Species of *Anatoma* (Gastropoda: Anatomidae) in Norwegian and adjacent waters, with the description of two new species

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ABSTRACT

The species of *Anatoma* Woodward, 1859 from Norwegian waters and from the Norwegian Sea are treated taxonomically. *Anatoma crispata* (Fleming, 1828) has until quite recently been regarded as the sole representative of this family in north European waters, but constant conchological differences make it evident that at least three species have been lumped under this name in Norwegian and other Scandinavian literature. Three species, *A. crispata*, *A. aspera* (Philippi, 1844) and *A. tenuisculpta* (Seguenza, 1877) are redescribed and two new species from deep water in the Norwegian Sea, *A. schioettei* new species and *A. schanderi* new species, are described based on shell characters. The distribution in inshore Norwegian waters and in the Norwegian Sea is described, and possible microhabitats suggested. Also geographical variability of conchological characters is discussed in some detail.

Additional keywords: Mollusca, Scissurelloidea, Vetigastropoda, Norwegian inshore waters, bathyal, Norwegian Sea

INTRODUCTION

Until recently it has been universally accepted that the family Anatomidae is represented in north European waters by a single species, *Anatoma crispata* (Fleming, 1828). In a paper, in which also *A. crispata* was recorded from Bergen, Lovén (1846) described, but did not illustrate, *Scissurella angulata*, from northern Norway. Except for Lovén, no one has questioned that *A. crispata* is the only species of the family in Norway, although several authors remarked that two or more varieties might be present. All early authors (e.g. Friele, 1874 and Verkrüzen, 1875), reported *A. crispata* without further discussion. However, Jeffreys (1870) and G.O. Sars (1878), remarked that the specimens found in Norway might be a larger variety of the British form, and G.O. Sars mentioned *A. aspera* and *A. angulata* as synonyms. Odhner (1912) is the first author to clearly distinguish between three varieties of *A. crispata* in northern waters: *A. crispata* sensu stricto, *A. crispata* "var. *angulata*" Lovén, 1846, and *A. crispata* "var. *aspera*," (= var. *paucicostata* Jeffreys, 1865) all of which he recorded from Norwegian waters, but without any clear differentiation of geographic localities.

Recently, Warén (in Hansson 2003) stated that both *A. aspera* and *A. crispata* are found in western Norway, and that there is a possibility that a third species is present in western Sweden and in northern Norway as well.

For several decades, one of us (T.H.) accumulated a sizeable material of *Anatoma* from the coast of Norway. This material, in addition to material graciously donated to T.H. (now deposited at ZMBN) by Per Bie Wikander, material from the H2Deep project, and available museum lots, has made it possible to reassess the genus in Norwegian waters and the Norwegian Sea. Constant conchological differences make it evident that at least three species have been lumped as *Anatoma crispata* in Norwegian and other Scandinavian literature. In this article, we designate **neotypes** and redescribe *A. crispata* and *A. aspera* based on material from the western Mediterranean, the north Atlantic, the Norwegian Sea and Norway. Additionally we resurrect and redescribe *A. tenuisculpta* (Seguenza, 1877) based on material from the western Mediterranean and the northeastern Atlantic Ocean. Furthermore, we describe two new species: *A. schioettei* new species, based on material from the shelf off East Greenland (75° N) and a hot vent locality northeast of Jan Mayen, and *A. schanderi* new species, from the bathyal and abyssal of the Norwegian Sea. Finally, the distribution of the three species in inshore Norwegian waters is discussed. Since *A. crispata* is the type species for the genus *Anatoma* in the family Anatomidae, it is of particular importance to unravel the taxonomic problems associated with this species, which has been misunderstood for such a long time.

MATERIALS AND METHODS

The geographic area covered is primarily the coast of Norway, but the availability of additional material from various parts of the Norwegian Sea (in this context used as a collective for the Norwegian Sea proper, the Iceland

Sea and the Greenland Sea) allowed for the inclusion of the entire area between Norway and Greenland as well. The study is based on material from five summer cruises along the Norwegian coast in the period 1967 to 1971. These cruises covered most of the coast from the Russian border to Stadt (70°15′ N to 62° N), and resulted in 164 specimens and 546 empty shells of species of *Anatoma*. In addition, Per Bie Wikander had collected 163 specimens (plus 20 empty shells) in the Skagerrak and Bodø regions, in the southern and northern part of Norway respectively. Seventy-four specimens and 26 shells were collected at various times between 1965 and 2010 near the Biological Stations of the University of Bergen. A few samples from the upper slope collected by Torleiv Brattegard (Høisæter, 2010) that contained specimens of *Anatoma* are included as well. A few specimens from the MAREANO program, and three small, but most interesting samples from ROV-assisted sampling of hot vents and other deep-water localities around Jan Mayen, during the H2DEEP program contributed to expand the geographic and bathymetric coverage. The scope of the investigation was further enhanced by museum material from Hamburg (ZMH) and Copenhagen (ZMUC) examined. In addition all material from the four university-based museums in Norway (TMB, ZMBN, ZMON, ZMTøN) have been examined. When relevant to our taxonomic goals, Recent and fossil material from Shetland and the Mediterranean was also studied.

The descriptions are primarily based on light microscopy (LM) and scanning electron microscopy (SEM). Standard procedures for SEM were followed (Geiger et al., 2007). To get a broader selection of material for description of variability, measurements were taken from LM photographs. Terminology follows Geiger (2003). Characters found to be of primary value in distinguishing species were: maximum size, shell shape, rate of increase in whorl width with growth, umbilicus width and presence or absence of a funiculus (a spiral cord in the wall of the umbilicus), the distance between selenizone and suture for the first few whorls, shape of aperture, especially inner edge and relation to umbilicus and any funiculus.

The sculpture is important and sometimes diagnostic, but generally rather variable. Details in the microsculpture of the protoconch and teleoconch I (e.g., Figure 1) are often important, but usually only visible in SEM images, and then only in fresh, uneroded shells.

Abbreviations used in the text are: DLG: Daniel L. Geiger collection, Los Angeles, USA; DMNH: Delaware Museum of Natural History, Wilmington, USA; JWC: John Wolff Collection, Lancaster, USA; MNHN: Muséum National d'Histoire Naturelle, Paris, France; MNW: National Museum Wales, Cardiff, United Kingdom; NHMUK: The Natural History Museum, London, United Kingdom; NHMW: Naturhistorisches Museum Wien, Vienna, Austria; NMR: Natural History Museum, Rotterdam, The Netherlands; NMSZ: National Museum Scotland, Edinburgh, United Kingdom; SBMNH: Santa Barbara Museum of Natural History, Santa Barbara, USA; SRC: Stefano Rufini Collection, Aguillara, Italy; TBS: Trondheim Biologiske Stasjon, Norway; USNM: National Museum of Natural History, Smithsonian Institution, Washington, USA; ZMBN: Zoological Museum, Bergen, Norway; ZMH: Zoologisches Museum, Hamburg, Germany; ZMON: Zoological Museum, Oslo, Norway; ZMTøN: Zoological Museum, Tromsø, Norway; ZMUC: Zoological Museum, Copenhagen, Denmark; H2DEEP: Ultraslow spreading and hydrogen based deep biosphere (Programme); MAREANO: Marine Areal database for Norwegian waters (Programme).

All material examined and not explicitely stated to belong to a particular museum collection has been deposited at the Zoological Museum in Bergen, Norway (ZMBN).

SYSTEMATICS

Anatomidae McLean, 1989

Anatoma Woodward, 1859

Type Species: *Scissurella crispata* Fleming, 1828 (by monotypy).

Remarks: *Anatoma* was long regarded as a subgenus of *Scissurella* d'Orbigny, 1824. *Schizotrochus* Monterosato, 1877 is an objective synonym. In the early 1960s *Anatoma* was rediscovered as the correct name for the group, but it was still regarded as a subgenus of *Scissurella*. Powell (1979) seems to have been the first to recognize that the conchological differences between *Scissurella* sensu stricto and *Anatoma* warranted full generic status for *Anatoma*. McLean (1989) introduced the taxon Anatominae at the subfamilial rank, to which Geiger and Thacker (2005) assigned full familial rank based on a molecular phylogenetic study. The family is found from Antarctica to the Arctic, from the intertidal to 5000 m, but is most common between 20 and 250 m (Geiger and Sasaki 2009). In inshore Norwegian waters, three species are found, and two additional ones in the Norwegian Sea.

Anatoma crispata (Fleming, 1828)

(Figures 1–18)

Scissurella crispata: Fleming, 1828: 385, pl. 6, Figure 3.

Scissurella crispata: Forbes and Hanley 1853: 544; Jeffreys 1865: 283; G.O. Sars, 1878 (in part): 126, pl. 8, fig. 7a, b; Norman, 1879 (in part?): 24; Schneider, 1886: 102; Norman, 1893 (in part?): 360; Friele and Grieg, 1901 (in part): 59; Brøgger, 1901 (in part?): 657, pl. 17, fig. 3; Norman, 1902: 357; Friele, 1903 (misidentification?): 15; Odhner, 1912 (in part): 13, pl. 2, figs 25–27; Dautzenberg and Fischer, 1912: 286; Soot-Ryen 1924: 50; Dautzenberg, 1927: 213; Odhner, 1960: 384; Fretter and Graham, 1976 (in part): 2; Bouchet and Warén, 1979 (misidentification?): 220; Graham, 1988: 60.

Anatoma crispata: Høisæter, 1986 (in part): 81; Sabelli et al., 1990 (misidentification?): 12; Smith and Heppell, 1991: 11.

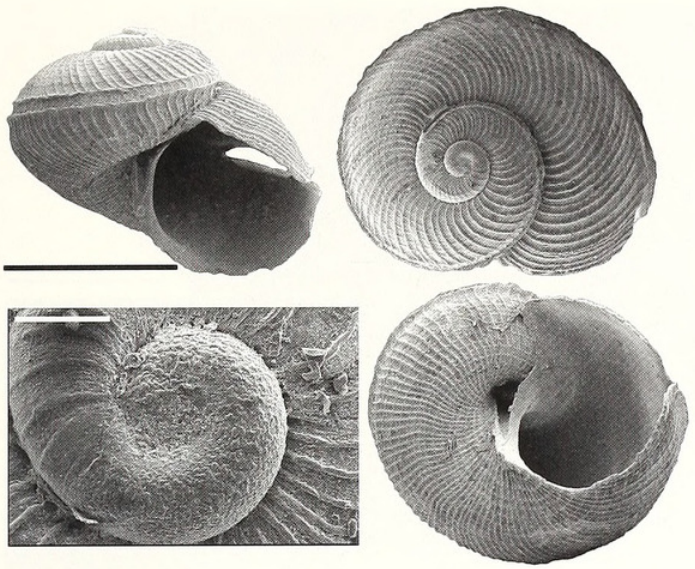


Figure 1. *Anatoma crispata*, **neotype**. SEM. Shetland, Great Britain, 60°30′ N, 1°15′ W (NHMUK, 1849.10.5.5–7). Scale bar shell = 1 mm; Scale bar protoconch = 100 µm.

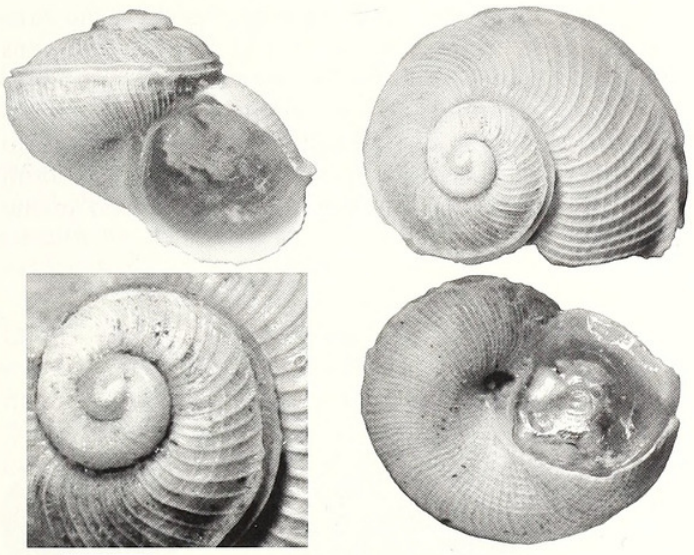


Figure 2. *Anatoma crispata*, Bremnesfjorden, Møre og Romsdal county, Norway (63°07′ N, 200–180 m), 2.1 mm diameter. Scale bar protoconch = 400 µm.

Scissurella angulata Lovén, 1846: 20 (see below under *A. tenuisculpta*).

Description: (Based mainly on the **neotype** [Figure 1] and a specimen from Bremnesfjorden, Norway [Figure 2]). Shell globular, small to moderate size (to 2.25 mm diameter, **neotype** 1.83 mm), trochiform, inflated, wider than tall. As in other species, juveniles "flatter" than adults. Protoconch of 0.75 whorls, with coarse flocculent sculpture, no apertural varix, apertural margin straight to slightly convex. Teleoconch I of 0.75 whorls, approximately 22 fine axials, weak spiral cord in position of selenizone. Teleoconch II of little less than two rapidly increasing, rounded whorls, suture adjacent to selenizone except near aperture of mature shells where up to five spirals separate suture and selenizone. Shoulder with 60–70 fairly strong axials on body whorl, sometimes rather crowded toward aperture; single spiral thread at or slightly behind start of selenizone, ca. 12–13 threads at apertural margin of mature shells, 1/3 to 1/2 width of axials. No spirals in adsutural 15% of shoulder. On base, 16–20 spirals cross the up to 65 rather strong axials, creating a grid-like pattern, approximately one of six to ten axials disappear at mid-base, remaining axials spirals into not very wide umbilicus. Rather narrow funiculus joins lower lip at columella starting point. Selenizone at periphery, of varying width but mostly wide, keels distinct, growth marks at least partly coordinated with axials. Margins of slit parallel. Aperture rounded, roof overhanging.

Operculum (Figure 2): Round, covering aperture, thin, transparent, multispiral, with central nucleus.

Radula (Figures 3–7): Rachidian tooth trapezoid, central cusp isolated, on either side four cusps arranged in fan shape. Lateral teeth 1–3, similar, innermost of 3–4 cusps largest. Lateral tooth 4 reduced, outermost of four cusps largest. Lateral tooth 5 enlarged, four cusps on inner margin, terminal one largest, one cusp on outer margin. Inner marginal teeth with triangular tip, terminal cusp largest, inner margin with four small cusps, outer margin with five larger cusps. Outer marginal teeth spoon shaped, approximately eight fine cusps on either side.

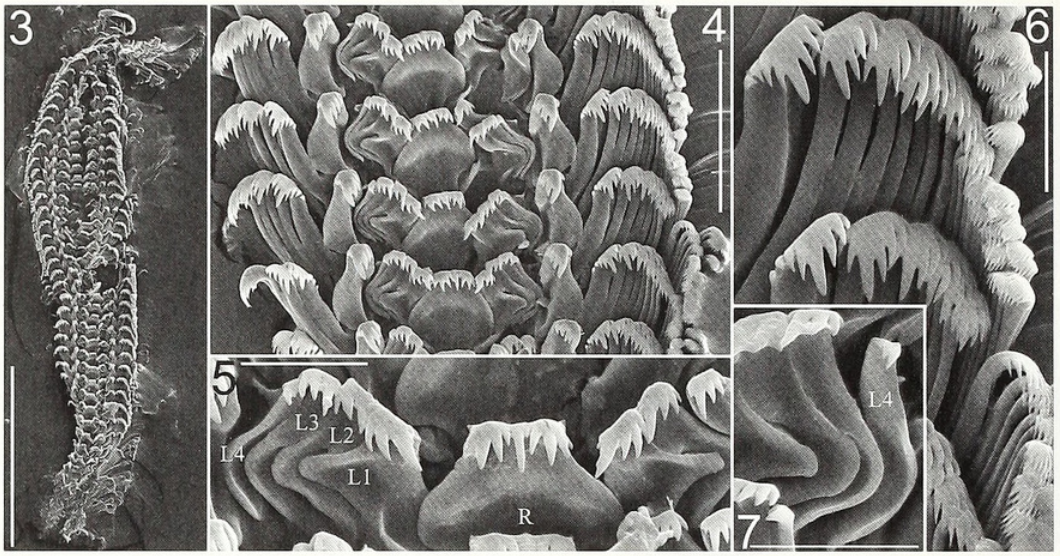
Differential Diagnosis: *Anatoma tenuisculpta* reaches a much larger size than *A. crispata* (5 mm vs. 2.25 mm) and is less globular and with more regular sculpture; it has no funiculus at any growth stage. The protoconch is smaller (216 vs. 255 µm) and the whorls increase more slowly. The shoulder is less convex, as is also the base. The edges of the slit and selenizone are also more regular than in *A. crispata*, and the slit has slightly converging margins in mature shells.

Anatoma aspera is taller and has a smaller protoconch (172 vs. 255 µm) and "tighter" spiral whorls, with a wide-angled funiculus starting fairly deep inside the umbilicus. The suture is significantly below the selenizone. The selenizone keels are wider, more prominent, and the axials on the shoulder are stronger, more "costae"-like.

Anatoma schioettei is more lenticular, has a distinct space between the start of the selenizone and the suture of the subsequent whorl, and has about half as many and more distinct axials.

Anatoma schanderi has a much larger shell (4.5 vs. 2.25 mm), is more turreted, has reticulate protoconch sculpture, and the axials are weaker and more similar in strength to the spirals.

Type Material: Whereabouts of Fleming's syntypes are unknown (McLean, 1967); they could not be found in either NHMUK, NMW, or NMSZ, and are presumed



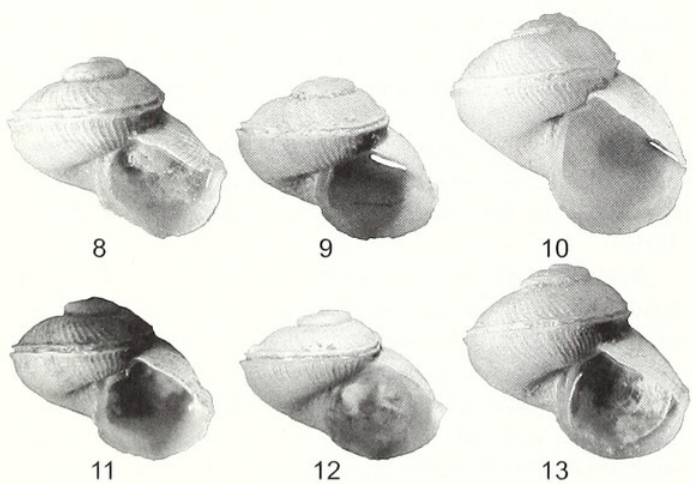
Figures 3–7. *Anatoma crispata*, radula, Fleslandsskjær, Raunefjorden, Hordaland, Norway, 60°18′ N, 5°13′ E, (DMNH 23176, 1). **3**. Whole radula. Scale bar = 200 µm. **4.** Whole width of radula. Scale bar = 30 µm. **5.** Central field with rachidian tooth (R) and lateral teeth 1–4 (L1–4). Scale bar = 10 µm. **6**. Marginal teeth. Scale bar = 10 µm. **7**. Lateral tooth 4. Scale bar = 10 µm.

to be lost. **Neotype** here designated, Shetland, Great Britain, 60°30′ N, 1°15′ W, NHMUK 1849.10.5.5-7.

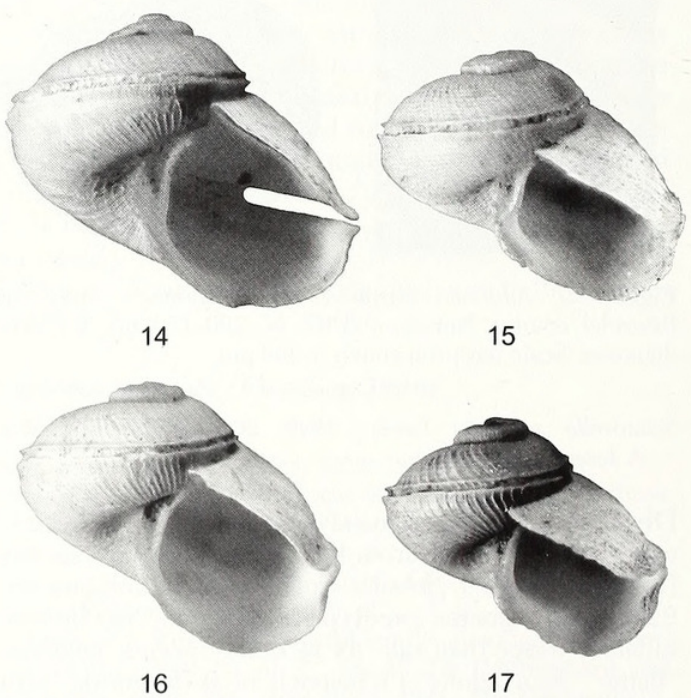
Type Locality: Noss Island [outside Lerwick] in Shetland (60°10′ N, 1°00′ W), where it was found in shell sand on the beach after a storm (Jeffreys, 1865).

Other Material Examined: 20/7 specimens/shells from Skagerrak, 29/15 from western Norway (own material), 0/10 (ZMON), 1/1 (ZMBN); 65/307 from middle Norway (63–65° N) (own material); 152/135 from northern Norway (66–71° N) (own material), 9/41 (ZMON), 4/0 (ZMBN), 4/20 (ZMTø). Material from Shetland 0/37 (NHMUK, MNHN, NMSZ).

Variability: *Anatoma crispata* has a wide distribution, both geographical and bathymetrical, and its shell morphology varies accordingly. Thus it is possible to recognize certain geographical morphotypes along the Norwegian coast (Figures 8–13, 15 and 17), as specimens from northern Norway (67–68° N) are somewhat larger (to 2.23 vs. 2.03 mm) and much more globular than those from further south (H/D varies from more than 0.9 to 0.8 or less). The shell morphology of the **neotype** (from Shetland, Figure 1) falls within the variation seen among



Figures 8–13. *Anatoma crispata*, six specimens from inshore Norwegian waters. **8, 11.** South coast (58°15′ N, 90–80 and 57 m respectively). **9, 12.** West coast (60°30′ N, 70–75 and 190 m respectively). **10, 13.** North coast (67°10′ N, 30 m). All specimens to scale, the largest (10) 2.23 mm diameter.



Figures 14–17. *Anatoma crispata*, four specimens from ca. 62–63° N. **14, 16.** Iceland-Faroe Ridge (63°35′ N, 12°51′ W, 574 m). **15, 17.** Coast of Møre og Romsdal (62°28′ N, 120–60 m). All specimens to scale, the largest (14) 2.42 mm diameter.

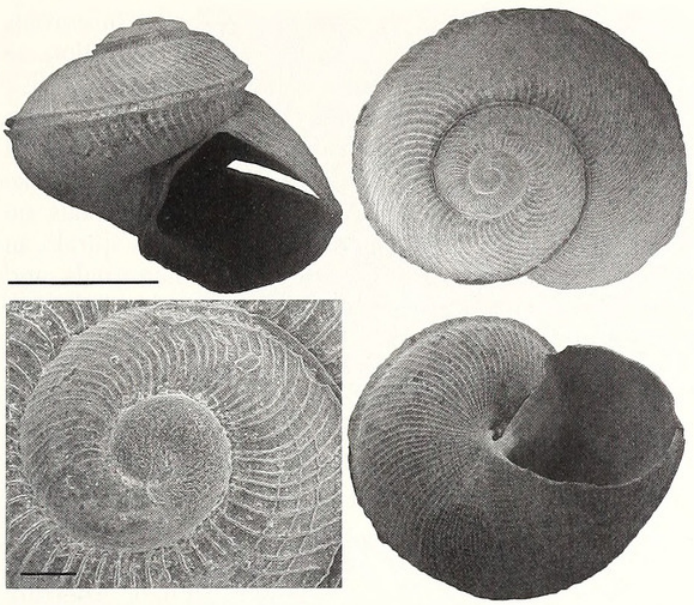


Figure 18. *Anatoma angulata*, **lectotype, here designated,** SEM (SMNH 4394), 2.25 mm diameter. Scale bar shell = 1 mm; Scale bar, protoconch = 100 µm.

inshore southern Norwegian specimens (Figures 2 and 8–13).

Shells from the southern side of the Iceland-Faroe ridge (Figures 14 and 16) are larger (to at least 2.45 mm) than material from inshore Norwegian waters at roughly the same latitude (Figures 15 and 17) which do not surpass 2.25 mm.

Distribution: Based on literature data the species is widely distributed, from the Mediterranean to the Barents Sea, from several hundred meters in fjords and the upper slope, to 10–20 m in northern Norway. It is, however highly doubtful that *Anatoma crispata* really occurs in the Mediterranean, as all Mediterranean specimens previously identified as *A. crispata* belong to different species (*A. aspera, A. tenuisculpta, A. eximia* (Seguenza, 1877), *A. umbilicata* (Jeffreys, 1883), *A.* new species Geiger, ms), and all illustrations of sufficient quality show species other than the true *A. crispata*). The main distribution is probably the northern part of the North Atlantic, in special the coast of Norway. The distribution extends south along the western coast of Britain and Ireland and farther south, but is insufficiently documented south of Ireland.

In material examined, there are specimens from 12–15 m (Vefsnfjorden, 65° 52′ N) and 20–10 m (Trondheimsleia, 63°24′ N) to 848 m (upper slope at 68° 39′ N, Mareano) and an empty shell from 1083 m (on the slope at 69° N, Mareano). Inshore, it is found down to 200–180 m in Bremnesfjorden, (Figure 2) and 190 m (Hjeltefjorden, 60°33′ N) and empty shells at 680 m in Korsfjorden (60°08′ N). The majority of living specimens have been taken between 70–50 m in southern and western Norway, and 40–25 m in northern Norway.

Remarks: *Anatoma crispata* is the first described species of the family, and has consistently been confused with a host of other species worldwide (e.g., the Australian *A. australis* (Hedley, 1903) and the northeastern Pacific *Thieleella kelseyi* (Dall, 1905): see Geiger and Jansen 2004a, Geiger and McLean, 2010, and also *A. atlantica* Bandel, 1998: see Tunnell et al. 2010) and in north-European waters with at least two other species treated here. Beginning with Jeffreys (1877), a number of species have been described from various deep water expeditions in the North Atlantic, but, until recently, few attempts have been made to subdivide the ubiquitous "*A. crispata*" on the shelf/upper slope of mainland Europe. The first may have been Dautzenberg (1927) who decided that the available evidence favored *A. aspera* to be a distinct species rather than just a variety of *A. crispata*. Nevertheless, until around 2000, most checklists still listed *A. crispata* as the only member of the European marine fauna, sometimes in addition to the deep water species *A. umbilicata* (Jeffreys, 1883) another mostly misidentified species (see entry for this species below).

In summary, the identity of *A. crispata* is highly confused, both regionally as well as globally. Additionally, *A. crispata* is the type species of the genus *Anatoma*, but the whereabouts of Fleming's syntypes is unknown. Accordingly, we designate here a **neotype** with the explicit intent to stabilize the nomenclature of the taxon. The specimen selected is from as close to the original type locality as possible (Shetland Islands) and corresponds to Fleming's (1828) description and illustration as well as possible. It is a well-preserved specimen with the protoconch. The specimen is at 1.83 mm slightly larger than Fleming's measurement of 1/15″ [=1.67 mm].

Given the equally contentious identity of *A. angulata* (see also under *A. tenuisculpta* below), we designate herein the sole surviving syntype (SMNH 4394) of the species as the **lectotype** (Figure 18), with the explicit purpose of nomenclatural stabilization of this taxon, in case non-conspecific syntypes should be located.

The present work documents that both *A. aspera* and *A. tenuisculpta* are distinct from *A. crispata*, and that these three species are all members of the Norwegian fauna. Even *A. crispata* sensu stricto seems to be a variable taxon, with a very wide distribution, both geographically and bathymetrically. In Norwegian waters, it dominates the samples from northern Norway (north of 64°N). Most (but not all) of the live-caught specimens from this part of the coast are from shallow (10–25 m), inshore, hard-bottom, environments. Museum-material documents it from the eastern, cold-water Barents Sea (71°42′ N, 271 m, –1.4°C) (ZMBN 21014), and Bøkfjord in Sør-Varanger (15–10 m) (ZMTø St. 4, 24/6 1937), as well as from Vadsø in Varangerfjorden (ZMON D 391). Southward, it is found around the Skagerrak coast, at least east to 9° E, near Risør. Hansson (2003) and Warén (pers. comm.) report that, in the last few decades, this species has become very scarce on the west coast of Sweden, after having been regularly collected in

earlier years. It is unclear whether this is the case also for the south coast of Norway. A number of the specimens from the Skagerrak coast were collected by Per Wikander in 1986–1988 (see further below under Remarks for *A. aspera*).

***Anatoma aspera* (Philippi, 1844)**
(Figures 19–33)

Scissurella aspera Philippi, 1844: 160, pl. 25, Figure 17.
Scissurella aspera: Weinkauff, 1862: 349; Munier-Chalmas, 1862: 396; Hidalgo, 1867: 144; Norman 1888: 21; Odhner, 1960: 385, 387.
Scissurella crispata var. *aspera*: Jeffreys, 1883: 88; Odhner, 1912: 13, pl. 2 fig. 25.
Schizotrochus asper: Monterosato, 1884: 39; 1890: 143.
Scissurella (*Schizotrochus*) *aspera*: Dautzenberg, 1927: 213.
Anatoma aspera: Anistratenko and Starobogatov, 1997: 76, fig. 4; Ardovini and Cossignani, 2004: 19; (misidentified: is *A. tenuisculpta* their *A. crispata* is *A. aspera*); Høisæter, 2009: 20.
Anatoma crispata Giannuzzi-Savelli et al., 1994: 13 (is *A. aspera*).
Scissurella crispata var. *paucicostata* Jeffreys, 1865: 284 [Figure 27 below].

Description: (Based mainly on **neotype** (Figure 19) and specimen from Raunefjorden, Hordaland county, (Figure 20)). Shell globular, of medium size (to 3.3 mm diameter). Height equal to or slightly less than diameter. As in other species, juveniles "flatter" than adults. Protoconch (Figures 21–22) of 0.75 whorl, with wide, open, irregular sculpture; varix present (in some specimens apparently doubled), barely connected to embryonic cap. Teleoconch I of 0.75–1 whorl, 20 (or more) axials, often partly eroded in larger shells, interaxials smooth except for strong spiral cord in position of selenizone (may also be eroded in larger shells). Teleoconch II up to 3¼ rapidly increasing whorls, with 5–12 spirals on base, visible between suture and selenizone. Shoulder with up to 65–67 high, crest-like axial costae on body whorl, additional fine axials on keel of selenizone; at least 15 very fine spirals in interaxials, an order of magnitude finer than axials, and not crossing the latter. On base, 25–30 spirals cross up to 90 slightly sinusoid axials creating a grid-like pattern (axials dominating but finer and denser than axials on shoulder); some axials disappear at midbase; remaining axials spiral into wide, deep umbilicus. Characteristic, almost triangular, funiculus departing columellar lip at roughly 40–45° near upper end of latter. Selenizone at periphery or a little above, wide (15–20% whorl height), keels distinct, somewhat flaring, growth marks not coordinated with axials. Margins of slit parallel. Aperture round, columellar lip somewhat flared, partly obscuring the umbilicus. Shell grayish white, empty shells often glassy, transparent, often with blackish "deposit" in some of cavities created by grid-like sculpture on base. "Dirty" aspect of specimen in Figure 20 largely representative of Norwegian specimens.

Operculum: Round, covering aperture, thin, transparent, multispiral, with central nucleus.

Radula (Figures 23–26): Rachidian tooth with central cusp strongest, curved arrangement of 3–4 cusps on each side. Lateral teeth 1–3 similar, apical cusp strongest, 3–4 on outer edge. Lateral tooth 4 smaller, apical

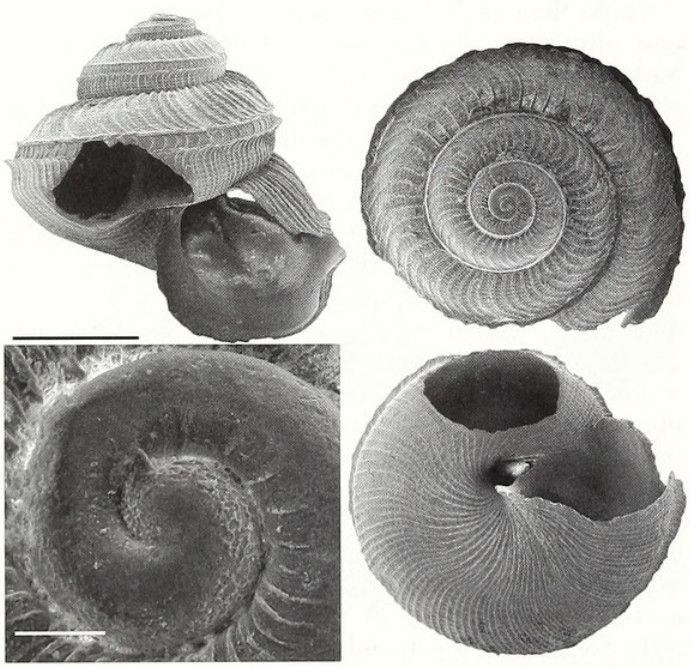


Figure 19. *Anatoma aspera,* **neotype**, Terreti - Cellantoni Bridge, 567 m above sea level, Pleistocene epibathyal facies, muddy clay, Italy, 38°07′ N, 15°43′ E, SBMNH 149681, 2.66 mm diameter.

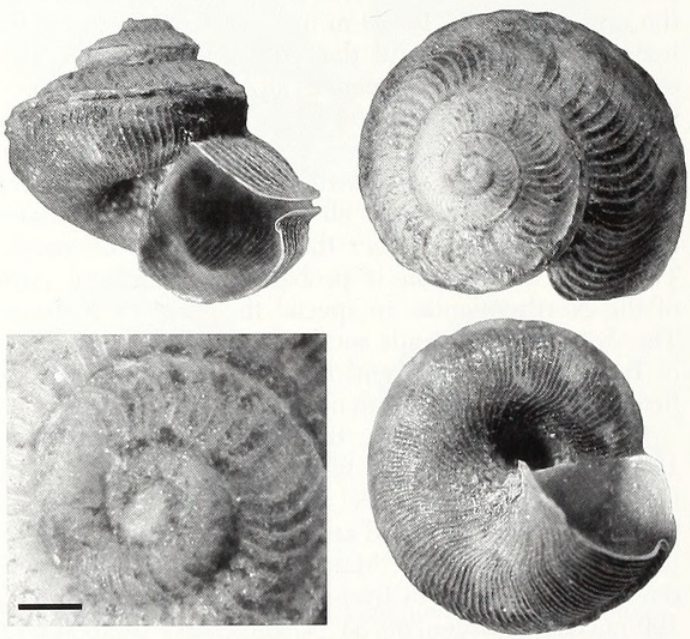
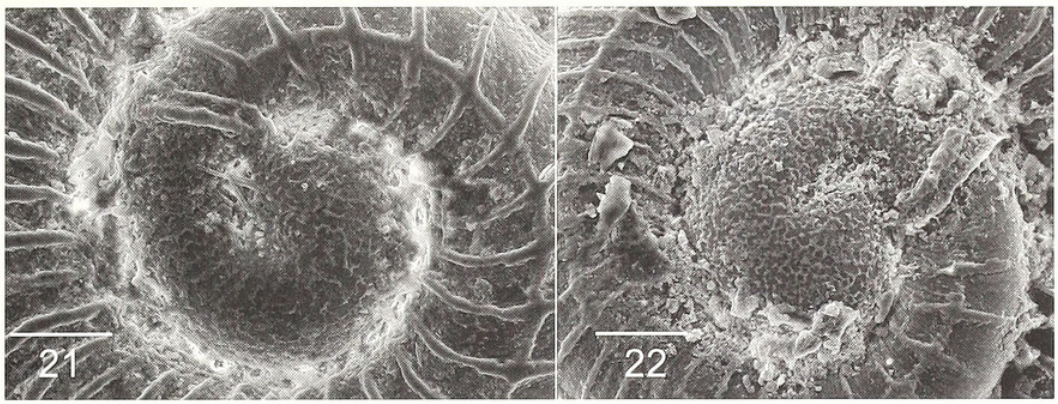
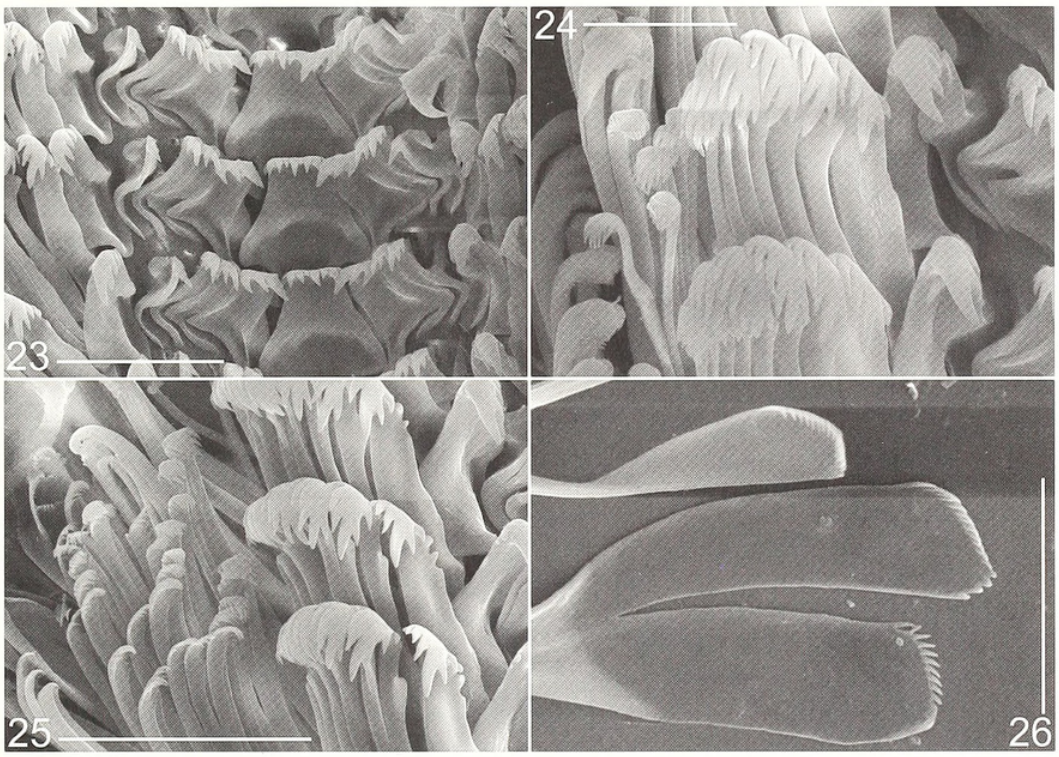


Figure 20. *Anatoma aspera*, Liholmsrennen, Raunefjorden, Hordaland county, (60°18′ N, 70–55 m), 5 mm diameter. Scale bar protoconch = 100 µm.



Figures 21–22. *Anatoma aspera*, protoconchs. **21.** Northern Tyrrhenian Sea, Italy. 70–100 m (DLG 311, 6). **22.** Liholmsrennen, Raunefjorden, Hordaland, Norway, 60°18′ N, 5°09′ E, 70–55 m. Scale bars = 50 µm.



Figures 23–26. *Anatoma aspera*, radula, Liholmsrennen, Raunefjorden, Hordaland, Norway, 60°18′ N, 5°09′ E, 70–55 m. **23.** Central field. **24, 25.** Marginal teeth. **26.** Outermost marginal teeth. Scale bars 23, 25 = 20 µm; 24, 26 = 10 µm.

cusp strongest, 3 smaller cusps on inner margin. Lateral tooth 5 elongated, apical cusp largest, approximately 6 cusps on inner edge. Inner marginal teeth inequilaterally triangular, apical cusp largest, 3 on inner margin, 4–5 on outer edge, outer marginal teeth with spoon-shaped tip. Outermost marginal teeth paddle-shaped with many small bristles at distal edge; no food groove. Radular interlock of central field moderate.

Differential Diagnosis: *Anatoma tenuisculpta* is larger than *A. aspera* (5 vs. 3.3 mm) and wider at same height, and has much narrower space between the suture and the selenizone at any given number of whorls; the former has a much finer axial sculpture, and more regular and prominent spiral sculpture. The distance between axials is more or less the same above and below the selenizone in *A. tenuisculpta* and with less dominating axials on the shoulders. In *A. tenuisculpta*, the keels of the slit and selenizone are less prominent, and the width of the selenizone is about 20% smaller. There is no funiculus in the narrower umbilicus. The shell is often yellowish gray-white although this varies in preserved material. The axial sculpture on the base is evenly rounded, and the base is sloping more gradually down from the selenizone.

Anatoma crispata is smaller (2.25 vs. 3.3 mm), more globular, and somewhat wider at same height; the axial sculpture on the shoulder is less dominating and the axial sculpture on shoulder and base is equally well developed. On early whorls, the suture is immediately below

the selenizone, whereas in large specimens it is less than half the selenizone width. The keels of the selenizone are not as prominent and the selenizone is narrower. The protoconch is larger and the whorls increase more rapidly in width. The umbilicus is narrower and with a distinct funiculus starting at lower end of umbilical lip.

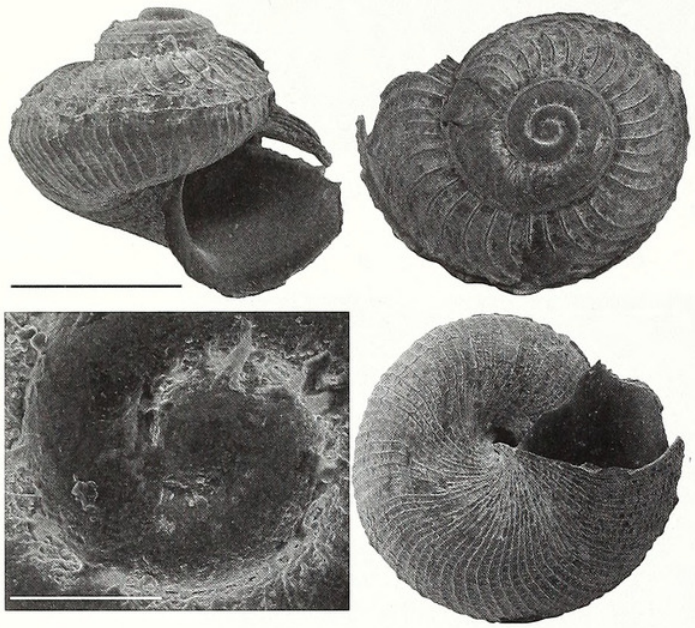


Figure 27. Holotype of *Anatoma crispata* "var. *paucicostata*," USNM 181580. Scale bar shell = 1 mm; Scale bar protoconch = 100 µm.

Anatoma schioettei has a much smaller (2.15 vs. 3.3 mm) shell, is much more disc-shaped, and has fewer axials that are crossed by almost imperceptible spirals.

Anatoma schanderi is larger (4.5 vs. 3.3 mm) has weaker axial sculpture that is approximately as strong as the spirals, sculpture on shoulder and base are approximately equally developed, and the protoconch has reticulate sculpture.

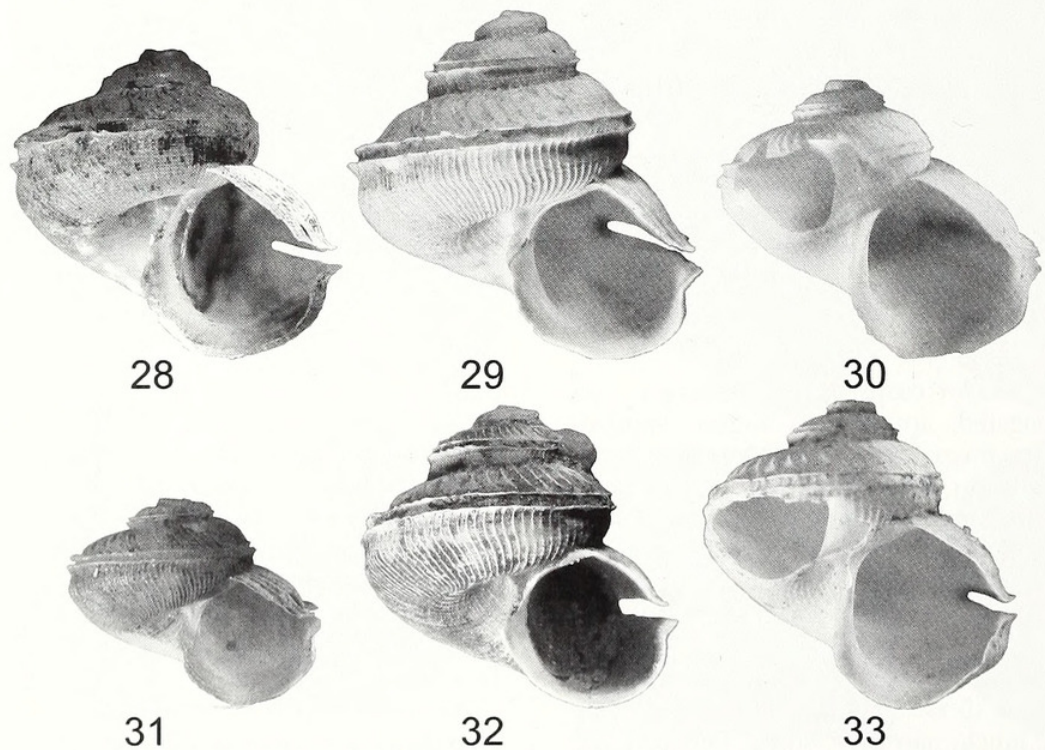
The radula of *A. aspera* is similar to the one of *A. tenuisculpta* and *A. schanderi*, in that the rachidian has a dominating central cusp with three smaller ones on each side, and wide lateral teeth 1–4 each with seven long and narrow cusps, the innermost dominating.

Type Material: Whereabouts unknown (not in Hamburg), presumed to be lost. **Neotype** is here designated, Terreti-Cellantoni Bridge, Italy, 38°07′ N, 15°43′ E, 567 m above sea level, Pleistocene, epibathyal facies, muddy clay, SBMNH 149681.

Type Locality: Punta Pezzo 13 km north of Reggio, Calabria, across the Strait of Messina from Sicily. Fossil of Pleistocene age from shelf deposits.

Other Material Examined: 42/52 specimens /shells of own material, 1/13 from the collections of ZMON, 6/9 from ZMBN, 1 shell from Trondheim Biologiske Stasjon, 0/1785 from throughout its range in various collections.

Variability: Figures 28–33 illustrate some of the variability of the species along the coast of Norway. The



Figures 28–33. *Anatoma aspera*, six specimens from the coast of Norway. **28, 31.** Raunefjorden, Hordaland county (60°18′ N, 70–55 m and 60°17′ N, 70–80 m). **29, 32.** North of Kirkelandet, Møre og Romsdal county (63°10′ N, 145 m). **30, 33.** Mouth of Andfjorden, Steinvær-revet, Nordland county (69°13′ N, 370 m). All specimens to scale, the largest (29) 3.3 mm diameter.

neotype (Figure 19) and the holotype of *A. crispata* "var. *paucicostata*" (Figure 27) from Shetland further testify to the morphological diversity of this species. The main variability seems to be associated with whorl expansion rates. Thus H/D ratios vary between 0.90 and 1.08 in Norwegian specimens of roughly the same size. The relative steepness of the shoulder (Figure 29 vs. 30) contributes to the different appearances of the shells as well. Further the relative strength of spirals and axials on the base varies (compare Figures 28 and 32). Three empty shells found around 69° N (Figures 30 and 33) have an extreme shape with the body whorl dominating completely, a wide selenizone and a longer more *"crispata"* like funiculus than in the forms found further south along the coast. Norwegian specimens generally reach a larger size than their Mediterranean counterparts, with maximum measured diameter of Mediterranean shells at 2.4 mm. The selenizone is generally wider and more open in Mediterranean specimens (see Figures 19 and 20).

Distribution: According to the literature and available museum material, mainly Mediterranean but also from the lower shelf and upper slope north along the Portuguese, Spanish and French coasts, and off the Irish and British western coasts. There are several lots from Rockall Trough between 550 to 680 m, a single lot from Porcupine Bank at 773 m, and a single specimen from the lower shelf north of the Faroes (250–400 m). Based on examined material, the species is found in Norway from Mosterhavn in Hardangerfjorden (59°42′ N) to Andfjorden (69°15′ N), but with a significant gap in distribution between 64°–69° N. (Possibly some of the 37 records of *Anatoma crispata* in Sneli et al. (2005) reporting the results from BIOFAR could represent *A. aspera*).

Remarks: The fossil assemblage described by Philippi (1844) is most likely a mixture of species of Pliocene to late Pleistocene age. This may be inferred from the frequent and sharp changes in depositional characters and fossil content due to strong Plio-Pleistocene tectonics at the location (Barrier, 1987). Thus, it is not unreasonable to accept Philippi's name for the Recent species discussed here. One of the leading fossils in the assemblage is in fact *Modiolula phaseolina* (Philippi, 1844), which is regarded in Norway as a "carpeting" species, creating a preferred substrate for a number of species at intermediate depths (50–200 m) in the fjords. The three inshore species of *Anatoma* discussed here are often found together with this bivalve. *Anatoma aspera* has been recognized as a valid Recent species in the Mediterranean by most conchologists. Weinkauff (1862) reported it from "Alger; très-rare"; Munier-Chalmas (1862) reported it also from Alger (may be the same record) and, surprisingly, from "Berghen, (Norwège)"; Hidalgo (1867) found a single, empty, but well preserved shell in the stomach of the fish *Peristedion cataphractum* (Linnaeus, 1758) near Mahon in Menorca (Balearic Islands, Spain). Later, Monterosato (1884) claimed that it was known from many localities in the Mediterranean, in contrast to *A. crispata,* which he claimed was scarce in the Mediterranean and the Adriatic Sea. Monterosato (1890) reported it without further comments as a member of the deep muddy bottom fauna near Palermo. (See also remarks above on possible confusion of *A. tenuisculpta* with *A. crispata*).

During the 1860s and 1870s, the species was not reported from the Atlantic, and Jeffreys (1865: 285) clearly had not seen it when he wrote: "Believing the *S. aspera* of Philippi to be the same species as *S.angulata* of Lovén, and that the latter is merely a large form of *S. crispata*,...". He thus set a pattern for *A. aspera* to be considered a variety of *A. crispata*. That Jeffreys was not familiar with Philippi's species is evident from his naming of a new variety of *A. crispata* "var. *paucicostata*" in the same work: "Spire more raised, and the ribs on the upper side much fewer than usual" (Figure 27, holotype). This variety was based on material from Shetland. Jeffreys (1877: 234) stated "I regard *S. aspera* of Philippi as a variety of the present species [i.e. *S. crispata*]. The height of the spire is an unreliable character". Later (Jeffreys 1883:88), he synonymized the two varieties, "*S. angulata* of Lovén and *S. aspera* of Philippi are varieties [of *A. crispata*]; the latter corresponds with my variety *paucicostata*."

During the 1890s, *A. aspera* was reported from fairly deep water (1200–1400 m) in several localities in the southern North Atlantic (e.g., Jeffreys, 1883; Locard, 1899). Some considered it to be a distinct species, others as a variety of *A. crispata*. Dautzenberg (1927), although recognizing a number of gradually converging conchological characters, regarded it as a valid species with a more southern distribution than *A. crispata*. Dautzenberg (1927: 214) arguments for accepting it as a valid species (reversing his opinion in Dautzenberg and Fischer 1912): "...car l'*aspera* est constamment plus petit, sa spire est beaucoup plus élevée, ses tours sont étagés et ses plis longitudinaux plus accusés." ["because *aspera* is consistently smaller, its spire is much more elevated, its whorls are stepped and its longitudinal folds are more prominent"].

Most non-Mediterranean authors (G.O. Sars, 1878; Norman, 1879; Dautzenberg and Fischer, 1912 chose to follow Jeffreys rather than Monterosato and later Dautzenberg; Odhner (1912), and most later authors either mention *A. aspera* as a variety of *A. crispata*, or report *A. crispata* as the only species found in northeast Atlantic waters (e.g., Fretter and Graham, 1976, Smith and Heppell, 1991). This tradition has also been adopted by most recent Mediterranean authors (Sabelli et al., 1991, citing Schirò, 1986). Clear evidence of the confusion is found in Giannuzzi-Savelli et al. (1994), in which illustrations of *A. aspera* are misidentified as *A. crispata*.

In discussing the *Anatoma* spp. collected by the Swedish Josephine Expedition in 1869, Odhner (1960)

mentioned *A. aspera* (as a full species) from Josephine's Bank (ca. 380 km due west of the southern tip of Portugal, 200–935 m depth), in addition to three West Indian localities ranging from 180–720 m depth. These records from moderately deep water are supplemented by three records by Dautzenberg (1927) from around the Azores and the Canaries at 1230–1350 m. We have not been able to locate any references to *A. aspera* as a full species from northern waters in more recent literature.

Anatoma aspera thus seems to be known as a Recent species from three or four different geographic/bathymetric zones, the Mediterranean in moderately deep water (20–1200 m: collection records DLG, MNHN) in the southern part of the North Atlantic on or near seamounts, from 200 m to 4400 m (collection records RMNH from Azores), and in Norwegian inshore waters [plus the record of *S.* "var. *paucicostata*" from Shetland by Jeffreys (1865)]. A statement that indicates that the material from the southern part of the North Atlantic might be specifically different from our northern form, is that according to Dautzenberg (1927: 214 [translated from French]) "*aspera* is consistently smaller [than *A. crispata*]", which does not fit the Norwegian material. The Norwegian shells of *A. crispata* never reaches the size (maximum diameter 2.4 mm) of a fully grown *A. aspera* (maximum diameter at least 3.3 mm). Mediterranean specimens, however, seem generally to be smaller than Norwegian specimens (to 2.5 mm).

In Norwegian waters, the species is definitely less common than *A. crispata*, and is mainly a southern form. Except for three shells from a *Lophelia* reef at 69°14′ N, we have no records of specimens from north of 64°40′ N. Two shells from the collection of the Zoological Museum in Tromsø, from respectively Lofoten and Bjarkøy (ca. 69° N) may also belong to this species. The species is rarely found shallower than 50 m or deeper than 150 m, and the blackish "deposit" on all or part of the shell (Figure 20) indicates that its microhabitat is somehow associated with blackish, maybe anoxic, sediment.

It is perhaps of importance that in three recent (Sep.–Oct. 2007) attempts to obtain some new material from one of the most reliable localities from the 1960s, only specimens of *A. aspera* have been found, and only two specimens at that, whereas more than 30 specimens of all three species were collected in a single sample in the 1960s.

Given the confusing identities of the specific epithets *crispata* and *aspera*, representing species for which no type material is extant, it is important to stabilize both taxa by designating neotypes. We designate here a **neotype** for *A. aspera*, with the explicit intention of taxon stabilization. As discussed above, the species was described based on Pleistocene fossil material and is widely recognized as extending its temporal range into the Recent. We have selected a fairly well-preserved fossil specimen from as close as possible to the original type locality.

Anatoma tenuisculpta (Seguenza, 1877)

(Figures 34–47)

Scissurella tenuisculpta Seguenza, 1877: 273, pl. 16, Figure 29.
Scissurella tenuisculpta: Monterosato 1890: 143; Vazzana, 1996: 150, Figure 13.
Anatoma tenuisculpta: Lozouet 1986: 114.
Scissurella crispata auct. not Fleming, 1828: Lovén, 1846: 20; Jeffreys 1870: 444; Friele 1874: 15; G.O. Sars 1878 (in part): 126; Norman 1879 (in part?): 24; 1893(in part?): 360; Friele and Grieg (in part): 59; Brøgger(in part?) 1901: 657; Odhner 1912 (in part): 13; Grieg 1914: 76; Hubendick and Warén 1974: 25; Fretter and Graham 1976 (in part): 2.
Scissurella crispata var. *angulata* auct. not Lovén, 1846: Odhner 1960: 384.
Scissurella argutecostata Seguenza, 1877: 273, pl. 16, Figure 30.
Scissurella funnazzensis de Gregorio, 1889: 13, pl. 1, fig. 9a–d.
Anatoma umbilicata auct. not Jeffreys, 1883.
Anatoma n.sp. Høisæter 2009: 21.

Description: (Largely based on **neotype**, Figure 34, and specimen from Tomfjorden, Norway, Figure 35 and from Rovdefjorden, Norway, Figure 36). Shell large (to 5.0 mm diameter), trochoid, biconical, wider than high, particularly in juveniles. Protoconch of slightly more than 0.75 whorls, with very fine flocculation; apertural varix not connected to embryonic cap, apertural margin slightly sinusoid. Teleoconch I of 0.5 to 0.65 whorls, with 17–30 fine axial cords, often partly eroded, spiral cord in position of selenizone. Teleoconch

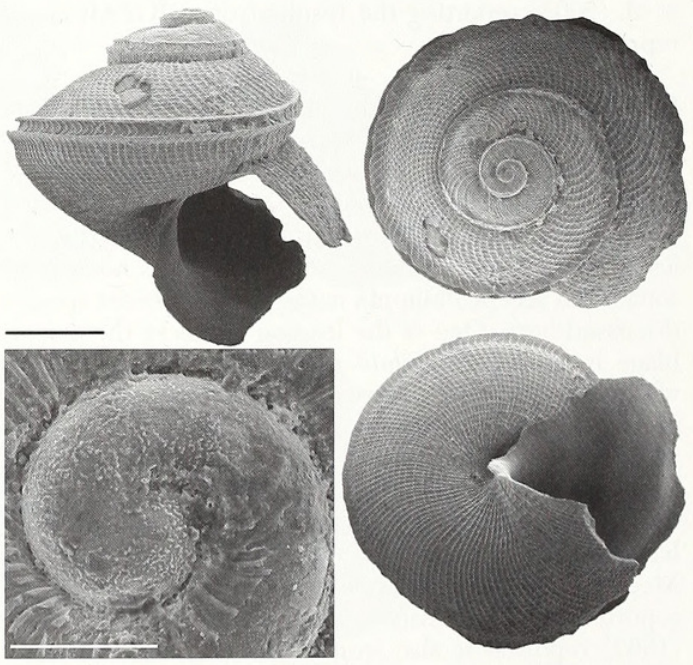


Figure 34. *Anatoma tenuisculpta*, **neotype,** SEM, Terreti-Cellantoni Bridge, 567 m above sea level Pleistocene epibathyal facies, muddy clay, Italy (38°07′ N, 15°43′ E), SBMNH 149680, 3.55 mm diameter.

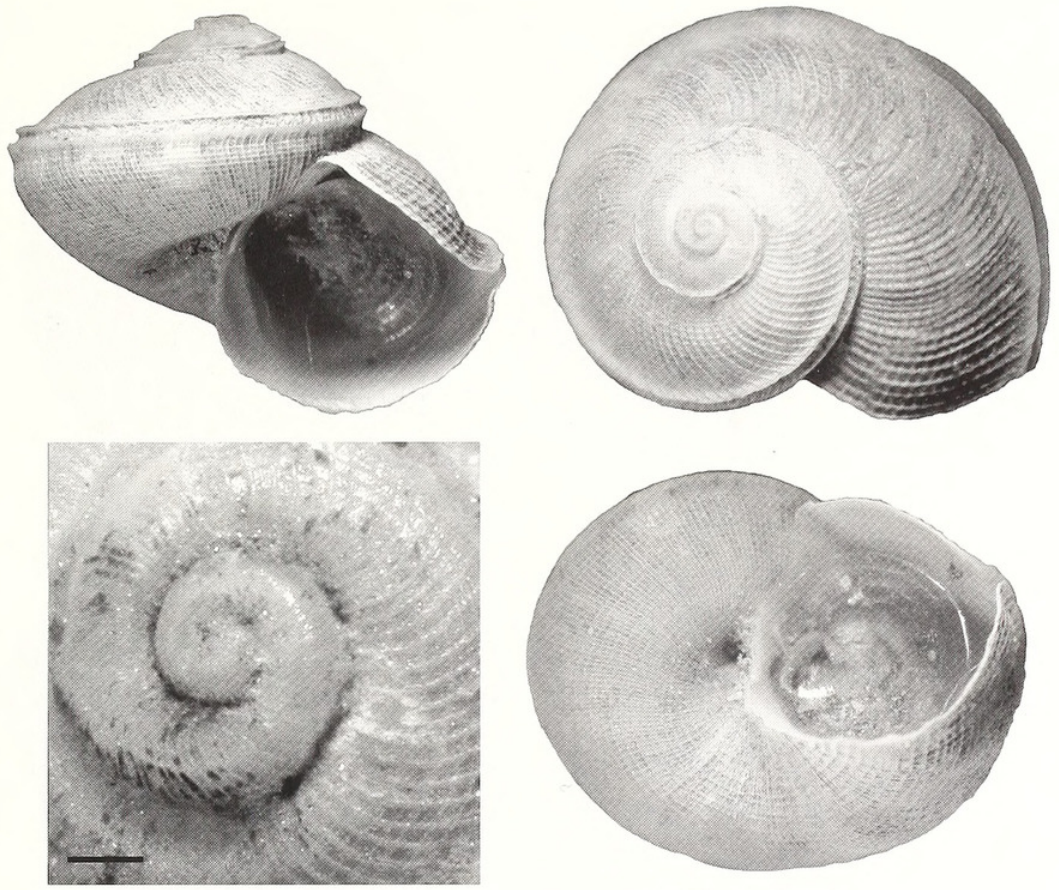


Figure 35. *Anatoma tenuisculpta*, Tomfjorden, Nordland county, Norway (66°15′ N, 380–300 m), 4.1 mm diameter. Scale bar protoconch = 100 μm.

II up to three whorls, suture approximately one to three selenizone widths below selenizone (one to three spirals between suture and selenizone), convex shoulder with 89–90 axials on body whorl (5 mm specimen); spirals starting with one median spiral between axials 4 and 5, after two axials, one new spiral on each side of first (all three on slightly concave lower part of shoulder), number of spirals increasing rapidly to 8–10 on next half whorl, then gradually to 17–18 spirals at aperture; spirals one order of magnitude finer than axials, not crossing axials completely, but creating a series of small nodules on axials of body whorl. Adsutural spiral-free band not much wider than distance between spirals. Base slightly convex, with 28–30 spirals crossing approximately 130 (5 mm specimen) only slightly stronger axials, creating regular grid of rectangular "pits"; these axials descending into fairly wide, deep umbilicus. Umbilicus open, without funiculus. Selenizone at periphery, narrow, keels distinct, axial lamellae distinct at least partly coordinated with axials. Margins of slit mostly parallel but slightly converging towards end. Aperture round; lower, inner lip flared, especially in juveniles. Columellar lip evenly rounded. Snails collected alive with translucent, yellowish hue, with rust-colored deposits in pits of sculptured surface.

Operculum (Figure 40): Round, thin and transparent, multispiral with central nucleus.

Radula (Figures 37–39): Rachidian tooth trapezoid, apical cusp largest, five cusps on each side. Lateral teeth 1–3 similar, innermost lateral tooth with five cusps, innermost largest. Lateral teeth 2 and 3 similar with each four equal-sized cusps. Lateral tooth 4 reduced, narrow with a single cusp. Inner marginal teeth with triangular tip, apical cusp largest, 5–6 cusps on each side. Outer marginal teeth with spoon shaped tip, many fine bristles. Radular interlock of central field moderate.

Gut content (Figure 41): Amorphous matter.

Differential Diagnosis: *Anatoma aspera* is proportionally taller and smaller than *A. tenuisculpta* (3.3 vs. 5 mm), with much coarser and less regular axial sculpture, and less prominent spiral sculpture on the shoulder. There is a pronounced gap between the suture and the selenizone above, particularly in larger specimens. The selenizone is wider and the margins of the slit are not converging. It has a wide-angled funiculus deep inside the wide umbilicus. The curvature of both shoulder and base is more convex, meeting the lower selenizone keel at nearly a right angle.

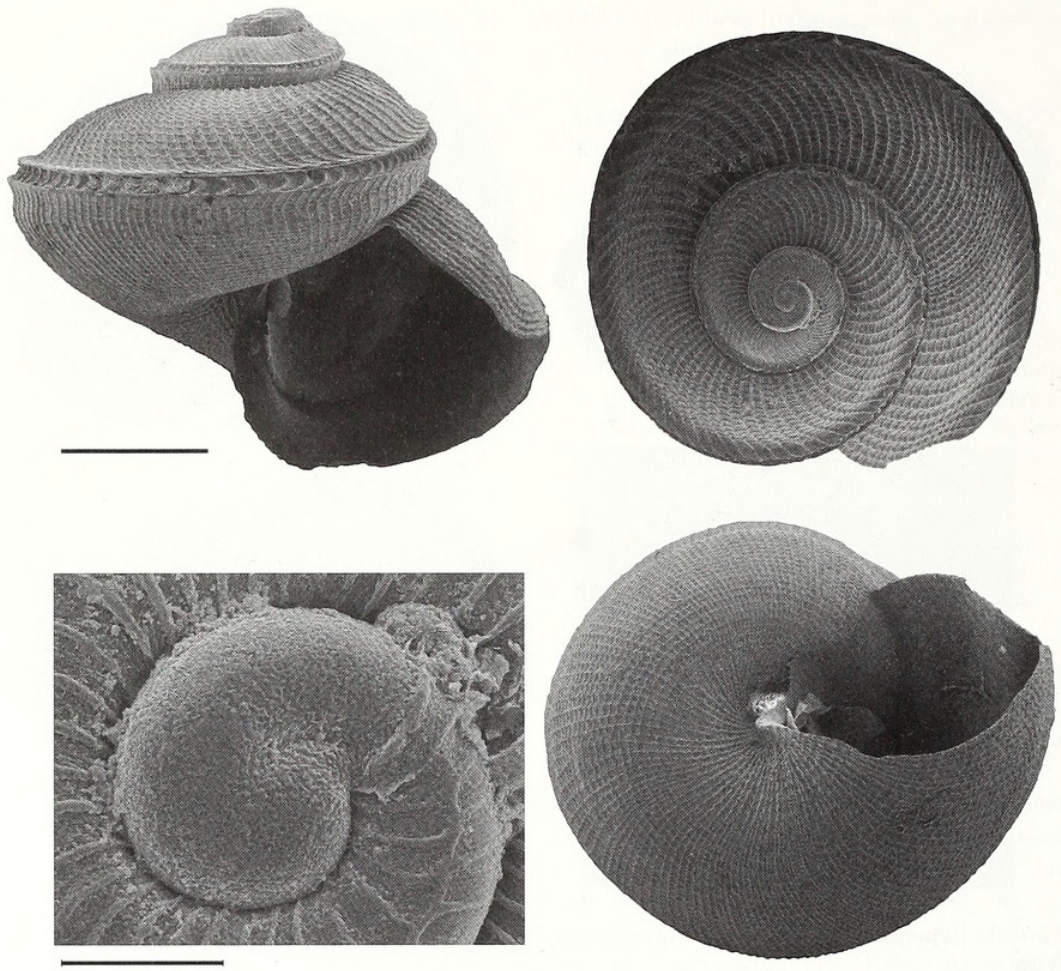
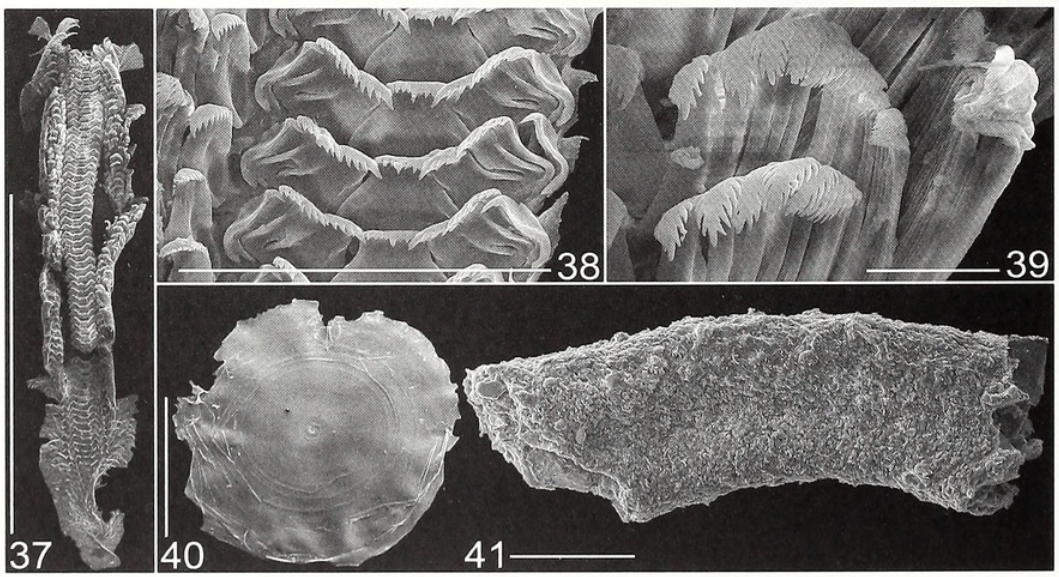
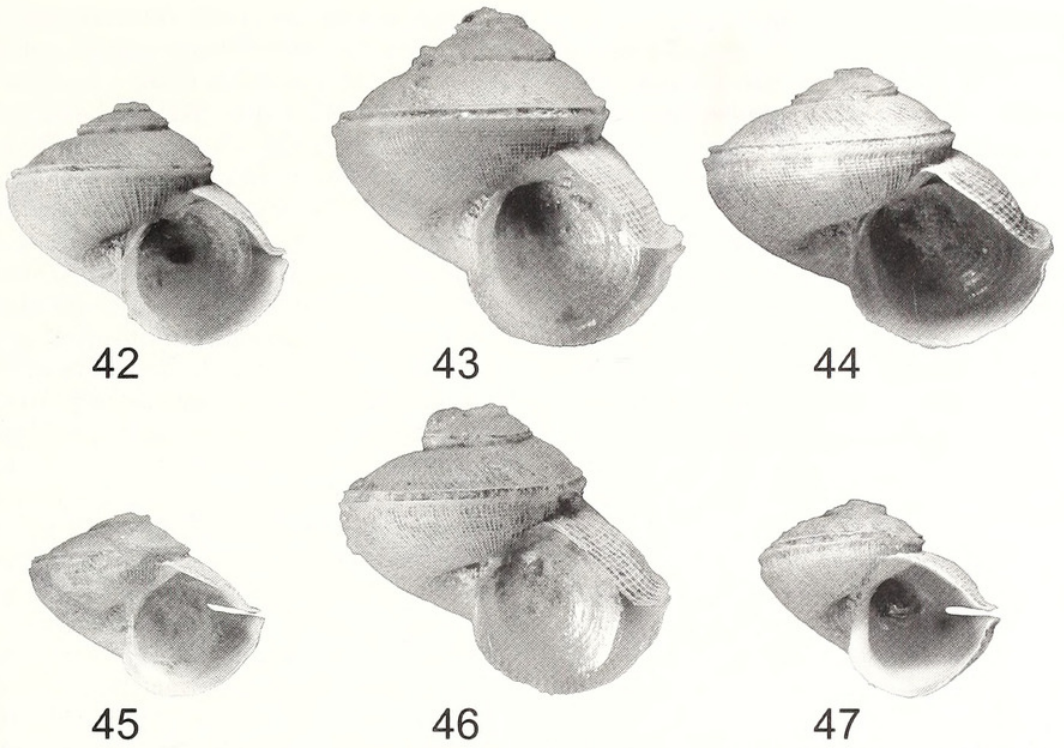


Figure 36. *Anatoma tenuisculpta*, SEM. Specimen from Rovdefjorden, Møre og Romsdal county, Norway (62°12′ N, 200–150 m), 3.8 mm diameter. Scale bars shell = 1 mm; Scale bar protoconch = 100 μm.



Figures 37–41. *Anatoma tenuisculpta*, 3.8 mm diameter. SEM. Radula, operculum and fecal pellet. A specimen from Rovdefjorden, Møre og Romsdal county, Norway (62°12′ N, 200–150 m). **37.** Entire radula. Scale bar = 200 μm. **38.** Central field. Scale bar = 20 μm. **39.** Marginal teeth. Scale bar = 10 μm. **40.** Operculum. Scale bar = 1 mm. **41.** Gut content of amorphous matter. Scale bar = 100 μm.



Figures 42–47. *Anatoma tenuisculpta*, six specimens from the coast of Norway. **42.** Straumsberget, Korsfjorden (60°10′ N, 300–150 m) **45.** Raunefjorden, Hordaland county (60°17′ N, 60–80 m). **43.** Rovdefjorden (62°12′ N, 200–150 m). **46.** Breisunddjupet (62°28′ N, 120–60 m), Møre og Romsdal county. **44, 47.** Tomfjorden, Nordland county (66°15′ N, 380–300 m). All specimens to scale, the largest (43) 4.2 mm diameter.

Anatoma crispata is smaller (2.25 vs. 5 mm), more globular, has a distinct funiculus, and more rapidly increasing whorls. The suture is adjacent to the selenizone of previous whorl. Teleoconch I has fewer and stronger axials. The shoulder is more convex with stronger, more irregular and strongly curved axials; spirals on the shoulder are fewer but more prominent, and with a wide adsutural sector devoid of spirals. The base has more widely spaced axials and spirals creating a grid with larger, almost square pits. The aperture has a less flaring lower and inner lip.

Anatoma schioettei is much smaller (2.15 vs. 5 mm) has a more elevated overall shell shape, has about half as many axials that are not crenulated, and the spirals are barely perceptible.

Anatoma schanderi is more turreted, has a protoconch with reticulate sculpture, the axials are much weaker, and about as strong as the spirals.

The radula of *A. tenuisculpta* differs from that of *A. crispata* mainly in having a broader rachidian tooth with 11 cusps, of which the central one is the longest, but is not isolated.

Type Material: Unknown whereabouts, presumed to be lost. **Neotype, here designated,** Terreti-Cellantoni Bridge, 567 m above sea level Pleistocene epibathyal facies, muddy clay, Italy, 38°07′ N, 15°43′ E (DLG 1421, 6), SBMNH 149680.

Type Locality: Pliocene/Pleistocene deposits near Reggio Calabria, southern Italy.

Other Material Examined: 92/80 specimens /shells of own material, 32/72 from the collections of ZMON, 22/38 from ZMBN, 3/12 from ZMTø and 7/0 from TBS. From other collections: Norway (NHMUK, 1): Dröbak, 59°40′ N, 10°38′ E (USNM 181590, 119; USNM 181591, 34; USNM 181589, 8); 60–130 m, Raunefjord, 60°16′ N, 5°09′ E (NMSZ 1973.59.1, 5); West of Ireland and Great Britain: 765 m, Rockall Trough, off W Scotland, 55°44′ N, 16°07′ W (NMR 993000033717, 32); 560 m, Rockall Trough, off western Scotland, 55°49′ N, 15°08′ W (NMR 993000033720, 6); 587 m, West of Rockall Trough, 55°30′ N, 15°48′ W (DLG 1217, 1); Southern North Atlantic: 621–786 m, Josephine Bank, Azores, 36°40′ N, 14°15′ W (USNM 181618, 1); 1920 m, Challenger Station SE342, 39°01′ N, 10°40′ W (NMSZ 1994128.60109, 8: complete); 1818 m, off W Portugal, 40°N, 9°15′ W (USNM 181602, 6); 2500 m, Challenger Station ES347, 41°38′ N, 11°20′ W (NMSZ 1994128.60110, 18: complete); 543m, Bahia de Cadiz, Spain, 35°30′ N, 6°08′ W (NMR 993000033757, 12); Mediterranean; 350 m, Fiumicino, Roma, 41°42′ N, 12° E (NMR ex 993000033735, 1); 400 m, Capraia, 43°03′ N, 9°54′ E (SRC, 1); 70–100 m, Northern Tyrrhenian Sea (SRC, 1). Palermo, 38°08′ N, 13°23′ E (ZMUC, 3).

Variability: In the Norwegian material the only significant variability seems to be difference in shape (Figures 42–47). This is partly due to change with growth, older specimens always being taller than younger ones, but comparison of shells in Figures 43 and 46 shows that shells of same size within a population may also differ. No geographical trends in the Norwegian material are evident. Shells from the Mediterranean agree in all significant respects with the Norwegian material.

Distribution: The majority of records are from the coast and fjords of Norway, but a few museum specimens indicate that it can be found in moderately deep water (60–800 m) on the shelf and upper slope of the northeast Atlantic ocean, possibly from the Faroe Islands and southward to west of Gibraltar, with various deep-water localities farther south. A very few records are from Italian waters, 70–400 m. The species is probably overrepresented in museum material from Norway because of its size. With a single exception, a few shells from Drøbak in Oslofjorden, all museum specimens are from western and northern Norway. In the material from ZMBN (22/38 specimens/shells), records of *A. tenuisculpta* are from five to ten times more frequent than each of the other two inshore species. Our own material indicates that it is far less common in Norwegian waters than *A. crispata*, of which we have three times as many specimens and six times the number of empty shells. The confirmed latitudinal distribution is from 67°10′ N, south to Korsfjorden (60°10′ N). The few shells from museum collections show that there is (or was) an isolated (?) population near Drøbak and scattered records north to Lofoten (68°25′ N) and southern Troms county (68°50′ N). The main depth distribution in Norwegian fjords is 80–200 m, with a few finds up to around 50 m (50–25 m dredge haul) and down to a little more than 300 m (380–300 m). A couple of empty shells from a fjord bottom at 680 m indicate that it might have been living even deeper than 380 m.

Remarks: This is the species called *Anatoma* n. sp. in Høisæter (2009). Despite it having been figured and described repeatedly from Norwegian waters, the species has never been properly identified. This is partly due to the confusion surrounding *Scissurella angulata* Lovén, 1846, which was accepted by most authors as the name for this form, either as a full species or as a form of *A. crispata*. Lovén (1846) described but did not illustrate *Scissurella angulata* from northern Norway in a paper in which he also recorded *A. crispata* from Bergen. This indicates that he did observe differences that he regarded to be of specific value. His diagnosis in Latin (four lines) is not detailed enough to let us decide which of his two species is the real *A. crispata*. Luckily, one of two syntypes is in SMNH, and SEM of this specimen (Figure 18 above) clearly shows that what Lovén regarded as the new species *S. angulata* in fact is a specimen of *A. crispata*.

The species is thus in need of another name. *Anatoma richardi* (Dautzenberg and Fischer, 1896), *A. josephinae* (Odhner, 1960), *A. umbilicata* (Jeffreys, 1883), and *A. tenuis* (Jeffreys, 1877) are all species described from deep water (360–2650 m) in the North Atlantic. None of these names has ever been used for the "large" Norwegian species, and studies of the type material have eliminated all of them (Geiger, unpublished data). However, Seguenza (1877) described three species of *"Scissurella"* from Pleistocene/Pliocene deposits from the Reggio Calabria region in southern Italy (northern shore of the Messina Strait). Two of these, *S. tenuisculpta* and *S. argutecostata*, have shell morphologies indistinguishable from our Norwegian form. Later (Gregorio 1889), described a species, *S. funnazzensis* from 140–180 m depth off Sicily. Examination of his illustrations shows that this species is indistinguishable from Seguenza's two fossil "species". Warén (pers. comm.) studied material of *S. tenuisculpta* from the type locality (any types have most likely been destroyed during one of many earthquakes in the region during the first half of the last century; Warén, 1980) and considers specimens from these deposits indistinguishable from Recent specimens from Mediterranean and Norwegian waters. We agree and apply the first reviser's principle in selecting *tenuisculpta* as name for the species. We cautiously apply this species epithet to the Norwegian material. We designate here a **neotype** (Figure 34) for *A. tenuisculpta* with the explicit intention of taxon stabilization.

Starting with Jeffreys (1865), many authors have regarded Lovén's *A. angulata* as a variety of *A. crispata*, "As I suspected, *S. angulata* of Lovén is a large form of this species [*A. crispata*]" (Jeffreys 1870: 444). Jeffreys, familiar with the British forms of *A. crispata*, got acquainted with the large Scandinavian "variety" on a dredging excursion to Oslofjorden (Drøbak), and probably assumed that the form described as new by Lovén was this large form. Friele (1874), G.O. Sars (1878), Norman (1879, 1893), Schneider (1886) all accepted *A. angulata* as a form or variety of *A. crispata* (mostly implicitly as they did not necessarily mention *A. angulata*, although, judging from museum material, they certainly were mainly studying *A. tenuisculpta*). Both G.O. Sars (1878), and Norman (1893) remarked that the Norwegian form of *A. crispata* attains a much larger size than the British form of the species. Norman did not mention Lovén's species, but G.O. Sars followed Jeffreys and synonymized both *A. aspera* and *A. angulata* with *A. crispata*, and even ventured the fanciful hypothesis that the British specimens studied were all juveniles. Monterosato (1890), in his survey of the molluscs of the depths of the waters of Palermo, discussed both *S. tenuisculpta* and *S. angulata*, the latter based on the description and illustration in G.O. Sars (1878). Monterosato left no doubt that he regarded the large form from Norway as a species separate from *A. crispata*, and that it should be identified

as *S. angulata* Lovén. He compared the fossil, *S. tenuisculpta* with *S. affinis* O.G. Costa (which he synonymized with *S. funnazzensis* de Gregorio, 1889) and consequently regarded (Monterosato, 1890: 143) the large Norwegian species ("The largest European species and probably the largest known species, living or fossil, confused by all with *S. crispatus*") as distinct from *S. tenuisculpta*. The only comment on *S. tenuisculpta* is its "restricted umbilicus".

The first author to seriously discuss the relationship between the three forms from Scandinavia was Odhner (1912: 13), who provided the following description of *Scissurella crispata* var. *angulata*: "Shell less depressed (than *S. crispata* s.s.); whorls more flattened above; body-whorl therefore more angulated; aperture = 2/3 the spire; H. 4.2, D. 5 mm; whorls 4 3/4 - var. *angulata* Lovén, 1846." This description undoubtedly refers to our *A. tenuisculpta*. Odhner, however was not consistent in his concepts of *"angulata"* and *"crispata"*. In Odhner (1960) he again referred to *A. crispata* var. *angulata* when describing his species *A. josephinae*. By including specimens from Trondheimsfjorden and Bohuslän (western Sweden) under the var. *angulata* umbrella, he demonstrates that his idea of the variety was not in accordance with *tenuisculpta*. Lovén's original material from "Finmark" (might be from anywhere in northern Norway, not necessarily in Finnmark county) consisted of two specimens (the only remaining shell is designated by us as **lectotype**, illustrated in Figure 18 above), both of which were studied by Odhner (1912); Lovén gave the maximum diameter as 2.4 mm (corresponding height 1.8 mm), quite different from the 5 mm he gave as the diameter in the diagnosis for *A. crispata* "var. *angulata*."

In more recent literature from the northeastern Atlantic, several illustrations of *A. crispata* are based on *A. tenuisculpta*. This is also true for the drawing in Hubendick and Warén (1974) from the Bergen area, western Norway, and the one in Fretter and Graham (1976) and thus also Graham (1988), which is the drawing by Poul Winther based on another shell from the Bergen area. Fretter and Graham (1976) also presented two SEM images of the spire of what is actually a specimen of *A. tenuisculpta* from the Bay of Biscay.

In Norway, *Anatoma tenuisculpta* is often found (alone or with *A. crispata* and/or *A. aspera*) at intermediate depths, from 50 m downwards, at least down to 460 m (Trondheims-fjorden; Norman, 1893). The substrate varies, but when a mixture of silt, shell gravel and small stones (and often with an abundance of *Modiolula phaseolina*) is present, the chances of finding this species are good. As late as June 2010, eight specimens were found in outer Korsfjorden (60°08′ N, 255–289 m). The depth distribution of the three species is discussed further in the Discussion below.

Anatoma schioettei new species
(Figures 48–60)

Description: (Largely based on holotype, Figure 48). Shell of moderate size (to 2.15 mm diameter), trochiform, stepped. Protoconch of 0.75 whorls, loose flocculent sculpture with some of the flocculae organized into a distinct spiral on top of protoconch and another, smaller and indistinct spiral near the inner part of the protoconch. No apertural varix, apertural margin straight, clearcut. Teleoconch I of ca. 0.75 whorl, with approximately 15 axial cords, (weak) spiral cord in position of selenizone. Teleoconch II of up to 2 whorls, suture one to two selenizone widths below selenizone. Shoulder slightly convex, strong axial cords, approximately 30–35 on first teleoconch II whorl. Weak spiral threads starting late, with a single thread increasing gradually to three to five near aperture. Base with same axial sculpture as on shoulder, 30–55 per whorl, one out of five or six fading out near middle of base. Around 16 weak spiral cords on base, getting gradually weaker towards the periphery. Umbilicus open, wide, distinct narrow funiculus. Aperture rounded oblong. Selenizone at periphery, keels moderately elevated, weak.

Radula (Figures 49–53): Rachidian tooth trapezoid, central cusp largest, four cusps in arc on each side of tip. Lateral teeth 1–3 similar, apical cusp largest, 4–5 progressively smaller cusps on outer edge of tip. Lateral tooth 4 reduced, hook-shaped, with 1–2 cusps on outer edge. Lateral tooth 5 enlarged, apical cusp largest, 6–7 cusps along inner edge, 2–3 along outer edge. Inner marginal teeth with triangular tip, apical cusp largest, 4–5 cusps on each side of tip. Outer marginal teeth with spoon-shaped tip, many small cusps along edge. Outermost marginal teeth paddle-shaped with many fine bristles along tip. Radular interlock of central field moderate.

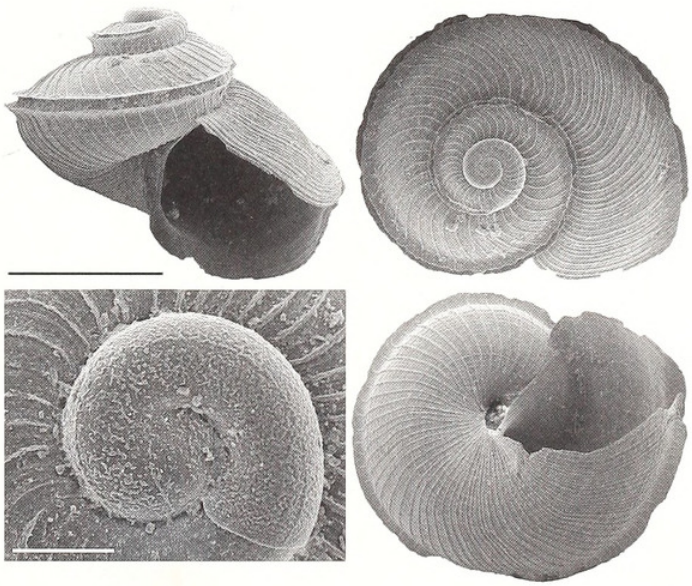
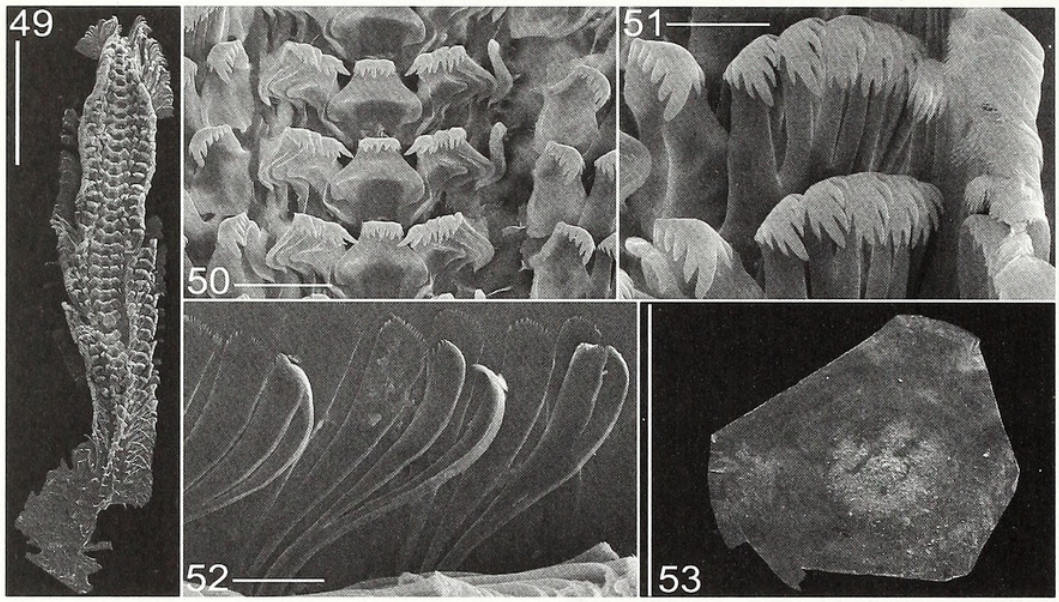


Figure 48. *Anatoma schioettei* new species, holotype, SEM, from 749–774 m, off Greenland, 75°01′ N, 12°38′ W (ZMH K–42704), 2.15 mm diameter. Scale bar shell = 1 mm; Scale bar protoconch = 100 µm.



Figures 49–53. *Anatoma schioettei* new species, 2.15 mm diameter, radula and operculum. Specimen from 749–774 m, Greenland, 75°01′ N, 12°28′ W (ZMH K–42705). **49.** Entire radula. Scale bar = 200 μm. **50.** Central field. Scale bar = 20 μm. **51.** Lateral tooth 5 and marginal teeth. Scale bar = 10 μm. **52.** Outermost marginal teeth. Scale bar = 10 mm. **53.** Operculum. Scale bar = 1 mm.

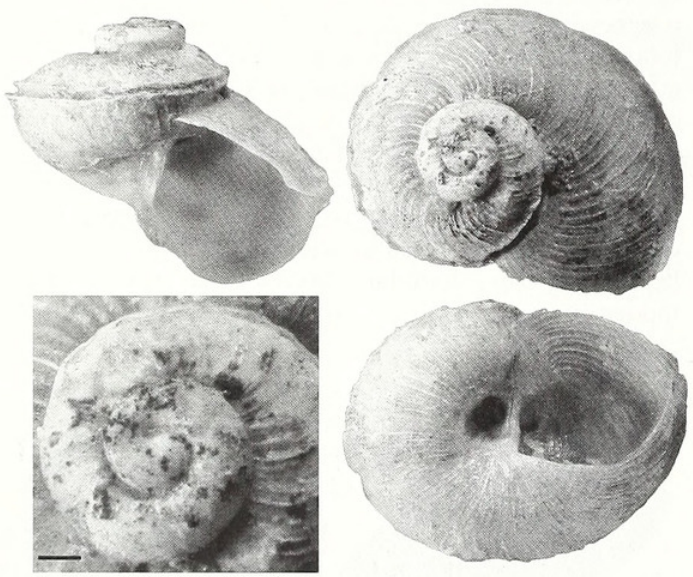


Figure 54. *Anatoma schioettei* new species, Trollveggen vent field just north east of Jan Mayen, 71°18′ N, 5°47′ W, 574 m, 1.95 mm diameter. Scale bar protoconch = 100 μm.

Differential Diagnosis: *Anatoma crispata* has whorls that are closer to the selenizone of the previous whorl, has at least twice as many axials, crossed by stronger spirals, and has a more narrow umbilicus.

Anatoma tenuisculpta is much larger (5 vs. 2.15 mm), has suture closer to the selenizone of the previous whorl, has at least twice as many axials, which have a crenulated appearance due to the crossing spirals, and lacks a funiculus.

Anatoma aspera has a taller overall shell, has stronger axials on the shoulder, and lacks a funiculus.

Anatoma schanderi has a taller shell with the base visible between suture and selenizone at an angle towards the spindle, is much larger (4.5 vs. 2.15 mm), spirals and axials of approximately equal strength, and a protoconch with more regular net sculpture.

The radula of *A. schioettei* is similar to the one of *A. crispata*, narrow necked rachidian with an isolated central cusp with three smaller cusps on each side. Lateral teeth 1–3 similar, each with three strong cusps. Lateral tooth 4 narrow with only one cusp. Lateral tooth 5 wide with at least seven cusps of which no. six from center is the strongest.

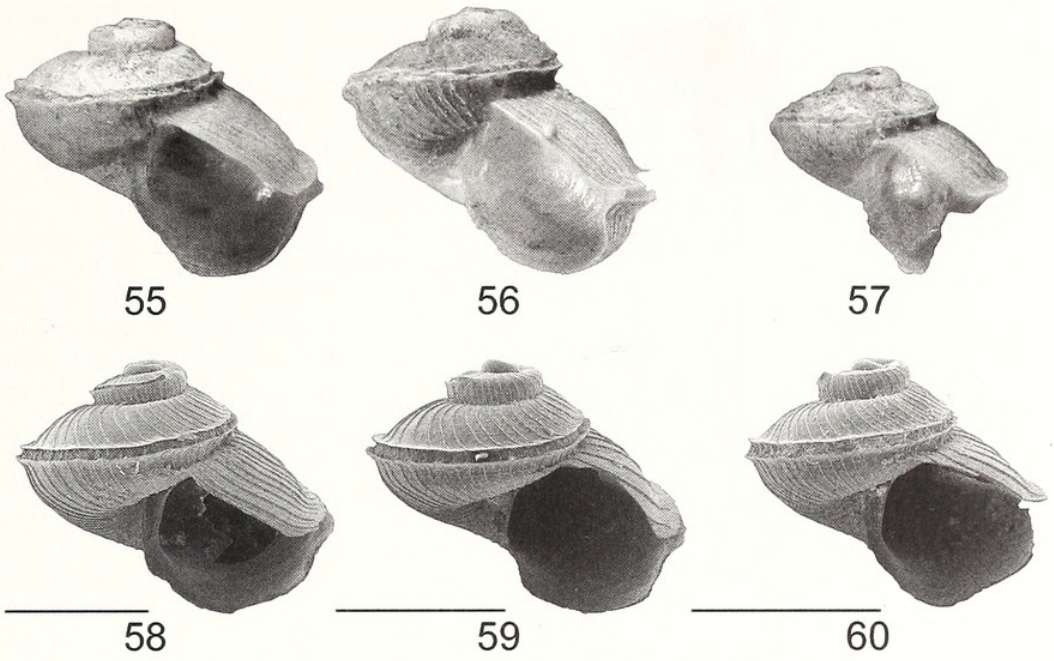
Type Material: Holotype, ZMH K 42704, Paratypes ZMH K 42705–42710, ZMUC GAS–427, 428.

Type Locality: 749–774 m, upper slope off East Greenland, 75°01′ N, 12°38′ W.

Other Material Examined: Three specimens from 574 m, H2Deep ROV dive 22-2008, the Trollveggen vent field just NE of Jan Mayen, 71°18′ N, 5°47′ W; 70 m, Greenland, 76°33′ N, 69°23′ W (ZMUC, 3: complete); 100–110 m, Greenland, 76°33′ N, 69°0′ W (ZMUC, 1: complete); 197–198 m, Greenland, 75°01′ N, 13°48′ W (ZMUC, 1, 1: complete) (ZMUC – GAS – 427, 428).

Etymology: Named after Tom Schiøtte of ZMUC. He generously provided material that he had been working on himself, which provided the radulas for the two new species.

Variability (Figures 55–60): Number and density of axials vary, as does the presence or distinctness of spirals on the shoulder, normally three but sometimes five weak spirals are present on the middle of the shoulder. The



Figures 55–60. *Anatoma schioettei* new species, six specimens from the northern Norwegian Sea. **55–57.** Three (LM) from the Trollveggen vent field, 574 m. **58–60.** Three (SEM) from the upper slope off northeast Greenland, 749–774 m (ZMH K – 42705–42710.). Scale bars all = 1 mm.

spirals are always much weaker than the axials, and at times only visible under very high magnification.

Distribution: The main distribution, judged by the limited material available, appears to be the shelf and upper slope off northeast Greenland, but as the two records from northern Baffin Bay show, it probably has a wide distribution in Arctic waters. As shown below, variants of the species may extend to "shallow" water hot vents near Jan Mayen, and to the upper slope off western Norway (ca. 62° N).

Remarks: Two "forms" of this species appear to be present in the Norwegian Sea, one on the upper slope off Greenland, at a depth from around 70 to 750 m at 75° N (Figures 58–60), the other one at the "Trollveggen" vent locality just northeast of Jan Mayen at 71°18′ N, at 574 m (Figures 54, 55–57). The main shell differences appear to be erosion and deposit of dark brown and black particles (microbes?) on shell surface.

In contrast to other known vent faunas, the vent faunas on the two investigated vent fields in the Norwegian Sea seem to be recruited from the surrounding soft bottom. Thus, two or three species of the skeneid gastropod *Skenea* are very similar to upper slope species on the "Trollveggen" hot vent, while the single *Skenea* species found on a much deeper hot vent locality in the same area, is similar to a species living on the adjacent soft bottom (Høisæter, unpublished). Whether or not the two "forms" are distinct species is impossible to ascertain from our material, but these subtle morphological similarities make it hard to support description of two new species (see the discussion below on why we accept *A. aspera* and *A. tenuisculpta* as Recent species although based on fossil types.) *Anatoma* spp. are not unknown from hot vent environments, as shown by the Japanese *A. fujikurai* Sasaki, Geiger and Okutani, 2010.

Anatoma* cf. *schioettei
(Figures 61–67)

Anatoma crispata (in part): Høisæter 2009: 21; 2010: 240, fig. 6A.

On the upper slope off Norway, an *Anatoma* (Figures 61 and 62) was found that was originally classified as a somewhat deviant "form" of *A. crispata* (see Høisæter 2010). Altogether four specimens and seven shells of this form were found in a dredge haul from 543 m and one specimen from 602 m, presumably from sandy/muddy sediment. On closer inspection (especially from SEM illustrations), the specimens turned out to be more similar to *A. schioettei* than to *A. crispata*. This similarity is based on a turreted and rather lenticular shell shape, and a protoconch that is pretty similar in the two forms. The protoconch is scattered with small irregular flocculae that merge onto a continuous spiral line on top of the protoconch in both forms. In addition the protoconch is in both cases terminated in a clean, straight apertural margin. This as opposed to the single irregular varix in *A. schanderi*, the "double" varix in *A. aspera* and the gradual transition between the two parts of the shell in *A. crispata*.

The main difference from *A. schioettei* sensu stricto is the strength of the axials, which can be variable in other species. Radulae are similar but the number and shape of the cusps on the rachidian and the laterals are different, *A.* cf. *schioettei* have more cusps on each tooth, and the cusps are generally less pointed than those of

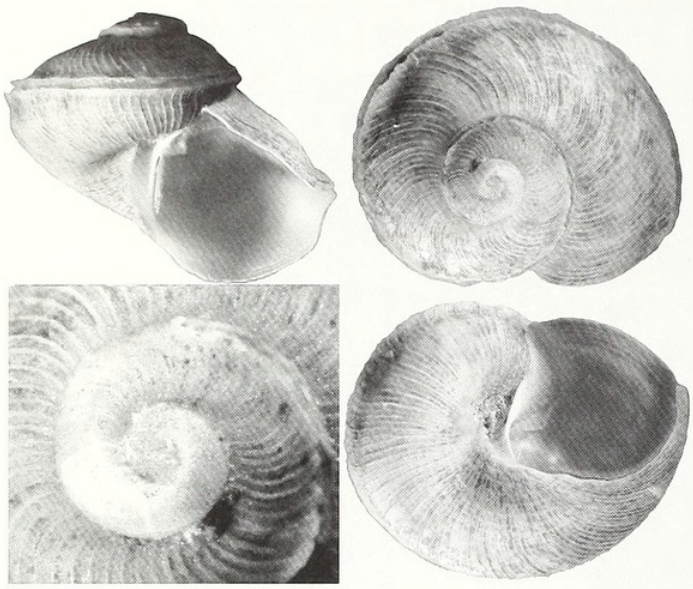


Figure 61. *Anatoma* cf. *schioettei* from upper slope off the Norwegian Trough, 62°20′ N, 543 m, 2.4 mm diameter. Scale bar = 200 µm.

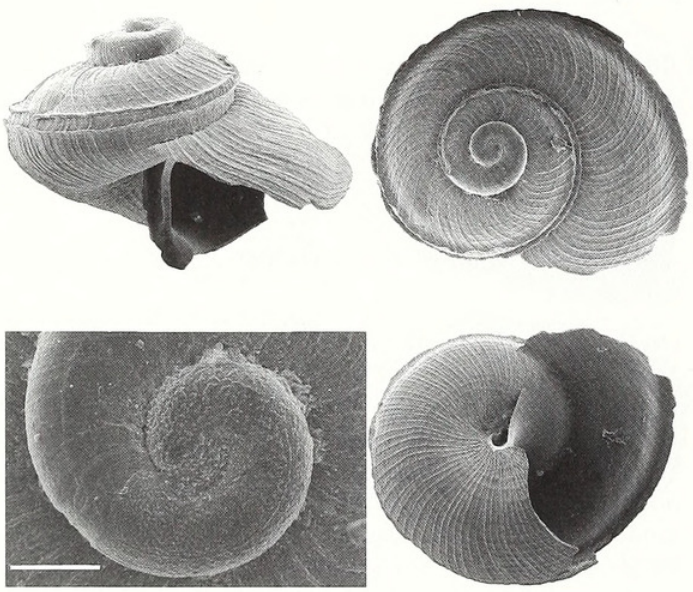


Figure 62. *Anatoma* cf. *schioettei*, upper slope off the Norwegian Trough, 62°20′ N, 543 m, 1.7 mm diameter. Scale bar = 100 µm.

A. schioettei. That this aberrant form have supernumerary lateral teeth (six instead of five) might be just an individual aberration.

Remarks: The distribution of this form is far from the known distribution of *A. schioettei* sensu stricto. The upper slope off Norway has a gastropod fauna apparently heavily influenced by the fluctuating temperature of the bottom-near water (Høisæter, 2010). The relationship of the fauna is with conspecifics or closely related species on the Faroe-Shetland Ridge or on the shelf/upper slope north of the Faroes. In this case the shelf/slope off Greenland, both East and West Greenland, also seems to be inhabited with a species closely related to a species from the upper slope off Norway.

***Anatoma schanderi* new species**
(Figures 68–83)

Description: (Largely based on holotype, Figure 68). Shell fragile, of medium to large size (to 4.5 mm diameter), trochiform, biconical, stepped. Protoconch of 0.75 whorls, reticulate sculpture (Figure 69), with distinct apertural varix, apertural margin straight. Teleoconch I comprising almost a full whorl, with approximately 30 axial cords, strong spiral cord in position of selenizone. Teleoconch II of up to 2.5 whorls, suture lightly impressed, well separated from selenizone by ca. 2 widths of selenizone (Figures 69 and 83). Shoulder convex, numerous and fairly weak axial cords, approximately 65–70 per whorl in fully grown specimens. Four to five rather indistinct spiral threads on middle of shoulder. Basal sculpture dominated by strong, widely spaced spiral cords, sometimes getting more conspicuous towards umbilicus, crossed by fine axial threads (Figures 68 and 69). Most axial threads fade away towards umbilicus, but 10–12 strong spiral cords continue into it (Figure 69). Umbilicus open, wide; funiculus narrow, indistinct. Aperture rounded-oblong, baso-adumbilical region flared. Selenizone slightly above periphery, keels of moderate strength.

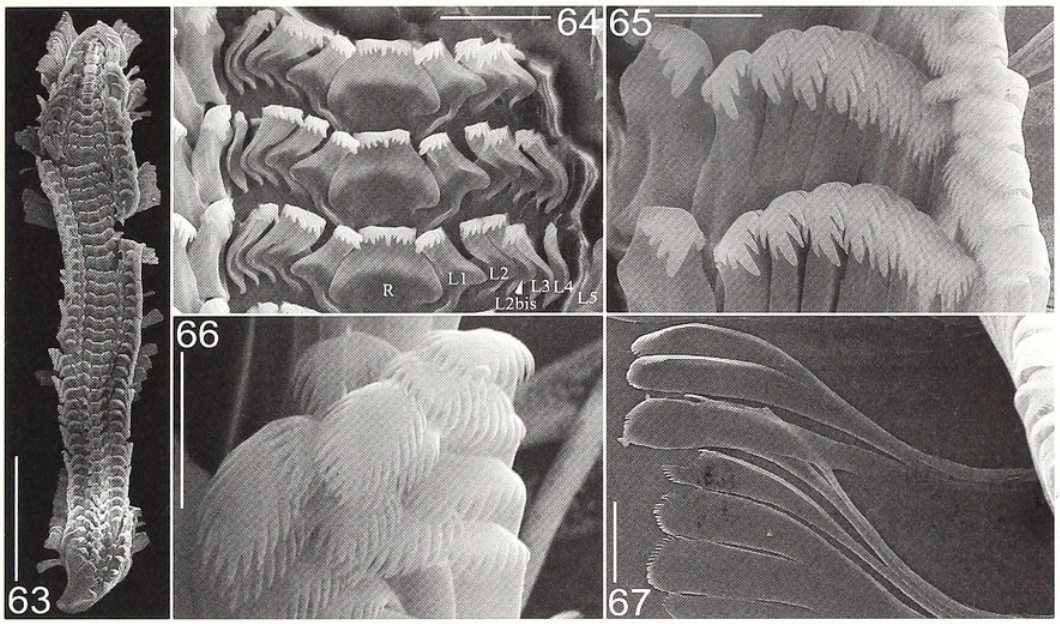
Radula (Figures 70–75): Rachidian tooth trapezoid, central cusp largest, 7–8 cusps in straight line on each side. Lateral teeth 1–3 similar, apical cusp largest, 4–5 cusps along outer edge of tip. Lateral tooth 4 reduced, hook-shaped. Lateral tooth 5 enlarged, apical cusp largest, 5–6 cusps along inner edge, 3–4 cusps along outer edge of tip. Inner marginal teeth with oval tip, apical cusp largest, 6–10 cusps along each side. Outer marginal teeth with spoon-shaped tip, many fine bristles along edge. Outermost marginal teeth paddle-shaped, with many fine bristles along tip. Radular interlock of central field moderate.

Differential Diagnosis: *Anatoma crispata* is smaller than *A. schanderi* (2.25 vs. 4.5 mm), has more pronounced axial sculpture, has a distinct funiculus, and the protoconch has flocculent sculpture.

Anatoma aspera is smaller (3.3 vs. 4.5 mm), has a taller, more turreted shell, and has much stronger axial sculpture on the shoulder.

Anatoma tenuisculpta grows somewhat larger (5.5 vs. 4.5 mm), has an overall more disc-shaped shell, and the axials are stronger with a crenulated appearance due to the crossing spirals.

Anatoma schioettei is much smaller (2.15 vs. 4.5 mm) has much more distinct axials, and the protoconch has flocculent sculpture.



Figures 63–67. *Anatoma* cf. *schioettei*, radula from specimen in Figure 62. **63.** Entire radula. Scale bar = 1 mm. **64.** Central field enlarged. Scale bar = 100 µm. **65.** Inner marginal teeth. Scale bar = 20 µm. **66.** Outer marginal teeth. Scale bar = 10 µm. **67.** Outermost marginal teeth. Scale bar = 20 µm.

Type Material: Holotype ZMBN 87296; four paratypes ZMBN 87297–87298.

Type Locality: The southern margin of the Greenland Basin (73°34′ N, 7°50′–8°01′ E) in the Norwegian Sea, 2560–2580 m. In a sample of semi-lithified sediment. (H2Deep ROV sample 7-2008.)

Other Material Examined: A fragment from H2Deep ROV Dive 1, 2430 m, near the Schultz Massif, 73°39′ N, 07°47.5′ E; 1509–1525 m, off eastern Greenland, 74°54′ N, 12°30′ W (ZMUC, 20); 749–774 m, Greenland, 75°01′ N, 12°38′ W (ZMUC, 20); 120 m, 10–15 km NW of Digby Neck, Nova Scotia, Canada, 44°36′ N, 65°45′ W (JWC 7286, 1).

Etymology: Named after Professor Christoffer Schander from the University of Bergen, who recognized the significance of what now are the type specimens during sorting of material.

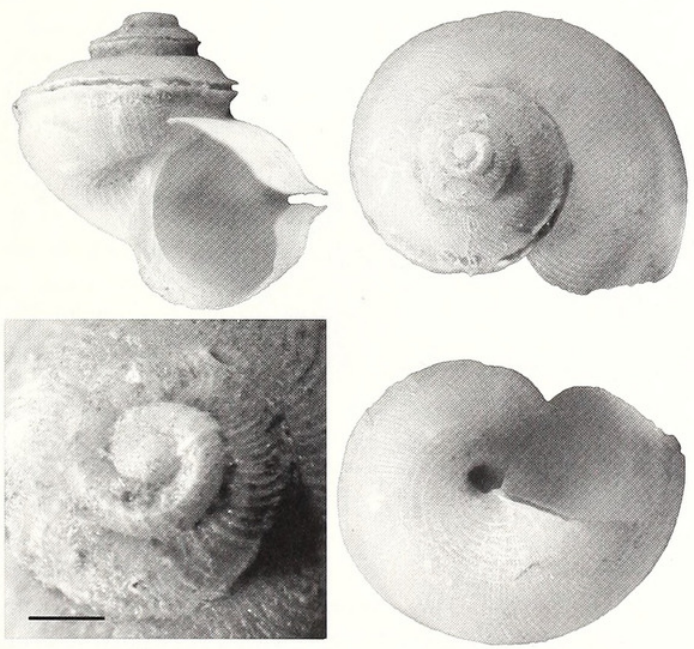


Figure 68. *Anatoma schanderi* new species, holotype (ZMBN 876296), southern margin of the Greenland Basin, 73°34′ N, 7°50′–8°01′ E, Norwegian Sea, 2560–2580 m, 2.5 mm diameter. Scale bar protoconch = 200 µm.

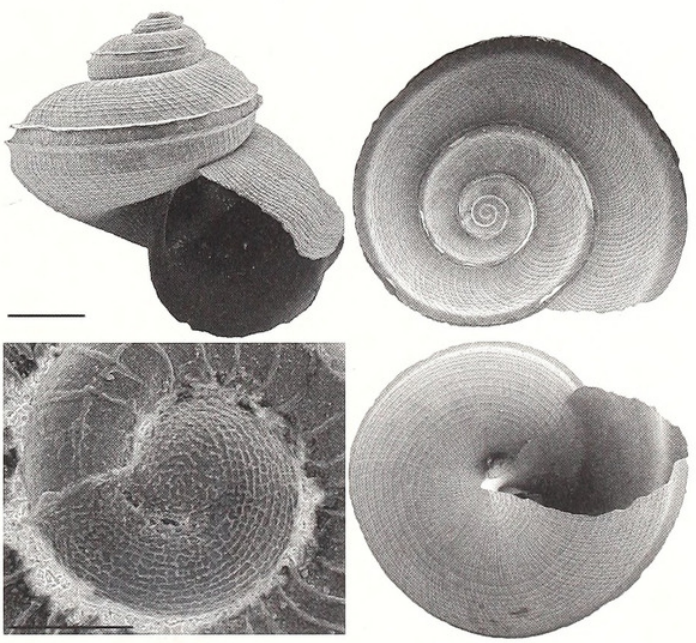
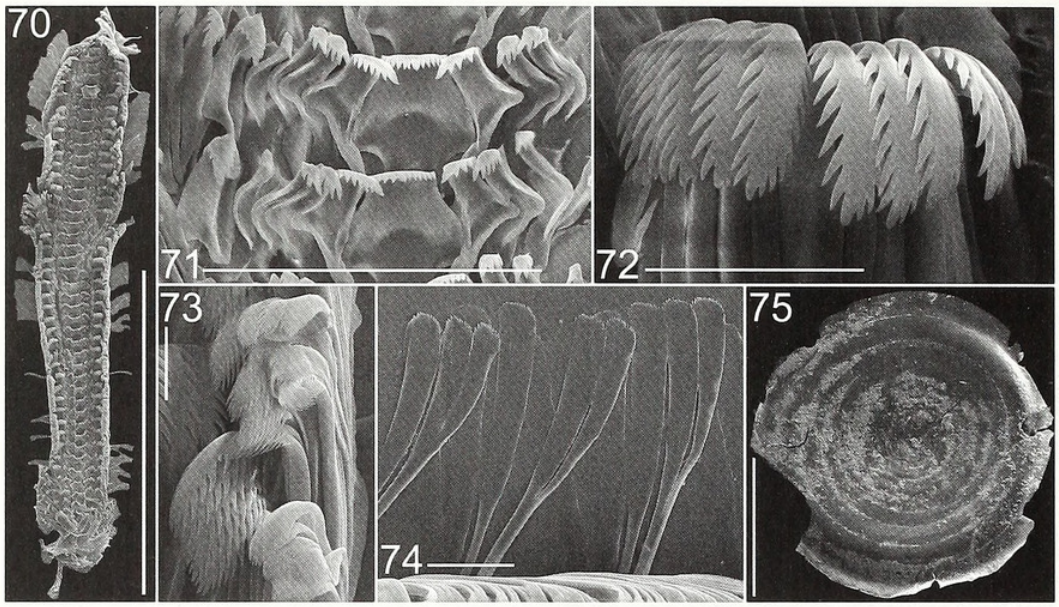
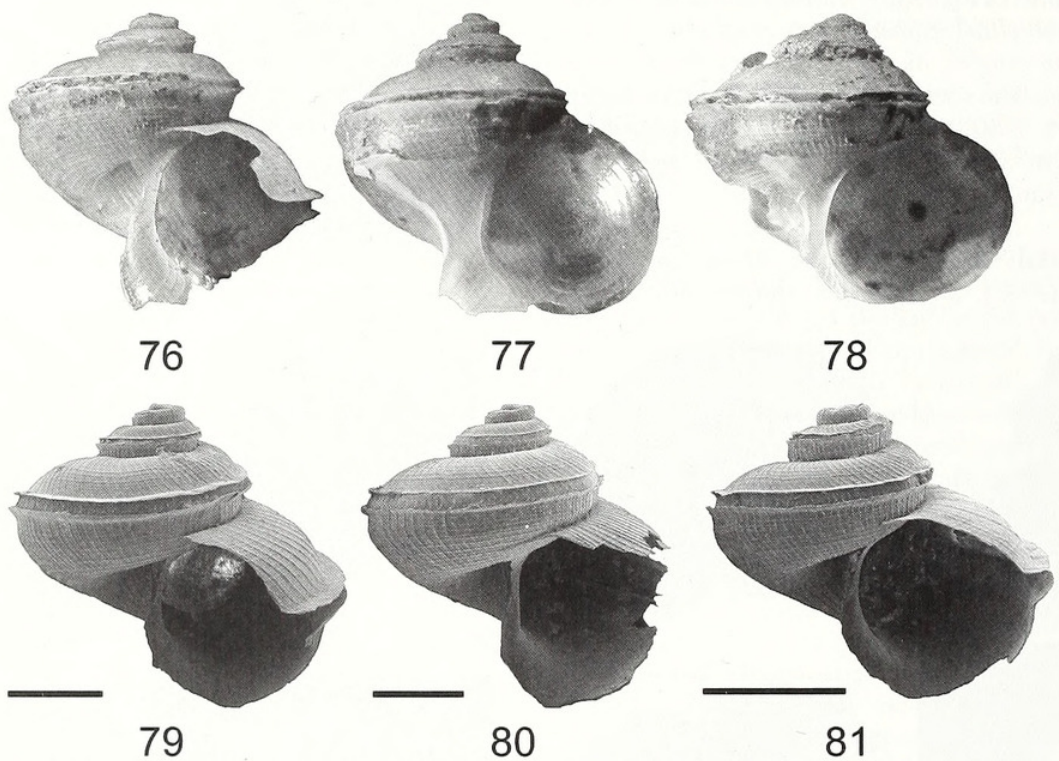


Figure 69. *Anatoma schanderi* new species, off eastern Greenland, 74°54′ N, 12°30′ W (ZMUC, 20), 1509–1525 m, 4.4 mm diameter. Scale bar shells = 1 mm; Scale bar protoconch = 100 µm. Radula shown in Figure 70.

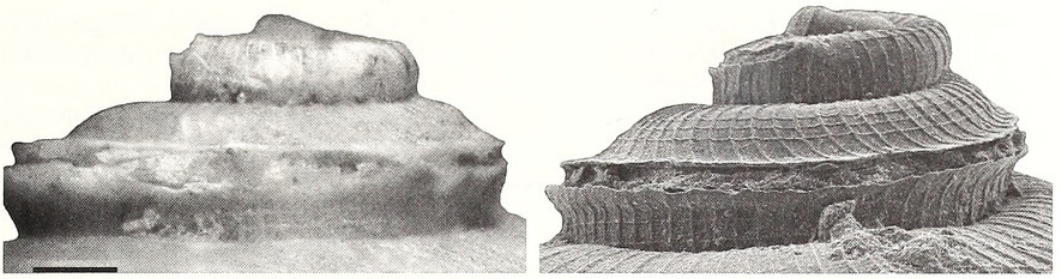


Figures 70–75. *Anatoma schanderi* new species, radula and operculum from specimen shown in Figure 69. **70.** Entire radula. Scale bar = 1 mm. **71.** Central field enlarged. Scale bar = 100 µm. **72.** Inner marginal teeth. Scale bar = 20 µm. **73.** Outer marginal teeth. Scale bar = 10 µm. **74.** Outermost marginal teeth. Scale bar = 20 µm. **75.** Operculum. Scale bar = 1 mm.



Figures 76–81. *Anatoma schanderi* new species, **76–78.** Three paratypes from the southern margin of the Greenland Basin, 73°34′ N, 7°50′–8°01′ E, in the Norwegian Sea, 2560–2580 m. **79–81.** Three specimens from the slope off East Greenland, ca. 1520 m. Scale bars = 1 mm.

Variability (Figures 70–75): Due to their fragility, the deep water paratypes are all poorly preserved, but what remain of the shells indicate that the variability is slight. Material from most other localities seems to fall within the range of variation of the type material. Only the relative strength of axials and spirals on the base varies somewhat. The selenizone of the specimen from Canada (see below) is wide and with a very narrow keel, and the shell is also more globular than the rest. It is impossible to tell if this is of taxonomic importance however (due to geographical isolation or just individual variation).



82 83

Figures 82–83. *Anatoma schanderi*, top whorls. **82.** Paratype in Figure 76. **83.** Specimen from the slope off Eastern Greenland, ca. 1520 m. Scale bars = 200 µm.

Distribution: Except for the single record from 120 m, Nova Scotia, Canada all material of this species are from rather deep water (750 to ca. 2600 m) in the Greenland Sea (the northwestern part of the Norwegian Sea.) The record from Canada indicates that the species has a mainly northwest Atlantic distribution, rather than being a purely deep water form.

Remarks: The reticulate pattern on the protoconch would have placed this species, according to the accepted generic taxonomy, in the genus *Thieleella* Bandel, 1998. For the purpose of this revision, we have decided to include *Thieleella* as a synonym of *Anatoma*. Figures 82–83 shows the uppermost whorls of two shells, LM photo at left and SEM photo at right. It illustrates that in spite of the lack of microscopic details in the LM photo, it is still possible to recognize some of the most important distinguishing characters without using SEM imaging.

Anatoma umbilicata (Jeffreys, 1883)

Scissurella umbilicata Jeffreys, 1883: 88–89, pl. 19, figs. 1–1a.

In Høisæter (2009) *Anatoma* cf. *umbilicata* is listed representing a specimen from the Norwegian Sea deep slope just north of the Faroes at 2222 m. The shell was very deteriorated and not suited for photography. In view of the presence of *A. schanderi* in this general area, the determination is quite dubious and needs verification.

Anatoma umbilicata is a mostly misidentified species. For instance, Sabelli et al., (1990), Gianuzzi-Savelli et al. (1994), and Adrovini and Cossignani (1999) record *A. crispata* and *A. umbilicata* as the only two species from the Mediterranean. The latter two references present respectively good quality SEM images and photographs, which make clear that both species were misidentified. We base our species concept of *A. umbilicata* on all extant type material examined by SEM (DLG, unpublished data).

DISCUSSION

After Geiger started looking closer at details on shells of Anatomidae from various parts of the world (Geiger, 2003; Geiger and Jansen, 2004a, b; Geiger, 2006a; Zelaya and Geiger, 2007; and Geiger and MacLean, 2010), it has become increasingly evident that the supposedly wide ranging *A. cristata* is a complex of several species. As demonstrated above, the complex is represented by three species in inshore Norwegian waters. The naming of these three species has not been straightforward though, as a number of early names, subsequently partly relegated to synonymy, are available for the species. *Anatoma crispata* was described from beach drift after a storm on small Noss Island just outside Lerwick on Shetland (Jeffreys, 1865: 285). Comparison with specimens from Shetland and our selection of neotypes have provided convincing arguments for assigning this name to the smallest of the three Norwegian species. For one of the remaining two species we have accepted the previously introduced name of a Pleistocene/Pliocene fossil from southern Italy, and for the last one we have resurrected the name of another fossil from about the same deposits.

The allocation of Recent specimens to species previously known only from the fossil record is always a tricky matter, and, when as in this case, the number of recorded specimens from the intervening localities (between the Mediterranean and Norway) is limited, this is even more problematic. There are examples in which extant marine species are known to have survived morphologically unaltered since the Pleistocene (and even the Pliocene, i.e., more than two million years). In Anatomidae, such an example is *Anatoma lyra* (Berry, 1947) described from the lower Pleistocene of Los Angeles, California, USA. Its holotype is indistinguishable from Recent material at the SEM level, including live-collected specimens (DLG, unpublished data). The synonymy of Mediterranean Pleistocene fossils with Recent North European inshore species represent a special case. As the various glacials forced boreal species living in the fjords of Norway in the warmer interglacials, to migrate south along the European shelf and slope, some of them were trapped in the Mediterranean, where they today are known as Pleistocene fossils. Some, but not all, succeeded in migrating north again to Norwegian waters when water temperatures increased, while others remained in the Mediterranean and evolved into "sister" species. Which of the fossils are genetically similar

enough to be regarded as conspecific with the forms today living in Norwegian fjords is an open question, but as long as there are Recent specimens both in the Mediterranean and in Norway, the question might be settled by molecular genetic investigations. If there is a continuous distribution of the morphospecies from Norway to the Mediterranean Sea close to the fossil deposits, this might also be a reasonable justification for accepting the name of the fossil. Those conditions seem to be met both with *A. aspera* and *A. tenuisculpta*.

Anatoma aspera has been accepted, mostly as a variety of *A. crispata*, by most modern authors as a form or species with a mainly south European distribution. Further research might demonstrate that differences between the Mediterranean and the north European populations are of a magnitude necessitating specific separation, in which case the name *A. paucicostata* (Jeffreys, 1865) is available. About the same argument holds for *A. tenuisculpta*, but in this case no synonym based on Recent material from the North Atlantic is available.

Within Anatomidae, recently elevated to full family rank (Geiger and Jansen, 2004a; Geiger 2006a), three genera, *Anatoma* Woodward, 1859, *Thieleela* Bandel, 1998, and *Sasakiconcha* Geiger, 2006 have been accepted by Geiger and collaborators (e.g., Geiger 2006b; Geiger and McLean, 2010; Zelaya and Geiger, 2007) as well as some other authors (e.g., Marshall, 2002). Of these, *Anatoma* and *Thieleella* are distinguished by a single character, the microsculpture on the protoconch, invisible except under very high magnification (i.e. under SEM). Thus *Thielleella* is characterized by a reticulate pattern, while *Anatoma* is either smooth or with flocculent pattern. Of the five species treated here, *A. schanderi* has a typical *Thieleella* reticulate pattern, while both *A. crispata* and *A. tenuisculpta* have protoconchs with very dense flocculation. *Anatoma schioettei* and *A. aspera* have protoconch microsculpture somewhat intermediate between these extremes, with a very open flocculation where some of the flocculae link together in an irregular reticulation (Figures 22 and 48). For the purpose of this revision we therefore include *Thieleella* as a synonym in *Anatoma*. This is done mainly for practical reasons, as specimens studied only by LM or specimens with worn protoconchs are impossible to place in the correct genus if the *Anatoma*/*Thielleella* dichotomy is retained.

The species of *Anatoma* all seem to occupy specific microhabitats although they often occur together in sledge or dredge hauls. Thus two of the inshore species co-occur in several samples and all three inshore species have been found together (alive) in two of our samples from western Norway. *Anatoma crispata* is found all around the Norwegian coast (and beyond), in depths from 10 to at least 200 m inshore (at least to 1000 m on the upper slope), and in temperatures from +12°C to –1.4°C. It appears to be associated with clean, hard bottom habitats and is often (in Norwegian waters) accompanied by species such as *Gibbula tumida* (Montagu, 1803), *Margarites striata* (Leach, 1819), *Lacuna vincta* (Montagu, 1803), and *Pusillina inconspicua* (Alder, 1844).

Anatoma aspera is found occasionally in waters not deeper than 40 m, it has its main distribution in depths between 60–100 m, but with records also from dredge hauls taken from 260 to 180 m. The conspicuous break between 64°40′ N and 69° N in the otherwise largely continuous distribution along the coast may provide support for the theory that *A. aspera* is mainly a southern species, having invaded the Norwegian coast at around 63° N and from there spread northward and southward. The shells (not in very well preserved condition, Figures 30 and 33) found at 69°14′ N at the considerable depth of 370 m, might be remnants of a separate invasion farther into the north. *Anatoma aspera* is (in Norwegian waters) most often found in, or near hypoxic, blackish mud, and is often found accompanied by *Puncturella noachina* (Linné, 1771), *Melanella lubrica* (Monterosato, 1890), *Trophonopsis barvicensis* (Johnston, 1825), and several pyramidellids, especially *Chrysallida eximia* (Jeffreys, 1849).

Anatoma tenuisculpta is the inshore Norwegian species living deepest, being usually found between 150–300 m, but with occasional records from 50 m and as deep as 500 m. This seems to agree with the known distribution (based on scattered museum material) along the lower shelf/upper continental slope of the northeast Atlantic, from the Faroes south to Gibraltar. *Anatoma tenuisculpta* is (in Norwegian waters) most commonly found on mixed bottoms often with some shells of *Modiolula phaseolina*, silt and shell gravel. Common accompanying gastropods are *Trophonopsis barvicensis* (Johnston, 1825), *Teretia teres* (Reeve, 1844), *Spirotropis modiolus* (de Cristofori and Jan, 1832) and (in the Møre og Romsdal part of the distribution) *Solariella amabilis* (Jeffreys, 1865).

Except for its part-time association with hot vent habitats, *A. schioettei* seems to be most common in upper slope habitats in the western part of the Norwegian Sea, at depths of 200–800 m. The bottom substrate is presumably silt or ooze, and the temperature is probably fluctuating between positive and negative values. The only Anatomidae known from hot vents in the Norwegian Sea most likely belong to this species as well. *Anatoma schanderi* has (with a single exception, see above) so far only been found in the bathyal parts of the Norwegian Sea, from 1500–2600 m, where the bottom substrate may be semi-lithified and the temperature is constant at –0.9°C.

The conclusion in Geiger and Sasaki (2009) that no members of Scissurellidae occur in these northern latitudes, neither in shallow nor in deep water, is supported by this revision. The five species of *Anatoma* are, on the other hand, nicely distributed on various depth zones so that the whole depth spectrum seems to be occupied by this family of gastropods.

The large majority of museum-material from south of 62° N in Norway belong to *A. tenuisculpta*. This may be

partly because this species is appreciably larger than the other two species, especially *A. crispata*, but we regard it as unlikely that this should be the only reason. Thus we conclude that this species is (or has been) the main representative of the genus in western Norway, becoming gradually less common further north along the coast. It is not known from the Norwegian south coast or the Swedish west coast (A. Warén, pers. comm.). (A notable exception is the occurrence of *A. tenuisculpta* at Drøbak in Oslofjorden).

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