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

KAI INGEMANN SCHNETLER & JESPER MILÀN


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.

Keywords: Gastropoda, Aporrhaidae, Spinilomatinae, Danian, early Paleocene, Faxe Quarry.

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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).
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 Rasmusen. 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.

Systematic Palaeontology

Class Gastropoda Cuvier 1797

Subclass Caenogastropoda Cox 1960

Order Latrogastropoda Riedel 2000

Superfamily Stromboidea Rafinesque 1815

Family Aporrhaidae Gray 1850

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.
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 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.

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

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

Squires & Saul (2001) established the genus Spinigeropsis with the type species Spinigeropsis calafia 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). Wiencke (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.
A new Cenozoic record of spinilomatine aporrhoids (Stromboidea, Caenogastropoda) 

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(Kaim 2004, fig. 137A) and Pietteia (Kaim 2004, fig. 137A) resemble that of Toarctocera. However, the adult teleconchs of these genera differ considerably from that of Toarctocera. Spiniloma differs from these genera by having long lateral spines on each teleconch 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

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 teleconch 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 teleconchs of “Spinigera’ (= Spiniloma) (Kaim 2004, fig. 137A) and Pietteia (Kaim 2004, fig. 137A) resemble that of Toarctocera. However, the adult teleconchs of these genera differ considerably from that of Toarctocera. Spiniloma differs from these genera by having long lateral spines on each teleconch 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.

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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.
spinigera 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 stratigraphical 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. schultz 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 aporrhinae 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 palaeocene 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? faxesis 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

We are grateful to the late Alice Rasmussen and her son Leif Rasmussen for finding and securing the specimen. Sten Lennart Jakobsen made the cast and the photographic work and furthermore identified the scleratinian coral Dendrophyllia candelabrum. We are very grateful to Klaus Bandel, Hamburg, for taxonomical discussions and advice concerning literature. Han Stoutjesdijk, Numansdorp, The Netherlands, is thanked for taxonomic help and help with literature. Ulrich Wieneke, Murnau, Germany, is thanked for fruitful discussions of the taxonomy and help with literature. We are very grateful to the referees Andrzej Kaim, Warsaw, Poland, and Alexzander Nützel, Munich, Germany, whose suggestions and helpful remarks improved the final manuscript considerably.

References

Bandel, K. 2007: About the larval shell of some Stromboidea, connected to a review of the classification and phylogeny of the Strombimorpha (Caenogastropoda), Freiberger Forschungshefte C 534, 97–206.
Bernecker, M. & Weidlich, O. 1990: The Danian (Paleocene) bryozoan 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.

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