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Aporrhais dingdenensis, a new species from the Miocene of the North Sea Basin (Gastropoda, Caenogastropoda, Aporrhaidae)

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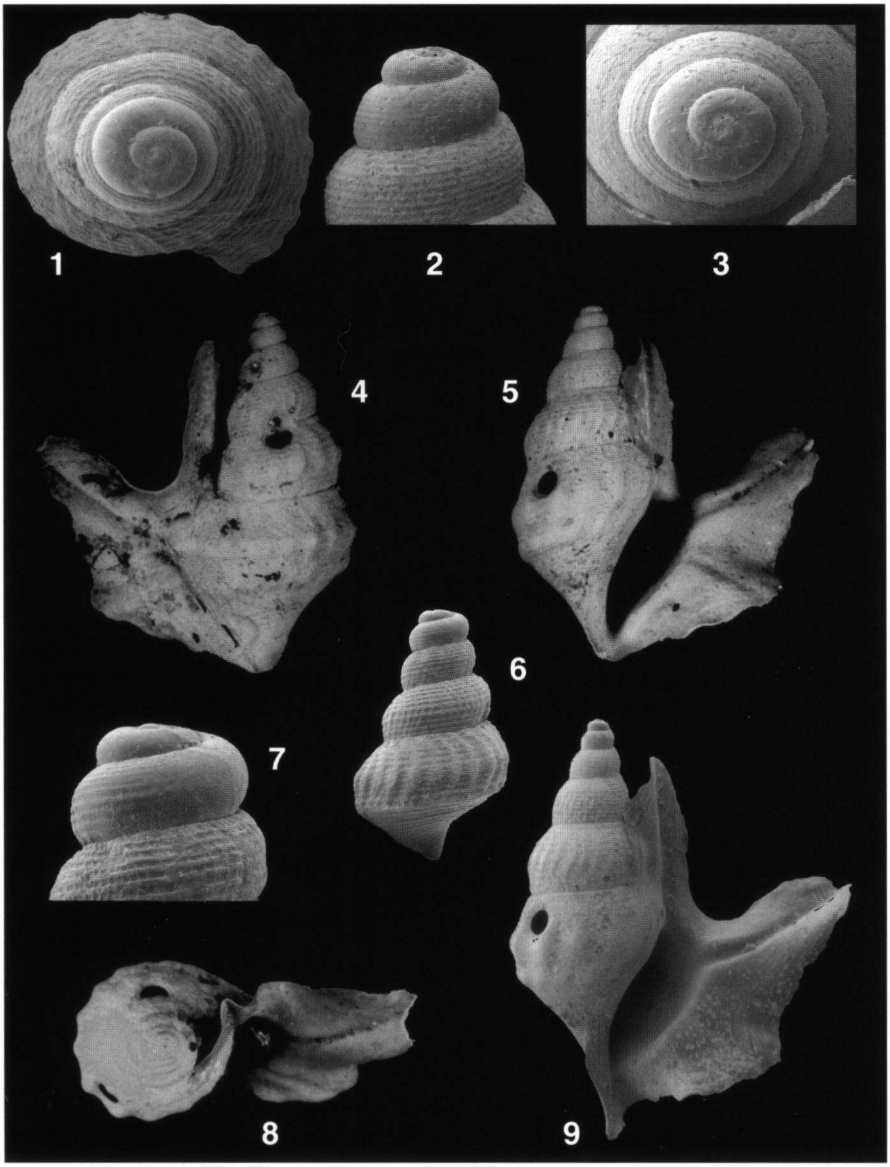
Thirteen species of the gastropod family Aporrhaidae can be distinguished in the European Oligocene and Neogene. All are briefly described here and a number of them is illustrated. Up to now, the most common North Sea Basin Miocene species of *Aporrhais* was known as *Aporrhais (Ap.) alata* (Eichwald, 1830). This taxon, however, is based on specimens from the Badenian (Middle Miocene) of Poland, which are now classified with the Miocene to Recent *Aporrhais (Ap.) pespelecani* (L., 1758) or *Aporrhais (Ap.) uttingeriana* (Risso, 1826) (Bałuk, 1995). This change in identification requires a new name for the North Sea Basin form, herein described as *Aporrhais (Ap.) dingdenensis* spec. nov. This is another example of the development of a highly endemic Neogene gastropod fauna in the North Sea Basin, without much contact with the Atlantic in the Southwest or the Paratethys to the East.

Key words: Gastropoda, Caenogastropoda, Aporrhaidae, new name, North Sea Basin, Miocene.

INTRODUCTION

The presence of two Aporrhaidae species in the North Sea Basin Miocene is known from the literature for over 150 years: *Aporrhais (Arrhoges) speciosus* (Schlotheim, 1820) found in the Early Miocene Edegem Member of the Berchem Formation of Belgium (Antwerp region) and a species, identified as *Aporrhais (Aporrhais) alata* (Eichwald, 1830), which is very common in the Early to Late Miocene of Belgium, The Netherlands, Germany and Denmark. Beyrich (1854) first recorded this species from the German Middle Miocene and considered it conspecific with the shell described by Eichwald from the Polish Middle Miocene Badenian.

Recently the specimens from the Paratethys known as *A. alata* have come under close taxonomic scrutiny by Strausz (1966), Bałuk (1995), Solsona (1998) and Solsona et al. (2000). We agree with their conclusion that this population does not differ significantly from the Miocene to Recent *Aporrhais (Ap.) pespelecani* (L., 1758), while also *Aporrhais (Ap.) uttingeriana* (Risso, 1826) is present in the Paratethys Basin. However, more species are distinguished here in the Paratethys Miocene. We also are in agreement with the



Figs 1-9. *Aporrhais* spec. Figs 1, 6, 7. *A. pespelecani* (L., 1758), juvenile; Santa Catalina, near Bonares, prov. Huelva, Spain; Grey Sands, Zanclean, Early Pliocene; height 4.0 mm (IRScNB IST 6576). Figs 2, 3, 4, 5, 8, 9. *A. dingdenensis* spec. nov. 2, 3, 9, holotype; Koningsbach, Dingden, Westfalen, Germany; Bislicher Schichten, Dingdener Feinsand, Langhian, Middle Miocene; height 12.1 mm (IRScNB IST 6488). 4, 5, 8, paratype; Metro Station Schoolplein, Antwerp, Belgium; *Glycymeris* bed 2-3, Antwerp Sand Member, Berchem Fm., Burdigalian, Early Miocene; height 13.1 mm, diameter 10.5 mm (IRScNB IST 6492).

northern European authors in that the North Sea Basin species is clearly distinct. This, however, leaves the North Sea Basin species without a name.

Abbreviations used: BML - collection B.M. Landau, Albufeira; IRScNB - Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MG - collection M. Grigis, Ninove, Belgium; RM - collection R. Marquet, Antwerp, Belgium (to be transferred to IRScNB in the near future); SMF - Senckenberg Museum, Frankfurt am Main, Germany; sp. - specimens.

A NEW MIOCENE *APORRHAIS* SPECIES

Aporrhais (Aporrhais) dingdenensis spec. nov. (figs 2-5, 8-9)

Aporrhais alata; Beyrich, 1854: 176, pl. 11 figs 7-8 (non Eichwald). Von Koenen, 1882: 276. Van Voorthuysen, 1944: 40, pl. 4 figs 6-14, 16-20. Glibert, 1952: 68, pl. 5 fig. 7. Rasmussen, 1956: 56, pl. 4 fig. 4. Sorgenfrei, 1958: 182, pl. 33 fig. 116. Anderson, 1964: 221, pl. 17 fig. 143.

Aporrhais pes-pelicani; Nyst, 1861: 40 (partim, non L.).

? *Aporrhais alata*; Ravn, 1907: 304, pl. 3 fig. 25.

Chenopus alata; Kautsky, 1925: 276.

Aporrhais (Aporrhais) alata; Janssen, 1984: 183, pl. 7 fig. 18, pl. 52 fig. 3. Wienrich, 2001: 417, pl. 67 fig. 10, pl. 83 fig. 10.

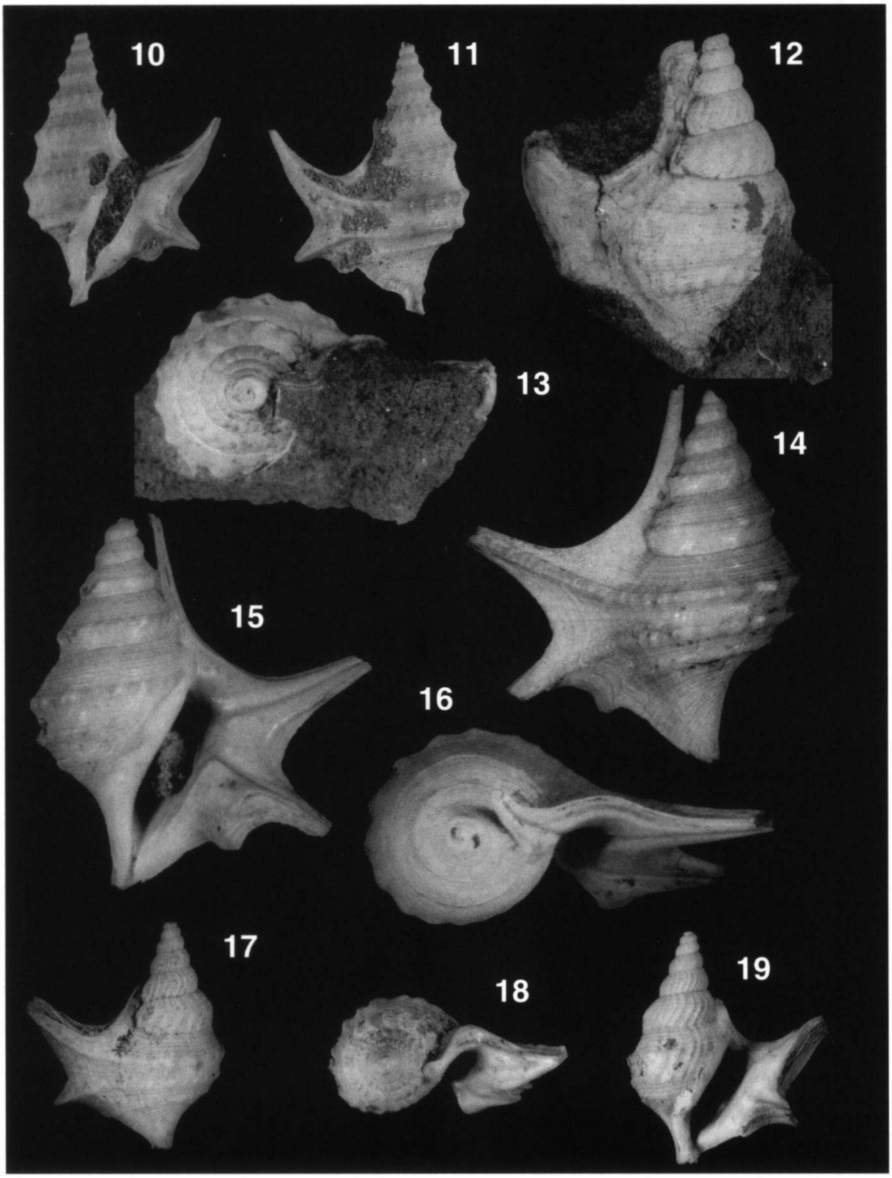
Material. — IRSNB: Holotype, IST 6488, and paratypes, IST 6489-6491, from type locality and stratum: Germany, Westfalen, Dingden, Koningsbach (see Janssen [1967] for details about this locality); Dingdener Feinsand, Reinbek Stufe, Langhian (Hinsch, 2001), Middle Miocene. IST 6492, Antwerp (Schoolplein), Belgium; Antwerp Sand Member, Berchem Fm., Early Miocene. Additional material listed by Glibert (1952) for the Belgian collection and Glibert (1963) for the 'foreign' collection. Material added to the collections later on: 70 sp. from the type locality and level.

RM: 5 sp., Antwerp (Ring, access Borgerhout), Antwerp Sand, Berchem Fm., (level 18) Burdigalian, Early Miocene; 6 sp., same locality, level with *Panopea*; 8 sp., Antwerp (Metro station Schijnpoort), same level; 8 sp., same locality, *Glycymeris* level; 4 sp, Antwerp (Metro station Schoolplein), *Panopea* level; 27 sp., same locality, *Glycymeris* level; 32 sp., Antwerp (Ring Berchem), level unknown; 188 sp., Antwerp (Kennedy Tunnel), Edegem Sand (Berchem Fm., Burdigalian, Early Miocene); 2 steinkerns, Ramsel (prov. Antwerp, old quarry Hermans), level with *Tasadia* (Berchem Fm.); 248 sp., Heist-Op-Den-Berg (prov. Antwerp, pit near Bergebeekstraat, Zonderschot), Zonderschot Sand (Berchem Fm., Burdigalian, Early Miocene); 8 sp., Winterswijk (Achterhoek, The Netherlands; Corleseweg 1), Miste (Breda Fm., Aalten Mbr., Middle Miocene); 358 sp., Winterswijk (Berenschot property), same level.

SMF: 178 sp., type locality and stratum; 8 sp., Langenfeld (near Hamburg, Germany), Langenfeld Stufe (Late Miocene); 55 sp., Beringen (Peel area, The Netherlands), Middle Miocene; 5 sp., Hemmoor (Germany), Hemmoor Stufe (Middle Miocene); 1 sp., Bersenbrück (near Osnabrück, Germany), Twistringer Schichten (Middle Miocene, Reinbekian); 1 sp., Made (near Esbjerg, Denmark), Middle Miocene; Morsum Kliff (Sylt, Denmark); Syltian (Late Miocene); 92 sp., Twistringen (Germany), Twistringer Schichten (Middle Miocene, Reinbekian).

MG: 25 sp., Heist-Op-Den-Berg (prov. Antwerp, pit near Bergebeekstraat, Zonderschot), Zonderschot Sand (Berchem Fm., Burdigalian, Early Miocene).

Description. — Shell small for genus, with an elevated turriculate spire, consisting of about six teleoconch whorls and an outer lip bearing elongated digitations characteristic of the genus. Protoconch smooth, consisting of two conical whorls. Junction with tele-



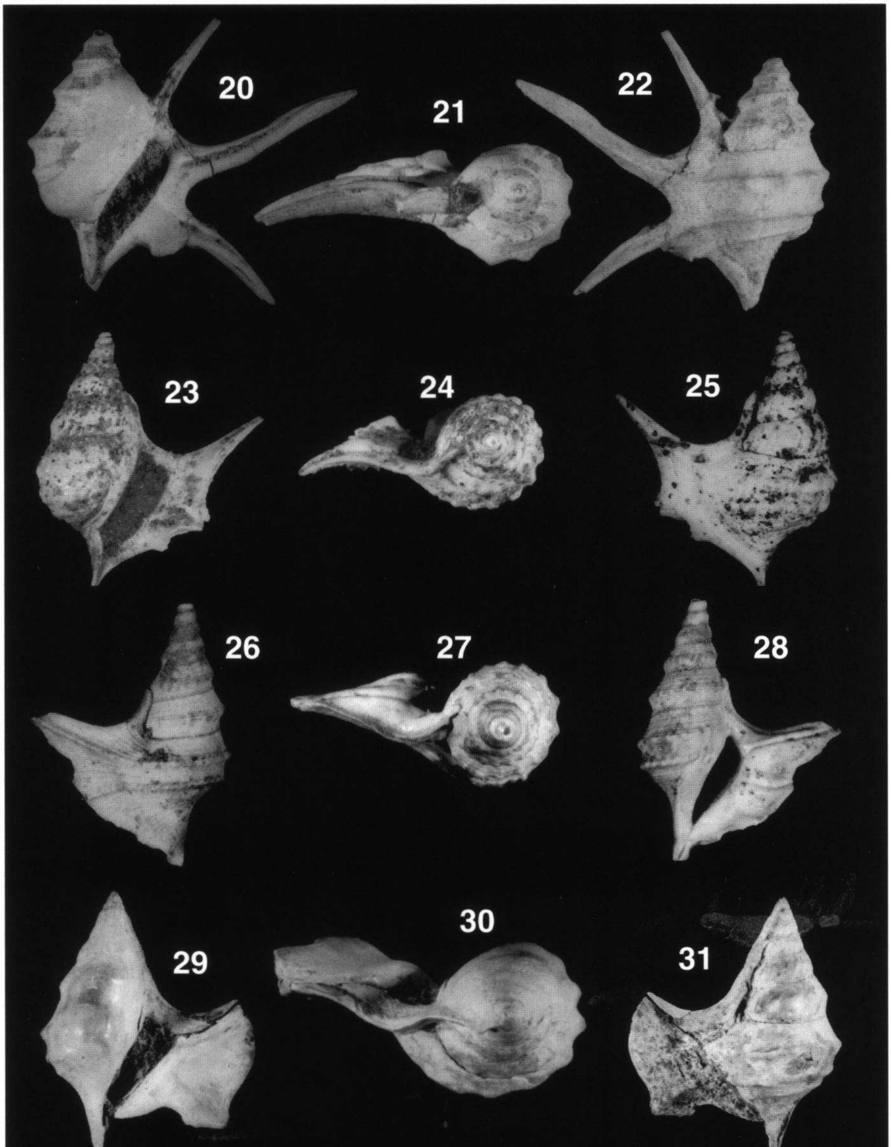
Figs 10-19. *Aporrhais* spec. Figs 10-11. *A. burdigalensis* (d'Orbigny, 1852); Le Coquillat, Léognan, dept. Gironde, France; Falun de Léognan, Burdigalian, Early Miocene; height 15.8 mm (MG). Figs 12-13. *A. speciosus* (Schlotheim, 1820); Wind claypit, Eger, Bükk Mountains, Hungaria; Egerian, Oligo-Miocene; height 21.9 mm (IRScNB IST 6577). Figs 14-16. *A. dactylifera* (Boettger, 1901). Paralectotype; Kostej (Coçteiul), Western Rumania; Badenian, Middle Miocene; height 19.5 mm (SMF). Figs 17-19. *A. oxydactylus* (Sandberger, 1861); Waldböckelheim, Mainz Basin, Germany; Unteres Meeressand, Rupelian, Early Oligocene; height 11.4 mm (SMF).

oconch marked by onset of spiral sculpture. Early teleoconch whorls rounded, becoming carinate abapically, with a prominent carina just below mid-whorl on penultimate whorl. Body whorl comprising about half of total height, with a weaker abapical second carina, which coincides with the suture on older whorls; in some specimens, a very weak third carina can be present. Spiral sculpture consists of fine cords, 8-10 on first teleoconch whorl, increasing to 15 on penultimate whorl, slightly wider than their interspaces. Axial sculpture starts on the second or third teleoconch whorl and consists of oblique opisthocline ribs, prominent mid-whorl, but not reaching the sutures. On the body whorl the axial ribs are indistinct, marked only by weak to prominent tubercles on the carinae. Aperture elongate oval, about 40% of total height. Outer lip extended into four labial digitations in adult specimens, of which the two central ones correspond with the carinae. Adapical digitation almost parallel to spire, detached or fused with the spire, usually remaining low, about the height of the second teleoconch whorl, but exceptionally extending to the apex. This digitation very typically turns behind the spire, when seen from above. Second digitation clearly separated from first, forming an angle of about 45° with it. Both first and second digitations bear a central incision on the apertural side. Third digitation much shorter, relatively broader and connected on nearly its entire length with the second one; in some specimens, this digitation is almost absent. Abapical digitation parallel to the first, relatively short, forming the siphonal canal. These digitations are hollow, the outer surface often eroded at the junction with the body whorl. On the outer apertural lip, very weak teeth can exceptionally be present before the onset of the digitations. Columella almost rectilinear, with a thickened, well-delimited, closely adherent band of columellar callus.

Differentiation. — *Rostellaria alata* Eichwald, 1830 (p. 225) was characterised as follows: "... und von Rostellarien, *R. alata*, m.[85]), bei Shukowze, Salisze, Kamionka und Tarnaru-da, wofern diese nicht eine andre Art bildet; sie ist ganz verschieden von *R. pes carbonis*, Brongn." Footnote 85: "*Testa turrita, transversim striata longitudinaliter costata, anfractie ultimo in marginem latum excurrente, bicarinato, carina utraque tuberculata in processum digitiformem prolongata; terte processus columellari ad tertium usque anfractum adscendente, spira extrema omnino libera.*" This diagnosis does not make it possible to decide which species is meant here. Although *Aporrhais (Ap.) uttingeriana* is in general the most common species in the Paratethys Badenian, *Aporrhais (Ap.) pespelecani* is found commonly in the Polish Middle Miocene. Bałuk (1995) synonymised *A. alata* with this species and his interpretation is adopted here.

In the Early Miocene Edegem Sand in the Antwerp region, Belgium, the new species is accompanied by a rarer form, which already appears in the Rupelian of the same region, i.e. *Aporrhais (Arrhoges) speciosus* (Schlotheim, 1820). This species, however, clearly differs by its larger, comma shaped tubercles (especially on the oldest whorls), its much higher extended callus (reaching nearly to the umbo), by the fusion of second and third digits and by the absence of a ventral incision on the digits.

Another allied species, *Aporrhais (Ap.) oxydactylus* (Sandberger, 1861), illustrated by Kuster-Wendenburg (1973: pl. 5 fig. 8) rather resembles the new species but differs by its broader shell, reticulate ornament, shorter adapical digit and larger angle between first and second digit. A common trait with the new species is the adapical digit, which can be turned slightly dorsally. The lineage, leading to *A. dingdenensis*, characterised by its low number of labral digits, could start with this species, which should have spread then to the Atlantic in the Late Oligocene, but not by means of the North Sea Basin, in which it is absent in the Chattian.



Figs 20-31. *Aporrhais* spec. Figs 20-22. *A. digitatus* (Telegdi-Roth, 1914); Wind claypit, Eger, Bükk Mountains, Hungaria; Egerian, Oligo-Miocene; height 31.2 mm (IRScNB IST 6578). Figs 23-25. *A. oxydactylus* (Sandberger, 1861); Weinheim near Alzey, Mainz Basin, Germany; Unteres Meeressand, Rupelian, Middle Oligocene; height 16.6 mm (SMF). Figs 26-28. *A. praeteritus* (Boettger, 1906); Valea Coçulue, Lapugy (Lăpugiul), Western Rumania; Badenian, Middle Miocene; height 16.3 mm (SMF). Figs 29-31. *A. speciosus* (Schlotheim, 1820); Gralex claypit, Kruibeke, prov. Oost-Vlaanderen, Belgium; Rupel Clay, Rupelian, Early Oligocene; height 40.7 mm (IRScNB IST 6579).

Aporrhais (Ap.) tridactylus has a noticeably broader shell than the new species, its tubercles are heavier, adults have five digitations and the adapical one is attached to the spire, forming an angle of about 90° with the second digit.

Aporrhais (Ap.) burdigalensis has a very heavy second digit and can start developing a fifth one, as figured by Cossmann & Peyrot (1922: pl. 8 fig. 11). Its ornament on the older whorls is much stronger than that of the new species.

Aporrhais (Ap.) meridionalis was figured by Cossmann & Peyrot (1922) and by Sacco (1893). It is as small as the new species, but its adapical digit is less well developed, the second is very weak and the third is hardly developed. It is not impossible that the new species is derived from this form, as it is the only Neogene form in which the number of digits is lower than in *A. dingdenensis*.

Aporrhais (Ap.) dactylifera is about as large as the largest specimens of the new species but has more (up to five) and especially stronger digitations, the adapical one never curves around the spire to the dorsal side and the siphonal one is straight and longer.

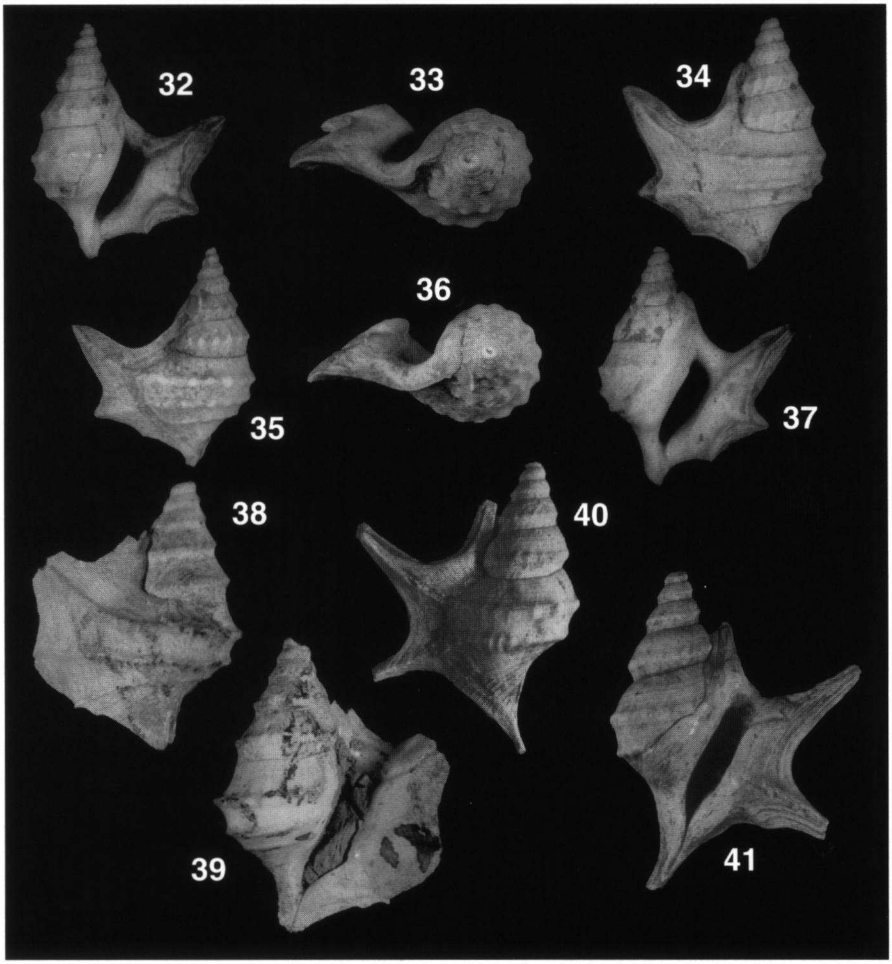
Aporrhais (Ap.) praeteritus has a weaker adapical digit, which is fused with the spire, the tubercles are heavier and more clearly delimited.

Aporrhais (Ap.) dingdenensis is much smaller than *A. pespelecani* and differs in details of the labial digitations. The adapical one never diverges dorsally of the spire in *A. pespelecani*, it never broadens in the new species and the abapical digitation is relatively shorter and finer in *A. dingdenensis*. The third digit is relatively shorter and less well developed in the new species. Furthermore, *A. pespelecani* can develop a fifth digit, which is never the case in the Miocene species. The Aporrhaidae, however, can vary considerably in digit development and fusion. A connection between second and third digit can also occur in *A. pespelecani* (*bilobatus* form) and *A. serresiana* (*macandrewae* form); it is however much more common in the new species. The strong curve of the abapical digit also is a variable feature, present in many but not all *A. pespelecani*. The protoconch of *A. pespelecani* is half a whorl larger than that of *A. dingdenensis* and its shape is cylindrical, while that of the new species is conical. This is here considered to be the most significant character. Sacco (1893) described two Miocene and two Pliocene forms of *A. pespelecani* from Italy, which are smaller than average and show some resemblance to the new species: *A. pespelecani taurominor* (Sacco, 1893), *A. p. dertominor* (Sacco, 1893), *A. p. crenulatina* (Sacco, 1893), *A. p. parvicincta* (Sacco, 1893). These all, however, have a tendency to form an extra digit between the third and the abapical digit (see Sacco, 1893: pl. 2 fig. 30) and are consequently only forms of *A. pespelecani*. He also described *Aporrhais uttingeriana peralata* (Sacco, 1893) (our figs. 38-39) from the Italian Pliocene, which also superficially resembles the North Sea Basin species, but has five digits, the second, third and fourth of which are completely fused; its characters come closer to *A. pespelecani* than to *A. uttingeriana* and it is considered here as a form of the first species.

Aporrhais (Ap.) uttingeriana differs from the new species by its four much stronger and longer digits, especially the abapical digit, which is particularly long; furthermore, the adapical digit is always fused with the spire. The protoconch of this species was figured by Solsona et al. (2000: pl. 1 figs 7-8). It has, like that of the previous species, three to three and a half whorls, so at least one more than the new species.

Aporrhais (Ap.) serresiana (Michaud, 1828), is easily distinguished by having five labial digitations instead of four and these are much longer and narrower. The first digit diverges from the spire and is not attached as seen in the previous species.

The Recent West African and Pleistocene Mediterranean *Aporrhais (Ap.) senegalensis* (Gray, 1848) figured by Nicklès (1950) has a stronger, broader shell than *A. dingdenensis*



Figs 32-41. *Aporrhais* spec. Figs 32-37. *A. tridactylus* (Braun, in Sandberger, 1861). 32-34, Kuhhimmel, Wöllstein, Mainz Basin, Germany; Schleichsand, Rupelian, Early Oligocene; height 21.3 mm (SMF). 35-37, Sulzheim, Mainz Basin, Germany; Cyrenenmergel, Rupelian, Early Oligocene; height 19.1 mm (SMF). Figs 38-39. *A. pespelecani* (L., 1758) form *peralata*, Campore, prov. Parma, Italy; Zanclean, Early Pliocene; height 24.2 mm (MG). Figs 40-41. *A. uttingeriana* (Risso, 1826); Bad Vöslau, Vienna Basin, Austria; Badenian, Middle Miocene; height 31.5 mm (IRScNB IST 6580).

and can have five labial digitations; its adapical digit comes close to that of *A. uttingeriana*, of which it could be a synonym; for this reason, it does not figure in the above list of Neogene European Aporrhaidae.

In the North Sea Basin Middle Pliocene *Aporrhais (Ap.) scaldensis* occurs, figured by Marquet (1998). This species differs by the second digit after the abapical one, which is very small if present, the upper digitation, which diverges widely from the spire and the strong, ventrally turned siphonal digitation. It is tempting to derive this species from *A. dingdenensis*, which occurs in the same region until the Late Miocene. In the North Sea Basin Early Pliocene (Kattendijk Formation) however, only *A. pespelecani* seems to occur, while in the Early-Middle Pliocene Luchtbal Sand no recognisable *Aporrhais* are found. So this connection is far from certain.

Derivatio nominis. — After the type locality.

THE OTHER EUROPEAN NEOGENE APORRHAIDAE

Next to *Aporrhais (A.) dingdenensis* spec. nov., twelve additional species are here recognised among the European Oligocene and Neogene Aporrhaidae. These are the following.

Aporrhais (Arrhoges) speciosus (Schlotheim, 1820) (figs 12-13, 29-31). — Late Eocene (Latdorfian) from Germany and Britain, Rupelian (Early Oligocene) from the North Sea Basin and the Etampes (France) region, Chattian and Early Miocene from the North Sea Basin and Paratethys. It is a large species, with large, comma-shaped tubercles (especially on the oldest whorls), its callus often reaches nearly to the umbo, the second and third digit are fused and a ventral incision on the digits is lacking. The specimens, figured by Báldi (1973, pl. 30 figs 3-4, pl. 31, figs 3-4), from the Hungarian Egerian (Oligocene-Miocene boundary) probably belong to this species, but adult specimens with fully developed callus were not encountered. Material from Kruibeke, Belgium (Rupelian), Edegem, Belgium (Early Miocene) and Eger, Hungaria was studied (IRScNB, RM).

Aporrhais (Ap.) digitatus (Telegdi-Roth, 1914) [= ? *A. callosa* (Telegdi-Roth, 1914)] (figs 20-22). — Egerian (Chattian-Aquitanian transition) from the Eger region, Hungaria. A very broad shell, with three rows of tubercles, the adapical one is very strong, carrying well separated small tubercles. Callus very strong. Four very long digitations are present. The adapical one is completely free from the spire, the second one is the longest, siphonal one short and broad. Betweeen third and siphonal digit, an outgrowth occurs, the adapical margin of which coincides with the abapical spiral. Material in RM.

Aporrhais (Ap.) oxydactylus (Sandberger, 1861) (figs 17-19, 23-25). — Rupelian from the Mainz Basin, Germany and the Etampes (France) region. Broad shell, with thick spire; on oldest teleoconch whorls, a reticulate sculpture is present; on the last whorl, thick tubercles occur. Adapical digitation short, touching the spire and slightly bending dorsally. Second digit very long and pointed, abapical one very short. Material studied in SMF and RM.

Aporrhais (Ap.) tridactylus (Braun, in Sandberger, 1861) (figs 32-37). — Rupelian and Chattian from the Mainz Basin, Germany. Rather broad shell with ornament consisting of heavy tubercles, never reticulate. Juveniles with four digitations, adults with five. Adapical one attached to spire, forming an angle of about 90° with second digit. Siphonal digit very short, broad, turning ventrally. Material studied in SMF and RM.

Aporrhais (Ap.) burdigalensis (d'Orbigny, 1852) (figs 10-11). — Aquitaine (France) Early and Middle Miocene Burdigalian and Sallomacian. Small species, with weak digitations, which resemble those of *A. (Ap.) pespelecani*. Characteristic are the strongly angular older whorls, which have a very clearly delimited narrow axial ornament. Probably it comes close to *A. (Ap.) pespelecani*, characterised mainly by its smaller shell and more strongly developed sculpture. A separation at species level consequently is uncertain; it could be the ancestral form of the *A. pespelecani* lineage, as it is the oldest known until now. Material studied in IRScNB, MG and RM.

Aporrhais (Ap.) meridionalis (Basterot, 1825). — Early and Middle Miocene (Aquitanian, Burdigalian and Sallomacian from Aquitaine, Southern France and the Italian Tortonian. Small species, with very weak adapical digit, well-developed second and weaker third digit. This may be only a form of *A. burdigalensis*. We prefer however, to keep it as a separate species, as the short adapical digit seems to be a constant character in all the specimens we have studied. Material studied in BML.

Aporrhais (Ap.) dactylifera (Boettger, 1896) (figs 14-16). — Middle Miocene (Badenian) from the Paratethys (Rumania). This species strongly resembles *Aporrhais (Ap.) uttingeriana* in the shape of its digits, but differs by the upper digit, which is free from the spire and consequently forms a smaller angle with the second digitation. Material studied in SMF.

Aporrhais (Ap.) praeteritus (Boettger, 1906) (figs 26-28). — Middle Miocene (Badenian) from the Paratethys (Rumania and Austria). A small and slender species, with a very weak adapical digit, which is fused to the spire, forming an angle of about 120° with the second one, third and fourth digit very weak, abapical one short; tubercles heavy and clearly delimited. Material studied in SMF.

Aporrhais (Ap.) pespelecani (L., 1758) (figs 1, 6, 7). — Middle Miocene (Badenian) of the Paratethys (rare), the Mediterranean and Atlantic France (including the Loire Basin), Pliocene to Recent of the Mediterranean, the Atlantic and the North Sea Basin. Characterised by the large shell, with five digitations in fully adult specimens, strong adapical digit, which remains free of the spire, broadens in its upper part in adult shells and forms an angle of about 90° with the second digit. Siphonal digitation well developed and mostly bent ventrally. Material studied in SMF, IRScNB, MG and RM.

Aporrhais (Ap.) uttingeriana (Risso, 1826) (figs 40-41). — Mediterranean Tortonian (Miocene) to Piacenzian (Pliocene) and in the Paratethys Badenian (where it is much more common than the previous species), now living off the coasts of West Africa (Solsona et al., 2000). Large species, with four to five well developed, long and pointed digitations, except for the adapical one, which is small and fused with the spire. It characteristically forms an angle of more than 100° with the second digit. Material studied in SMF, IRScNB, MG and RM.

Aporrhais (Ap.) serresiana (Michaud, 1828). — Pliocene to Recent Mediterranean. This rare, large species has five labial digitations, which are very long and narrow. The first digit diverges from the spire and is not attached as seen in the previous species. Three of these digits have an incision. In the opinion of Sacco (1893), this and the previous species could form an evolutionary lineage, characterised by elongation of the digits. The material for deciding this question is not available to us, but it is clear that *A. serresiana* must be a phylogenetically derived species, appearing much later than either *A. pespelecani* or *A. uttingeriana*. Material studied in MG and RM.

Aporrhais (Ap.) scaldensis Altena, 1954. — Middle and Late Pliocene of the North Sea Basin, endemic. Medium-sized species, with four to five digits, among which the second after the abapical one is very small if present at all, both middle ones are well separated and strongly pointed, the upper one diverges widely from the spire, the siphonal digitation is well developed and turns ventrally, the tubercles are very small and numerous on the last whorl. Material studied in IRScNB, MG and RM.

REMARKS

Aporrhais dingdenensis first appears in the Early Miocene of the North Sea Basin, in the Edegem Sand Member of the Belgian Berchem Formation. It is very common in the Middle Miocene Antwerp and Zonderschot Sand Member of Belgium, in the Miste Beds of The Netherlands and in the Reinbek Stufe of the type locality. The species then becomes less common in the Late Miocene deposits of northern Germany and Denmark (Gram, Sylt and Langenfeld deposits). Few complete specimens have been found in these deposits. They are larger than typical Early and Middle Miocene specimens and resemble *A. pespelecani. A. dingdenensis* is also represented in the Belgian Late Miocene Deurne Sand Member of the Diest Formation, albeit under the form of steinkerns.

Although most common in Antwerp, Zonderschot and Miste, these specimens are of the smallest size, whereas those found in the Edegem Sand and Langenfeld Stufe can become twice as large, without, however, reaching the size of *A. pespelecani.* The deposits with the smallest specimens of the new species seem to occur in localities with sandy substrates, the largest on more clayey bottoms; the exception on this is the clayey Dingdener Feinsand. The size of Aporrhaidae is very variable, depending on the habitat. The inverse phenomenon can be observed in the Recent *A. pespelecani,* specimens living on muddy substrates being smaller in size than those inhabiting sandy bottoms, while also salinity seems to have an influence.

The Neogene North Sea Basin has a highly endemic fauna. The Middle Miocene Miste fauna monographed by Janssen (1984) has about a 60% endemic gastropod species. This percentage is an underestimate, as firstly it does not include any species not definitely classified, many of which are probably endemic and, secondly, under closer scrutiny, some of the species initially considered conspecific with specimens from other Basins are in fact separate species, examples being *A. dingdenensis* and probably *Natica tigrina* Janssen, 1984, non Defrance, 1825 (Solsona, 1998). This shows there was little contact between the North Sea Basin and the Atlantic, with little species migration. The same trend persists during the Pliocene, as can be seen in the study of Marquet (1998) about the Kallo (Belgium) gastropods: 49 % of the marine species encountered is endemic. In contrast to the Gastropoda, the Bivalvia only show little endemicity, while their species usually have a much longer time range. This could be a consequence of the easier way of dispersion of bivalves compared with paucispiral gastropod species. The local evolutionary lines of North Sea Basin gastropods became extinct during the Pleistocene, nearly none of them having been able to spread into the Atlantic.

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