A new Cenozoic record of spinilomatine aporrhaids (Stromboidea, Caenogastropoda) in the early Paleocene of Faxe, Denmark

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A new find is identified as a representative of the subfamily Spinilomatinae, *viz. Spiniloma? faxensis* sp. nov. The specimen was found as an impression in coral limestone of the early Paleocene (middle Danian) Faxe Formation in the Faxe quarry in Denmark. The genus *Spiniloma* was until now known exclusively from the Mesozoic of Europe. The new find extends the stratigraphic range of the genus into the early Paleocene. Furthermore, the gastropod fauna of the Faxe Formation is dominated by gastropods with a preference for hard substrates, while soft- substrate genera like *Spiniloma* are extremely rare.

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The Middle Danian Faxe Formation of the Faxe Quarry, eastern Denmark (Fig. 1), contains a very rich mollusc fauna where especially gastropods are very well represented with more than 220 recorded species (Ravn 1902a, b, 1933; Nielsen 1919; Schilder 1928; Rosenkrantz 1960; Schnetler *et al.* 2001; Schnetler & Petit 2006; Schnetler & Lozouet 2012; Schnetler 2012, 2013; Lauridsen & Schnetler 2014). The gastropods are found in sizes ranging from 0.45 mm (Lauridsen & Schnetler 2014) and up to 16 cm in height (Schnetler & Milàn 2011) for adult specimens. A unique specimen is attributed to the Spinilomatinae and represents the first post-Mesozoic occurrence of this subfamily in Europe.

Geological setting and stratigraphy

The middle Danian Faxe Formation (Fig. 2) represents an extraordinarily well-preserved deep-water coral-mound complex (Lauridsen *et al.* 2012). The coral-mound complex is dominated by three frame-building azooxanthellate scleratinian coral species of which *Dendrophyllia candelabrum* is by far the most common, followed by *Faksephyllia faxoensis* and a minor content of *Oculina becki* (Bernecker & Weidlich 1990, 2005; Lauridsen *et al.* 2012). The Faxe Formation is unique to the area and represents the oldest and best developed cold-water coral-mound complex of its kind, with only a few limited patch reefs known from elsewhere in the Danish basin (Bjerager *et al.* 2010; Lauridsen *et al.* 2012). Within the Faxe Formation there are isolated pockets of the Baunekule Facies (informally known as 'Næsekalk'), where aragonitic-shelled fossils were recrystallized to calcite during the early burial, preserving the morphology of primarily aragonitic shells (Lauridsen *et al.* 2012). The Faxe Formation interfingers laterally with the bryozoan limestone of the Stevns Klint Formation, which is the common type of Danian limestone in southern Scandinavia (Bjerager & Surlyk 2007a, b). The described specimen is found within the coral limestone of the Faxe Formation.

Material and Methods

The only specimen described herein has been collected in the Faxe quarry as an impression in consolidated coral limestone (Fig. 3). The specimen was found in 1994 by the late Mrs. Alice Rasmussen (1932–2013). The

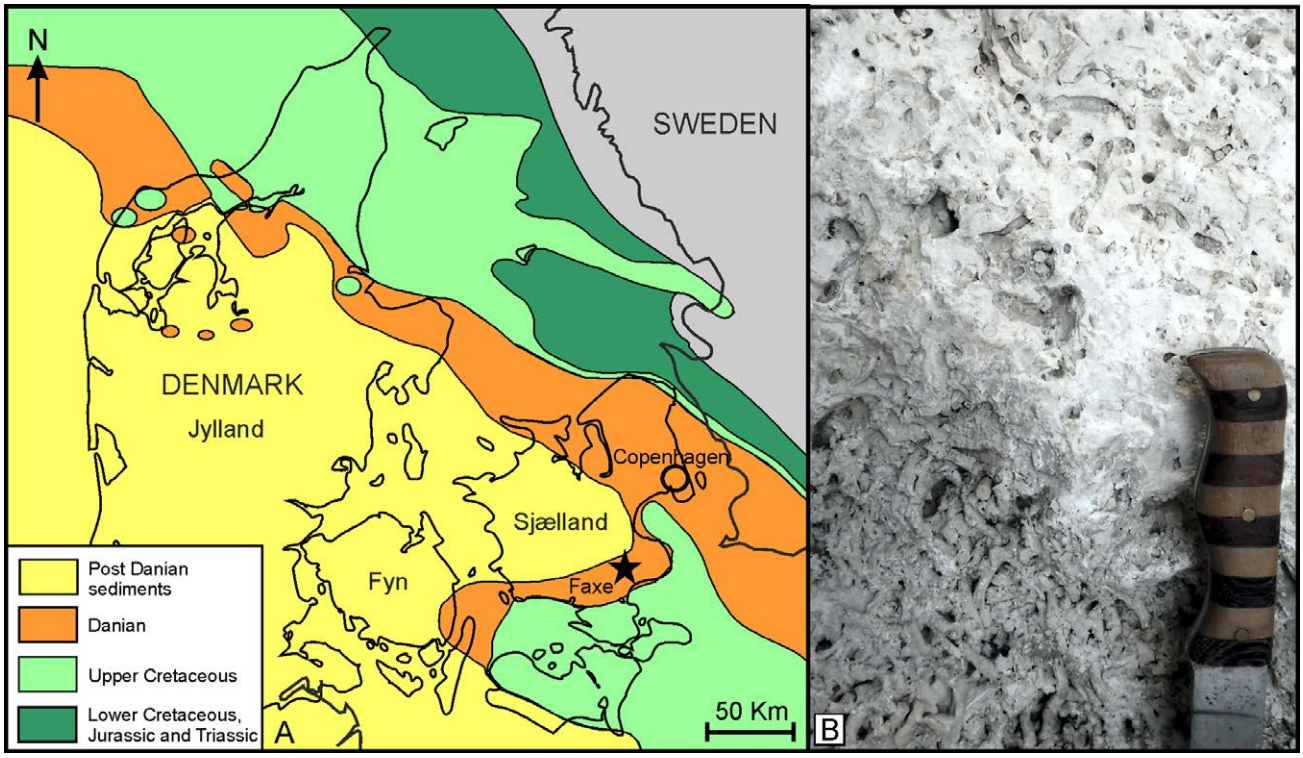

Fig. 1. **A**: The Faxe Limestone Quarry (black star) is located by the town of Faxe, approximately 70 km south of Copenhagen on the Danish island Sjælland. Modified after Thomsen (1995). **B**: Typical coral limestone of the Faxe Formation, scale on knife handle 10 cm.

original aragonitic shell had been dissolved after hardening of the sediment, and a perfect natural cast of the shell morphology was obtained by making a silicone latex cast of the impression in a vacuum chamber (Fig. 4). The specimen was not collected *in situ*, but impressions of scleratinian corals in the same slab could be identified as *Dendrophyllia candelabrum* by preparator Sten Lennart Jakobsen (Natural History Museum of Denmark) who made the cast. Thus, the provenance of the specimen is fully secured. The specimen is now part of the collection of Østsjællands Museum, Denmark, catalogue number OESM-10059-21631.

Systematic Palaeontology

Class Gastropoda Cuvier 1797

Subclass Caenogastropoda Cox 1960

Order Latrogastropoda Riedel 2000

Superfamily Stromboidea Rafinesque 1815

Family Aporrhaidae Gray 1850

Subfamily Spinilomatinae Gründel, Nützel & Schulbert 2009

Genus ***Spiniloma*** Gründel, Nützel & Schulbert 2009 (= *Spinigera* d'Orbigny 1850; inv.)

Type species: *Ranella longispina* Eudes-Deslongchamps 1843 (Bajocian of France)

Spiniloma? faxensis sp. nov.
Figures 3, 4
Holotype. Figures 3b, 4; OESM-7116, leg. Alice Rasmussen. The holotype is the only specimen known.

Type locality. Faxe quarry, Sjælland, Denmark.

Type stratum. Coralline Limestone, Faxe Formation, middle Danian.

Derivation of name. The species is named after the type locality, the Faxe quarry.

Diagnosis. The species is characterized by one keel on the whorls and hollow spines on all whorls, situated as continuations of the keel. The columella is slightly concave and the canal is rather short and slightly turned to the left.

Measurements. Height 22 mm (estimated 30 mm), width 20 mm (estimated 25 mm), height of body whorl 14 mm, height of aperture 7 mm (estimated 11 mm).

Description. One impression of an incomplete specimen has been collected. It consists of a little more than three teleoconch whorls and the body whorl and shows both sides of these whorls. The presumed spines on the left side are not preserved and the anterior part of the canal and the labrum are broken off. On the base an axial varix opposite the labrum is indicated by a weak axial fold and an old aperture, which clearly suggest a spine. The protoconch is not preserved. The whorls are angular and have a carina because of a rather strong and projecting spiral, situated somewhat below the middle of the whorl. The carina divides the whorl into two parts with almost straight outline. The first teleoconch whorl is only partly preserved and has only part of the spiral ornament preserved. On the following whorl, there are three primary spirals cords above the carina and two below the carina, which is spiral cord number four. Spiral cord number one is situated at about one fourth of whorl height below the adapical suture, and spiral cords number two and three are of almost the same strength and equally spaced. The spirals are considerably thinner than their interspaces. The carina is smooth and considerably stronger than the other spirals. Below the carina there are primary spiral cords number five and six, the latter is partly covered by the following whorl. Weaker secondary spiral lirae are inserted from the first completely preserved whorl onward, which has such spirals between the adapical suture and spiral number one and between the spirals number two, three, four, five and six. On the following whorls three further generations of secondary spirals are inserted, especially between spiral number three and the carina. On the body whorl, the adapical part of the whorl has 15 spirals of varying strength above the carina and eight below. On the base, spiral number six is of almost the same strength as the carina and demarcates the almost flat base which has a similar spiral ornament as the whorls. About 20 spirals of varying strength are visible on the base and the neck of the canal. On the right side of all preserved whorls there are varices which have hollow spines at the continuations of the carina. These spines are increasing in length abapically and almost perpendicular to the axis. On the body whorl, the spine is directed distinctly downwards. A few almost opisthocyrt axial folds are visible on the first intermediate whorls. Furthermore, fine growth lines are visible. On the adapical part of the whorl they are almost orthocline with a very shallow sinus near spiral number three and then they run slightly opisthocline to the carina. Under the carina, they are almost orthocline. The growth lines suggest that the first intermediate whorl may have had a reticulate pattern. The aperture is subovate with a slightly concave columella which is partly covered by a thin callus. The rostrum is partly broken and seems to have been rather short and turned to the left.

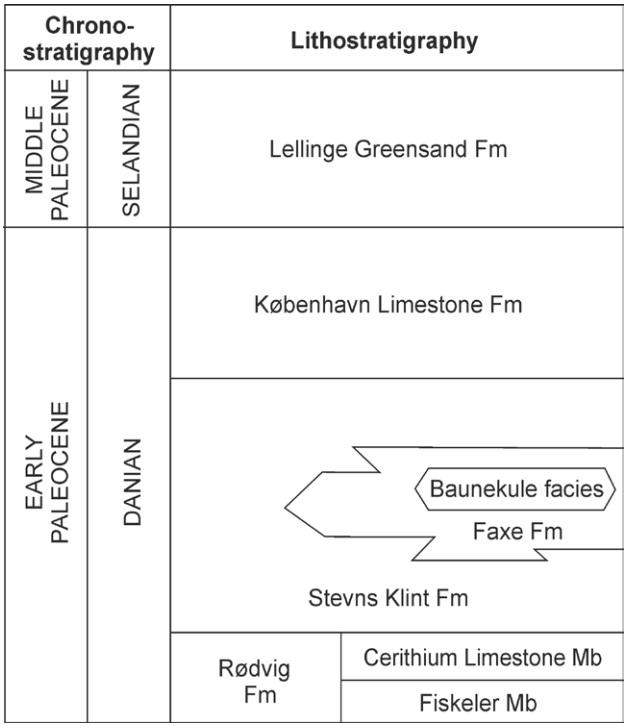

Fig. 2. Stratigraphic scheme of the Lower to Middle Paleocene section in the Danish Basin. The *Spiniloma* specimen is found in the Middle Danian Faxe Formation, which is geographically restricted to the Faxe Limestone Quarry. Modified from Lauridsen *et al*. (2012) and Surlyk *et al*. (2006, 2013).

Discussion

The new species is assigned to the subfamily Spinilomatinae because of the spines on both sides of the spire and the prevailing spiral ornament. As neither the protoconch, first intermediate whorl nor the anterior part of the rostrum are preserved, the assignment to genus is somewhat uncertain.

The new species matches *Spiniloma* Gründel *et al*. 2009 (replacement name of *Spinigera* d'Orbigny 1850, type species: *Ranella longispina* Eudes-Deslongchamps 1843 from the Bajocian of France) with regard to the presence of projecting spines on all teleoconch whorls, spines on the carina, one spine on the labrum and the general outline with prevailing spirals on the teleoconch whorls. The new species differs from the type species of *Spiniloma* especially by having a wider

aperture, a slightly concave columella and a curved and shorter rostrum.

Squires & Saul (2001) established the genus *Spinigeropsis* with the type species *Spinigeropsis calafia* Squires & Saul 2001 from the late Paleocene of southern California. *Spinigeropsis* differs from *Spiniloma* by having no digitations on the uppermost spire, shorter digitations on the middle part of the spire, two rather than one digitation on the left side of the body whorl, posteriorly directed digitations, and a bent and much shorter rostrum (Squires & Saul 2001). Wieneke (2015) assigned the genus to the family Spinilomatidae. The new species matches *Spinigeropsis* with regard to the rather short and bent rostrum, axial ribs (suggested on first intermediate whorl) and the broader basis and rostrum, but differs by having spines on all teleoconch whorls and only one spine on the labrum.

Guzhov (2014) established the genus *Undoriptera* which has a carinated teleoconch with reticular ornamentation on the first teleoconch whorls and prevailing spiral ornamentation on later whorls. The carina is situated approximately in middle of whorl. The external lip is more or less expanded, having three processes which are slightly curved posteriorly. The genus *Undoriptera* thus has only the spiral ornament similar to *Spiniloma*. Guzhov (2014) assigned it to the family Aporrhaidae. The new species has only one process on the external lip, whereas *Undoriptera* has

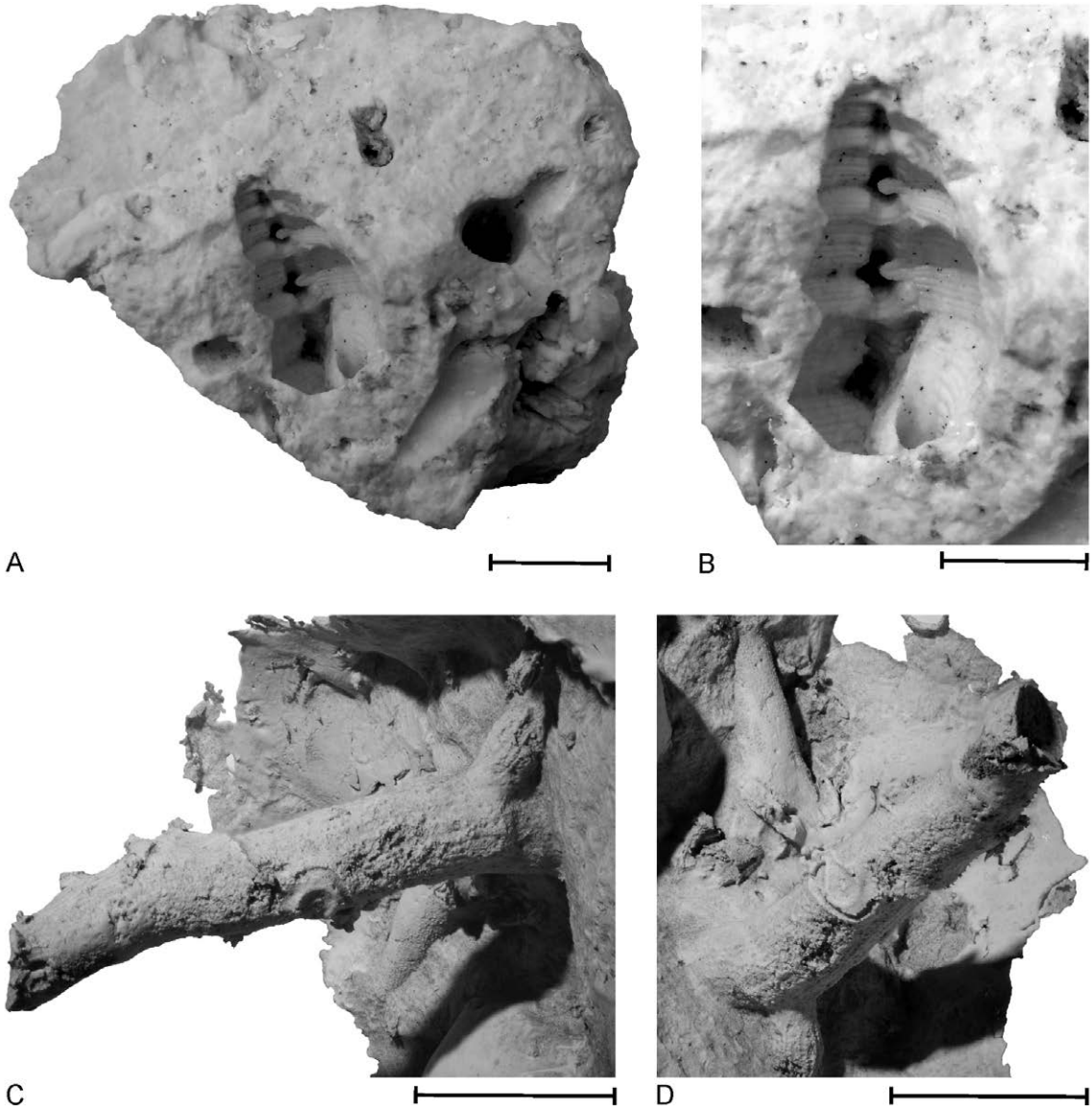

Fig. 3. The specimen OESM-7116. **A**: The complete specimen with the impressions of the gastropod and corals. **B**: Close-up of the gastropod impression in the limestone. **C** and **D**: Silicone casts of the coral voids that enable the identification as the scleratinian species *Dendrophyllia candelabrum*. Scale bars equal 10 mm. Photos by Sten Lennart Jakobsen.

three, and thus it cannot be assigned to the genus *Undoriptera*.

Gründel *et al*. (2009) established the genus *Toarctocera*. This genus has a smooth protoconch and the first teleoconch whorls are ornamented with two strong spiral ribs which angulate the whorl face, and numerous axial ribs. After one or two whorls, the axial ribs and the abapical spiral disappear and the adapical spiral rib continues as a strong, crenulated keel. A second keel is situated at the edge to the base and emerges at the abapical suture. It becomes fully visible on the last whorl. The outer lip of the aperture of adult specimens is extended to a rectangular plate on which both keels extend as strong ribs. The distal edges extend into two long spines. The adapical spine is bending to the right (in apertural view) posteriorly, until it is parallel to the shell axis. The abapical spine runs straight in an abapical direction oblique to the shell axis. The anterior rostrum is bent to the left (in apertural view) in a posterior direction until it is almost parallel to the shell axis. Thus, *Toarctocera* differs considerably from *Spiniloma* and was assigned to the family Aporrhaidae by Gründel *et al*. (2009). *Toarctocera* has an outer lip, extended to a rectangular plate with two long spines in the distal edges, whereas the new species has only one spine on the external lip and thus cannot be assigned to the genus *Toarctocera*.

Kaim (2004, fig. 137) provided an overview of the early whorls of the aporrhaid genera *Spinigera*, *Dicroloma*, *Pietteia*, *Quadrinervus*, *Anchura*, and *Aporrhais*. The early teleoconchs of ''*Spinigera*'' (= *Spiniloma*) (Kaim 2004, fig. 137A) and *Pietteia* (Kaim 2004, fig. 137A) resemble that of *Toarctocera*. However, the adult teleoconchs of these genera differ considerably from that of *Toarctocera*. *Spiniloma* differs from these genera by having long lateral spines on each teleoconch whorl. Thus, the new species differs from all genera discussed, but matches *Spinigeropsis* and *Spiniloma* best. The study of more material may result in an establishment of a new genus, but preliminarily we prefer to assign it to the genus *Spiniloma* because the new species comes closest to this genus in general outline, spiral ornament and the arrangement of spines. As the assignment is somewhat uncertain, we suggest the name *Spiniloma*? for the new species.

According to Global Biodiversity Information Facility (2016) the genus *Spiniloma* has been reported from Germany, France, Poland and Austria. Moreover, it has been recorded from Western India (Jaitly & Szabo 2007). *Spiniloma*? *faxensis* sp. nov. is different from the Lower Jurassic (Toarcian) species *Spiniloma dumortieri* (Piette 1891) because the latter has a rounded carina abapically and four strong spiral bands above it, and the spines are much shorter. *S. semicarinata* (Münster *in* Goldfuss 1844) from the Middle and Upper Jurassic (Callovium–Oxfordium) has projecting spines which are directed slightly upwards and a spiral ornament consisting of 11 spiral ribs. *S. recurva* from the Middle Jurassic (Bajocian) (Hudleston 1888) has spines directed adapically and *S. macrocephali* (Quenstedt 1884) from the Middle Jurassic (Doggerian) has spines directed abapically. *S. compressa* (d'Orbigny 1850) from

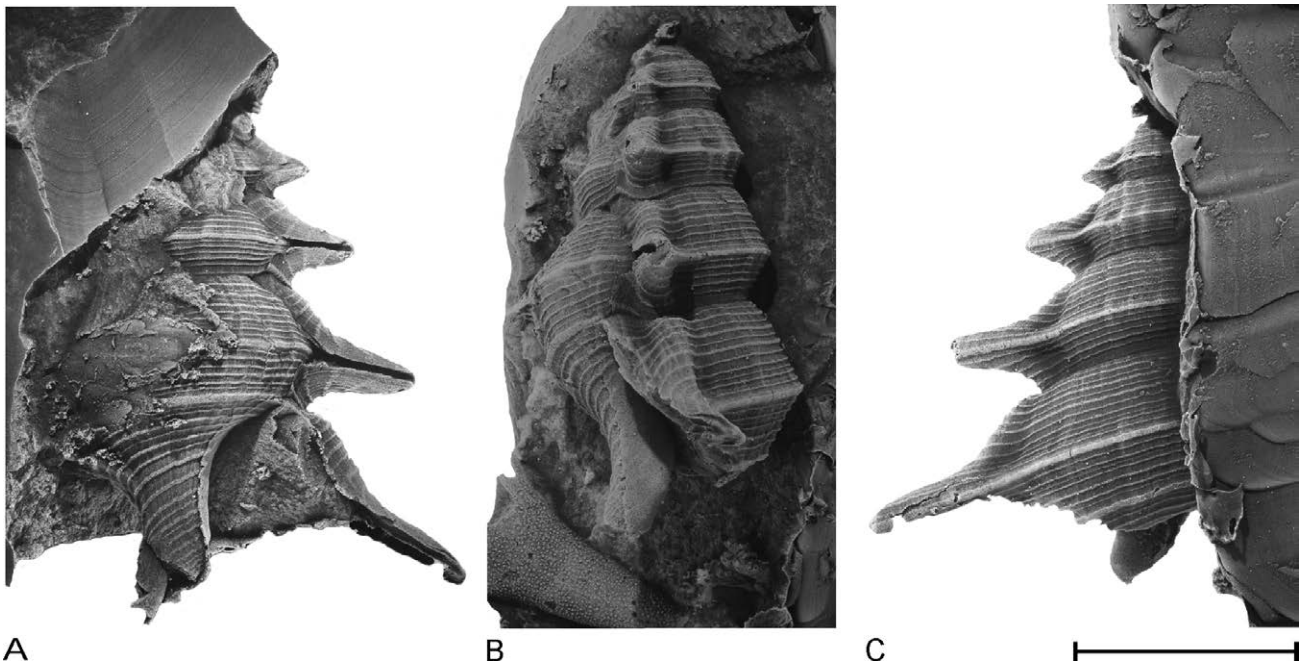

Fig. 4. Silicone cast of holotype of *Spiniloma? faxensis* sp. nov. OESM-7116. **A**: Apertural view, **B**: Lateral view, **C**: Rear view. Scale bar equals 10 mm. Photos by Sten Lennart Jakobsen.

the Middle Jurassic (Callovian) has a spiral ornament consisting of seven broad spiral bands separated by narrow interspaces above the carina and four weaker spirals under the carina which is broad and smooth. The spines are not hollow. *S. spinosa* (Münster 1841) from the Late Jurassic (Malmian) and *S. trinitatis* (Tawney 1874) from the Middle Jurassic (Bajocian) have only spines opposite to the aperture. *S. fragilissima* (Quenstedt 1857) (Middle Jurassic, Callovian) has spines only on the apertural side of the shell. *Spinigera paueri* Böhm 1891 (Maastrichtian, Cretaceous) has more convex whorls and axial ribs on the intermediate whorls. The spines are only visible on the apertural side of the shell (but are presumed to have been present on both sides).

Note on the classification of Spiniloma d'Orbigny 1850

Wenz (1939, p. 924–925) described the subgenus *Spinigera* s. str. as medium sized, rather slender, with convex, in most cases carinated, whorls with spiral bands and varices on both sides. On the last whorl, a long and acute spine is placed perpendicularly to the axis. Last whorl with a rather concave base. Aperture small with a long straight rostrum which is closed anteriorly by a folded margin. Labrum not widened, with a long narrow spine with an interior furrow. Columella straight and smooth, not sharply demarcated. Wenz (1939, p. 924) considered *Spinigera* d'Orbigny 1850 as a member of the Aporrhaidae, which he did not subdivide into subfamilies.

Wenz (1939) interpreted *Spinigera* s. str. and *Diempterus* Piette 1876 as subgenera of *Spinigera* and stated that *Spinigera* s. str. has a stratigraphical range from the Upper Triassic (Rhaetian) to the Jurassic (Toarcian–Oxfordian) in Europe, while *Diempterus* has a range from the Middle Jurassic (Bathonian) to the Upper Cretaceous (Gault) in Europe. Roy (1994) reported that *Spinigera* s. str. had a stratigraphic range from the Middle Jurassic (Bajocian) to the Early Cretaceous (Hauterivian).

Since then, several families and subfamilies have been introduced, e.g. Korotkov (1992), Kiel & Bandel (1999), Bandel (2007) and Kollmann (2009). Bouchet and Rocroi (2005) considered Korotkov´s families as subfamilies of the Aporrhaidae. Bandel (2007) raised the subfamily Spinigerinae to family rank, while Kollmann (2009) considered Spinigerinae as a subfamily of Aporrhaidae. Schulze *et al.* (1937, p. 3245) and Bouchet & Rocroy (2005, p. 161) stated that *Spinigera* d'Orbigny 1850 (Gastropoda) is a junior homonym of *Spinigera* Lesson 1842 (Mammalia). Korotkov (1992) established the family Spinigeridae, which for this reason is an invalid family name. Recently, Gründel *et al.* (2009) replaced the genus name *Spinigera* with *Spiniloma* and divided the family Aporrhaidae into the subfamilies Aporrhainae and Spinilomatinae. Bouchet (2015) considered the subfamily Spinilomatinae to be a synonym of Aporrhaidae Gray 1850. Wieneke (2016) suggested that the Spinilomatinae should be raised to family rank. We agree with the classification by Bouchet & Rocroi (2005) and Kollmann (2009) in considering Spinilomatinae as a subfamily of Aporrhaidae, as morphological characters like e.g. carinate whorls, prevailing spiral ornament and hollow spines also occur on other Aporrhaidae. Squires & Saul (2001) established the genus *Spinigeropsis* with type species *Spinigeropsis calafia* Squires & Saul 2001 from the late Paleocene of southern California. According to Wieneke (2015) this genus should be assigned to Spinilomatidae and is thus the youngest representative of the subfamily.

Stratigraphic range of the Faxe gastropods

The stratigraphic range of the Faxe gastropod genera was studied by Lauridsen & Schnetler (2014). They concluded that 40 genera were spanning the K/Pg boundary, 49 are known solely from younger Cenozoic strata, and six genera are previously known only from the Recent. The genus *Spiniloma* was until now predominantly reported from the Mesozoic and the occurrence in the Danian fauna is surprising and supports the conclusion of Lauridsen & Schnetler (2014) that the Faxe gastropod fauna contains several older elements. Also the presence of the genera *Temnotropis* Laube 1870 and *Neoamphitomaria* Bandel 1988 is in favour of this.

Palaeoecology

Lauridsen & Schnetler (2014, p. 28) concluded that the Faxe gastropod fauna was dominated by species that had a preference for hard substrates, such as the coral mounds. Soft-substrate genera are rare and this explains that Aporrhaidae until now have never been encountered in Faxe. The spines or digitations on genera of this family are interpreted as a 'snowshoe' adaption to a soft bottom (Kollmann 2009, p. 49).

Conclusion

Spiniloma? faxensis sp. nov. is established as the first Cenozoic representative of the Mesozoic subfamily Spinilomatinae Gründel *et al.* 2009 in Europe and demonstrates that the genus *Spiniloma*, which previously was known exclusively from Jurassic and Cretaceous

strata, may have survived into the Middle Danian. Furthermore, the species is the first representative of the family Aporrhaidae Gray 1850 in the gastropod fauna of the Middle Danian Faxe Formation, and the subfamily Spinilomatinae thus survived the K/Pg boundary in Europe. The coral mound complex of the Faxe formation in the Faxe Quarry was dominated by gastropod species that had a preference for hard substrates, although soft-substrate genera such as *Spiniloma* were also present but extremely rare.

Acknowledgements

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