathonian to Callovian; France, ?Poland.

Genus *Gymnothilda* Schröder, 1995

Fig. 2A.

Type species: *Gymnothilda levata* Schröder, 1995, original designation; Early Cretaceous (Valanginian); Wąwał, Poland.

Included species: *Gymnothilda levata* Schröder, 1995, Valanginian; *Mathilda tomaszina* Schröder, 1995, Valanginian; *Gymnothilda dispidualis* Gründel, 1997, late Bathonian–early Callovian; *Gymnothilda torallolensis* Kiel and Bandel, 2001, Campanian; *Gymnothilda reesi* Kaim, 2004, Valanginian.

Diagnosis.—Shell broad, conical; protoconch transaxial to slightly medioaxial, smooth or with axial folds; early teleoconch with one or two primary spiral ribs; whorls keeled at one of primary spiral ribs; base sharply demarcated from whorl face by edge; additional spiral ribs absent or only present on keel; axial ornament lacking or only weak on early teleoconch whorls or only developed on the keel; micro-ornament may be present.

Remarks.—In its present composition, *Gymnothilda* is rather heterogeneous. However, only a few species are included so that a subdivision is not warranted. *Gymnothilda* contains species with one or two primary spiral ribs and with or without micro-ornament. Kaim (2004) restricts the genus to Early Cretaceous species (Valanginian). The oldest species assigned to *Gymnothilda* is the Bathonian *G. dispidualis* Gründel, 1997 (late Bathonian to early Callovian). However, Kaim (2004: 134) doubted this generic assignment and stated that it probably represents a species of *Promathildia*, and that its reduced axial ornamentation derived independently. We consider this as a possible interpretation but leave the Middle Jurassic *G. dispidualis* in *Gymnothilda* until we know more about this genus.

Stratigraphic and geographic range.—*Gymnothilda* as understood here, has its first occurrence in the late Bathonian and ranges with *G. torallolensis* Kiel and Bandel, 2001 into the Late Cretaceous (Campanian). *Gymnothilda pagodoidea* Kiel, 2006 (Albian) belongs to *Bathraspira* (see below). It is also possible that the only known specimen of *G. torallolensis* represents a juvenile of *Bathraspira*. The genus is known from Germany, Poland.

Genus *Bathraspira* Cossmann, 1906

Fig. 2B, C.

Type species: *Cerithium tectum* Orbigny, 1842, original designation; Albian, France.

Included species: The protoconch is known only for *Bathraspira pagodoidea* (Kiel, 2006). All the other species of *Bathraspira* remain therefore uncertain.

Remarks.—Usually, *Bathraspira* was assigned to the caenogastropod family Procerithiidae (for example Cossmann 1906; Abbass 1973; Kiel 2006). Protoconch and early teleoconch whorls have been unknown until Kiel (2006) described *Gymnothilda pagodoidea* from the Albian of Madagascar. This species unites a mature teleoconch which is typical for *Bathraspira* and a protoconch as well as early teleoconch whorls which are typical for *Gymnothilda*. If the juvenile specimen of this species illustrated by Kiel (2006: fig. 8/1) was

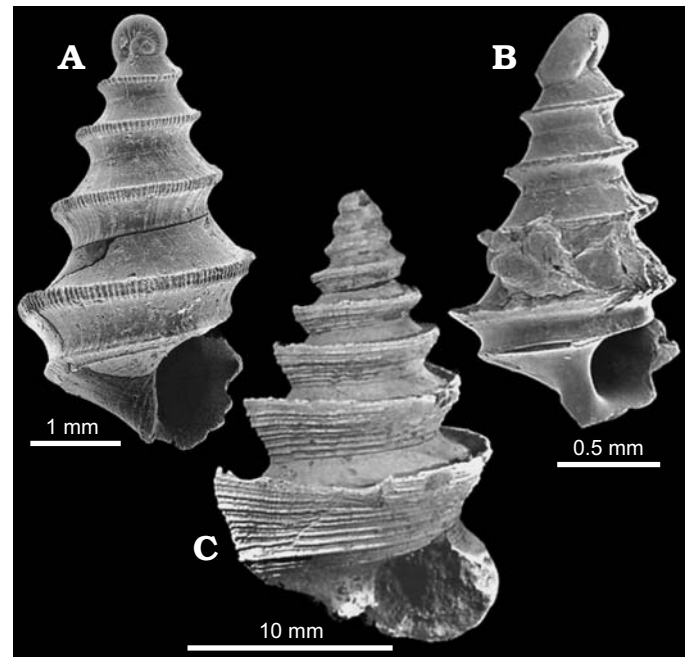


Fig. 2. Type species and examples for Cretaceous genera of the family Mathildidae. A. *Gymnothilda levata* Schröder, 1995, Wąwał, Valanginian; from Kaim (2004: fig. 113A₁). B, C. *Bathraspira pagodoidea* (Kiel, 2006), Mahajanga Basin/Madagascar, Albian; from Kiel (2006: figs. 8.1, 8.2). Juvenile (B) and adult (C) specimens.

found alone, it would be certainly assigned to *Gymnothilda*. Steffen Kiel (personal communication 2010) also agreed that “*Gymnothilda*” *pagodoidea* belongs to *Bathraspira*. It is yet unknown whether this ontogenetic change is also present in other *Bathraspira* species. In any case, *Bathraspira pagodoidea* (Kiel, 2006) is certainly a member of the Mathildidae. *Bathraspira* sp. sensu Kollmann 1982 (late Early Cretaceous) represents a juvenile specimen consisting of a protoconch and two teleoconch whorls; it shows the characters of *Tricarilda*.

Stratigraphic and geographic range.—*Bathraspira* is known only from the Cretaceous; France, England, Madagascar.

Genus *Carinathilda* Gründel, 1997

Fig. 3A.

Type species: *Carinathilda carinata* Gründel, 1997, original designation; Middle Jurassic; NW Poland.

Included species: *Carinathilda carinata* Gründel, 1997, Bathonian; *Carinathilda calteriana* Gründel, 1997, Callovian.

Emended diagnosis.—Protoconch (always?) coaxial; shell moderately broad with two primary spiral ribs and keeled whorls; whorl outline oblique and straight between keel and abapical suture, weakly convex above the keel; base strongly and evenly convex without demarcation to whorl face; weaker secondary spiral ribs and reinforced growth lines form a fine reticulate pattern; a distinct micro-ornament of numerous fine spiral threads is present.

Remarks.—Differences to *Angulathilda* are discussed below. *Jurilda* has a more slender teleoconch and the keel is less pronounced. Moreover, *Jurilda* lacks a distinct micro-ornament.

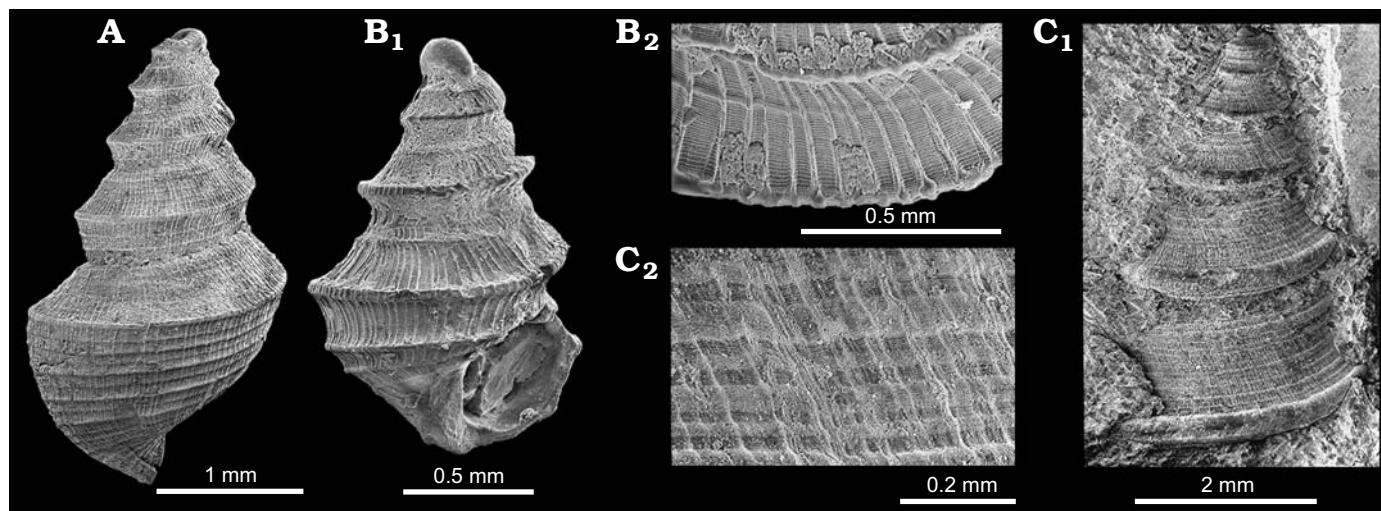


Fig. 3. Type species and examples for Jurassic genera of the family Mathildididae. **A.** *Carinathilda carinata* Gründel, 1997, bore Klęby (formerly Klemmen) 1/37, Poland, Bathonian; from Gründel (1997: pl. 7: 98). **B.** *Angulathilda calloviensis* (Gründel, 1997), erratic boulder from Hohendorf near Wolgast 3/96/3, Germany, Callovian; from Gründel (1997: pl. 7: 98, 101). Whole specimen (B₁), detail of the ornament (B₂). **C.** *Erratothilda erratica* (Gründel, 1990), erratic boulder from Bauer-Wehrland, Germany, Callovian; from Gründel (1997: pl. 7: 104, 105). Whole specimen (C₁), detail showing ornament (C₂).

Stratigraphic and geographic range.—Bathonian to Callovian; Germany, Poland.

Genus *Angulathilda* nov.

Fig. 3B.

Etymology: From Latin *angulatus*, angulated; because of the basal angulated edge; the ending *-thilda* refers to the ending of the related genus *Mathilda*.

Type species: *Carinathilda calloviensis* Gründel, 1997 from glacial erratic boulder, Hohendorf/Mecklenburg-Vorpommern, NE Germany; Callovian.

Included species: ?*Mathilda binaria* Hébert and Eudes-Deslongchamps, 1860 sensu Andreae 1887, Oxfordian; *Purpurina (Pseudalaria) guerreri* (Hébert and Eudes-Deslongchamps, 1860) sensu Couffon 1919; *Teretrina microstriata* Schröder, 1995, Oxfordian; *Teretrina tectispira* Schröder, 1995, Oxfordian; *Carinathilda calloviensis* Gründel, 1997, Callovian; *Carinathilda* sp., cf. *calloviensis* Gründel, 1997, late Bathonian-early Callovian; *Carinathilda bathoniensis* Gründel, 1999b, early Bathonian; *Carinathilda? naricatoidea* Kaim, 2004, Middle Bathonian; *Carinathilda saulae* Kaim, 2004, Valanginian; *Carinathilda squiresi* Kaim, 2004, Valanginian; *Carinathilda* sp. sensu Gründel 2005a, Callovian; ?*Carinathilda procera* Gründel, 2006, late Bathonian; *Carinathilda bandeli* Kiel, 2006, Albian; *Carinathilda* cf. *microstriata* (Schröder) sensu Kiel 2006, Albian; ?*Carinathilda parviruga* Kiel, 2006, Albian.

Diagnosis.—Protoconch medio- to coaxial, smooth or with radial wrinkles; shell moderately broad with two primary spiral ribs and strongly keeled whorl face; whorl face somewhat concave below and above keel; numerous fine axial ribs (or strong growth lines); base slightly to moderately convex; whorls face joins base at distinct angulation with strong spiral rib; micro-ornament of numerous fine spiral threads present.

Remarks.—*Mathilda binaria* Hébert and Eudes-Deslongchamps, 1860 sensu Andreae (1887) and *Carinathilda procera* Gründel, 2006 do not show any micro-ornament (in the latter, this could be due to preservation) and are therefore placed only tentatively in *Angulathilda*. The Cretaceous

Carinathilda parviruga Kiel, 2006 has a distinct umbilicus which is not present in other species of this genus. Several species which were described before SEM studies were possible cannot neither be included nor excluded with certainty because the diagnostic relevant presence of a micro-ornament was not tested.

In contrast to *Angulathilda*, *Carinathilda* has a strongly convex base which is not demarcated from the whorl face by an edge; moreover the whorl face is slightly convex below the keel in *Carinathilda*. *Erratothilda* has three or more primary spiral ribs.

Stratigraphic and geographic range.—Bathonian to Early Cretaceous; Germany, ?France, Poland, Russia.

Genus *Erratothilda* Gründel, 1997

Fig. 3C.

Type species: *Eucycloidea erratica* Gründel, 1990, original designation; glacial erratic boulder from Bauer-Wehrland/Mecklenburg-Vorpommern, NE Germany, Callovian.

Included species: *Eucycloidea erratica* Gründel, 1990, Callovian; *Erratothilda dziki* Kaim, 2004, Valanginian; *Erratothilda krawczynski* Kaim, 2004, Valanginian; ?*Erratothilda wascherae* Gründel, 2006, Late Bathonian.

Emended diagnosis.—Shell and ornament basically as in *Angulathilda*. However, *Erratothilda* has three or more primary spiral ribs. *Erratothilda* has a pronounced micro-ornament.

Remarks.—The characteristic micro-ornament has not been shown for *Erratothilda wascherae* Gründel, 2006 which comes from a locality at which the preservation is not sufficient to show such fine details.

Stratigraphic and geographic range.—Questionable Bathonian, certainly from the Callovian to Early Cretaceous; Germany, ?France.

Family Gordenellidae Gründel, 2000

Remarks.—In our opinion, the diagnostic differences between Mathildidae and Gordenellidae as outlined by Gründel (2000) remain valid despite Guzhov's (2007) doubts. Gordenellids differ from mathildids in the rather large size, slender to very slender shape, high number of whorls, early teleoconch whorls with mathildid ornament (three primary spiral ribs, middle and abapical spiral strongest and angulating whorl profile, numerous opisthocyrt axial ribs), and change of the ornament on mature teleoconch whorls (sometimes complete reduction) (see below).

Genus *Promathildia* Andreae, 1887 (Synonym: *Clathrobaculus* Cossmann, 1912)

Figs. 4A–C, 5A–C.

Type species: *Mathilda janeti* Cossmann, 1885, here designated; Bathonian; France.

Included species: There are certainly more than the here listed species, which belong to the genus *Promathildia*. However, descriptions and illustrations are commonly insufficient for a reasonable assignment. For the majority of the species listed below, the protoconch is unknown so that the placement of these species is also somewhat uncertain (the transaxial, strongly emerging protoconch is diagnostic). Included species: *Cerithium amoenum* Eudes-Deslongchamps, 1843, Bajocian; *Cerithium ziczac* Eudes-Deslongchamps, 1843 (= type species of *Clathrobaculus*), Pliensbachian; *Turritella eucycla* Hébert and Eudes-Deslongchamps, 1860, Callovian; *Turritella subulatissima* Hébert and Eudes-Deslongchamps, 1860, Callovian; *Clathrobaculus fistulosus* (Stoliczka, 1861), Sinemurian; *Cerithium collenoti* Martin, 1862, Sinemurian; *Cerithium sinemuriensis* Martin, 1862, Sinemurian; *Mathilda janeti* Cossmann, 1885, Bathonian; *Rigauxia gracilis* Daresté de la Chavanne, 1912, Hettangian; *Promathildia* (*Clathrobaculus*) *doncieuxi* Cossmann, 1913, Oxfordian; *Tricarilda plana* with aberrant protoconch sensu Gründel 1997, Callovian; *Clathrobaculus* sp., cf. *eucyclus* Hébert and Eudes-Deslongchamps, 1860 sensu Gründel 2000, Callovian; *Clathrobaculus? humberti* Martin sensu Gründel 2003b, Hettangian; *Clathrobaculus* sp. 1 sensu Kaim 2004, Valanginian; *Clathrobaculus* sp. 2 sensu Kaim 2004, Callovian; *Clathrobaculus* sp. 3 sensu Kaim 2004, Bathonian; *Clathrobaculus demissus* Gründel, 2006, late Bathonian; *Clathrobaculus medidilatatus* Guzhov, 2007, Oxfordian.

Spelling.—In the literature, both spelling variants, *Promathildia* and *Promathilda* are commonly used. Andreae (1887) introduced the genus as *Promathildia*. It was emended to *Promathilda* because this name refers to the progenitor of the modern genus *Mathilda* Semper, 1865 (Bieler 1995). However, Phillippe Bouchet (personal communication 2010) pointed out to us that the emendation *Mathildia* dates from Bosquet (1869): “This suggests that the spelling *Promathildia* is not an original incorrect spelling but that Andreae voluntarily used the emendation *Mathildia* combined with the prefix *Pro-*.”

Emended diagnosis.—Shell slender, relatively large, with many whorls; protoconch heterostrophic, transaxial, distinctly emerged, detached or almost detached from initial teleoconch whorl; teleoconch whorls with 3 (4) primary spiral ribs, convex with distinctly deepened suture, angulated at two of the primary spiral ribs (octagonal whorl outline) or with one of the primary spiral ribs as keel. Numerous fine ax-

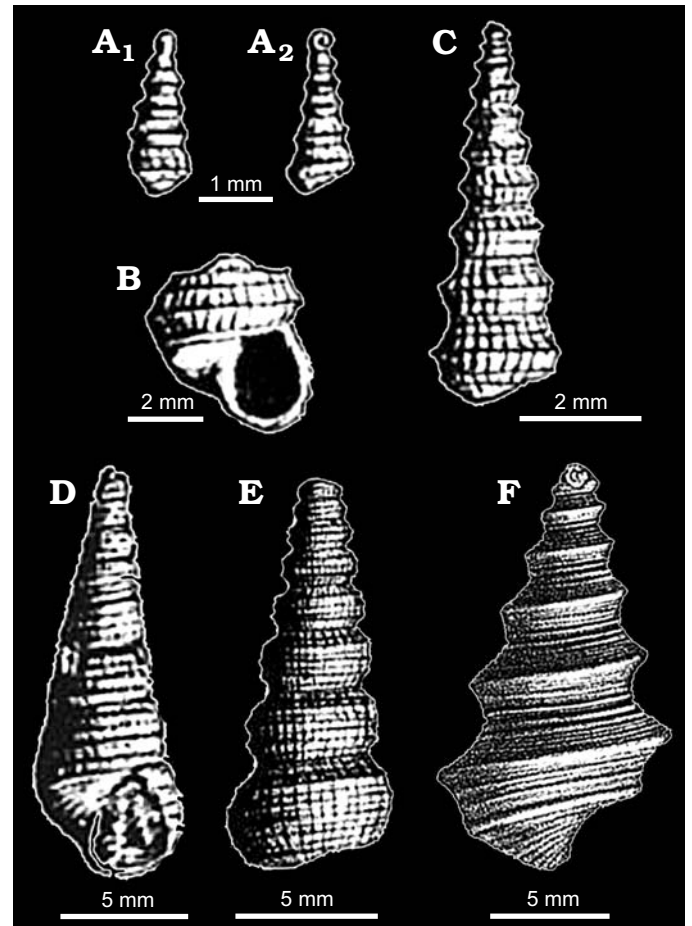


Fig. 4. Jurassic species originally included in *Promathildia* (family Gordenellidae) (see also Fig. 1E, F). A–C. *Mathilda janeti* Cossmann, 1885 is designated as type species of *Promathildia* herein; Hérouvillette, France, late Bathonian. A. From Cossmann (1885: pl. 14: 20, 21), with protoconch in lateral (A₁) and axial (A₂) views. B. Last whorl with aperture; from Cossmann (1885: pl. 14: 19). C. *Mathilda janeti* Cossmann, 1885; from Cossmann (1885: pl. 14: 18). D. *Mathilda reticularis* (Piette, 1855), Le Wast, late Bathonian; from Cossmann (1885: pl. 8: 9). E. *Mathilda reticularis* (Piette, 1855), Rumigny, France, late Bathonian; from Cossmann (1885: pl. 17: 34), lectotype. F. *Pterocera cassiope* d'Orbigny, 1850, France, Oxfordian; from Piette (1864–91: pl. 35: 4).

ial ribs or strong growth lines; teleoconch ornament does not change during ontogeny or changes are only minor.

Remarks.—*Promathildia* is now included in Gordenellidae because *Mathilda janeti* is here designated as type species of this genus and this species is a gordenellid. Andreae (1887) introduced the genus *Promathildia* in a work on Late Jurassic (Oxfordian) gastropods from Alsace (east France). It was introduced as follows (Andreae 1887: 23–24, translated from German): “The affiliation of certain Jurassic turritellid forms to the Recent genus *Mathildia* Semper was first recognized by Laube (1867) and again confirmed by Cossmann (1885) by the finding of inverse and perpendicularly situated embryonic whorls in *Mathildia Janeti* Coss. Anyhow, it seems conspicuous to us that the Jurassic mathildids (which could possibly be called *Promathildia*) exceed their living relatives so

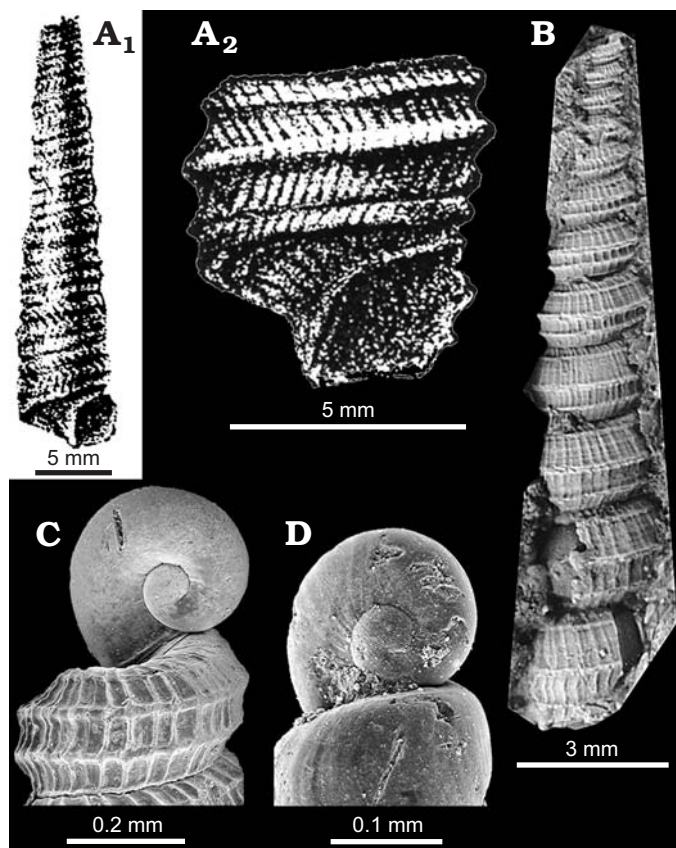


Fig 5. Type species and examples for the Jurassic genus *Promathildia* (family Gordenellidae) and protoconch of *Falsoebala* for comparison. **A.** *Promathildia ziczac* (Eudes-Deslongchamps, 1842), type species of *Clathrobaculus*, France, Early Jurassic; from Eudes-Deslongchamps (1843: pl. 11: 8, 9). Whole specimen (A₁), last whorl enlarged (A₂). **B.** *Promathildia* sp., cf. *eucycla* (Hébert and Eudes-Deslongchamps, 1860), erratic boulder from Vorpommern (NE Germany), Callovian; from Gründel (2000: pl. 1: 2). **C.** *Promathildia* sp., bore Usedom 3/63 (NE Germany), Late Bathonian, protoconch; from Gründel (1997: pl. 4: 48). **D.** *Falsoebala compacta* Gründel, 1998, bore Kłęby (formerly Klemmen) 1/37, Poland, Callovian, protoconch.

eminently in size. As far as I can overview the Jurassic mathildids, they seem split into at least 2 morpho-groups. The more slender ones with pronounced reticulate ornament group around *Mathildia Janeti* Coss., *M. reticularis* Piette etc. by almost lacking a siphonal outlet of the aperture. In the others, the spiral keels exceed the fine transverse ribs by far and its type is formed by *M. binaria*. These are broader and have a rather wide but flat anterior outlet of the aperture. According to this aperture shape, they resemble *Messalia* and *Mesostoma*. The latter Tertiary genus has also the same ornament. I am retaining these forms in *Mathildia* because I found one of the most important characters, the inverse embryonic end, in a good specimen from the Pfirt. Species related to *M. binaria* have commonly been assigned to *Alaria* as is the case in the previously mentioned species *Alaria clathrata* Terq. & Jourd. and *Pterocera Cassiope* d'Orbigny from the Oxfordian of Neuvizy, which was assigned to *Alaria* by Piette". This citation shows that *Promathildia* was

originally meant as a kind of chronotaxon encompassing the Jurassic mathildids which are allegedly larger than living members of *Mathilda* (size is the only diagnostic feature mentioned by Andreae 1887). It is clear that Andreae (1887) did not designate a type species for *Promathildia* and did not provide a sufficient diagnosis. He distinguished two morpho-groups within *Promathildia* but this is irrelevant for nomenclature because he did not name these groups. The designation of *M. binaria* as "type" for one of the unnamed subdivisions of *Promathildia* does not represent the designation of a type species because it relates not to a name bearing group. This is also true for Koken's (1889: 458–459) treatment of *Promathildia*. This author repeated Andreae's (1887) text verbally and as Andreae (1887), he did not name any of the two proposed subgroups of *Promathildia*. Andreae (1887) mentioned five nominate Jurassic species as members of *Promathildia* and one of those originally included taxa can be designated as type species:

- *Mathilda janeti* Cossmann, 1885,
- *Mathilda reticularis* (Piette, 1855),
- *Alaria clathrata* Terquem and Jourdy, 1871,
- *Turritella binaria* Hébert and Eudes-Deslongchamps, 1860
- *Pterocera cassiope* Orbigny, 1850.

Koken (1889) used the genus *Promathildia* for Triassic mathildoids including for "*Cerithium bisertum*" from the Cassian Formation. Kittl (1894) was the first to formally assign species (from the Triassic Cassian Formation) to the genus *Promathildia* in binominal form (Nützel and Erwin 2004). Cossmann (1912) designated *Cerithium bisertum* Münster, 1841 from the Late Triassic Cassian Formation as type species of *Promathildia*. However, this designation is invalid because *Cerithium bisertum* has not been originally included by Andreae (1887) (ICZN article 67.6, 69.1, 69.2.2). Moreover, this species differs significantly from the Jurassic species that were mentioned by Andreae (1887) as examples for *Promathildia*. Thus this designation is in conflict with Andreae's (1887) intention. In the following, we will discuss each of the originally included species as possible type species for *Promathildia*:

- *Mathilda janeti* Cossmann, 1885 (Fig. 4A–C) represents probably a species of the genus *Clathrobaculus* Cossmann, 1912 according to its overall morphology. Cossmann (1885: pl. 14: 20, 21) reported a heterostrophic protoconch of the *Mathilda*-type for *M. janeti* (see Fig. 4A herein); therefore this species is certainly a mathildoid. Obviously, Cossmann (1885) had only juvenile specimens at hand. The heterostrophic, transaxial protoconch and the slender shell of *M. janeti* would support an assignment to *Clathrobaculus*.
- *Mathilda reticularis* (Piette, 1855) (Fig. 4D, E) was insufficiently described by Piette (1855) and no illustration was given. It was described and illustrated by Cossmann (1885). One specimen (Cossmann 1885: pl. 17: 34; see Fig. 4E herein) is from the Piette's (1855) collection and comes from the type locality (Rumigny, Bathonian) according to Cossmann. We designate this specimen as lectotype of

Mathilda reticularis. It is a teleoconch fragment which is 13.6 mm high. The whorl face is ornamented with four spiral ribs, two of which are more pronounced on the earliest preserved whorls. Protoconch, primary spirals on the early teleoconch, and aperture are unknown. Due to this incomplete preservation, it is not suitable as type species of *Promathildia*.

- *Alaria clathrata* Terquem and Jourdy, 1871 (Bathonian; Fig. 1E) and *Turritella binaria* Hébert and Eudes-Deslongchamps, 1860 (Callovian; Fig. 1F) closely resemble each other and both species are congeneric (see above). Both were repeatedly assigned to the genus *Teretrina* Cossmann, 1912. *Teretrina* has a Triassic type species which differs significantly from both Jurassic species (AN and JG own observations) so that this generic assignment can be refuted. *Alaria clathrata* and *Turritella binaria* occupy a certain place within the Jurassic Mathildoidea (see below). The teleoconch of both species is relatively well known. However, protoconch and early teleoconch including primary spiral ribs have not been described or illustrated to this point. If one of these species would be chosen as type species of *Promathildia*, these important characters would remain unknown and therefore the status the genus would be unclear.
- *Pterocera cassiope* Orbigny, 1850 (Fig. 4F) (= nom. nov. pro *Rostellaria bispinosa* Phillips, 1829) (illustrated by Phillips 1829: pl. 4: 32 and Piette 1864–91: pl. 35: 1–4, non pl. 1: 7, which probably is a *Dicroloma* or *Bicorempterus* species and insufficiently known). This species is not suitable as type species of *Promathildia* because many important characters are unknown and the species probably represents the caenogastropod family Aporrhaidae.

Andreae (1887) identified some of his Oxfordian specimens as *Mathilda binaria* (Hébert and Eudes-Deslongchamps, 1860), a species which was originally described from the Callovian of France. However, this is certainly a misidentification—there are strong differences in shape and ornament. For instance, Andreae's (1887: pl. 1C: 1–3) illustrations show a hardly convex base bordered by a strong spiral rib so that the basal edge is angular. It probably represents an undescribed species of the genus *Angulathilda*. A description of a new species is not warranted yet because of the insufficient knowledge of this species. It is very likely that it represents a mathildid because Andreae (1887: 24) mentioned that the protoconch is heterostrophic.

In conclusion, of all species which were mentioned by Andreae (1887) when introducing the genus *Promathildia*, only *Mathilda janeti* is sufficiently known to characterize the genus. Therefore, we designate *Mathilda janeti* Cossmann, 1885 as a type species of *Promathildia* Andreae (1887). This species is most probably congeneric with the type species of the genus *Clathrobaculus* Cossmann, 1912 (Fig. 5A) and therefore *Clathrobaculus* is a junior synonym of *Promathildia*. *Promathildia janeti* is slender, with numerous convex whorls separated by deep suture and has an ornament of two strong spiral ribs; the protoconch is relatively large and trans-

axial. These characters are also typical of *Clathrobaculus* (Cossmann 1912; Guzhov 2007). The relatively small size of the originals of *Mathilda janeti* as illustrated by Cossmann (1885) probably indicates that he had only juveniles at hand. Our designation of a type species from those species which were originally included by Andreae (1887) changes the previous concept (e.g., Bandel 1995; Gründel 1997; Kaim 2004) and the genus should now be included in the family Gordenellidae Gründel, 2000 (see discussion of the Gordenellidae below); this group had its greatest diversity in the Jurassic.

The protoconch is known for the following species of *Promathildia*: *Mathilda janeti* Cossmann, 1885 (Bathonian), *Tricarilda plana* Gründel, 1973 with aberrant protoconch sensu Gründel 1997 (Callovian), *Clathrobaculus* sp. 3 sensu Kaim (2004) (Bathonian), and *Clathrobaculus demissus* Gründel, 2006 (Bathonian). All other species listed above have a teleoconch morphology which agrees with the diagnosis of *Promathildia* as given above.

Haas (1953) described several species from the Late Triassic and the transition to the Early Jurassic of Peru which closely resemble *Promathildia*. He assigned some of them to *Clathrobaculus* (see also Guzhov 2007), e.g., *Promathildia* (*Teretrina*) *bolinoides* Haas, 1953, *Promathildia* (*Teretrina*) *aculeata* Haas, 1953, and *Promathildia* (*Clathrobaculus*) *subulata* Haas, 1953. For some of these species Haas (1953) could report a heterostrophic protoconch. However, these protoconchs cannot be evaluated from the illustrations provided by Haas (1953). According to their teleoconch morphology, it is very likely that these species belong to *Promathildia* or are closely related to this genus. *Promathildia* seems to be absent in the Late Triassic Cassian Formation; none of the species reported by Bandel (1995) seems to represent this genus.

Gordenella Gründel, 1990 differs from *Promathildia* in having straight to concave sides of mature teleoconch whorls. Moreover, in *Gordenella* the middle primary spiral is moving toward the abapical suture during ontogeny; at the same time, the primary spiral rib becomes weaker (in some cases it fades completely). *Gordenella* also differs in showing an ontogenetic weakening of the axial ribs.

Stratigraphic and geographic range.—The stratigraphic occurrence of *Promathildia* can only be given preliminarily, because many species which probably belong to this genus are insufficiently known. The oldest certain species is of Hettangian age (*Cerithium collenoti* Martin, 1862). The genus is probably as old as Late Triassic. The last representative is of Early Cretaceous age (*Clathrobaculus* sp. 1 sensu Kaim 2004). The genus is known from Germany, Austria, France, Poland, ?Russia.

Genus *Gordenella* Gründel, 1990

Fig. 6A, B.

Type species: *Cerithium?* *pommeranum* Schmidt, 1905, original designation; Oxfordian; Poland.

Included species: *Turritella fahrenheiti* Rouillier, 1848, Callovian–Oxfordian; *Turritella krantzi* Rouillier, 1848, Oxfordian; *Turritella schlumbergi* Eudes-Deslongchamps, 1866, Bajocian; *Cerithium?* *pommeranum*

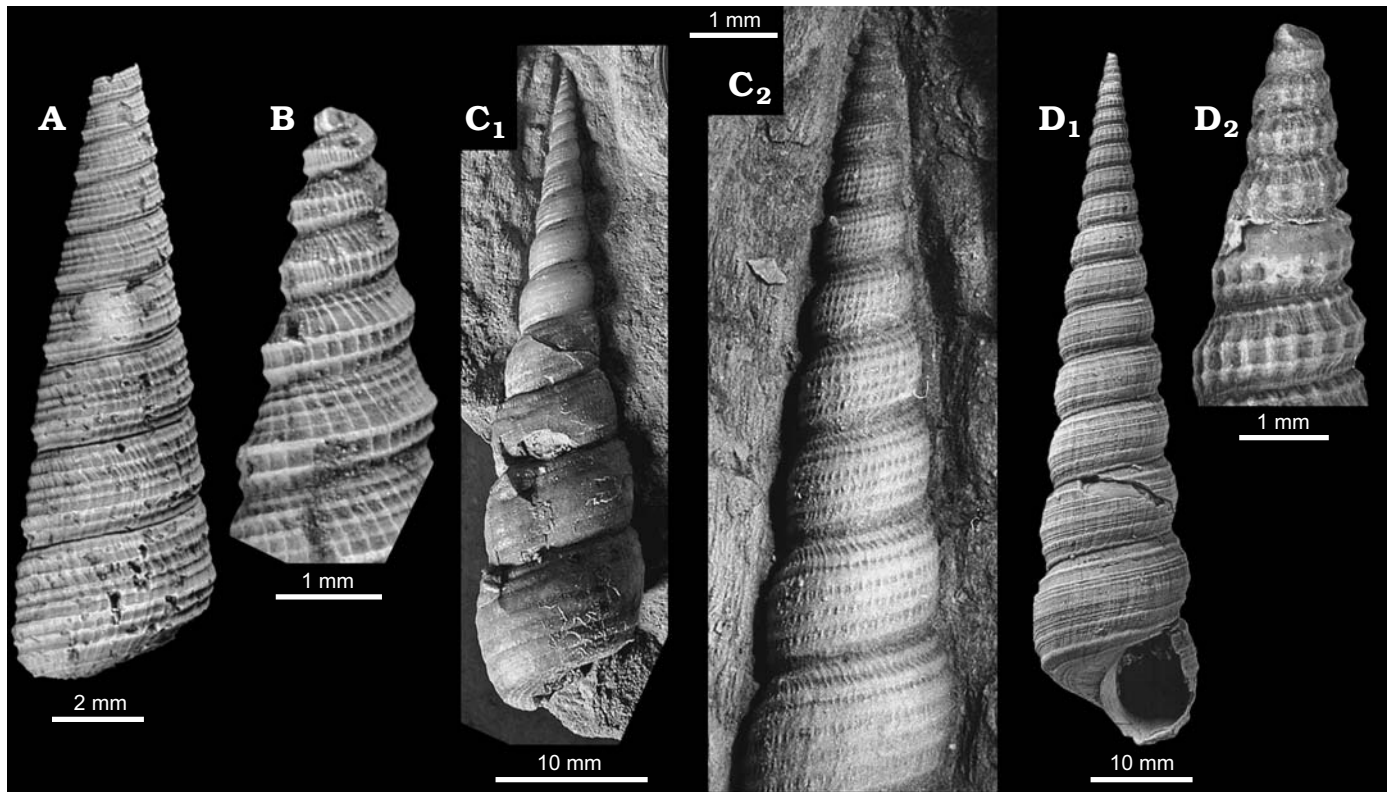


Fig. 6. Type species and examples for Jurassic genera of the family Gordenellidae. **A, B.** *Gordenella pommerana* (Schmidt, 1905), Kłęby (formerly Klemmen), Poland, late Oxfordian. **A.** From Gründel (2000: pl. 1: 8). **B.** From Gründel (2000: pl. 1: 11). **C.** *Turritelloidea opalina* (Quenstedt, 1852), Mistelgau, Germany, late Toarcian, see also Gründel (2005: figs. 2/1, 3). **D.** New genus, new species to be described elsewhere, Buttenheim, Germany, late Pliensbachian; whole specimen (**D**₁), early whorls (**D**₂).

Schmidt, 1905, Oxfordian; ?*Procerithium* (*Cosmocerithium*) *kunzeviense* Gerasimov, 1992, Tithonian; *Gordenella wehrlandia* Gründel, 2000; *Gordenella* sp., cf. *wehrlandia* Gründel, 2000 sensu Gründel 2003a, Bathonian; *Clathrobaculus inconstantiplicatus* Guzhov, 2007, late Callovian?, Oxfordian; ?*Gordenella*? sp. sensu Schubert et al. 2008, Pliensbachian. According to Guzhov (2007), *Turritella sauvagei* Buvignier, 1852, *Turritella divisa* Ilovaisky, 1904, *Turritella complanata* Brösamlen, 1909, and *Promathildia bigoti* Cossmann, 1913 are synonyms of *Turritella fahrenheiti*; *Turritella bicostata* Ilovaisky, 1904 and probably also *Turritella praecursor* Andreae, 1887 are synonyms of *Gordenella krantzi*.

Emended diagnosis.—Shell slender, large, with many whorls; protoconch heterostrophic, transaxial, distinctly emerged, detached or almost detached from initial teleoconch whorl; early teleoconch whorls with two strong and often several weaker spiral ribs as well as numerous opisthocyrt axial ribs; strong abapical spiral rib moves down towards the abapical suture until it is positioned slightly above the abapical suture; this spiral becomes stronger during ontogeny; at the same time, strong adapical spiral is weakening and may fade entirely; below adapical suture one or two spiral ribs become increasingly stronger; whorl face straight to concave (the latter in most species); axial ribs are reduced to strong growth lines on the last whorls of adult specimens.

Remarks.—The name *Clathrobaculus*, as cited in older literature, is replaced in the following discussion with *Promathildia* according to its new definition. Guzhov (2007) described the

characteristic type of protoconch for several species representing *Gordenella*. The same type is also present in *Promathildia*. When Gründel (2000) introduced the family Gordenellidae, he considered *Clathrobaculus* as being closely related to *Gordenella* Gründel, 1990. However, he decided that the separation line between Mathildidae and Gordenellidae runs between both genera because *Clathrobaculus* lacks an important character of the Gordenellidae, namely the conspicuous ontogenetic change of the teleoconch sculpture which can even result in a complete reduction of the ornament in mature teleoconch whorls. *Clathrobaculus* and *Gordenella* share the relatively large size (for mathildoids), the very slender multi-whorled shell and especially the transaxial protoconch which is widely elevated and not covered by the initial teleoconch whorl. Therefore, *Clathrobaculus* (= *Promathildia*) is assigned to Gordenellidae. All genera of the Gordenellidae have an early ontogenetic “*Clathrobaculus*”-stage, which has also been identified by Guzhov (2007).

Guzhov (2007) assumed a fluent transition from *Clathrobaculus* sensu stricto in his sense (= *Promathildia* herein) and species of *Gordenella* sensu Gründel (2000). Therefore, he considered *Gordenella* to represent a synonym of *Clathrobaculus*. *Clathrobaculus medidilatatus* Guzhov, 2007 has a relatively weak ontogenetic change of the teleoconch ornament i.e., rounded whorl flanks, minor displacement of the strongest spiral rib in an abapical direction, weakening of

the axial ornament associated with an increase in the number of axial ribs per whorl. Even if this species is included in the genus *Clathrobaculus*, there are still pronounced differences between *Clathrobaculus* sensu stricto = group 1 according to Guzhov (2007) and groups 2+3 as defined by Guzhov (2007) (= *Gordenella* sensu Gründel 2000): (i) *Clathrobaculus* has convex and keeled/angulated teleoconch whorls and its teleoconch ornament does not change during ontogeny (or only minor changes occur); (ii) groups 2+3 as defined by Guzhov (= *Gordenella* sensu Gründel 2000) has mostly a concave whorl face (or it is straight) and a pronounced ontogenetic change of the teleoconch ornament which was described in detail by Gründel (2000). The morphological differences between groups 1 and 2+3 sensu Guzhov are much more pronounced than the differences between groups 2 and 3 (subgenera of *Gordenella*?). Therefore we consider *Gordenella* to represent a valid genus, separate from *Clathrobaculus* (= *Promathildia*).

Stratigraphic and geographic range.—Certain *Gordenella*-species with known protoconch and first teleoconch whorls including an early *Promathildia*-like stage are known from the Callovian and Oxfordian. Specimens with typical *Gordenella*-like mature teleoconch whorls were reported from the Bathonian by Gründel (2000) and from the Bajocian by Eudes-Deslongchamps (1866). It is very likely that this material represents *Gordenella*. The generic assignment of *Gordenella*? sp. from the Late Pliensbachian as reported by Schubert et al. (2008) remains doubtful. *Procerithium* (*Cosmocerithium*) *kuncevicense* Gerasimov, 1992 is also insufficiently known. Thus, *Gordenella* ranges from the Bajocian to the Oxfordian according to the current state of knowledge. The genus is known from Germany, France, Luxembourg, Poland, Russia.

Genus *Turritelloidea* Walther, 1951

(= *Turritilda* Schröder, 1995; = ?*Costacolpus* Marwick, 1966)

Fig. 6C.

Type species: *Turritella opalina* Quenstedt, 1852, original designation; Toarcian to Aalenian; South Germany.

Included species: *Turritella minuta* Koch and Dunker, 1837, Kimmeridgian–Tithonian; *Turritella opalina* Quenstedt, 1852, late Toarcian–early Aalenian; *Cerithium*? *decipiens* Hébert and Eudes-Deslongchamps, 1860, Callovian; ?*Turritella anomala* Moore, 1867, Pliensbachian; ?*Turritella* (*Mathilda*) *abbas* Hudleston, 1892, Toarcian–Aalenian; *Turritella* (*Mathilda*) *strangulata* Hudleston, 1892, Aalenian; ?*Turritella solitaria* Wilckens, 1922, Late Cretaceous; ?*Promathildia turritella* (Dunker, 1847) sensu Meier and Meiers 1988, Hettangian; gen. nov. *terquemi* (Bistram, 1903)? sensu Gründel 2003b, Hettangian; ?*Turritelloidea* sp. sensu Schubert et al. 2008, Pliensbachian.

Diagnosis.—Shell median-sized to large and highly conical. The heterostrophic protoconch of the *Mathilda*-type is nearly coaxial. On the first teleoconch whorl two strong keel-like spiral ribs and numerous axial ribs are developed. The last whorls have 6–7 spiral ribs of almost the same strength. In this part of the shell, the ribs are very broad (broader than the spiral furrows between them). The axial ribs become also broader and

at the same time weaker. The ornament of the last whorls of adults consists only of broad spiral ribs (the base included).

Remarks.—The protoconch is only known for the type species. Hudleston (1892: 230) made the following remark for *T.?* *abbas*: “Indications of a sinistral apex have been observed on one specimen”. However, *T.?* *abbas* lacks the broadened, band-like spiral ribs and therefore is placed in *Turritelloidea* only tentatively (see also Gründel et al. 2011). The protoconch and the early teleoconch whorls of most of the species listed above are unknown and therefore, the generic assignment of these species is not beyond doubt. These species are placed in *Turritelloidea* because their mature teleoconch resembles that of the type species. The protoconch is also unknown for the type species of the genus *Costacolpus* Marwick, 1966 (*Turritella solitaria* Wilckens, 1922, Late Cretaceous). Its early teleoconch whorls have an ornament of axial and spiral ribs whereas the mature whorls have exclusively spiral ribs. The spiral ribs become very broad and are separated from each other by narrow furrows. The base has sometimes varix-like thickenings. *Costacolpus solitaria* closely resembles *Turritelloidea opalina* in general shape and ornament. Thus, it seems to be likely that *Costacolpus* represents a junior synonym of *Turritelloidea*.

In Fig. 6D a yet undescribed genus close to *Turritelloidea* is illustrated. It is from the Late Pliensbachian of Germany and will be described in the near future in the frame of a larger monograph. Because this genus is important for this work, we give a preliminary description herein. The shell is high-spired with numerous whorls. The early teleoconch whorls are ornamented with few, widely spaced, strong axial ribs. The earliest preserved teleoconch whorls show two median spiral ribs which somewhat angulate the whorl profile. In addition a weaker subsutural spiral is present. The intersections of axial and spiral ribs are nodular in early whorls. The position of the primary spiral ribs remains approximately stable during ontogeny. The spiral and axial ribs become weaker during ontogeny and intersections are not nodular any longer. Numerous additional spiral striae are added on mature teleoconch whorls and axial ornament consists of numerous densely spaced strengthened growth lines. The base is flat and is ornamented with narrow spiral ribs and broader furrows. The protoconch is unknown.

This yet undescribed new genus resembles *Turritelloidea*. However, *Turritelloidea* has broad spiral ribs separated by narrow furrows on mature teleoconch whorls. The type species of *Gordenella* (Fig. 6A, B) has a straight whorl profile; its mature teleoconch whorls does not show numerous spiral striae. The relatively large size, the high number of whorls and the suppression of axial ribs during ontogeny suggest that the new genus belongs to Gordenellidae.

Stratigraphic and geographic range.—*Turritelloidea* is certainly as old as Late Toarcian. It is likely that the genus ranges from the Hettangian to the Bajocian and even to the Late Jurassic or to the Late Cretaceous (e.g., *T. minuta* from the latest Jurassic and *Costatrochus solitaria* from the Late Cretaceous).

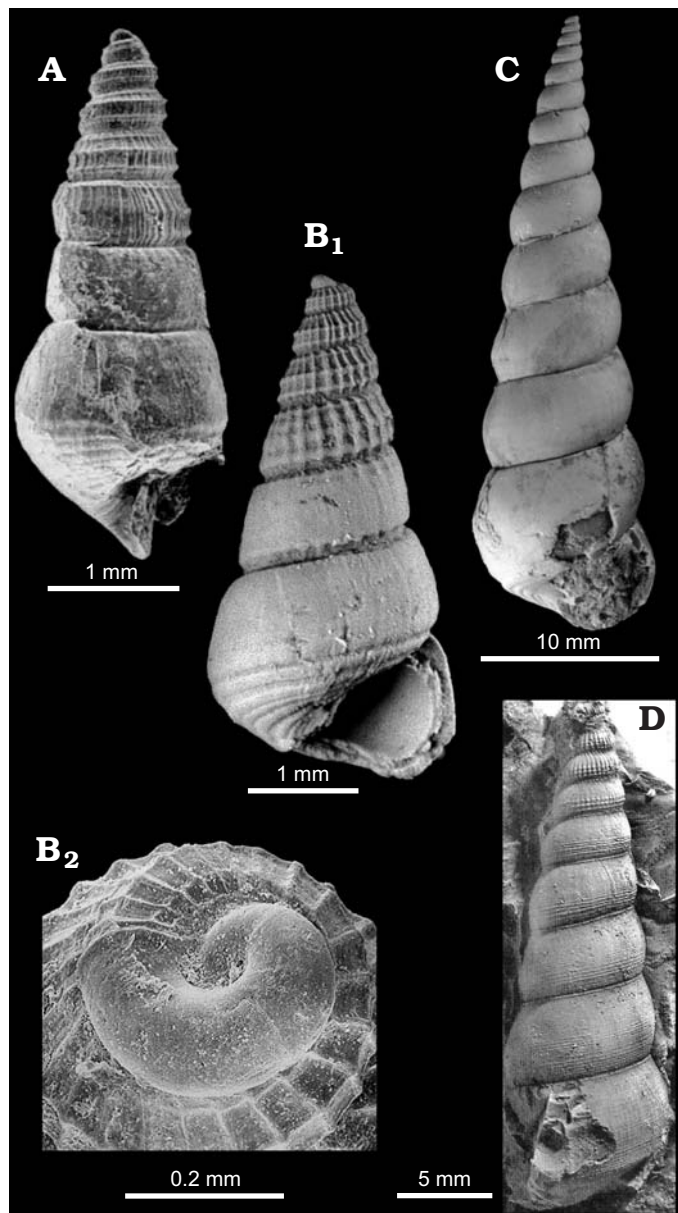


Fig. 7. Type species and examples for Triassic and Jurassic genera of the family Gordenellidae. **A.** *Camponella pianozensis* (Zardini, 1985), Cassian Formation, S Tyrol, Italy, Late Triassic; from Bandel (1995: pl. 8: 7). **B.** *Proacirsa* sp., cf. *struvii* (Lahusen, 1883), Dubki near Saratov, Russia, late Callovian; from Gründel (2005: pl. 5: 12, 16). Whole specimen (**B**₁), protoconch (**B**₂). **C.** *Proacirsa laevigata* (Eudes-Deslongchamps, 1843), erratic boulder from Bauer-Wehrland, Germany, Callovian; from Gründel (2000: pl. 1: 15). **D.** *Schafbergia crenata* (Stoliczka, 1861), Schafberg near St. Wolfgang, Austria, late Pliensbachian; from Szabó (2008: fig. 87B).

The genus is known from Germany, England, France, ?Luxembourg.

Genus *Camponella* Bandel, 1994

Fig. 7A.

Type species: *Coelostylina pianozesis* Zardini, 1985, original designation; Late Triassic; North Italy.

Included species: Only the type species is known.

Diagnosis.—"The small shell has a high spire with numerous

flat-sided whorls and distinct suture. The protoconch is coiled sinistral and inclined with respect to the axis of the teleoconch. The first whorls (c. 5) of the juvenile teleoconch are covered with axial and spiral costae, of which the spiral ones are dominant. Later whorls are smooth or have indistinct spiral threads up to the edge of the base, while the base is covered by spiral carinae. The umbilicus is narrow and may form the opening to a hollow columella" (Bandel 1995: 18).

Remarks.—*Camponella* and *Proacirsa* share important characters: Protoconch morphology, ornament of the early teleoconch as well as reduction of this ornament during ontogeny, and broad spiral ribs on the base. *Camponella* differs from *Proacirsa* in being much smaller, in having fewer whorls and in having an umbilicus. *Camponella* is probably ancestral to *Proacirsa*.

Stratigraphic and geographic range.—Late Triassic; North Italy.

Genus *Proacirsa* Cossmann, 1912

Fig. 7B, C.

Type species.—*Turritella inornata* Terquem and Jourdy, 1871, original designation; Bathonian; France.

Included species: *Cerithium laevigatum* Eudes-Deslongchamps, 1843, Bajocian; *Cerithium januale* Trautschold, 1860, Pliensbachian (?); *Chemnitzia dilatata* Laube, 1867, Callovian (?); *Turritella similis* Moore, 1867, Pliensbachian; *Turritella inornata* Terquem and Jourdy, 1871, Bathonian; *Chemnitzia struvii* Lahusen, 1883, Callovian–Oxfordian; *Cerithium semiornatum* Greppin, 1888, Bathonian; *Zygopleura (Anopychia) bigoti* Cossmann, 1913, Pliensbachian; *Hudlestoniella lahusei* Gerasimov, 1962, Tithonian–Berriasian; *Turritella zlotniki* Kaim, 2004, Valanginian; *Proacirsa* sp., cf. *struvii* (Lahusen, 1883) sensu Gründel 2005a, Callovian.

Emended diagnosis.—The protoconch consists of about 1.5 whorls, is heterostrophic and almost coaxial. The early teleoconch has two or three spiral ribs; the adapical rib is distinctly weaker than the abapical spiral ribs. The spiral ribs are intersected by numerous axial ribs; the intersections are more or less nodular. After a few teleoconch whorls, the ornament fades. Only in some cases, remains of a spiral ornament are present on the last whorls. The base is moderately convex and is ornamented with broad spiral ribs.

Remarks.—The protoconch of a species belonging to *Proacirsa* was described by Gründel (2005b).

Stratigraphic and geographic range.—Pliensbachian to Valanginian, Early Cretaceous; Germany, England, France, Luxembourg, Switzerland, Poland, Russia.

Genus *Schafbergia* Gatto and Monari, 2010

Fig. 7D.

Type species: *Chemnitzia crenata* Stoliczka, 1861, original designation; Pliensbachian; Austria.

Included species: *Chemnitzia crenata* Stoliczka, 1861, Pliensbachian; ?*Chemnitzia turgida* Stoliczka, 1861, Sinemurian; *Proacirsa (Schafbergia) zirettoensis* Gatto and Monari, 2010, Sinemurian–Pliensbachian.

Emended diagnosis.—Shell shape similar to that of *Proacirsa*; protoconch unknown; early teleoconch whorls orna-

mented with several spiral ribs on the abapical whorl portion which are intersected by numerous axial ribs; intersections of axial and spiral ribs nodular; axial ribs reduced after a few whorls; mature teleoconch whorls with numerous weak spiral ribs which are somewhat more distinct in the abapical portion of the whorls; base with numerous somewhat broadened spiral ribs.

Remarks.—*Proacirsa* differs in having three spiral ribs which are distributed over the entire whorl face and in having fewer axial ribs in the early teleoconch whorls, in having rather broad spiral ribs on the base and a smooth whorl face in mature teleoconch whorls.

Stratigraphic and geographic range.—Sinemurian to Pliensbachian, Early Jurassic; Italy, Austria, Hungary.

Family Tofanellidae Bandel, 1995

Remarks.—The Tofanellidae are characterized by coaxial protoconchs with a morphology that is considered to be diagnostic for the family (Bandel 2005: 19): “Its embryonic whorl is left coiled and immersed in the apex of the larval shell. The rounded whorls of the larval shell gradually change from left coiling to plane coiling and finally to dextral coiling.” However, even some Mathildidae have coaxial protoconchs (e.g., *Erratohilda*). It seems that the differentiation between Mathildidae and Tofanellidae is unclear in such cases. For instance, why is the protoconch of *Mathilda bolina* von Münster, 1841 sensu Bandel (1995: pl. 2: 2) of the mathildid type whereas that in pl. 11: 8 (*Tofanella cancellata* Bandel, 1995) allegedly tofanellid (see Fig. 8A, B)? And is *Tricarilda octoangulata* Gründel, 2006 then really a species of the Mathildidae or does it belong to *Tofanella*? Obviously these cases need further clarification.

The representatives of the Tofanellidae are generally small and have been overlooked in many studies. It seems to be likely that only a small part of the gone species diversity and distribution have been assessed. So far, the family has not been reported from the Late Cretaceous and Cenozoic. However, Bandel (2005) reported Recent representatives of the family. At least some tofanellid genera seem to be long ranging although all range dates must be treated with caution. Gründel (1998) subdivided the family Tofanellidae into the two subfamilies Tofanellinae Bandel, 1995 and Usedomellinae Gründel, 1998. Kaim (2004) refuted this subdivision and even Bandel (2005: 19) was sceptical: “Gründel (1998) suggested to split the taxon into the subfamilies Tofanellinae and Usedomellinae, but the genera held herein contain species which are sometimes very difficult to place in one genus or the other or to a representative of one subfamily or the other. These subfamilies may, therefore, not be very useful.” Despite this statement, Bandel (2005) continued to use both taxa in his paper. However, it is indeed difficult to apply Gründel’s (1998) concept in some cases (e.g., *Camponaxis*). Therefore we are reluctant to propose a subdivision of Tofanellidae into subfamilies and further studies of more fossil representatives are needed.

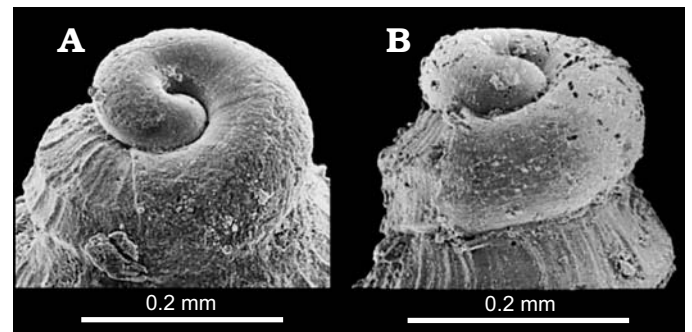


Fig. 8. Coaxial heterostrophic protoconchs of *Mathilda* and *Tofanella* sensu Bandel (1995) do not show principal differences. **A.** *Mathilda bolina* (von Münster, 1841) sensu Bandel (1995), Alpe di Specie, N Italy, Late Triassic; from Bandel (1995: pl. 2: 2). **B.** *Tofanella cancellata* Bandel, 1995, Cassian Formation, Campo, Dolomites, N Italy, Late Triassic; from Bandel (1995: pl. 11: 8).

Genus *Tofanella* Bandel, 1995

Figs. 8B, 9A, B.

Type species: *Turritella decussata* von Münster, 1841, original designation; Late Triassic, North Italy.

Included species: *Turritella decussata* Münster, 1841, Late Triassic; *Tofanella cancellata* Bandel, 1995, Late Triassic; *?Tricarilda octoangulata* Gründel, 2006, Bathonian; several undescribed species from the Pliensbachian of England (JG, own observation).

Diagnosis.—“The turriculate shell has a major keel on the first whorls of the teleoconch, which disappears on later whorls as they become almost flat. The spiral sculpture is crossed by few collabral elements. The protoconch has a smooth surface, and the embryonic shell is immersed in its apex. In the larval whorls the sinistral coiling changes into dextral coiling before onset of the teleoconch. With transition from larval to adult shell sculpture and whorl shape change drastically” (Bandel 1995: 21).

Stratigraphic and geographic range.—Late Triassic to Pliensbachian; England, ?France, North Italy.

Genus *Cristalloella* Bandel, 1995

Remarks.—Kaim (2004) and Bandel (2005) considered *Wonwalica* Schröder, 1995 (December) to represent a junior synonym of *Cristalloella* Bandel, 1995 (November). The species known to date form two morpho-groups which have been used as subgenera by Gründel (2006): *Cristalloella* (*Cristalloella*) and *Cristalloella* (*Wonwalica*).

Subgenus *Cristalloella* (*Cristalloella*) Bandel, 1995

Fig. 9C.

Type species: *Cristalloella cassiana* Bandel, 1995, original designation; Late Triassic; North Italy.

Included species: *Cristalloella cassiana* Bandel, 1995, Late Triassic; *Wonwalica spiralocostata* Gründel, 1998, Callovian; *Cristalloella parva* Bandel, Gründel, and Maxwell, 2000, late Early Jurassic–early Middle Jurassic; *Cristalloella* (*Cristalloella*) *carinata* Gründel, 2006, Bathonian.

Emended diagnosis.—Shell often very slender and with numerous whorls. Axial and spiral ribs cover the whorls. The

keel is strong. Shell with flat and angular base. A strong border rib is developed.

Stratigraphic and geographic range.—Late Triassic to Callovian; Germany, France, New Zealand, North Italy.

Subgenus *Cristalloella* (*Wonwalica*) Schröder, 1995
Fig. 9D.

Type species: *Wonwalica minuta* Schröder, 1995, original designation; Valanginian, Poland.

Included species: *Cristalloella sinuata* Bandel, 1995, Late Triassic; *Cristalloella delicata* Bandel, 1995, Late Triassic; *Wonwalica minuta* Schröder, 1995, Valanginian; *Wonwalica* n. sp. sensu Gründel 1999b, early Bathonian; *Cristalloella boczarowskii* Kaim, 2004, Valanginian; *Cristalloella* (*Wonwalica*) *pusilla* Gründel, 2006, late Bathonian; *Cristalloella* (*Wonwalica*) sp. nov. sensu Gründel 2007b, Pliensbachian; *Cristalloella* (*Wonwalica*) *bandeli* Gründel, 2007a, late Toarcian–early Aalenian.

Diagnosis.—Shell mostly relatively broad and with only few whorls (in relation to the typical subgenus). The keel is as strong as in *C.* (*Cristalloella*). The base is always convex and lacks a bordering rib against the whorl face.

Stratigraphic and geographic range.—Late Triassic to Early Cretaceous; Germany, France, North Italy.

Genus *Neodonaldina* Bandel, 1996

Fig. 9E.

Type species: *Spirocyclina elongata* Zardini, 1978, original designation; Late Triassic, North Italy.

Included species: *Spirocyclina elongata* Zardini, 1978, Late Triassic; *?Neodonaldina ampezzana* Bandel, 1996, Late Triassic; *Neodonaldina sinuata* Gründel and Nützel, 1998, Pliensbachian; *Neodonaldina sterpa* Gründel, 2006, late Bathonian; *Neodonaldina carixiana* Gründel, 2007b, Pliensbachian.

Diagnosis.—Shell slender with convex whorls; whorls not shouldered; suture deep; protoconch tofanellid, consisting of about two whorls; teleoconch whorls ornamented with spiral ribs which can become weaker during ontogeny; growth lines opisthocyrt to parasigmoidal; base convex, not demarcated from whorl face.

Remarks.—*Neodonaldina* has been assigned to the family Donaldinidae. However, the type species (Bandel 1996: fig. 5d; see also Fig. 9E₁ herein) as well as other species (e.g., *N. carixiana*; Gründel 2007b: pl. 6: 23) do not have a donaldinid protoconch but a tofanellid one sensu Bandel (2005: 8, 19).

Stratigraphic and geographic range.—Late Triassic to Bathonian; Germany, France, North Italy.

Genus *Graphis* Jeffreys, 1867
(= *Rotfanella* Gründel, 1998)

Fig. 9F, G.

Type species: *Turbo unicus* Montagu, 1803 (= junior subjective synonym of *Turbo albidus* Kanmacher, 1798), original designation; Recent; North Atlantic and Mediterranean.

Included Jurassic species: *Rotfanella rotundata* Gründel, 1998, Callovian; *Rotfanella* sp. nov. sensu Gründel 1998, Bathonian; *Rotfanella herriigi* Gründel, 1999b, Bathonian; *Rotfanella weissii* Gründel, 1999b, late Toarcian–early Aalenian; *Graphis sinecostata* Gründel, 2007a, late

Toarcian–early Aalenian; *Graphis* sp. sensu Gründel 2007b, Pliensbachian.

Diagnosis.—Shell small with a blunt apex; protoconch with two whorls, broader than the first teleoconch whorl, with or without radial ribs; teleoconch whorls convex with distinct suture; ornament consists of numerous parasigmoidal axial ribs, crossed by numerous weak spiral striae; base convex and without any border rib to the flank; aperture rounded, small.

Remarks.—Bandel (2005: 21, figs. 64–67) re-described and illustrated the type species of *Graphis*. This species has the same characters as Jurassic species of *Rotfanella* (see Fig. 9G). Therefore *Rotfanella* Gründel, 1998 represents a synonym of *Graphis*. However, Bandel's (2005) synonymization of *Urlocella* Gründel, 1998 with *Graphis* is unjustified. *Urlocella* differs from *Graphis* in having a narrower protoconch (smaller diameter than first teleoconch whorl) and in showing a conspicuous reduction of the ornament during ontogeny.

Stratigraphic and geographic range.—Early Jurassic (Pliensbachian) to Recent; Germany, Poland.

Genus *Camponaxis* Bandel, 1994

Fig. 9H.

Type species: *Cerithium* (?) *lateplicatum* Klipstein, 1843, original designation; Late Triassic, North Italy.

Included species: *Cerithium* (?) *lateplicatum* Klipstein, 1843, Late Triassic; *Coronaria subcompressa* Kittl, 1894, Late Triassic; *Katosira beneckeii* Kittl, 1894, Late Triassic; *Camponaxis zardiniensis* Bandel, Gründel and Maxwell, 2000, late Early Jurassic–early Middle Jurassic; *?Rotfanella costigera* Gründel, 2003c, Callovian (?); *?Graphis* sp., cf. *costigera* Gründel, 2003 sensu Gründel 2007b, Pliensbachian; *Iravadia* (*Pseudonoba*) *ponderi* Kiel and Bandel, 2003, Late Cretaceous.

Emended diagnosis.—Shell slender; whorls convex; suture deep; protoconch tofanellid; teleoconch ornamented with strong, straight axial and weak to absent spiral ribs; base convex, not demarcated from whorl face.

Remarks.—*Rotfanella costigera* and *Graphis* sp., cf. *costigera* differ from typical *Graphis*-species in size, in having fewer but stronger axial ribs which are not or only weakly parasigmoidal, and in lacking a spiral ornament. According to these characters, they are closer to the type species of *Camponaxis* and they can be considered to represent descendants of this genus. *Iravadia* (*Pseudonoba*) *ponderi* has also a tofanellid protoconch and the ornament of the first teleoconch whorl (the only preserved one) consists exclusively of relatively few, strong, straight axial ribs. According to its shell shape, protoconch morphology, and teleoconch ornament, this species could also represent a species of *Camponaxis*. Kiel and Bandel (2003) suggested that *Iravadia* (*Pseudonoba*) *ponderi* resembles *?Chevallieria* sp. sensu Schröder (1995) (= *Usedomella schroederi* Gründel, 1998) and placed this species in the family Iravadiidae (Rissoidea, Caenogastropoda).

Stratigraphic and geographic range.—Late Triassic to Early–Middle Jurassic boundary; Callovian to Late Cretaceous questionable; North Italy, Poland, ?Germany.

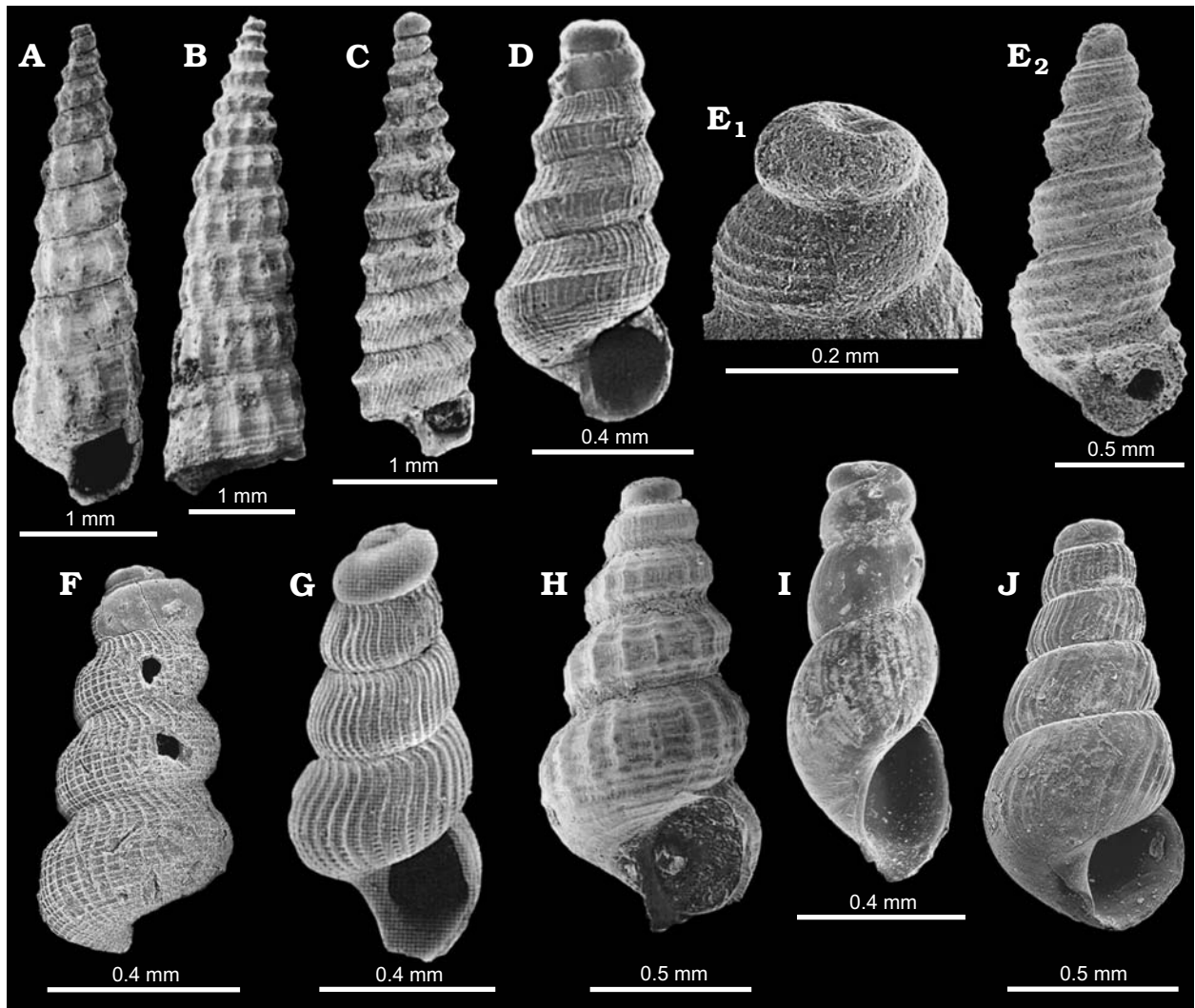


Fig. 9. Type species and examples for Triassic and Jurassic genera of the family Tofanellidae. **A, B.** *Tofanella laevigata* (von Münster, 1841), Cassian Formation, Alpe di Specie, Dolomites, N Italy, Late Triassic **A.** From Bandel (1995: pl. 10: 1). **B.** From Bandel (1995: pl. 10: 2). **C.** *Cristalloella (Cristalloella) cassiana* Bandel, 1995, Cassian Formation, Campo, Dolomites, N Italy, Late Triassic; from Bandel (1995: pl. 10: 9). **D.** *Cristalloella (Wonwalica) minuta* Schröder, 1995, Wąwał, Poland, Valanginian; from Schröder (1995: pl. 10: 1). **E.** *Neodonaldina elongata* (Zardini, 1978), Cassian Formation, Alpe di Specie, Dolomites, N Italy, Late Triassic. Protoconch (**E₁**) from Bandel (1996: fig. 5d), whole specimen (**E₂**) from Bandel (1996: fig. 6a). **F.** *Graphis rotundata* (Gründel, 1998), borehole Heringsdorf 4/63, Germany, middle Callovian; from Gründel (1998: pl. 1: 5). **G.** *Graphis albida* (Kanmacher, 1798), Pliocene, Nice/France; from Bandel (2005: fig. 64). **H.** *Camponaxis lateplicata* (Klipstein, 1843), Cassian Formation, Misurina, Dolomites, N Italy, Late Triassic; from Bandel (1995: pl. 14: 3). **I.** *Usedomella laevigatoidea* (Gründel, 1993), borehole Kłęby 1/37 (formerly Klemmen), Poland, Callovian; from Gründel (1998: pl. 2: 19). **J.** *Urlocella minuera* Gründel, 1998, borehole Kłęby 1/37, late Bathonian; from Gründel (1998: pl. 1: 11).

Genus *Usedomella* Gründel, 1998

Fig. 9I.

Type species: *Hyala? laevigatoidea* Gründel, 1993, original designation; Callovian, erratic boulder from North Germany.

Included species: *Hyala? laevigatoidea* Gründel, 1993, late Bathonian–Callovian; *Usedomella schroederi* Gründel, 1998, Pliensbachian; *Usedomella lata* Gründel, 1998, late Bathonian–Callovian; *Usedomella magnoconcha* Gründel, 1998, late Bathonian; *Usedomella winkleri* Gründel, 1999b, late Toarcian; *Usedomella* cf. *laevigatoidea* (Gründel, 1993) sensu Gründel 1999b, Middle Callovian; *Usedomella* sp. sensu Gründel 2007a, late Toarcian–early Aalenian.

Emended diagnosis.—Shell small, slender; whorls convex; suture deep; protoconch tofanellid, broader than the first

teleoconch whorl, consisting of about two whorls; teleoconch whorls including base smooth; growth lines weakly parasigmoidal; aperture round to oval.

Stratigraphic and geographic range.—Pliensbachian to Callovian; Germany, Poland.

Genus *Urlocella* Gründel, 1998

Fig. 9J.

Type species: *Urlocella minuera* Gründel, 1998, original designation; Bathonian to Callovian, Poland and NE Germany.

Included species: *Urlocella minuera* Gründel, 1998, Bathonian–Callovian; *Urlocella* sp. nov. sensu Gründel 1998, Pliensbachian; *Urlocella* cf. *minuera* Gründel, 1998 sensu Bandel 2005, Pliensbachian.

Emended diagnosis.—Shell slender; whorls convex; suture deep; protoconch tofanellid, consisting of about two whorls; first teleoconch whorl wider than protoconch; teleoconch ornament consists of parasigmoidal axial ribs and spiral ribs; teleoconch ornament reduced during ontogeny; base convex, not demarcated from whorl face; aperture broadly oval.

Remarks.—Kaim (2004) considered *Urlocella* to represent a synonym of *Chrysallida* Carpenter, 1856. However, Bandel (2005) did not accept this because *Chrysallida* has no tofanellid protoconch and therefore represent a genus of the Pyramidellidae. Instead Bandel (2005) considered *Urlocella* to represent a synonym of *Graphis*. We consider this synonymy to be unlikely as was outlined above (see Remarks under *Graphis*).

Stratigraphic and geographic range.—Pliensbachian to Callovian; Germany, Poland.

Genus *Conusella* Gründel, 1999b

Fig. 10A.

Type species: *Conusella conica* Gründel, 1999, original designation; late Pliensbachian; Northeast Germany.

Included species: *Conusella conica* Gründel, 1999a, Pliensbachian; *Conusella? pacifica* Bandel, Gründel, and Maxwell, 2000, late Early–early Middle Jurassic; *?Conusella?* sp. sensu Gründel 2003c, Callovian; *Conusella torusa* Gründel, 2006, late Bathonian; *?Conusella* sp. sensu Gründel 2006, late Bathonian; *Conusella* sp. sensu Gründel and Kaim 2006, Oxfordian.

Emended diagnosis.—Shell conical; protoconch tofanellid, comprising about two whorls; first teleoconch whorl broader than protoconch; whorls broad in relation to height; suture shallow; whorls smooth except straight growth lines; base convex, not demarcated from whorl face; base indistinctly umbilicated; aperture broadly oval.

Stratigraphic and geographic range.—Pliensbachian to Oxfordian; Germany, Poland, France, New Zealand.

Genus *Reinbergia* Gründel, 2007b

Fig. 10B, C.

Type species: *Reinbergia inflata* Gründel, 2007c, original designation; late Pliensbachian; NE Germany.

Included species: Only the type species.

Diagnosis.—Shell broadly conical with distinct suture and a tofanellid protoconch. The last whorl is higher than the spire; whorls smooth; growth lines strongly parasigmoidal; base with a distinct umbilicus; umbilicus surmounted by edge; aperture broadly oval (after Gründel 2007: 90).

Stratigraphic and geographic range.—Late Pliensbachian; Germany.

Discussion

The evolution of the Mathildidae in the Jurassic.—Numerous species of the Jurassic Mathildidae are insufficiently known and commonly protoconch and early teleoconch are

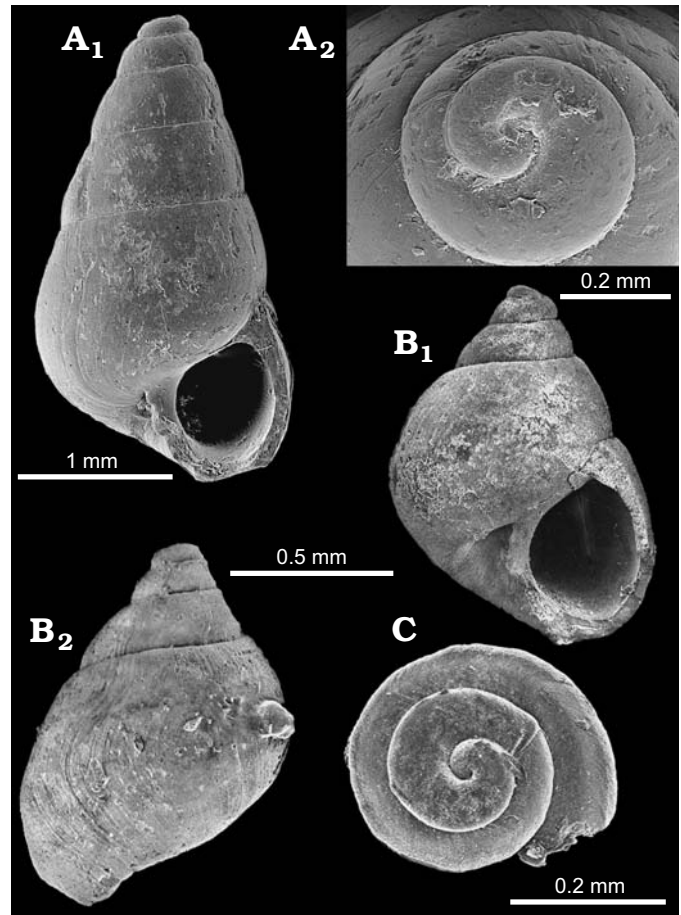


Fig. 10. Type species and examples for Jurassic genera of the family Tofanelidae. A. *Conusella conica* Gründel, 1999, Grimmen, Germany, late Pliensbachian. Whole specimen (A₁) from Gründel (1999: pl. 8: 8); protoconch in apical view (A₂) from Gründel (1999: pl. 9: 2). B, C. *Reinbergia inflata* Gründel, 2007, borehole Kb Rnb Gm 4/66 Reinberg, Germany, late Pliensbachian. B. From Gründel (2007: pl. 7: 6, 7). C. From Gründel (2007: pl. 7: 8).

unknown. Micro-ornaments can only be studied with a SEM and therefore, they have only been depicted in some recent studies. Modern studies were almost exclusively conducted on Early and Middle Jurassic faunas from clay and sandstone rocks of central and western Europe deposited in moderately deep water. There are, however, almost no recent studies on mathildoids from calcareous shallow water deposits which were dominant during the Late Jurassic. Even studies about Mesozoic mathildoids from other regions of the world are rare. As outlined above, the status of taxonomically relevant characters is insufficiently known. For these reasons, the stratigraphic ranges (originations and extinctions) of the genera discussed here, must be treated with caution and certainly must be continuously updated.

Bandel (1995) showed that Mathildoidea were richly diversified in the Late Triassic. There was a considerable diversity decline at the Triassic–Jurassic boundary but the *Jurilda*-group survived. However, it should be kept in mind that most of the Triassic diversity has been reported from tropical intra-platform basins partly with transported shallow water material

(Cassian Formation). In contrast most of the Jurassic data come from offshore soft bottoms of Central Europe with a more temperate climate. Both occurrences differ considerably in facies and depositional environment. Therefore, evolutionary considerations based on the composition of these Mesozoic mathildoid faunas (including Gordenellidae and Tofanellidae) must take into account facies differences as well as their different age. Mathildoid faunas from other parts of the world are poorly known or completely unknown. Therefore, the impact of the end-Triassic extinction is certainly biased. Gründel (1997: 153, table 2) gave an overview over the evolution of the Mathildidae from the Triassic to the Recent. The present study on Jurassic Mathildidae corroborates and improves these results.

Kaim (2004: 168, fig. 138) constructed a stratophenetic phylogenetic tree of Mathildoidea, which is on the species-level at least for Jurassic representatives. In this tree, Mathildidae are descendants of the Late Paleozoic Donaldinidae. *Tricarilda* is considered to represent a synonym of *Mathilda*. This tree also shows *Promathildia* (= *Jurilda* herein) and *Mathilda* as being present as early as Triassic. *Carinathilda* and *Gymnothilda* are descendants of *Promathildia*. *Erratothilda* (adelphotaxon of *Carinathilda*) together with *Tuba* Lea, 1833 (not yet found in the Jurassic) represents a lineage of equal rank to the group previously outlined. However, according to Kaim (2004) it is also possible that *Carinathilda* and *Erratothilda* are congeneric.

After an apparent considerable decline of Mathildoidea at the Triassic/Jurassic-transition, the *Jurilda*-group radiated in the Early and early Middle Jurassic. Numerous species with generally rather conservative morphology evolved. Since the Bathonian new genera occur indicating an increasing morphological disparity. Gründel (1997) also discussed the possible relationships of genera within the group.

Tangarilda differs from other Jurassic Mathildidae in having opisthocyrt growth lines with the backmost point between adapical and middle spiral rib. The genus seems to stand somewhat isolated in the family in this respect. The phylogenetic meaning of this character is not yet clear. In fact, such growth lines are not present in Mathildidae after the Hettangian (Sinemurian?) although numerous well-preserved mathildids are known from the post-Hettangian Jurassic.

It seems possible that there are closely related Late Triassic taxa with similar growth lines (AN personal observation) and that these taxa represent an old evolutionary line which became extinct in the late Early Jurassic.

According to the current state of knowledge, the first certain occurrence of *Jurilda* is of Hettangian age. Bandel (1995) reported very similar "*Promathildia*"-species from the Late Triassic Cassian Formation e.g., *Promathildia decorata* (Klipstein, 1843). However, the phylogenetic relationships of the diverse Mathildoidea from the Cassian Formation to Jurassic and younger forms are far from being clear (AN and JG unpublished data). It is for instance unclear, whether Triassic species with two primary spiral ribs can be assigned to the genus *Jurilda*. At least in some of these Triassic species, the growth line pattern differs from that of typical *Jurilda* species

and resembles that of the genus *Tangarilda*. Other late Triassic species, e. g., *Promathildia sculpta* (Kittl, 1894) sensu Bandel (1995), have numerous weak spiral ribs and this pattern resembles the micro-ornament of some Jurassic species but is distinctly coarser.

At present, it can be stated that either *Jurilda* itself or closely related forms were present as early as Late Triassic. This represents a continuous evolutionary lineage which crosses the critical Triassic–Jurassic boundary. This *Jurilda* lineage continues at until the Early Cretaceous and comprises species with a rather conservative morphology. The younger history of this group is unknown. None of the Recent species described by Bieler (1995) belongs to the *Jurilda*-group.

Gymnothilda can be derived from *Jurilda* by a reduction of the ornament. The oldest known species is *Gymnothilda dispiralis* from the Bathonian. This species has two primary spiral ribs. Forms with a single primary spiral rib are known from the Early Cretaceous. There are also Cretaceous species with two primary spiral ribs. Possibly a reduction of primary spiral ribs occurred within this genus. *Gymnothilda tomaszina* from the Valanginian has a micro-ornament which resembles that of *Carinathilda*. *Gymnothilda*-species have been reported only from a few stages (Bathonian, Valanginian, Campanian) and some are only known from juvenile specimens. Therefore, the evolution of this genus is still largely unknown.

The genus *Bathraspira* is only known from the Cretaceous. Protoconch and early ontogeny have been unknown until recently and the genus was assigned to the Procerithiidae or Cerithiidae. Kiel (2006) described a species with protoconch and early teleoconch whorls (*Gymnothilda pagodoidea*); this species combines a mature teleoconch typical for *Bathraspira* and an early stage typical for *Gymnothilda* with a single primary spiral rib. At least this species can be interpreted as a descendant of *Gymnothilda*. However, it is unclear whether this is true for other or all species of *Bathraspira*.

The evolution of the *Jurilda*–*Gymnothilda*–*Bathraspira* lineage encompasses a reduction of the sculpture. However, another lineage related to *Jurilda* is characterized by a strengthening and complication of the ornament. *Carinathilda* has two primary spiral ribs and a conspicuous ornament of fine spiral ribs. It is very likely that *Carinathilda* originated from a *Jurilda*-like ancestor. *Jurilda naricata naricata* (Gründel, 1973) represents a transitional stage. It resembles *Carinathilda* in having a strongly convex base, in the ornament of spiral ribs on the base, and in having keeled whorls. A micro-ornament may be present or lacking. In any case it is weaker than in *Carinathilda* (Gründel 1997: 137). If the micro-ornament was stronger and would form a constant character of this subspecies, then it could be placed in *Carinathilda*.

Angulathilda closely resembles *Carinathilda*. However, the base of *Angulathilda* is less convex and the base is demarcated from the whorl face by a strong spiral or a pronounced edge. The keel is more pronounced in *Angulathilda* and the whorls are concave above and below it. These differences may be easily derived from the bauplan of *Carinathilda*.

Both genera seem to appear in about the same time interval, during the Bathonian.

The oldest mathildoid with three primary spiral ribs is *Tricarilda*. This genus is probably as old as Hettangian and certainly as old as Sinemurian. Bandel (1995) reported Late Triassic mathildoids with three primary spiral ribs but those taxa differ in several other characters and are probably not members of the family Mathildidae. *Tricarilda* ranges into the late Early Cretaceous and its younger fate is unknown. The genus is not present among the modern forms reported by Bieler (1995).

Mathildoids with more than three primary spiral ribs are assigned to the genus *Mathilda*. Such species are known from the Toarcian onward and range into the Late Cretaceous (Dockery 1993). Whether these Mesozoic forms are congeneric with the Pliocene type species of *Mathilda* (see Gründel 1976 for a re-description) and with the modern species described by Bieler (1995) remains unclear.

Turrithilda cassiana Bandel, 1995 and *T. dockeryi* Bandel, 1995 from the Late Triassic Cassian Formation represent mathildid species with four primary spiral ribs. These species have been assigned to *Bandelhilda* Gründel, 1997 by Gründel (1997). They differ from Jurassic *Mathilda*-species in having smaller, coaxial protoconchs, two primary spiral ribs being strengthened, and angulate the whorl face; the whorls are parallel to the shell axis between these angulations. It needs to be tested whether these species belong to the stem group of *Mathilda* (Nützel and Gründel in preparation).

Erratohilda resembles the *Jurilda*-group in having a conspicuous micro-ornament. However, *Erratohilda* has three or more primary spiral ribs. Weak spiral striae are also present in some *Tricarilda* species (e.g., *T. plana* [Gründel, 1973] and *T. waltheri* Gründel, 1997). We therefore assume that *Erratohilda* is derived from *Tricarilda*. *Erratohilda* resembles *Angulathilda* in shell shape (keeled whorls, concavity above and below keel, strong spiral rib at edge to base). *Erratohilda* has been reported from the Callovian to the Early Cretaceous. Mathildoids with a distinct micro-ornament have also been reported from the Late Cretaceous e.g., *Echinimathilda microstriata* Dockery, 1993.

In conclusion, Mathildidae are as old as Late Triassic and had a first radiation during the Late Triassic including various species and several genera. Most of these taxa became extinct at the end-Triassic mass extinction event. According to the current state of knowledge, at least one evolutionary line survived the end-Triassic extinction: the *Jurilda*-group. It is still unknown whether the genus *Jurilda* itself was present in the Late Triassic or whether closely related forms were present. *Tangarilda* represents an additional evolutionary lineage which probably originates as early as Late Triassic. *Tricarilda* is probably a descendant of the *Jurilda*-group. In the Early Jurassic, only a radiation on the species level can be recognized. The Pliensbachian–Toarcian crisis had no impact on the genus level in mathildids. *Mathilda* originates in the Toarcian. A distinct radiation can be recognized in the Bathonian; *Gymnohilda*, *Carinathilda*, *Angulathilda*, and

Erratohilda appeared at about the same time. With the exception of *Carinathilda*, these genera as well as *Jurilda*, *Tricarilda*, and *Mathilda* were still present in the Early Cretaceous. Together with the Early Cretaceous *Bathraspira*, these genera show that Mathildidae were diverse during the period from the Middle Jurassic to the Early Cretaceous.

The evolution of the Gordenellidae in the Jurassic.—Gründel (2000) and Guzhov (2007) suggested that *Promathildia* (= formerly *Clathrobaculus*) and *Gordenella* are closely related to each other. *Promathildia* has all diagnostic characters of Gordenellidae except of the concave whorl face and the ontogenetic reduction of the teleoconch ornament.

Promathildia and *Gordenella* share a transaxial widely exposed protoconch. In the Jurassic such protoconchs are only known from Ebalidae (see Fig. 5C, D; Schröder 1995; Gründel 1998; Kaim 2004). Even Guzhov (2007: 386) emphasized the characteristic protoconch morphology in *Gordenella* and *Promathildia*. This suggests that they are closely related and separates them from the Mathildidae. In summary, *Promathildia* is here considered to represent a member of the Gordenellidae (in contrast to Gründel 2000). According to our interpretation, this genus shows the most basal morphology of this family and represents a phylogenetic link to the Mathildidae. Guzhov's (2007) though we are aware that this phylogenetic scenario is rather hypothetical due to the insufficient knowledge of majority of involved species.

The family Gordenellidae contain only a few genera. Apparently, there are two evolutionary lineages. *Promathildia* is known since the earliest Jurassic. Very similar species which belong to *Promathildia* or a closely related genus have been reported from the Late Triassic (Haas 1953). However, these species are insufficiently documented. *Promathildia* share some characters with the mathildid *Tricarilda*: three primary spiral ribs and a basically mathildoid ornament throughout its teleoconch ontogeny. *Tricarilda* is known since the earliest Jurassic. *Promathildia* is more slender and has more whorls than *Tricarilda* and the protoconch morphology of both genera differs from each other. The relationships of both genera are not yet clear. It seems possible that both genera share a last common ancestor in the Triassic. *Promathildia* ranges into the Early Cretaceous; its younger evolution is unknown. Several Cretaceous mathildoid gastropods were described which could belong to Gordenellidae or Mathildidae (e. g., *Mathilda coxi* Abbass, 1962 and *M. ahmadi* Abbass, 1962). However, these taxa are insufficiently known so that a safe taxonomic assignment is unwarranted.

Gordenella closely resembles *Promathildia* in shape, ornament of the early teleoconch and the protoconch morphology. This suggests that *Gordenella* probably evolved from a *Promathildia*-like ancestor (Gründel 2000; Guzhov 2007). *Gordenella* differs from *Promathildia* by its pronounced ontogenetic change of the teleoconch ornament. *Gordenella* ranges from the Bajocian to the Oxfordian.

The yet unnamed genus and species (to be named elsewhere) illustrated herein (Fig. 6C) is known from the Pliens-

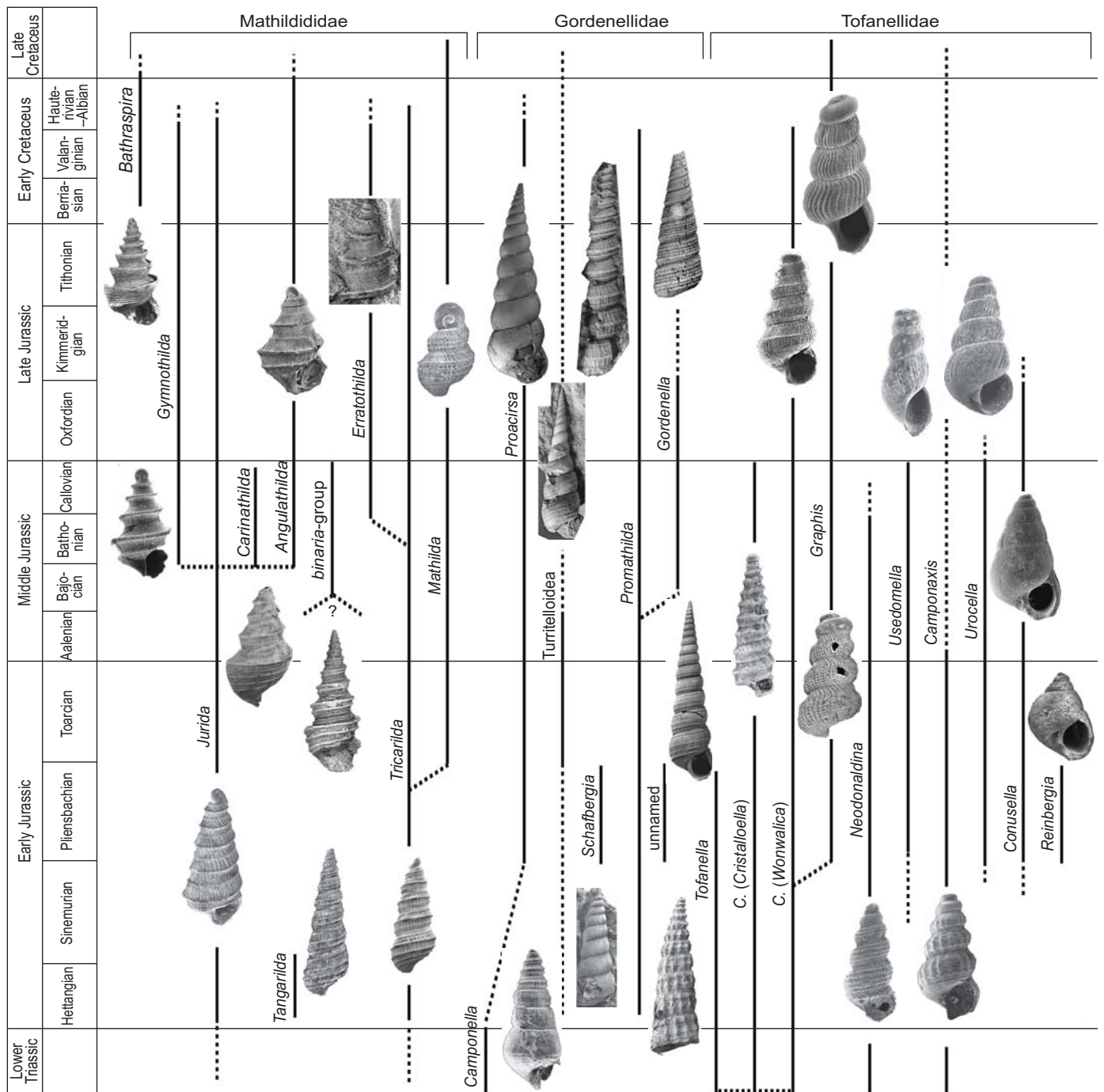


Fig. 11. Stratigraphic ranges of mathildoid genera with indications of some possible phylogenetic relationships.

bachian of Germany. Its early teleoconch has a “*Promathildia*-like” ornament as is typical for Gordenellidae. As in *Promathildia* the position of the spiral ribs remains fairly stable throughout ontogeny; however, they become weaker. In contrast to *Promathildia*, the new genus adds numerous spiral ribs and striae during ontogeny. At the same time the axial ribs are replaced by very numerous strengthened growth lines. The ontogenetic change of the teleoconch ornament differs from that in *Gordenella*. The new genus and *Gordenella* are probably not very closely related to each other. Moreover, the relationship of the new genus to *Promathildia* is not yet clear be-

cause the protoconch of the new Pliensbachian genus is unknown.

The second gordenellid lineage initiates with the Late Triassic *Camponella*. *Camponella* closely resembles *Proacirsa* (Pliensbachian–Early Cretaceous) but differs in being smaller, in having fewer whorls, and in having an umbilicus. It is very likely that *Proacirsa* evolved from a *Camponella*-like ancestor. The stratigraphic gap between the occurrences of both genera spanning the Carnian to Pliensbachian is probably a result of preservation. *Camponella* and *Proacirsa* closely resemble the genus *Schafbergia* Gatto and Monari, 2010 (Li-

assic, Alps). *Schafbergia* differs from these genera in having weaker spiral ribs which are confined to the abapical portion of the whorls. Moreover, in *Schafbergia*, the spiral ornament on the whorl flanks persists throughout the entire ontogeny and it lacks the broadening of the spiral ribs on the base. All three genera are probably closely related to each other although their exact phylogenetic relationships are unknown. *Turritelloidea* differs from *Proacirsa* by its teleoconch ornament of broad spiral ribs and narrow furrows throughout its ontogeny (a similar ornament is present on the base of *Proacirsa*). It differs from *Schafbergia* in having broadened spiral ribs on mature teleoconch whorls and in details of the early whorls. The genera *Camponella*, *Proacirsa*, and *Turritelloidea* share an almost coaxial protoconch (the protoconch of *Schafbergia* is unknown) which differentiates them from the *Promathildia*-branch. *Turritelloidea* seems to have the longest range and originates as early as Hettangian and probably ranges into the Late Cretaceous.

Seemingly, the end-Triassic crisis had no serious effect on the Gordenellidae. The *Proacirsa*-branch is certainly and the *Promathildia*-branch is probably as old as Triassic. Few new genera occur in the Jurassic and there seems to be no strong radiation of this group. *Promathildia* and *Proacirsa* are the most diverse and longest ranging genera.

Remarks on the family Anoptychiidae Bandel, 1994.—*Anoptychia* encompasses high-spined shells with axial ribs on the early teleoconch, which are reduced subsequently so that the shell is smooth. Bandel (1995: 16) based the new family Anoptychiidae on a heterostrophic species from the Cassian Formation, which he identified as *Melania suprapecta* Münster, 1841 (type species of the genus *Anoptychia* Koken, 1892). However, according to Nützel (1998) and Nützel et al. (2003), Bandel (1994, 1995) misidentified his material. The protoconch of the type species of *Anoptychia* is still unknown and therefore, its higher systematic placement is doubtful. High-spined species in which teleoconch ribs are reduced during ontogeny are also present in other gastropod groups, e.g., in the family Zygopleuridae (Caenogastropoda). Presently, it is unclear whether *Anoptychia* belongs to the Heterobranchia or Caenogastropoda and therefore *Anoptychia* is not considered here. The material presented by Bandel (1995) from the Late Triassic seems to represent a genus which has not been reported from the Jurassic.

The Jurassic evolution of the Tofanellidae.—The knowledge about the Tofanellidae is rather new. Nearly all Jurassic representatives have been described since 1995. Most of them are from Germany and Poland. The Late Triassic tofanellids were studied by Bandel (1995). All of these species are from the Carnian Cassian Formation (N Italy). Morphological details including the protoconch morphology of the minute species could only be studied after scanning electron microscopes were available. It is clear that only a small portion of the gone diversity of this group has been documented so far. Bandel (1995) and Gründel (1998) made first assumptions about the relationships of fossil tofanellids to modern

descendants. Kaim (2004) suggested a close phylogenetic relationship of tofanellids and *Graphis*. Bandel (2005) showed that the Recent genus *Graphis* belongs to the Tofanellidae and that there are closely related Jurassic forms which do not differ from their modern counterparts. Gründel (2007a, b) synonymized the Jurassic genus *Rotfanella* with the modern genus *Graphis* and thus *Graphis* represents an extremely long-lasting genus. There is almost no information about tofanellids from the Late Cretaceous to the Cenozoic.

Within the Tofanellidae, two groups with distinct shell morphology can be recognized. These groups may represent real phylogenetic lineages:

(i) The first tofanellid group is characterized by an inflated last protoconch whorl which is broader than the first teleoconch whorl and by a very slender, almost cylindrical teleoconch (slow increase of whorl width during ontogeny). The following genera belong to this group: *Tofanella*, *Cristalloella*, *Graphis*, *Neodonaldina*, and *Usedomella*. *Tofanella*, *Cristalloella* (including both subgenera), and *Neodonaldina* are as old as Late Triassic. The earliest reports of *Graphis* and *Usedomella* are from the Pliensbachian. Within this group, there is a tendency to reduce the ornament. *C. (Cristalloella)* and some representatives of *Tofanella* have keeled whorls and a strong ornament of axial ribs and weaker spiral ribs. The transition from the whorl face to the base is formed by an edge with a spiral rib. *Cristalloella (Wonalica)* has a weaker keel and the transition from the whorl face to the base is rounded. *Graphis*, *Neodonaldina*, and *Usedomella* have convex, rounded whorls without keel. *Graphis* has a complex ornament consisting of axial and spiral ribs. *Neodonaldina* has only spiral ribs which becomes rather weak in some species. *Usedomella* is smooth and only some species show remains of axial ribs in the subsutural portion of the first teleoconch whorl.

(ii) The second tofanellid group encompasses the genera *Camponaxis*, *Urlocella*, *Conusella*, and *Reinbergia*. Their protoconch is not inflated and the first teleoconch whorl is broader than the teleoconch. The teleoconch is not as slender as in the first group and the whorls increase more rapidly in width so that the habitus is broader conical. The oldest known genus of this group is *Camponaxis* from the Late Triassic. The oldest known representatives of the other genera have been reported from the Pliensbachian. *Camponaxis* has axial and weaker spiral ribs on all teleoconch whorls. In *Urlocella*, the ornament is restricted to the early teleoconch whorls. *Conusella* and *Reinbergia* are smooth.

To date, five genera (subgenera) of the Tofanellidae are known from the Late Triassic. All of them survived into the Jurassic. Therefore, the end-Triassic mass extinction obviously did not affect this family on the generic level. However, there is no tofanellid species which is known from the Triassic as well as from the Jurassic. On the one hand, this is preservation driven because no tofanellid occurrences are known between the Carnian and the Pliensbachian. On the other hand, the facies and geographic differences between the Late Triassic occurrences (all from the Cassian Formation) and the Ju-

rassic occurrences (German–Polish Basin) make it unlikely that identical species are found before and after the Jurassic–Triassic boundary. Seemingly, a tofanellid radiation occurred in the Early Jurassic. *Graphis*, *Usedomella*, *Urlocella*, *Conusella*, and *Reinbergia* seem to occur at about the same time in the Pliensbachian. However, it is possible or even likely that this contemporaneous appearance is result of preservation and/or sampling biases. *Tofanella* and *Reinbergia* have not been reported from the post-Pliensbachian. *Cristalloella* (*Cristalloella*), *Neodonaldina*, *Usedomella*, and *Urlocella* seem not to survive the Middle to Late Jurassic boundary according to the current state of knowledge. The younger evolutionary history of the Tofanellidae is largely unclear. Only *Graphis* is also known from the Recent.

In conclusion, the family Tofanellidae had a first radiation in the Late Triassic. The radiation could be somewhat older because only the Cassian Formation produces specimens which are so well-preserved that tofanellids can be recognized whereas older Triassic formations generally lack this excellent preservation. Seemingly it was not affected by the end-Triassic crisis. A second radiation occurs in the Pliensbachian and the family reaches its highest diversity between the Pliensbachian and the Callovian. Few taxa have been reported after this period. However, it must be kept in mind that tofanellids are known from very few occurrences. *Graphis* is a tofanellid genus which ranges from the Pliensbachian to the Recent. This is one of the longest generic ranges known from gastropods.

Conclusions

We have presented a synoptic classification of Mesozoic (and some modern) mathildoid taxa treated herein (for a key see Appendix 1). As stated above, it is based on shell characters of which the biological meaning is poorly known or unknown. In the absence of a phylogenetic framework based on anatomical and molecular studies, the present arrangement is justified especially that it largely concerns fossil taxa, which status would hardly be clarified by molecular studies. Nevertheless, such studies on living mathildoids certainly would help to better understand the phylogenetic meaning and significance of shell characters in Mathildoidea. We would like to emphasize that not all Mesozoic mathildoid species are included in this classification. We omitted especially those taxa which are so poorly known that any generic and family assignment is highly speculative.

About 150 early Mesozoic (mostly Early and Middle Jurassic) species of the heterobranch superfamily Mathildoidea are classified into four families and 27 genera. Most taxa are assigned to the families Mathildidae, Gordenellidae, and Tofanellidae while the Triassic family Anoptychiidae holds only a single genus and is restricted to the Late Triassic. A high mathildoid diversity has been recognized from the Late Triassic Cassian Formation (Kittl 1894; Bandel 1995, 1996). Many of these taxa are unknown from the Jurassic and prob-

ably became extinct during the end-Triassic mass extinction event. However, at least five genera (probably eight) survived the end-Triassic mass extinction event. *Tricarilda*, *Jurilda*, and *Promathildia* are rather conservative, long ranging groups of high Jurassic species diversity. They probably gave rise to the modern Mathildidae.

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Appendix 1

Key to mathildoid genera and subgenera.

Mathildidae

Protoconch of mathildid type, mostly transaxial or medioxial, not completely elevated, rarely coaxial; teleoconch with ornament of spiral ribs and reinforced growth lines or collabral axial threads; ornament normally not reduced during ontogeny (except for *Gymnothilda*).

- 1 Backmost point of growth lines between primary spiral ribs 1 and 2 *Tangarilda*
- 2 Backmost point of growth lines on primary spiral rib 2
 - 2.1 Microornament lacking or weak
 - 2.1.1 Ornament not reduced during teleoconch ontogeny
 - 2.1.1.1 2 primary spiral ribs *Jurilda*
 - 2.1.1.2 3 primary spiral ribs *Tricarilda*
 - 2.1.1.3 4 and more primary spiral ribs *Mathilda*
 - Ornament reduced during teleoconch ontogeny; 1 or 2 primary spiral ribs *Gymnothilda*
 - 2.2 Distinct microornament present; whorls with keel
 - 2.2.1 2 primary spiral ribs
 - 2.2.1.1 Transition from whorl face to base rounded *Carinathilda*
 - 2.2.1.2 Transition from whorl face to base with keel *Angulathilda*
 - 3 or more primary spiral ribs; transition from whorl face to base with keel *Erratohilda*

Gordenellidae

Protoconch and early teleoconch as in Mathildidae; later teleoconch in most cases with considerable ontogenetic change; shell mostly relatively large and slender with numerous whorls

- 1 Typical mathildid ornament during entire teleoconch ontogeny with no or few changes; protoconch transaxial and widely elevated *Promathildia*
- 2 Ornament changes considerably during teleoconch ontogeny
 - 2.1 Whorl face straight to concave; abapical primary spiral ribs shifts towards abapical suture *Gordenella*
 - 2.2 Whorl face of mature teleoconch whorls convex
 - 2.2.1 Ornament reduced in latest teleoconch whorls; base with broad spiral ribs
 - 2.2.1.1 Shell small with few whorls, umbilicated *Camponella*
 - 2.2.1.2 Shell tall with many whorls, not umbilicated *Proacirsa*
 - 2.2.2 All teleoconch whorls ornamented
 - 2.2.2.1 Whorl and base of late teleoconch whorls ornamented with broad ribbon-like spiral ribs *Turritelloidea*
 - 2.2.2.2 Early teleoconch whorls with few axial ribs which are as strong as spiral ribs; later whorls with numerous reinforced growth lines and spiral threads new unnamed genus
 - 2.2.2.3 Early teleoconch whorls with numerous axial and spiral ribs of about equal strength; later whorls with weak spiral ribs only *Schafbergia*

Tofanellidae

Shell small; protoconch tofanellid, i.e., coaxial with change from sinistral to dextral within larval shell and sunken initial whorl

- 1 Teleoconch strongly ornamented, without reduction in late whorls
 - 1.1 Whorls with keel
 - 1.1.1 Only early teleoconch with keel, whorl face more or less straight in later whorls *Tofanella*
 - 1.1.2 All teleoconch whorls with keel
 - 1.1.2.1 Shell very slender with numerous whorls, with keel or edge at transition to base *Cristalloella* (*Cristalloella*)
 - 1.1.2.2 Shell more or less stout, with few whorls, transition to base rounded *Cristalloella* (*Wonwalica*)
 - 1.2 Whorls convex, shell with few whorls
 - 1.2.1 Whorls with few, straight axial ribs; spiral ribs weak or lacking *Camponaxis*
 - 1.2.2 Whorls with numerous parasigmoidal axial ribs and weaker spiral ribs *Graphis*
 - 1.2.3 Whorls with spiral ribs only *Neodonaldina* (part)
- 2 Whorls convex, ornament reduced during ontogeny
 - 2.1 Whorls with spiral ornament becoming weaker during ontogeny *Neodonaldina* (part)
 - 2.2 Whorls with parasigmoidal axial ribs and weaker spiral ribs; axial ribs weakening during ontogeny *Urlocella*
- 3 Whorls convex, smooth
 - 3.1 Shell slender, protoconch wider than first teleoconch whorl *Usedomella*
 - 3.2 Shell broadly conical; protoconch narrower than first teleoconch whorl
 - 3.2.1 Growth lines straight; indistinct umbilicus *Conusella*
 - 3.2.2 Growth lines distinctly parasigmoidal, distinct umbilicus *Reinbergia*