GEOGRAPHICAL DIFFERENTIATION IN CLELANDELLA (GASTROPODA: TROCHIDAE) IN THE NORTHEASTERN ATLANTIC

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ABSTRACT

The trochid genus Clelandella is reviewed, taking into account new material collected on northeastern Atlantic seamounts and archipelagos, and in deep water of the Mediterranean. The type species C. miliaris (Brocchi, 1814) is illustrated with toptotypic material, and living representatives are reported ranging from north Norway to West Africa and into the Mediterranean. The insular populations of Clelandella are found to constitute discrete groups, which are treated as new species: Clelandella dautzenbergi n. sp. on the Lusitanian seamounts, C. perforata n. sp. in the Meteor group of the central North Atlantic, C. azorica n. sp. in the Azores and C. madeirensis n. sp. in Madeira. Within such groups, differentiation is not appreciable and variability is continuous notwithstanding distances of the order of 200 km. Between such groups, the geographical isolation of the insular populations has resulted in substantial divergence over distances in the range 300–600 km. A further species, C. myriamae n. sp., was collected on deep-water mud volcanoes of the eastern Mediterranean, and is broadly sympatric with C. miliaris.

INTRODUCTION

The trochid genus Clelandella has so far been considered monotypic, with the sole species C. miliaris (Brocchi, 1814) ranging from north Norway to West Africa and into the Mediterranean, where it has lived since Pliocene times.

The systematic position of ‘Trochus’ miliaris has been the subject of debate. Some authors placed it in the genus Calliostoma (e.g. Norman, 1893; Dautzenberg, 1927) or its subjective synonym Zyzyphinus (e.g. Brusina, 1866) in the Calliostomatinae, whereas others placed it with some doubt in the monodontine genus Jujubinus. Winckworth (1932) proposed the subgenus Clelandella with Trochus clelandi Wood, 1828, a synonym of T. miliaris, as type species, and later Nordsieck (1968) raised Clelandella to the status of a genus within the Calliostomatinae. The debate on the generic and familial position was closed when Crestella, Scibiani & Picardiello (1990) gave definitive arguments for the placement of Clelandella in the Monodontinae along with Jujubinus, based on the external head-foot morphology, radular morphology and allozyme data. Calliostoma differs in many respects and is currently placed in the distinct family Calliostomatidae (Marshall, 1995).

New material from hitherto unexplored areas has revealed more diversity in the genus Clelandella, which has undergone a substantial diversification. This paper describes four new species collected on eastern Atlantic seamounts or islands, and one more found in deep water communities associated with cold seeps in the eastern Mediterranean.

MATERIAL AND METHODS

Most of the material used in this paper derives from the extensive collecting programmes carried out by Muséum National d’Histoire Naturelle, Paris (hereafter MNHN), with the research vessels of Ifremer (the French marine research agency) in the past few decades. Material examined is housed in MNHN, unless otherwise stated, and is listed in the Appendix available as supplementary data at http://mollus.oupjournals.org.

Material from the North Atlantic seamounts was collected during two ‘Seamount’ expeditions, aimed at general collecting of the benthic fauna and a better understanding of the colonization of isolated sites by benthic species. ‘Seamount 1’ was conducted in September/October 1987 by Philippe Bouchet (MNHN) with R/V Le Noroit (Bouchet & Métivier, 1988), and visited Gorringe, Josephine, Ampère, Lion and Seine seamounts (57 dredge hauls and 10 beam trawl operations shallower than 1000 m). ‘Seamount 2’ was conducted in January/February 1993 by the author with R/V Le Suroît (Gofas, 1993) and visited the Great Meteor Bank, Hyères, Irving, Plato, Atlantis and Tyro seamounts (69 dredge hauls and 16 beam trawl operations shallower than 1000 m).

In this and other MNHN surveys, the coarse fractions, usually above 10 mm, were mostly sorted on board to phyla, then sorted to species level in the laboratory. The finer fractions were preserved on board, and later sieved on 5 mm, 2 mm, 1 mm, 0.5 mm and 0.3 mm sieves, and sorted under a stereomicroscope. Drawings of living animals were prepared wherever possible. Provisional listing of molluscs were made for the depth interval shallower than 500 m, recording several thousand specimens representing 242 species in the Lusitanian seamounts, and 182 species in the Meteor group seamounts. Most of the specimens and species are in the size range 1–5 mm. The largest part consisted of shells, and these were taken into account in the mollusc counts. The material from Seamount 1 is shared between the Swedish Museum of Natural History, Stockholm, and MNHN; that of Seamount 2 is deposited in MNHN.

Samples from around the Azores were collected in 1971 by the ‘Biações’ expedition of R/V Jean Charcot, conducted under the direction of J. Forest (MNHN), and a small collection (leg. H. Zibrowius) from the slope of Madeira was made by the ‘Zarco’ expedition, also of R/V Jean Charcot, in 1966.

Further relevant material for this study originated from the ‘Medinaut’ programme, a pluridisciplinary French-Dutch joint exploration of the mud volcanoes in the eastern Mediterranean, conducted by J. Woodside and J.P. Foucher. The ‘Medinaut’ expedition used R/V Le Nadir of Ifremer and the submersible Nautile to take site-specific samples, and biological collections were supervised by M. Sibuet (Ifremer).

Measurements of shells were taken as follows: height, measured between two lines perpendicular to the axis of coiling, one tangent to the apex and the other to the abapical edge of the aperture; maximum diameter or breadth, between two lines
parallel to the axis of coiling, tangent to the peripheral edges. The dimensions given refer to the largest specimen or shell in the lot.

Abbreviations used in text and appendix:

jv.: juveniles, specimens or shells which were not retained in the 2 mm sieve

spm.: specimen(s) (collected alive)

sh.: shell(s)

stn: station (in oceanographic cruises)

MCFE: Museo Civico Federico Eusebio, Alba, Italy

MCSN: Museo Civico di Storia Naturale, Milano

MNHN: Muséum National d’Histoire Naturelle, Paris

PMHU: Paläontologische Museum der Humboldt-Universität, Berlin

SMNH: Swedish Museum of Natural History, Stockholm

USNM: United States National Museum, Washington, DC

SYSTEMATIC DESCRIPTIONS

Genus Clelandella Winckworth, 1932


Description: Shell conical, solid, approximately as high as broad. Protoconch less than 1 whorl, smooth, bordered with a delicate lip. Spire sculptured with beaded spiral cords; periphery of last whorl with peripheral angle, usually with peripheral rim. Abapical surface also with spiral cords. Axis imperforate or with minute umbilicus. Aperture strongly prosocline, rhomboidal in outline, with brightly nacreous surface inside and thin, sharp outer lip. Shell colour variable, with flames or articulated pattern on cords, nacre showing through in some cases. Animal with relatively large head and elongate foot with flattened sole, truncated anteriorly. Cephalic tentacles tapering, with villose surface; two well developed cephalic lappets, with serrated edge, between tentacles. Eyes relatively large, at end of cylindrical stalk. Snout semicircular in section, with truncated anterior edge forming a fan in front of mouth. Neck lobes well developed, colourless, subequal in size, the left one (facing inflowing current) with serrated edge, the right one with smooth edge. Three pairs of epipodial tentacles, evenly spaced, with rugose surface. Base of each epipodial tentacle and of each neck lobe with single papilla.

*Clelandella miliaris* (Brocchi, 1814) (Figures 1–3, 12A, B, 13A, B)

*Trochus miliaris* Brocchi, 1814: 353, pl. 6, fig. 1 (northern Italy, no specified locality; lectotype from qualification as holotype [Rossi-Ronchetti, 1955: 93–95], MCSN 149).

*Trochus clelandi* W. Wood, 1828: 16, pl. 5, fig. 15.

*Trochus millegranus* Philippi, 1836: 183, pl. 10, fig. 25 (Palermo, Sicily; fossil in Neogene; 3 syntypes PMHU).

*Trochus martini* J. Smith, 1839: 99, pl. 1, fig. 26.

*Trochus millegranus* var. *pyramidata* Jeffreys, 1865: 826 (several British localities given; numerous syntypes from the Shetlands in USNM 179449 [Warén, 1980]).

Description: Shell conical, solid, as high as broad or slightly higher than broad, to 14.0 mm high £ 13.8 mm broad. Protoconch as in genus. Teleoconch up to 7–8 whorls. Spire sculptured with beaded spiral cords as wide as interspaces, and with rim running beneath suture and continued on peripheral angle of last whorl; beads aligned transversely in oblique rows parallel to growth lines; peripheral rim also somewhat beaded and covered by several (usually 3–4, up to 10 on large specimens) smaller spiral threads. First teleoconch whorl with three spiral cords and a fine subsutural thread, number of spirals later increased by intercalation of additional cords to 5–8 on last whorl. Profile of first

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**Figure 1.** *Clelandella miliaris* (Brocchi, 1814), fossils. A, B. Rio Torsero, Pliocene (height 8.2 mm; MCFE). C, D. Baldichieri, Pliocene (height 12.2 mm; MCFE). E, F. Syntypes of *Trochus millegranus* Philippi, 1836 from Palermo, Pleistocene (heights 16.7 mm and 15.0 mm; PMHU).

Figure 3. Clelandella spp. from West Africa. A, B. Clelandella miliaris, off Dakar, 135 m (spm., height 7.8 mm). C, D. Clelandella cf. miliaris, same locality (spm., height 7.8 mm). E, F. Clelandella cf. miliaris, off Dakar, 140–160 m (spm., height 10.2 mm).
teleoconch whorl convex, rapidly becoming flat; shell profile either regularly continued from one whorl to another, or slightly offset inwards from the conical shape; last whorl definitely set off inwards in most cases. Abapical surface flat, bearing 6–10 spiral cords as wide as or narrower than interspaces, more weakly beaded than spire cords. Axis imperforate, covered by columellar callus. Aperture as in genus. Shell colour whitish to yellowish, nacre showing through in some cases; broad brown flames starting from suture; peripheral rim white articulated by brown streaks; abapical surface usually paler, but with cords often articulated by smaller brown flecks.

Animal as in genus. Cephalic tentacles elongate, tapering, with brown line running on their upper surface; cephalic lappets, eye stalks and neck lobes colourless. Sides of foot with vertical brown streaks. Epipodial tentacles thin and tapering, colourless. Small papilla at base of each epipodial tentacle and of each neck lobe.

**Range:** Atlantic Ocean, northwards to Iceland (Oskarsson, 1982, and A. Warén, personal communication), the Faeroes (Spärck & Thorson, 1933), and material in SMNH, A. Warén, personal communication) and to 69°N in Norway (Hoisaeter, 1986); southwards to West Africa (see discussion below), and throughout the Mediterranean, usually in 100–300 m depth.

**Remarks:** This species was originally described as a fossil from northern Italy, where it is quite rare in Pliocene strata. A specimen was qualified as the holotype and figured by Rossi-Ronzetti (1955), which amounts to a lectotype designation following article 74.6 of the International Code of Zoological Nomenclature. The Recent Mediterranean specimens attributed to *Cleandella miliaris* are not different from the Pliocene fossils, neither in colour pattern (preserved in some specimens) nor in sculpture (Fig. 1A–D). *Trochus nillegranus* Philippi, 1836 (Fig. 1E, F) was described from Plio-Pleistocene deposits and also agrees with the current concept of *C. miliaris*, although it is somewhat stouter and one-third larger. Some North Atlantic specimens differ in being paler in colour, with the nacreous layer showing through, and have been known by British authors under the name *Trochus clelandi*. The animal of *C. miliaris* was reported by Cretella et al. (1990) to have a double papilla below the third epipodial tentacle, but this was not recorded on the material examined here.

Some specimens found in West Africa have a different shell profile, that is broader, at first slightly concave, then rather convex as the later whorls become slightly constricted; they also have a more blunt periphery without a distinct rim on large specimens (Fig. 3C–F). The colour is also distinct, with reddish tones being predominant over brown. The specimens from Côte d’Ivoire tend to be umbilicated but otherwise do not differ from those collected in Senegal. However, specimens with typical shell morphology of *C. miliaris* were also found in Senegal (Fig. 3A, B), and many of the examined specimens show intermediate features. The material at hand is not sufficient to assess if this is geographic variation or if an additional species is involved.

**Cleandella dautzenbergi new species** (Figures 4, 5, 13C, D)

*C. miliaris* var. *candida* Dautzenberg, 1927: 192.


**Type material:** Holotype (sh., 9.1 × 9.1 mm) MNHN, from Josephine Bank, ‘Seamount 1’ DW38 (36°41'N, 14°17'W, 233–243 m); 12 paratypes (6 spm., 10.2 × 9.9 mm; 6 sh., 15.2 × 13.8 mm) MNHN; 12 paratypes (6 spm., 10.9 × 10.5 mm; 6 sh., 13.8 × 13.2 mm) SMNH (type collection 5981), all from the type locality.

**Etymology:** This species is dedicated to Philippe Dautzenberg, one of the malacologists who have shaped the knowledge of European faunas, and who particularly pioneered the exploration of deep-water molluscs around the Azores and seamounts.

**Description:** Shell conical, solid, as high as broad or slightly higher than broad, to 15.0 mm high × 13.5 mm broad, more commonly up to 10 × 9.5 mm. Protoconch as in genus. Teleoconch up to 7–8 whors. Spire sculptured with beaded spiral cords, as wide as interspaces, one of which running beneath suture and continued on peripheral angle of last whorl; beads aligned transversely in oblique rows parallel to growth lines. First teleoconch whorl with three spiral cords and a fine subsutural thread, number of spirals later increased by intercalation of additional cords to 5–8 on last whorl. Profile of first teleoconch whorl convex, later whors becoming nearly flat but slightly swollen sublaterally; shell profile regularly continued from one whorl to another, the later whors very slightly constricted, offset inwards from the conical shape. Suture underlined by adapical spiral cord, therefore somewhat canaliculated. Peripheral cord of body whorl stronger, usually duplicate with adapical component strongly beaded and abapical one less so, rarely complemented abapically by 1–2 faint spiral threads. Abapical surface slightly convex and bearing 6–10 spiral cords, as wide as interspaces, crossed by growth lines. Axis imperforate, covered by columellar edge. Aperture as in genus. Shell colour whitish to yellowish, nacre showing through in some cases, broad brown flames starting from suture on early spire whors; later whors usually with cords and peripheral rim white articulated by white and brown streaks; abapical cords also articulated by smaller white and brown flecks.

Animal (Fig. 5) as in *C. miliaris*.

**Range:** On the upper part of the Lusitanian seamounts (Gorrinage, Ampère, Seine and Josephine Banks), alive in 165–360 m depth.

**Remarks:** Dautzenberg (1927) reported two colour morphs from Josephine Bank, and proposed for an entire white shell the varietal name *Calliostoma miliare* var. *candida*. However this must be interpreted as infrasubspecific, because Dautzenberg used it explicitly to distinguish colour morphs existing in the same population. Moreover, the epithet candidus has been used twice in connection with species of *Calliostoma*: *Zicyphalus candidus* Brusina, 1864 (a synonym of *Calliostoma zicyphalum*) and *Trochus glattertoni* var. *candida* Bucquoy, Dautzenberg & Dollfus, 1885. Dautzenberg’s specimen must have been a bleached shell, because not a single white morph was recorded in the abundant material examined here.

There are several consistent morphological differences from mainland populations assigned to *C. miliaris*. The periphery of the last whorl is bounded by a spiral beaded cord, usually double, smooth or occasionally with only one or two very faint spirals on the adapical side, contrary to *C. miliaris* which has a swollen peripheral rim covered by many distinct spiral threads (compare Fig. 13A, B and C, D), and to *C. perforata* or *C. madeirensis* which have distinct, crowded spirals on the adapical side of the keel. Compared to *C. miliaris*, there is a sharper difference in sculpture between the adapical surface of whors, with strong beads, and the abapical surface, with the cords hardly beaded at the intersection with the growth lines. The living animal is typical of *Cleandella*.
the morphological traits that diagnose it are stable across the four Lusitanian banks, with bank-to-bank distances in the same order of magnitude as the distances to the mainland. A single specimen collected alive off Gran Canaria resembles the others, although geographically quite remote.

**Clelandella perforata** new species (Figures 6–9, 12C, D, 13E, F)

**Type material**: Holotype (spm., 6.5 × 6.9 mm) and 14 paratypes (spm., 7.0 × 8.5 mm) MNHN, from Great Meteor Bank, ‘Seamount 1’ DW152 (30°02.00′ N 28°22.10′ W, 470 m).

**Etymology**: The name alludes to the constant presence of an umbilicus, unusual in the genus.

**Description**: Shell conical, moderately solid, as high as broad or slightly broader than high, to 8.7 mm high × 8.9 mm broad. Protoconch as in genus. Teleoconch up to 5–6 whorls. Spire sculptured with distinct beaded spiral cords, as wide as interspaces, one of which running beneath suture and continued on peripheral angle of last whorl; beads strong, aligned transversely in oblique rows parallel to growth lines. First teleoconch whorl with three spiral cords and a fine subsutural thread, number of spirals later increased by intercalation additional cords to 5–8 on last whorl. Profile of first teleoconch whorl convex, of later whorls less so but swollen subsuturally; shell profile regularly continued from one whorl to another. Suture underlined by adapical spiral cord, therefore somewhat canaliculated. Peripheral cord covered with 4–6 thin spiral threads. Abapical surface slightly convex, bearing 6–10 spiral cords, as wide as interspaces, crossed by growth lines but not beaded. Axis with distinct umbilicus, bordered by columellar edge. Aperture as in genus. Shell colour whitish with nacre generally showing through, some specimens without pattern, others with broad brown or reddish flames starting from suture and with peripheral rim white articulated by brown streaks; others with adapical cords and peripheral rim articulated; abapical cords generally colourless, sometimes articulated.

**Figure 4. Clelandella dautzenbergi** n. sp. from the Lusitanian seamounts. **A, B.** Holotype from Josephine Bank, ‘Seamount 1’ DW38, 235–245 m (sh., height 9.1 mm). **C, D.** Ampère bank, ‘Seamount 1’ DE38, 300–325 m (spm., height 9.3 mm). **E, F.** Gorringe bank, ‘Seamount 1’ DW09, 350–360 m (spm., height 9.3 mm).
Animal (Fig. 9) like *C. miliaris* but with stouter, distinctly more villose cephalic tentacles, stouter epipodial tentacles with comparatively larger papillae at their base. Sides of foot tinged with yellow and with small carmine flecks, remainder of animal colourless.

**Range:** On the upper part of the Meteor group seamounts (Meteor, Hyères, Irving and Atlantis Banks), alive in 280–520 m depth.

**Remarks:** This is a common species on the upper part of the seamounts. As noted for the Lusitanian banks, the populations of

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**Figure 6.** *Clelandella perforata* n. sp. from Great Meteor Bank, ‘Seamount 2’ DW152, 470 m. **A, B.** Holotype (spm., height 6.5 mm). **C, D.** Paratype with articulated colour pattern on shell (spm., height 7.0 mm). **E, F.** Paratype with white shell (spm., height 6.0 mm).

**Figure 7.** *Clelandella perforata* n. sp. from Irving Bank, ‘Seamount 2’ DW210, 320 m (sh., actual heights **A, B:** 6.8 mm; **C, D:** 6.7 mm; **E, F:** 7.2 mm).
Clelandella from the Meteor group seamounts are also homogeneous between banks. There are three discrete colour morphs (Figs 6–8), one of them with an entirely white shell, one with an articulated pattern on the adapical cords, and one with broad flames, and all three are found throughout the range. **Clelandella perforata** differs from *C. dautzenbergi* (and from the mainland species) in being distinctly umbilicate at all stages. As in *C. dautzenbergi*, there is a clear contrast between the strongly beaded adapical cords and the nearly smooth abapical cords, but the profile of the shell is different between the two species. *Clelandella perforata* has a distinctly channelled suture, resulting in a trochiform outline. Contrary to other species, the peripheral cord is not very much wider than the other adapical cords of the same whorl and does not form a conspicuous rim; it is covered by several minute spirals (Fig. 13E, F), which are never seen in *C. dautzenbergi*.

**Clelandella azorica** new species  
(Figures 10A–D, 13G)

**Type material:** Holotype (spm., 12.2 × 11.0 mm) and 9 paratypes (sh., 9.8 × 8.5 mm) MNHN, from S. of São Miguel, Azores, ‘Biaçares’ DP156 (37°37’ N, 25°54’ W, 350 m).

**Etymology:** The name alludes to the geographic range of this species in the Azores.

**Description:** Shell conical, solid, as high as broad or slightly higher than broad, to 12.2 mm high × 11.0 mm broad. Protoconch as in genus. Teleoconch up to 6.5–7.5 whorls. Spire sculptured with elevated, beaded spiral cords generally narrower than interspaces; beads aligned transversely in oblique rows parallel to growth lines and connected across interspaces by oblique threads; periphery with a compound twin cord, adapical part beaded like on spire, abapical part less distinctly, if at all beaded, and covered by several (usually 2–4) smaller spiral threads. First teleoconch whorl with three spiral cords and a fine subsutural thread, number of spirals later increased by intercalation of additional cords to 5–7 on last whorl; often with smaller second-order spiral cords or threads intercalated in broader interspaces. Profile of first teleoconch whorl convex, later becoming tumid, inflated subsuturally; shell profile either regularly continued from one whorl to another, or with later whorls offset inwards from the conical shape. Abapical surface flat, bearing 6–10 spiral cords as wide as or narrower than interspaces, weakly beaded or incised by evenly spaced lines parallel to growth lines; sometimes with second-order spiral threads in interspaces. Axis hardly perforate, umbilical chink bordered by thin columellar edge. Aperture as in genus. Shell colour variable, with whitish to yellowish...
background and brownish flames or blotches, or with small brownish spots tending to form an articulated pattern along cords; abapical surface usually paler but with cords often articulated by smaller brown flecks.

**Range:** Throughout the Azores archipelago, alive in 190–465 m range.

**Remarks:** The shells of *Clelandella* collected in the Azores are different from the seamount species *C. perforata*. They are larger, hardly umbilicate, have a distinct peripheral rim, and have a distinct sculpture on abapical cords, in these respects resembling more the mainland *C. miliaris*. However, they differ in having an umbilical chink and in the architecture of the spire whorls, which are tumid and have elevated, broadly separated cords with an oblique sculpture, giving a cancellate surface.

### Clelandella madeirensis new species
(Figure 10E, F)

**Type material:** Holotype (sh., 7.8 × 7.0 mm) and 4 paratypes (sh., 8.3 × 7.0 mm) MNHN, from off Porto Santo, Madeira Archipelago, ‘Zarco’ stn. 29 (33°01.1’ N, 16°16.0’ W, 300–340 m).

**Etymology:** The name alludes to the geographic range of this species in the Madeira Archipelago.

**Description:** Shell conical, solid, slightly higher than broad, up to 8.3 mm high and 7.0 mm broad. Protoconch as in genus. Teleoconch up to about 7 whorls. Spire sculptured with beaded spiral cords, narrower than or nearly as wide as interspaces, one of which running along suture and continued on peripheral angle of last whorl; beads aligned transversely in oblique rows parallel to growth lines. First teleoconch whorl with three spiral cords and a fine subsutural thread, number of spirals later increased by intercalation of additional cords to 6–8 on last whorl. Profile of first teleoconch whorl convex, rapidly becoming less so. Suture underlined by adapical spiral cord, therefore somewhat canaliculated. Peripheral cord broad and flat, beaded on adapical side, covered by several (usually 3–4) spiral threads on abapical side. Abapical surface convex bearing about 12–13 weak, unequal, nearly smooth spiral cords. Axis imperforate, covered by columellar edge. Aperture as in genus. Shell colour on spire, whitish with reddish flames more apparent over cords; periphery white articulated by reddish streaks; abapical surface reddish with whitish blotches and with darker reddish flecks on cords; whitish blotches not adjusted to cords but extending also on interspaces or onto neighbouring cords.

**Range:** Only known from Porto Santo, Madeira Archipelago, in 220–340 m.

**Remarks:** The material collected in the Madeira Archipelago is scanty, but is so clearly distinct from the neighbouring population of Seine seamount, only some 200 km distant, that it is considered worth describing. These specimens most resemble some West African specimens of *Clelandella* with which they share the reddish hue and rounded periphery covered by spiral sculpture. They are distinguished by smaller size, and sculpture of the base with attenuated cords, not beaded at all, and where the colour pattern does not adjust to the cords in an articulated pattern (contrary to all other species seen). *Clelandella dautzenbergi* is geographically the nearest neighbour, but differs in having a salient peripheral keel devoid of spirals, and a hue exclusively composed of brown tones on a white background, without any red tones observed in several hundred specimens. Despite the reduced sampling effort on the Madeiran archipelago, *C. madeirensis* can be considered as a rare species, compared to *C. dautzenbergi* which was found in large numbers in the same depth interval.
Clelandella myriamae new species
(Figures 11, 12E, F, 13H)

Type material: Holotype (spm., 6.8 × 7.5 mm) and 6 paratypes (1 spm. + 5 sh., 7.9 × 8.3 mm) MNHN, from Anaximander seamounts, ‘Amsterdamm’ mud volcano, ‘Medinaut’ dive MN13 (35°20’ N, 30°16.5’ E, 2030 m).

Etymology: This species is dedicated to Myriam Sibuet, who has extensively contributed to the knowledge of deep-sea faunas and in particular has supervised the biological collections in ‘Medinaut’.

Description: Shell conical, moderately solid, usually quite as high as broad but with a rather variable height/breadth ratio, to 10.5 mm high × 10.8 mm broad. Protoconch as in genus. Teleoconch of 6–7 whorls. Spire sculptured with spiral cords, as wide as interspaces; cords made rugose by intersection with growth lines, or nearly smooth. First teleoconch whorl with three spiral cords and a fine subsutural thread, number of spirals later increased by intercalation of additional cords to 6–10 on adapical part of last whorl. Profile of first teleoconch whorl convex, of later whorls less so; shell profile regularly continued from one whorl to another. Suture underlined by adapical spiral cord. Periphery of last whorl forming a blunt angle, covered by a cluster of 3–4 fine spiral threads. Abapical surface quite convex, bearing 10–12 spiral cords as wide as interspaces, crossed by growth lines but not beaded. Axis with a narrow umbilical chink, bordered or covered by columellar edge. Aperture as in genus. Shell colour whitish to yellowish, nacre generally showing through, some specimens nearly without pattern, others with cords articulated by brown or reddish flecks; flecks aligned to form axial flames on most intensely coloured individuals; abapical cords colourless or less intensely marked than adapical.

Animal not observed alive; on preserved specimen examined (MN12) similar to that of C. miliaris, with eyes equally developed. General colour pale, with a faint brown line on upper side of cephalic tentacles, and brownish flecks on sides of foot. Other appendages and sole of foot colourless.

Range: Only known from the eastern Mediterranean, around deep-water cold seeps, alive in 1700–2030 m.

Remarks: This species was collected in the remarkable context of deep-water mud volcanoes of the eastern Mediterranean. It is broadly sympatric with C. miliaris (see Fig. 2C, D from the south coast of Crete) from which it differs mainly in the spiral cords which are not beaded. The profile is also broader, the abapical surface has more cords and the axis has a small umbilical chink in most specimens.

DISCUSSION

The taxonomic recognition given here to discrete, allopatric groups of population reflects the observations that (1) within such groups, differentiation is not appreciable and variability is continuous and (2) between such groups, differentiation is such that it is best explained by an absence of genetic exchange. Trochids, and more generally the Vetigastropoda and Patello-gastropoda, have larvae with a short pelagic life, which should not enable long-distance dispersal.

The geographical isolation of the insular populations has resulted in substantial divergence, whereas the mainland stock has maintained a conservative morphology for several million years. It can be speculated that the insular populations are more likely to have originated from a limited number of migrants, and thus could undergo an early differentiation through the founder effect.

Within a particular archipelago or seamount group, the distances in the order of magnitude of 200 km do not seem to

Figure 11. Clelandella myriamae n.sp. from the Anaximander seamounts, eastern Mediterranean. A, B. Holotype from ‘Medinaut’ MN13, 2030 m (spm., height 6.8 mm). C, D. ‘Medinaut’ MN12, 1700 m (spm., height 5.1 mm). E, F. An aberrant individual from ‘Medinaut’ MN12 (spm., height 7.2 mm); note profile of early whorls as in other specimens.
be an obstacle to the circulation of larvae. There is a remarkable
continuity in morphology of the large samples collected in
different seamounts of the same group; in the Meteor group there
are several distinctive colour morphs (Figs 6–8) and the same
array of variants is repeated on each seamount of the group. The
threshold where isolation is ensured lies between the 600 km
separating Azores from Atlantis Bank, and the maximun
distances of 300 km found within the area comprising the
Canaries, Madeira and the Lusitanian seamounts (Fig. 14).

The distance from the Lusitanian banks to the mainland and to
Madeira is nevertheless of the same order of magnitude as the
distance between Gorringe, Josephine, Seine and Ampère
Banks. There, environmental factors probably contribute to
the differentiation. The seamounts differ markedly from

![Figure 12. Apical whorls and enlarged view of protoconchs of Clelandella. A, B. C. miliaris, off Marseille, Canyon de la Cassidaigne. C, D. C. perforata n. sp., paratype, Meteor Bank, 'Seamount 2' DW152, 470 m. E, F. C. myriamae n. sp., Kazan mud volcano, 'Medinaut' MN10, 1700 m (Scale bars = 100 μm).](image)

![Figure 13. Peripheral rim of the body whorl in Clelandella spp. Scanning electron micrographs, all shown with apex to the top and illuminated from abapical surface. A. C. miliaris, Rio Toeser (Pliocene fossil); B. C. miliaris, off Cap Sicié, Mediterranean France; C. C. dautzenbergi n. sp., paratype, Josephine bank, 'Seamount 1' DW38. D. C. dautzenbergi n. sp., Ampère Bank, 'Seamount 1' DE98. E. C. perforata n. sp., paratype, Meteor Bank, 'Seamount 2' DW152. F. C. perforata n. sp., Irving Bank, 'Seamount 2' DW210. G. Clelandella azorica n. sp., S. of São Miguel, 'Biaços' stn DR198. H. Clelandella myriamae n. sp., Kazan mud volcano, 'Medinaut' MN12 (Scale bars = 1 mm).](image)
the mainland in that they receive no terrigenous input, so that the sediments are mainly of bioclastic origin.

Another point regarding the seamount populations of *Clelandella* is the large numbers of specimens, which make up a substantial proportion of the total catch in these species-poor environments. Such high dominance values are not achieved with mainland *C. miliaris* and would render problematic the contribution of migrants, if any, to the local insular gene pools.

Among the vetigastropods and patellogastropods of the northeast Atlantic archipelagoes, some kind of differentiation is observed when data are available. Most other trochid species in the Atlantic archipelagoes are now recognized as endemic, even if early works have tentatively identified them with mainland taxa. In the littoral genus *Jujubinus*, the Canarian species *J. guanchus* Curini Galletti, 1985 and *J. poppei* Curini Galletti, 1983, the Madeiran species *J. vexatiosis* Curini-Galletti, 1990 and the Azorean species *J. pseudogravinae* Nordsieck, 1973 are now regarded as distinct from similar Mediterranean species (Curini Galletti, 1985, Curini-Galletti, 1990; Nordsieck, 1973; Segers, 2002 and personal observations). Another trochid genus, *Danilia*, occurs on the seamounts in the same depth range as *Clelandella*. Specimens from the Lusitanian seamounts are not separable from the mainland species *D. tinei*, whereas another species, *D. affinis* Dautzenberg & Fischer, 1896 is found on the Meteor group.

Among patellids, which have been subject to genetic investigation, a geographical divergence has also been recognized between archipelagoes but has been given taxonomic recognition at the subspecific rather than the specific level (Corre-Real, Hawkins & Thorpe, 1996a,b; Weber & Hawkins, 2002). Another trochid genus, *Danilia*, occurs on the seamounts in the same depth range as *Clelandella*. Specimens from the Lusitanian seamounts are not separable from the mainland species *D. tinei*, whereas another species, *D. affinis* Dautzenberg & Fischer, 1896 is found on the Meteor group.

Among patellids, which have been subject to genetic investigation, a geographical divergence has also been recognized between archipelagoes but has been given taxonomic recognition at the subspecific rather than the specific level (Cort-Real, Hawkins & Thorpe, 1996a,b; Weber & Hawkins, 2002). Whether the differentiation here recorded in insular *Clelandella* actually deserves specific status (i.e. would be irreversible if these populations were brought together) or should be held as subspecific (i.e. not accompanied by biological means of reproductive isolation) could be a matter of debate. However, as in most such cases of allopatric insular distributions, there are no objective criteria.

The occurrence of *Clelandella myriamae* belongs to a totally different context (Olu-le Roy et al., 2004). It is one of the commonest species on the deep-water eastern Mediterranean mud-volcanoes, together with another trochid *Putseysia wiseri* (Calcara, 1942), usually rare in Mediterranean bathyal environments. The benthic community in this environment depends on primary production by sulphur-reducing bacteria. The small trochids are unlikely to harbour bacterial symbionts within their tissues, but probably find accumulations of organic matter to graze on.

The deep-water faunas associated with mud volcanoes in the eastern Mediterranean lack most of the organisms typically associated with these features, and are probably too secluded to be colonized by those. Instead, they harbour a genuine community among which many are neoendemics derived from particular species of the non-vent Mediterranean fauna. Among the bivalves, this is the case of the lucinids *Lucinoma kazani* Salas & Woodside, 2002 (very similar to the littoral *L. borealis* Linné, 1767) and *Myrtea amorpha* (Sturany, 1896) (similar to the littoral *M. spinifera* Montagu, 1803). Therefore, it is likely that *C. myriamae* represents a local offshoot, with a drastic shift in habitat, derived from an ancestral stock of *C. miliaris*.

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