Taxonomy, biogeography and DNA barcodes of *Geodia* species (Porifera, Demospongiae, Tetractinellida) in the Atlantic boreo-arctic region

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Geodia species north of 60°N in the Atlantic appeared in the literature for the first time when Bowerbank described *Geodia barretti* and *G. macandrewii* in 1858 from western Norway. Since then, a number of species have been based on material from various parts of the region: *G. simplex*, *Isops phlegraei*, *I. pallida*, *I. sphaeroides*, *Synops pyriformis*, *G. parva*, *G. normani*, *G. atlantica*, *Sidonops mesotriaena* (now called *G. hentscheli*), and *G. simplicissima*. In addition to these 12 nominal species, four species described from elsewhere are claimed to have been identified in material from the northeast Atlantic, namely *G. nodastrella* and *G. cydonium* (and its synonyms *Cydonium muelleri* and *Geodia gigas*). In this paper, we revise the boreo-arctic *Geodia* species using morphological, molecular, and biogeographical data. We notably compare northwest and northeast Atlantic specimens. Biological data (reproduction, biochemistry, microbiology, epibionts) for each species are also reviewed. Our results show that there are six valid species of boreo-arctic Atlantic *Geodia* while other names are synonyms or mis-identifications. *Geodia barretti*, *G. atlantica*, *G. macandrewii*, and *G. hentscheli* are well established and widely distributed. The same goes for *Geodia phlegraei*, but this species shows a striking geographical and bathymetric variation, which led us to recognize two species, *G. phlegraei* and *G. parva* (here resurrected). Some *Geodia* are arctic species (*G. hentscheli*, *G. parva*), while others are typically boreal (*G. atlantica*, *G. barretti*, *G. phlegraei*, *G. macandrewii*). No morphological differences were found between specimens from the northeast and northwest Atlantic, except for *G. parva*. The Folmer cytochrome oxidase subunit I (COI) fragment is unique for every species and invariable over their whole distribution range, except for *G. barretti* which had two haplotypes. 18S is unique for four species but cannot discriminate *G. phlegraei* and *G. parva*. Two keys to the boreo-arctic *Geodia* are included, one based on external morphology, the other based on spicule morphology.

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INTRODUCTION

Continental shelves and slopes of the cold-temperate north Atlantic accommodate large accumulations of demosponges, so-called 'ostur' or 'cheesebottoms' by Faroese fishermen (Klitgaard, Tendal & Westerberg, 1997; Klitgaard & Tendal, 2004; Murillo *et al*., 2012). In these sponge grounds, Geodiidae and Ancorinidae species (sub-order Astrophorina) dominate in terms of size and biomass (Fig. 1). Specimens can reach 80 cm in maximum dimension and weigh more than 38 kg. Icelandic, Faroese, and Norwegian fishermen speak of single sponges that are more than 1 m in diameter, and that are so heavy that it takes the efforts of two men to throw them overboard again after having been caught in the trawl. In some areas up to 20 tonnes of sponges can be caught in a single trawling, the net being virtually filled up and so loaded that there is a danger of damage during the onboard hauling. These
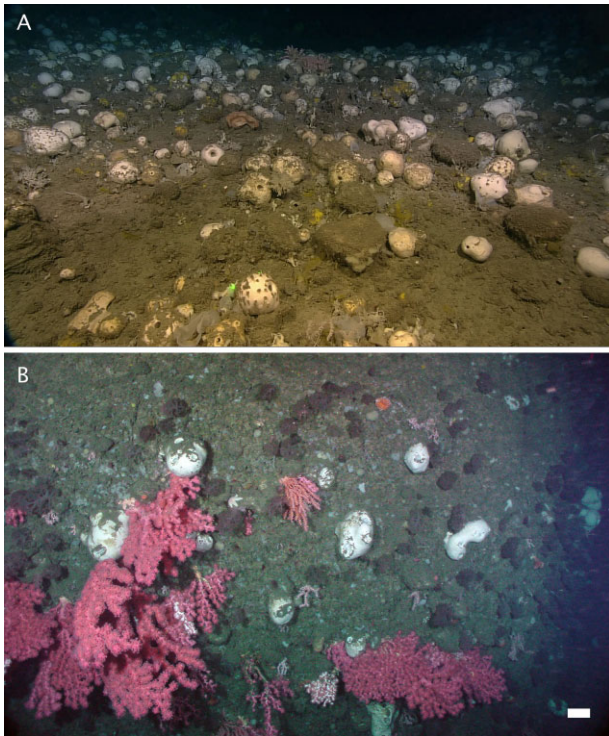

Figure 1. A, sponge ground on sand-bottom, Flemish Cap, 1581 m. HUD2010-029 campaign, dive 1339 of ROV *ROPOS*, 48°12.2′N, 43°56.7′W, each sponge is about 10–20 cm large; frame grab obtained with the software Topaz Moment (http://www.topazlabs.com/moment/) (Canadian DFO/ROPOS 2010). The *G. barretti* specimen R1339-10 was collected at this locality. B, *Geodia barretti* and gorgonians (*Paragorgia arborea*) on hard-bottom off Nova Scotia, HUD2007-025 campaign, 43°58′7″N, 59°0′46″W, *c.* 700 m depth. Scale: 10 cm. (Canadian DFO/ROPOS 2007).

very large sponges usually belong to the genus *Geodia* Lamarck, 1815 (family Geodiidae), comprising *c.* 150 species worldwide.

Geodia species are massive sponges with a conspicuous cortex. In small specimens and the periphery of large specimens the skeleton structure is radial, and without obvious arrangement in the interior of large specimens. They possess characteristic ball-shaped spicules called 'sterrasters' which make up the main part of the cortex (these sterrasters are an autapomorphy of the Geodiidae). *Geodia* species have a very diverse spicule repertoire, which can be used to identify species. In addition, *Geodia* species differ in their external morphology, colour, and cortex thickness. The subfamily Geodiinae Sollas, 1888 has been resurrected (Cárdenas *et al*., 2010) to include Geodiidae species with star-shaped microscleres (euasters) in the ectocortex (outer part of the cortex) and with ana/pro/mesotriaenes. The Geodiinae only contains *Geodia* species, some of which are distributed in well-supported clades (Cárdenas *et al*., 2010, 2011) (Fig. 2).

Geodia species from the northeast Atlantic (NEA) north of 60°N appeared in the literature for the first time in 1858 when Bowerbank described *Geodia barretti* and *Geodia macandrewii* from western Norway. Since then, a number of species have been based on material from various parts of the region, namely *G. simplex* Schmidt, 1870 (western Greenland), *Isops phlegraei* Sollas, 1880b (western Norway), *Isops pallida* Vosmaer, 1882, *Isops sphaeroides* Vosmaer, 1882, *Synops pyriformis* Vosmaer, 1882 (all from northern Norway), *Geodia parva* Hansen, 1885 (Norwegian Sea, uncertain location), *Cydonium normani* Sollas, 1888 (western Norway), *G. atlantica* Stephens, 1915 (off Ireland), *Sidonops mesotriaena* Hentschel, 1929 (Spitsbergen) and *Geodia simplicissima* Burton, 1931 (northern Norway). In addition to these 12 nominal species four names of species described from elsewhere are claimed to have been identified in material from the boreo-arctic region of the NEA, namely *Geodia cydonium* Jameson, 1811, *Cydonium muelleri* Fleming, 1828, *Geodia gigas* Schmidt, 1870, and *Geodia nodastrella* Carter, 1876. The nomen nudum *Geodia norvegica* used by Lankester (1882) must be a miswriting; it is not connected with a description or any known material.

Boreo-arctic *Geodia* species are large whitish deep-sea sponges which usually live on coarse gravel/sand (Fig. 1A), coral rubble, or on hard bottoms (Fig. 1B). Therefore, geographical and bathymetric distributions of these species reach far wider than the mass accumulations, and solidly built as they are, *Geodia* species can, at least as fragments, be taken with any kind of gear working on the localities where they live. Large undamaged specimens are normally easy
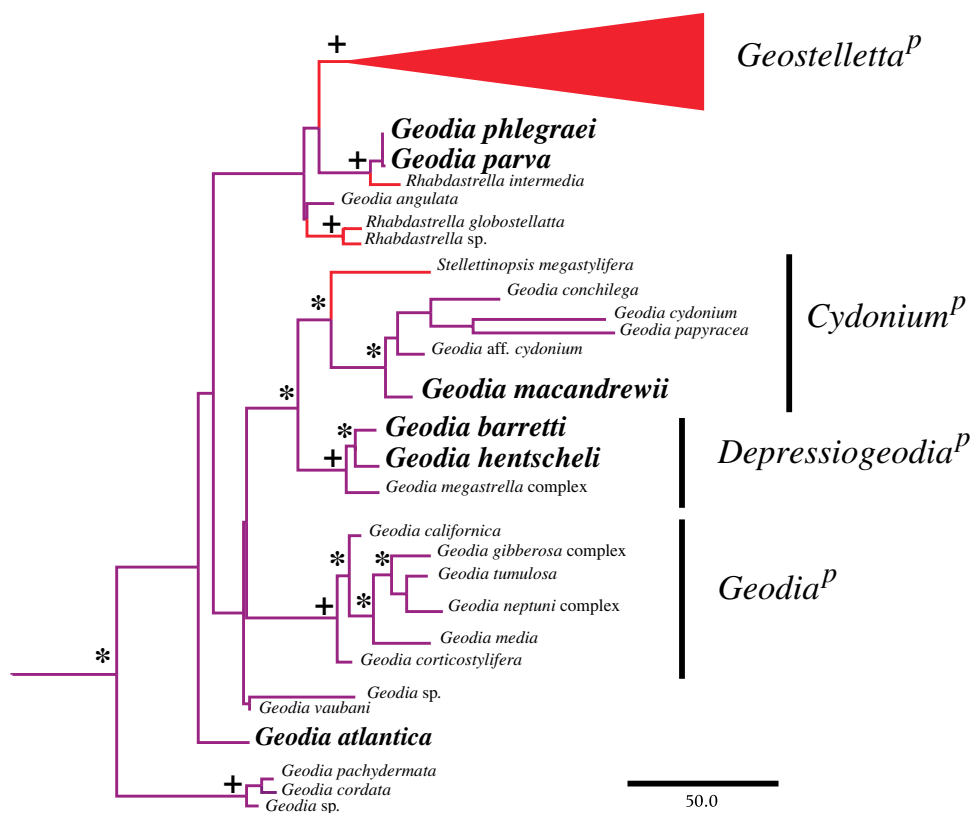
Figure 2. Molecular phylogeny of the *Geodia* genus, modified from Cárdenas *et al*. (2011: figure 2). Maximum-likelihood tree made from concatenated sequences of COI (Folmer fragment) and 28S (C1-D2 domains). Bootstrap nodal support values are given above the nodes: *, $\geq 75\%$; +, $\geq 99\%$ (2000 replicates).

to identify thanks to characteristic external morphologies, while it is often more difficult with fragments and with small (i.e. young) specimens. In the latter case, identification depends on spicule morphology, which is not straightforward for non-taxonomists. Adding to that, the fact that quite a number of names are available results in some misunderstandings of species and misidentifications occurring in the literature. Also, a number of less well-described species having been reported only once or a few times add to the general uncertainty about species identity. Rough morphological redescriptions of these species have been attempted (Hougaard *et al*., 1991b) but the most comprehensive taxonomic review is still that of Koltun (1966, in Russian). Koltun (1966) based his review on specimens from the collections in St Petersburg, most of which were collected in north-eastern boreal and arctic waters. The main achievements of Koltun's review include the first key to these species with detailed comprehensive spicule plate drawings, along with good-quality black and white photographs that are as yet the main reference for these species. On the other hand, Koltun (1966) did not examine types, he did not give spicule measurements for individual specimens (so the spicule variation within a specimen or populations is unknown), and, again, the distributions and descriptions he gave were biased by the single collection he studied. Furthermore, he did not have access to molecular data and microscopic data using scanning electron microscopy (SEM). So, 47 years after Koltun's landmark paper, a revision of this group is required using new approaches, and reviewing the literature on the other sources of data which are now available for these animals (e.g. phylogeny, biochemistry, microbial communities).

Since reports of north-west Atlantic (NWA) *Geodia* are scarce (Wagoner *et al*., 1989; Fuller *et al*., 2008; Kenchington *et al*., 2010) the boreo-arctic *Geodia* species revised here were usually considered to be typical of the NEA sponge fauna. But recent NWA records of *G. barretti*, *G. macandrewii*, and *G. phlegraei* were confirmed in international waters off Newfoundland, i.e. Flemish Cap, Flemish Pass, and south-eastern Grand Bank (Fuller, 2011; Murillo *et al*., 2012) (Fig. 1A). This revision is therefore an opportunity to study these NWA specimens and compare the genetics and the morphology of western and eastern populations. By mapping the records of

these species, we also hope to get a clearer picture of the biogeography and ecology of these species.

MATERIAL AND METHODS

The major part of the material originates from our own participation in a large number of cruises. The geographical area thus covered comprises the Denmark Strait, areas around the Faroe Islands and Iceland, the Norwegian and Swedish coasts, Spitsbergen, different parts of the Norwegian and Greenland Sea, south-eastern Grand Bank off Newfoundland, Flemish Cap, and Davis Strait. Sampling and station lists in which O.S.T. and A.B.K. took part are listed in Klitgaard & Tendal (2004: table 1). P.C. and H.T.R. mainly recovered material from the Skagerrak (BIOSKAG 2006), the Norwegian/Swedish coasts, the Barents Sea (R/V *Polarstern* ARK-XXII/1a cruise in 2007 and the 'Ecosystem Barents Sea' cruise in 2007), from Iceland (IceAge cruise with R/V *Meteor* in 2011) and from the Schultz Massive Seamount in the Greenland Sea (BIODEEP2007, H2DEEP2008 expeditions on board R/V *G.O. Sars*). P.C. collected and observed *Geodia* species *in situ* during a dive in Trænadjupet (northern Norway) with the manned-submersible *Jago* (*Polarstern* ARK-XXII/1a-2007). NWA records came from trawl surveys (Murillo *et al.*, 2012), from rock dredge samples, and boxcores obtained in 2009–2010 in the NAFO Regulatory Area (Divs. 3LMNO), on board the Spanish R/V *Miguel Oliver* as part of the NEREIDA Project (cf. Acknowledgements). *Geodia* specimens from NEREIDA 2009-10 were examined for this study. M.B. also participated in the HUD2010-029 cruise, on board *CCGS Hudson*, using the ROV *ROPOS* in the Flemish Cap and Orphan Knoll mounds. *Geodia* samples from the Davis Strait were dredged during the R/V *Paamiut* survey 'PA2010-009'. Specimens from Spitsbergen were collected by A. Plotkin (University of Bergen) during the course 'Marine Benthic Fauna of Svalbard' on board the R/V *Helmer Hanssen*. In addition to the recently collected material, we have visited and examined the extensive collections of the Zoological Museums of Copenhagen and Uppsala, the Swedish Museum of Natural History in Stockholm, the National Museum of Natural History in Paris, the Bedford Institute of Oceanography in Dartmouth, and borrowed type material and specimens for control or comparison from several other museums and laboratories (see below). *Geodia* material from previous publications has also been re-examined (Fristedt, 1887; Lundbeck, 1909; Hentschel, 1929; Burton, 1934; Burton, 1959; Kingston *et al.*, 1979; Wagoner *et al.*, 1989; Boury-Esnault, Pansini & Uriz, 1994; Voultsiadou & Vafidis, 2004; Nichols, 2005; van Soest *et al.*, 2007). Additional Arctic records for *G. phlegraei*

or *G. parva* were found in the Global Biodiversity Information Facility (GBIF) website (http://www .gbif.org, accessed 30 March 2012); these identifications were made by Koltun (I. Kröncke, pers. comm.) and thus were trusted. More records came from underwater picture databases: that of the Marine area database for Norwegian waters (MAREANO, http://www.mareano.no) and that of habitat mapping studies in the West Shetland Channel (pictures courtesy of K. L. Howell) (Howell, Davies & Narayanaswamy, 2010), when identifications to the species level was possible. All the records obtained from our identifications and the literature were compiled and mapped with GeoMapApp version 3.3.2 (http://www.geomapapp.org), using the North Polar base map projection and the default Global Multi-Resolution Topography Synthesis (Ryan *et al.*, 2009). When the latitude/longitude information was missing but the locality was given, we reconstructed the geographical coordinates using Google Earth. Temperature ranges for each species were obtained from the campaigns in which bottom temperatures were recorded (e.g. Ingolf Exp., BIOICE, BIOFAR, PA1994, PA2010-009) and from the literature. A list of the specimens examined by us in various campaigns/museum collections and the compiled records for all species – including geographical coordinates, museum collection or reference, temperature and salinity when available – were deposited in the Dryad Repository (http://www.datadryad.org) under the following Dryad Package Identifier: http://dx.doi.org/10.5061/dryad.td8sb.

Samples collected during the cruises were coarsely sorted once on deck and either fixed in 4% borax-buffered formaldehyde (O.S.T., A.B.K.), directly in 70% ethanol (NEREIDA), 96% ethanol (P.C., H.T.R., A. Plotkin) or frozen at sea before being fixed in 70% ethanol (PA2010-009). When fixed in formaldehyde, the sponges were rinsed in freshwater and transferred to 80% alcohol after 2 weeks, as was the case for the specimens stored in the Zoological Museum in Copenhagen. Spicule preparations for light microscopy and SEM, as well as thick sectioning, follow protocols from Cárdenas & Rapp (2012). For each species SEM observations were made for NEA and NWA specimens. Sequences of the Folmer fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene and a 28S ribosomal gene partial fragment (C1–D2 domains) of our specimens were obtained in previous phylogenetic studies where protocols are described (Cárdenas *et al.*, 2010, 2011). The COI Folmer fragment (659 bp) was obtained using primers LCO1490 and HCO2198 (Folmer *et al.*, 1994) while the 28S (C1-D2) marker (802 bp) was amplified using primers C1′ASTR (Cárdenas *et al.*, 2011) and D2 (Lê, Lecointre & Perasso, 1993). To investigate the

intraspecific variation of the COI Folmer fragment we sequenced more specimens for the present paper, following the same protocol. In addition, 18S was obtained for all the species revised. The complete 18S of *Geodia neptuni* retrieved from GenBank (AY737635) is 1802 bp. We have used primers originally designed for Platyhelminthes (Norén & Jondelius, 1999) along with the protocol used by Wallberg *et al*. (2007) to obtain a nearly complete 18S sequence (1708–1710 bp). The 18S was amplified in two parts with two sets of primers: 4FB/1806R and S30/5FR. For the sequencing, these same primers were used, plus additional sequencing primers: 4FBK, 5F, 7F, and 7FK. PCR products were then purified using the ExoSAP-IT® kit (USB Europe, Staufen, Germany) and sent for sequencing (Macrogen). 18S sequences were assembled and blasted using Geneious 5.6.4. (created by Biomatters, http://www.geneious.com/).

The following abbreviations are used for the institutions from which we have examined material, or where material will be deposited: BIO, Bedford Institute of Oceanography, Halifax, NS, Canada; BNHM, The Natural History Museum, London, UK; IEO, Instituto Español de Oceanographía, Vigo, Spain; INHM, The Icelandic Natural History Museum, Iceland; KLF, The Kaldbak Laboratory, The Faroe Islands; MNHN, Muséum national d'Histoire naturelle, Paris, France; MOM, Musée Océanographique de Monaco; PC, University of Bergen collection (H.T.R.), Norway; RMNH, The Royal Museum of Natural History, Leiden, Netherlands; SMNH, Swedish Museum of Natural History, Stockholm; TSZY, Tromsø Museum, Norway; UPSZMC, The Zoological Museum of Uppsala, Sweden; ZMB, Museum für Naturkunde, Berlin, Germany; ZMBN, Bergen Museum, Bergen, Norway; ZMH, Zoologisches Museum, Hamburg, Germany; ZMUC, The Zoological Museum, Copenhagen, Denmark; ZMO, University of Oslo, Natural History Museum, Oslo, Norway.

RESULTS AND DISCUSSION

For each species valid name, synonymy, material examined (http://dx.doi.org/10.5061/dryad.td8sb), description (of specimens in general, and type material in particular), DNA barcodes, distribution, and facts on the biology of the species are provided. In the synonymy part (sorted according to the chronology of names, except for misspellings included under the correctly written species), we have mainly included references to taxonomy, phylogeny or distribution of the species. Species name established under the rules of the *PhyloCode v.4c* (http://www.ohiou.edu/phylocode) are also given here; these *PhyloCode* species names are those suggested by molecular phy-

logeny results (Cárdenas *et al*., 2011: fig. 5) according to the *PhyloCode* defined clades they belong to (Fig. 2). The six boreo-arctic species described here belong to well-supported clades (the *PhyloCode* defined *Depressiogeodia*^{p} [Cárdenas *et al*., 2010] and *Cydonium*^{p} Fleming, 1828 [Cárdenas *et al*., 2010]) or have poorly resolved phylogenetic relationships (Cárdenas *et al*., 2011) (Fig. 2).

In the spicule overview of each species we have included the minimum–maximum of each measurements for each spicule category based on (1) our measurements of specific specimens (Tables 1–5), (2) additional measurements from other specimens (data not shown in Tables 1–5), and (3) the literature. SEM spicule figures usually focus on the microscleres as the megascleres are often visible on the thick sections presented here, and were already accurately represented by Koltun (1966). In this study, we have also investigated sterraster characters that may potentially be relevant for *Geodia* species discrimination (da Silva, 2002; Cárdenas *et al*., 2009): sterraster thickness, hilum diameter, rosette diameter, and morphology and number of the rosette rays.

CLASS DEMOSPONGIAE SOLLAS, 1885

ORDER TETRACTINELLIDA MARSHALL, 1876

SUB-ORDER ASTROPHORINA SOLLAS, 1888

FAMILY GEODIIDAE GRAY, 1867

SUB-FAMILY GEODIINAE SOLLAS, 1888

GENUS *GEODIA* LAMARCK, 1815

GEODIA ATLANTICA (STEPHENS, 1915)

GEODIINAE^p *ATLANTICA* (*PhyloCode* SPECIES NAME)

(FIGS 3–6, TABLE 1)

Sidonops atlantica, Stephens, 1915: p. 18. *Sidonops* cf. *atlantica*, Cárdenas *et al*., 2010: p. 89.

Geodia sp., Hougaard *et al*., 1991a: p. 225, b: p. 470; Warén & Klitgaard, 1991: p. 55; Cedhagen, 1994: p. 67; Klitgaard, 1995: p. 2 (synonymy by this study).

Geodia atlantica, Klitgaard & Tendal, 2004: p. 57; Todt *et al*., 2009: table 1; Schöttner *et al*., 2013: p. 2. *Geodia* cf. *atlantica*, Cárdenas *et al*., 2011: table S1.

Misidentifications:

Isops pallida, Vosmaer, 1882: p. 16 (in part).

Geodia macandrewii, Reitner & Hoffmann, 2003: Tafel 2, figure 1.

Geodia barretti, van Soest *et al*., 2007 (in part?): table 2.

Type material examined.

Isops pallida, near Hammerfest, Norway, 71°12′5N, 20°30′5E, 247 m, Willem Barents Exp. 1878–79, RMNH Por 652, wet specimen (only pictures were seen); RMNH, Vosmaer slide collection, box number 37, three spicule preparations with number 64.
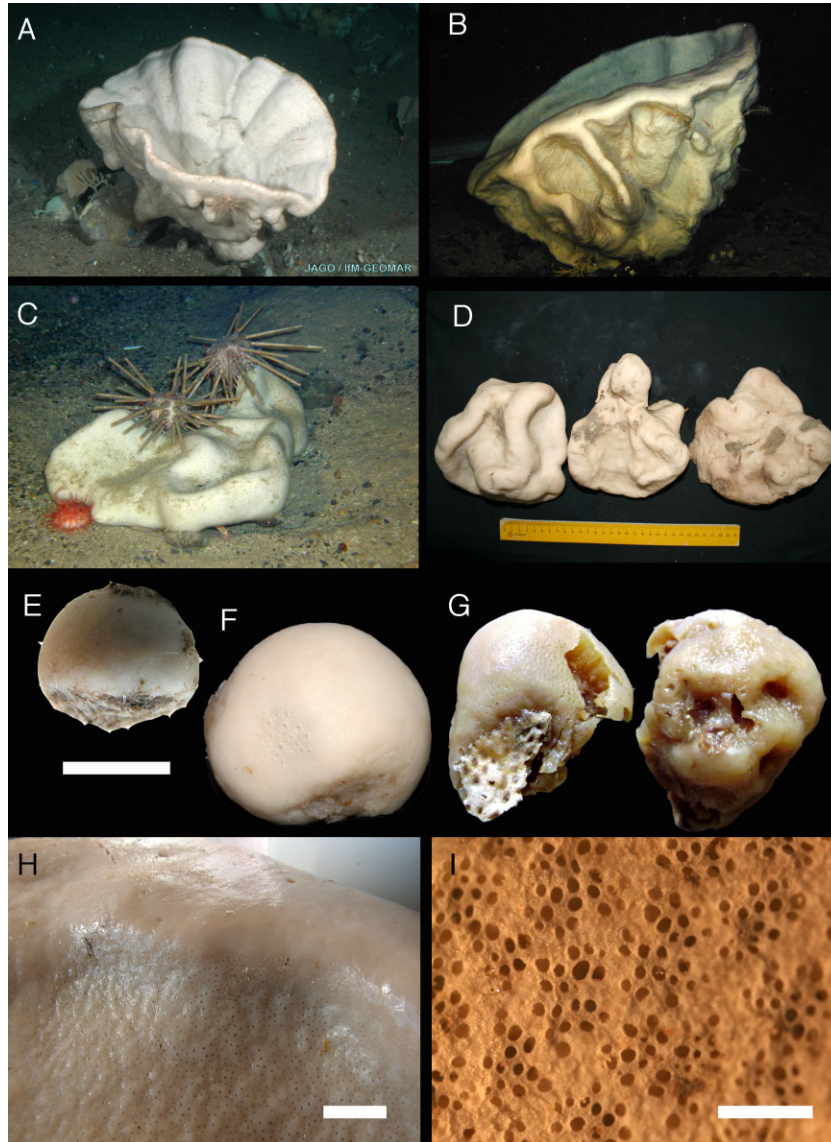
Figure 3. External morphology of *Geodia atlantica* (Stephens, 1915). A, specimen PC222 *in situ*, Trænadjupet, northern Norway, 66°58′N, 11°7′E, 292 m, specimen is *c*. 40 cm in diameter (picture: J. Schauer, Polarstern ARK-XXII/1a, 2007). B, specimen observed *in situ* but not collected, Schiehallion, West Shetlands, 60°20′30″N, 04°05′56″W, 450 m depth, unknown scale (picture supplied by Daniel Jones, SERPENT Project 2006, http://www.serpentproject.com). C, sea urchins (*Cidaris cidaris* and ?*Gracilechinus alexandri*) on *G. atlantica*, West Shetlands, 450 m, unknown scale (picture supplied by Daniel Jones, SERPENT Project 2006). D, three specimens just after being dredged off Newfoundland, NEREIDA 0509 exp., field # DR19-1(2) (photo courtesy of NEREIDA Project). E, specimen PC77 from Korsfjord, western Norway. Scale: 1 cm. F, specimen ZMAPOR 21406 from Norway, 319 m. Scale: 4 cm. G, holotype S.R.151-27/364-1914, size is 2.7 × 2 cm. H, uniporal oscules from a specimen collected in the Korsfjord. Scale: 1 cm. I, cribriporal pores (ZMBN 77927, Korsfjord). Scale: 5 mm.

Geodia atlantica, holotype, off western Ireland, 54°17′5N, 11°33′5W, 709 m, stones and rock, 9.15 °C, number S.R.151-27/364-1914.

External morphology and cortex: Colour alive and in ethanol is whitish (Norway, Flemish Cap) to light brown (Bay of Biscay, Rockall Bank). Choanosome colour alive and in ethanol is brownish (always darker than cortex). Large specimens can be funnel shaped with a deep cavity with irregular swellings and ridges (Fig. 3A, B). From fragments we have seen in large trawl catches at the Faroe Islands, we had
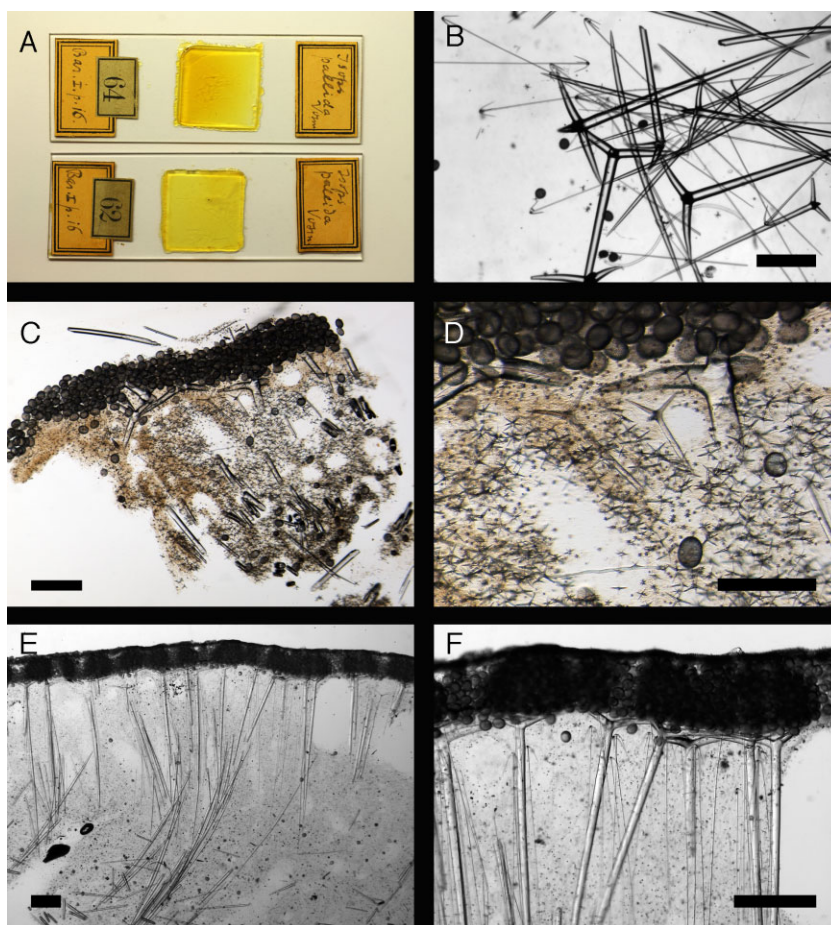
Figure 4. A, type slides of *Isops pallida* Vosmaer, 1882 for specimen numbers 62 (= α, here designated as lectotype) identified as *G. phlegraei*, and 64 (= β) identified as *G. atlantica*. B, orthotriaenes and abundant anatriaenes from one of the slides 64 (= β). C and D, thick sections of the holotype of *Sidonops atlantica* Stephens, 1915, specimen S.R.151-27/364–1914. E and F, thick sections of ZMBN 77927, Korsfjord, 200–400 m depth. Scale bars: B, 400 μm; C, E, F: 500 μm; D, 300 μm.

the impression that in very large specimens the bottom of the funnel could disappear with time, and that the sponge maintained a ring-shaped wall, 80–100 cm in diameter. The largest specimen found measures 72 × 40 × 39 cm. Other specimens are irregularly plate-shaped and convoluted (Fig. 3C, D). Young specimens are subspherical (Fig. 3E, G). The surface is smooth. The lower sides of the specimens are sometimes covered with stones incorporated in the cortex. Uniporal oscules (0.3–0.5 mm in diameter) are scattered on the top surface of small specimens, and oscules are sometimes surrounded by a raised lighter-coloured boundary. Oscules are scattered on the inner side of funnel-shaped specimens so that pores and oscules are on opposite sides (Fig. 3H). Cribriporal pore areas (0.3–0.5 mm in diameter) are on the outer side of funnel-shaped specimens and on one side of plate-shaped specimens; they are in small groups, which are evenly scattered over the surface

(Fig. 3I). The cortex is elastic, *c.* 0.5 mm thick (with ectocortex: 30–100 μm) (Fig. 4). Anatriaenes within the choanosome are fairly common (Fig. 4F).

Description of type material: Three spicule preparations (with number 64) (Fig. 4A) of the syntype β of *Isops pallida*. Pictures of the spicules are shown (Fig. 4B). We have seen only pictures of the wet specimen of syntype β: it is a whole spherical specimen about 4 cm in diameter, with very small roots, a thin cortex (< 1 mm thick), slightly raised uniporal oscules and cribriporal pores on opposite sides. It looks similar to specimen ZMAPOR 21406a from Norway (Fig. 3F).

The holotype of *G. atlantica* is a small subspherical specimen (2.7 × 2 cm). This specimen is represented in plate II of Stephens (1915) and Figure 3G. In the Dublin Museum, there are also five spicule preparations made by Stephens (four spicule slides and one
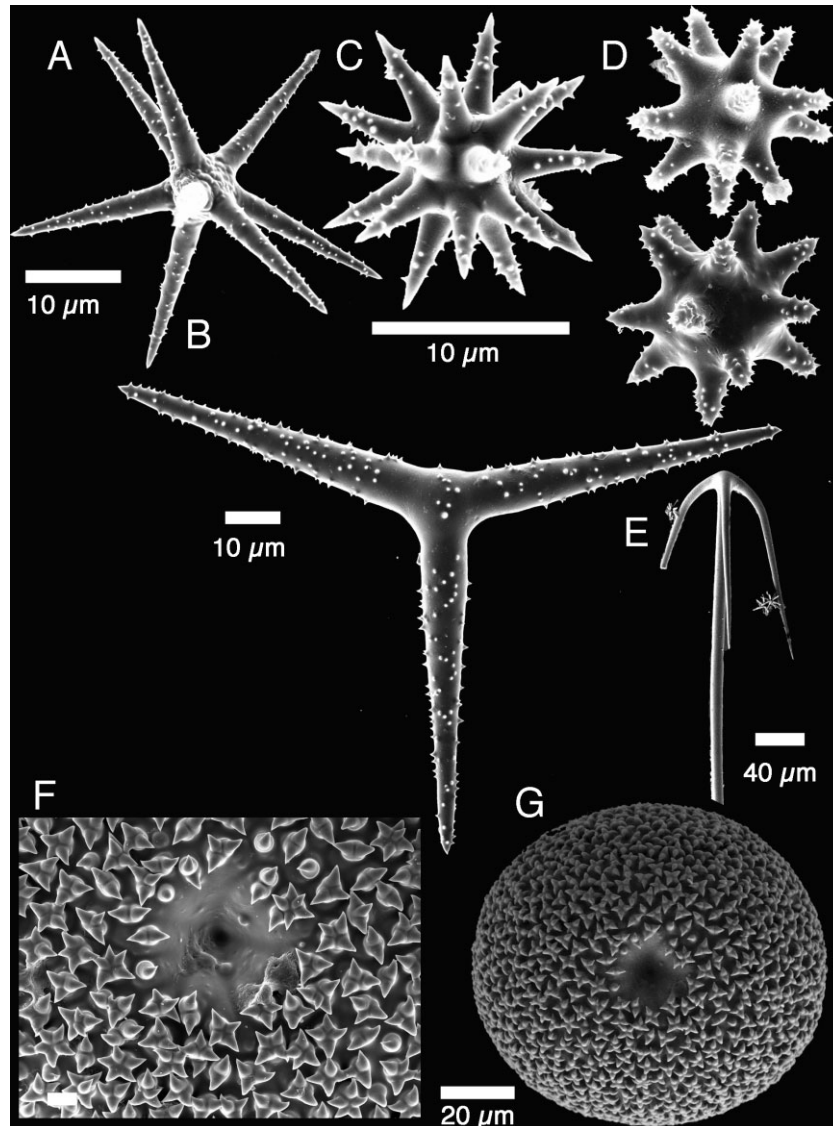
Figure 5. Spicules of *Geodia atlantica* (Stephens, 1915). All spicules are from the holotype of *Sidonops atlantica* Stephens, 1915, S.R.151-27/364-1914, except E from ZMBN 77927. A and B, oxyaster I. C, oxyaster II. D, spheroxyasters. E, anatriaene. F, close-up on a sterraster showing hilum and rosettes. Notice the smooth rosettes. Scale bar: 4 µm. G, sterraster.

section). New thick sections were made for this study (Fig. 4C, D). Figure 5 shows SEM pictures of this holotype.

Spicules (Figs 4–5, Table 1): Megascleres: (a) oxeas, straight or bent, length: 1275–4440 µm; width: 11–68 µm. (b) Orthotriaenes, rarely dichotriaenes, straight or slightly bent rhabdome, rhabdome length: 630–4400 µm; width: 18–125 µm; orthotriaene clad length: 95–750 µm; protoclad length: 190–430 µm; deuteroclad length: 90–300 µm. (c) Anatriaenes, straight or slightly bent rhabdome, rhabdome length: 376–5200 µm; width: 2–32 µm; clad length: 9–300 µm.

(d) Protriaenes, very rare [one reported in the type (Stephens, 1915) and one observed in PC626], rhabdome length: 3000 µm; width: 8–15 µm; clad length: 96–130 µm. Microscleres: (e) sterrasters, slightly elongated, more rarely spherical, length: 80–125 µm; width: 75–112 µm; thickness: 70–88 µm. Rosettes are made of 2–6 smooth rays; rosette diameter: 4–7 µm; hilum diameter: 10–20 µm. (f) Spheroxyasters, rough actines, 5–16 µm in diameter. (g) Oxyasters I, 3–8 rough actines, diameter: 22–110 µm [maximum measured in type by Stephens, (1915)]. (h) Oxyasters II, 9–25 rough actines, usually with a larger centrum than oxyasters I, diameter: 12–35 µm.
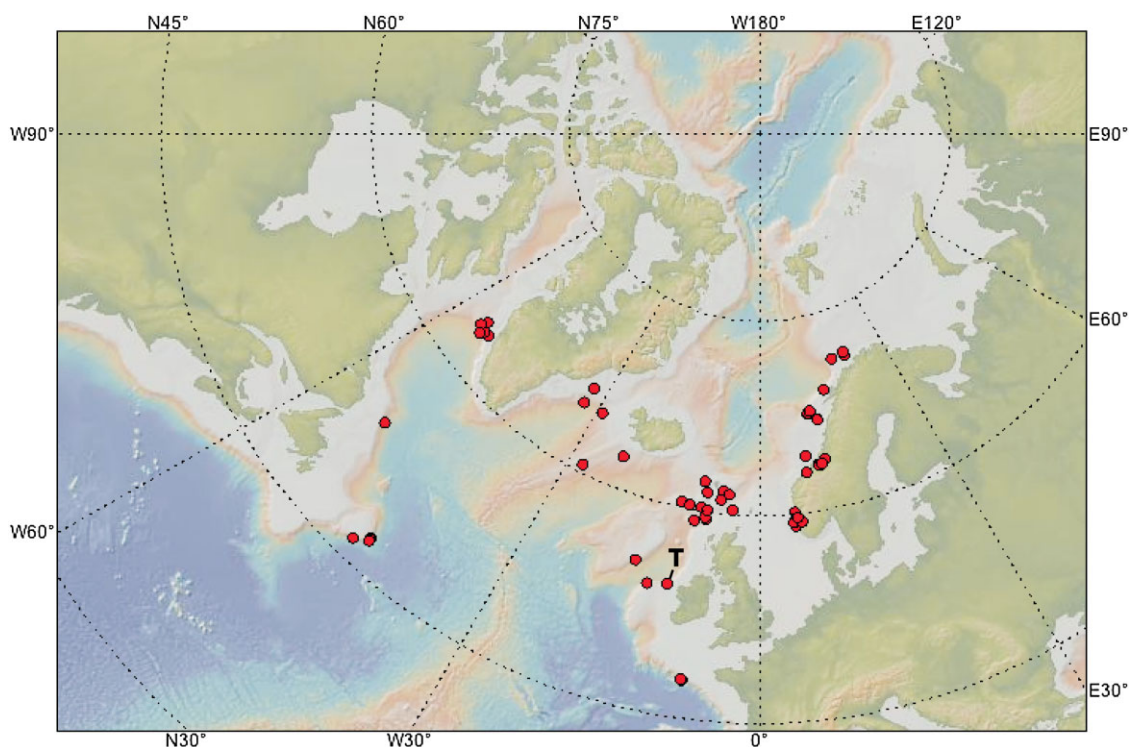
Figure 6. Distribution of *Geodia atlantica* (Stephens, 1915) (map made with GeoMapApp, http://www.geomapapp.org). T, type locality.

DNA barcodes: GenBank accession nos. HM592679, HM592695, EU442195 (Folmer COI): we have sequenced specimens from western and northern Norway (10), Rockall Bank (1), and Flemish Cap (1): the Folmer COI is identical in all these specimens. No. KC481227 (18S), obtained from ZMBN 77927 (Korsfjord, Norway).

Distribution (Fig. 6): This species has an amphi-Atlantic boreal distribution. It has been recorded at depths of 65–2338 m, the shallowest record being from divers in Sandsfjord, Rogaland, Norway (Moen & Svensen, 2008), the deepest boreal records being from south of Iceland and off south-east Greenland, while the deepest record overall is from the Bay of Biscay. *Geodia atlantica* seems only to be present in the south-western Barents Sea and absent in Arctic waters, which might explain why it is not mentioned by Koltun (1966). It has been found at temperatures between 1.4 °C (Denmark Strait) and 10.5 °C, but is usually found at temperatures higher than 3 °C.

Biology: We found no indications of asexual reproduction. The predatory chiton *Hanleya nagelfar* Lovén, 1846 and the parasitic foraminiferan *Hyrrokkin sarcophaga* Cedhagen, 1994 have been found living on *G. atlantica* (Warén & Klitgaard, 1991; Cedhagen,

1994; Todt *et al.*, 2009). Sea urchins are also possibly feeding on this sponge; the two species observed in Figure 3C were tentatively identified from the photo as *Cidaris cidaris* (L., 1758) and *Gracilechinus alexandri* (Danielsen & Koren, 1883) (T. Saucède, pers. comm.). *Cidaris cidaris* (Rouho, 1888; Mortensen, 1928) and other cidarids (Bo *et al.*, 2012) are indeed considered to be sponge predators whereas *G. alexandri* is more of an omnivore opportunist which may be more interested in the small organisms living around and on the sponge. Other associated fauna has been investigated by Klitgaard (1995). The chemistry (elemental analysis, amino acids, sterols, and quaternary ammonium compounds) has been investigated by Hougaard *et al.* (1991a, b).

Distinctive characters: External morphology: The deep funnel shape or plate convoluted shape, with smooth surface. The pattern of distribution of pores and oscules: when one finds a fragment of a funnel or plate-shaped specimen, oscules are on one side, pores on the other. Spicules: Lack of microxeas (as in *G. phlegraei* and *G. parva*) and very common anatriaenes.

Remarks: Burton (1930) synonymized *I. pallida* with *G. phlegraei* by stating that he had compared type

Table 1. Individual spicule dimensions and cortex thickness for specimens of *Geodia atlantica* (in µm) collected at different depths

Material	Depth (m)	Cortex thickness (mm)	Spheroxyasters (diameter)	Sterrasters (length/width)	Oxyasters I (diameter)	Oxyasters II (diameter)	Ortho/ dichotriaenes (rhabdome: length/width)	Ortho/ dichotriaenes (ortho/proto/ deuteroclads)
I. pallida Barents Sea slide 64, specimen β	247	n.o.	7-**13.5**-16	100-**107.2**-115/ 85-**91.6**-100	35-**57.3**-72	15-**22.1**-30 (10)	630-**2181.8**-2600/ 18-**83.1**-100	95-**473.6**-750/ n.o./n.o.
Trænadjupet, Norway PC222	292	n.o.	9-**11.9**-15	88-**102.6**-112/ 84-**93.7**-100	25-**36.9**-55	12.5-**17.3**-25	3080-**3826.6**-4360/ 70-**79.6**-90 (6)	400/ 200-430(2)/ 90-300(2)
Korsfjord, Norway ZMBN 77927	200-400	0.5-0.6	6-**11.1**-16	80-**93.2**-110/ 75-**85.4**-95	22-**41.2**-65	12.4-**16.6**-21	1625-**2741.9**-3500/ 25-**58**-80	190-**377.9**-525/ n.o./n.o.
Off Ireland SR151-27 holotype (Stephens, 1915)	709	0.4	5-10	100/ 80	75-110	15-20	2000-3000/ –	400-550/ –/ –
SR151-27 holotype (this study)	709	0.4	7.5-**12**-14.6*	88.5-**95.6**-105/ 78.6-**84.7**-90.8 (18)	35.9-**63.9**-104.2*	12.2-**18**-26.5*	–/ 18-**68.9**-100(10)	105-**300**-510(6)/ 190-**200**(2)/ 200-300(2)
Rockall Bank ZMAPOR 19647	750-762	1	7.5-**10.9**-13	104-**116.1**-125/ 100-**106.4**-112	32.5-**53.2**-87	12.5-**19.2**-30	3600-**3950**-4120(4)/ 60-**101.5**-112(17)	250-**506.6**-650(9)/ n.o./n.o.
Bay of Biscay MNHN Thalassa Z407	1085	1	7.5-**11.1**-13	104-**116.6**-124/ 92-**99.2**-112	30-**52.7**-76	12.5-**21**-35	1375-**3629.6**-4400(14)/ 40-**107.7**-125	160-**499.2**-670(20)/ 250-**303**-370(20)/ 150-**228.6**-300(20)
Flemish Cap UPSZMC 78293 (DR20-01b)	1122	1	5-**10.1**-13	89-**97.7**-104	32-**53.4**-72	12-**19.5**-32	2120-**2735**-3440(4)/ 64-**85.1**-120 (7)	300-**438.4**-510 (16)/ 140-170(2)/ 210-300(2)

Table 1. *Continued*

Material	Oxeas (length/width)	Anatriaenes (rhabdome: length/width)	Anatriaenes (clad)	Protriaenes (rhabdome: length/width)	Protriaenes (clade)
I. pallida Barents Sea slides 64, specimen β	1575-**2671.5**-3450/ 35-**52.6**-65	860-**2564**-3850/ 6-**11.8**-16	55-**138.4**-190	n.f.	n.f.
Trænadjupet, Norway PC222	1700-**2450.4**-2840/ 16-**26.1**-32 (12)	450-**1272.2**-1825/ 2-**6.4**-10	20-**98.7**-172	n.f.	n.f.
Korsfjord, Norway ZMBN 77927	1625-**3030.4**-3650(23)/ 11-**44.1**-65(24)	430-**2247.8**-3000/ 2-**10.1**-15	9-**155.7**-250	n.f.	n.f.
Off Ireland SR151-27 holotype (Stephens, 1915)	2400-3400/ 45-60	2000-3000/ 10-20	90-160	3000/ 15 (1)	130 (1)
SR151-27 holotype (this study)	n.o.	-/ 12.8	134	n.f.	n.f.
Rockall Bank ZMAPOR 19647	1275-**3771.1**-4440/ 14-**52.6**-68	1625-**2375.5**-3050/ 3-**11.1**-24	18-**125.6**-190	n.f.	n.f.
Bay of Biscay MNHN Thalassa Z407	2600-**3604**-4080/ 34-**59.5**-68	4560-5200(2)/ 16-**25.7**-32	68-**216.7**-300	n.f.	n.f.
Flemish Cap UPSZMC 78293 (DR20-01b)	1500-**2767.1**-3480/ 12-**47.2**-68	376 to >3040/ 2.5-**11.6**-20	25-**149.4**-250	n.f./ 8 (1)	96 (1)

Means are in bold; other values are ranges; $N = 30$ unless stated otherwise in parentheses, or unless measurements come from other studies. A dash indicates that this measurement is not given in the literature. n.f, not found; n.o., not observed in the subsample in our possession.
*SEM measurements.

slides from the 'Norman collection', and taxonomists followed his conclusions. Even Vosmaer (1933: 141–142) accepted the synonymy after having examined a slide of *G. phlegraei* sent to him by Sollas. However, the only slides of *I. pallida* that we found in the Norman collection (BMNH 10.1.1.1149 to 1156 and MNHN-DN45) had labels saying '*Isops pallida* Vosmaer/Lervig, Norway, 1879'. In 1879, Norman did stay in Leirvik (current name of 'Lervig') on the island of Stord in the Hardangerfjord in western Norway (Norman, 1893), so these are clearly not from the type of *I. pallida* (which was collected near Hammerfest in northern Norway). Interestingly, the thin cortex (0.5 mm), the large spiny oxyasters, and spheroxyasters showed that these slides from the Norman Collection were not from a *G. phlegraei* but from a *G. atlantica*. So Burton (1930) had probably not examined type slides and had not noticed the difference between *G. atlantica* and *G. phlegraei* spicules. However, in the course of this study, Rob van Soest (Naturalis, Leiden) rediscovered in the Vosmaer slide collection (box 37) five slides with labels stating '*Isops pallida* Vosm' and 'Bar. I p. 16' (Fig. 4A) which was understood as a reference to the Barents Sea expedition 1st publication, and to the page number of the original description of *I. pallida* in Vosmaer (1882). We therefore concluded that these five slides were the syntype slides of *I. pallida*. Three slides had the number 64 while two slides had the number 62 (Fig. 4A); the spicule morphologies and abundance corresponded to the descriptions given of syntype α (= 62) and syntype β (= 64), the latter being the one represented in the original plates (external morphology and spicules). Indeed, Vosmaer (1882) clearly notes that specimen α has considerably fewer oxyasters and anatriaenes than specimen β. This is because Vosmaer (1882) simply mixed one specimen of *G. phlegraei* (α) with one specimen of *G. atlantica* (β): spicule morphologies (spheroxyasters, large spiny oxyasters, abundant anatriaenes) (Fig. 4B) and sizes (Table 1) clearly show that specimen β of *I. pallida* type material is conspecific with *G. atlantica*. Since Vosmaer, (1882) did not explicitly designate a holotype, we have the possibility to designate a lectotype. We formally designate the syntype α as the lectotype of *Isops pallida* Vosmaer, 1882. Recommendation 74B of the 'International Code of Zoological Nomenclature' states that in choosing a lectotype among syntypes, preference should be given to the illustrated specimen, in our case syntype β. But we decide to go against this recommendation for the following reasons: (1) α comes before β in the alphabet, (2) *atlantica* has been used far more in the literature than *pallida* and, above all, (3) *I. pallida* has always been considered a junior synonym of *G. phlegraei* (so our deci-

sion will preserve the stability of the nomenclature). Following our decision, specimen β then becomes a misidentification, and *I. pallida* does *not* become a junior synonym of *G. atlantica*.

Just before the publication of this revision, Rob van Soest discovered in 2013 a jar (RMNH Por. 652) labelled: '*Isops sphaeroides* Vosm (type v. *I. pallida* Vosm.) W. Barents exp. 1878/79, 71°12′5″N 20°30′5″O, Coll. G.C.J. Vosmaer 12 Juli 1879'. Inside are two specimens and another small label written in pencil '*Isops pallida*, N. Archive Suppl. 1' which refers to the original description of *I. pallida* by Vosmaer in 'Niederlaendisches Archiv fuer Zoologie Supplementband 1'. We therefore believe that these two specimens are the two syntypes of *I. pallida*. The external morphologies (observed from pictures, courtesy of R. van Soest) of the largest specimen (α = lectotype) and of the smallest specimen (β) confirm the above conclusion based on spicules: α is a *G. phlegraei* and β a *G. atlantica*.

We noted that *G. atlantica* had a second smaller category of oxyasters that Vosmaer (1882) has seen in specimen β, but not Stephens (1915). Stephens (1915) states that the cortical spheroxyasters become larger in the choanosome; these are actually the oxyasters II. Admittedly, spheroxyasters and oxyasters II can be difficult to separate in spicule preparations, unless carefully measured and examined in thick sections (spheroxyasters are in the ectocortex, oxyasters II usually in the choanosome just below the cortex). In some specimens anatriaenes may be separated into two size categories (e.g. UPSZMC 78293 from the Flemish Cap), especially based on the rhabdome length (376–530 vs. > 2000 μm), but since a continuum of anatriaene sizes exists in other specimens (e.g. PC222 from northern Norway), we refrained from doing so. There is usually a clear predominance of orthotriaenes over dichotriaenes (but not always the case, see MNHN-ThalassaZ407).

The main difference between the type and the Norwegian specimens is that, in the Norwegian specimens, the asters are less spiny, and the oxyasters I are smaller and much less abundant (Fig. 5); this may be due to the shallower environment of the Norwegian specimens (200–400 m) compared with the type (709 m). No consistent morphological differences were found between specimens from the Flemish Cap and specimens from the NEA. A more NEA southern morph may be present (found in the MNHN Thalassa and Centob collections). These specimens are irregularly plate shaped, with a darker external colour and are usually found growing around coral. We have never seen it with the characteristic funnel shape but we have only seen small specimens (less than 15 cm long).

GEODIA BARRETTI BOWERBANK, 1858

DEPRESSIOGEODIA[P] *BARRETTI*

(*PhyloCode* SPECIES NAME)

(FIGS 7–10, TABLE 2)

Geodia barretti, Bowerbank, 1858: p. 290; 1862: p. 768, 794; 1864: p. 168, 171; 1872a: p. 198; Sollas, 1880a: p. 247; 1888: p. 250; Vosmaer, 1882: p. 23; Norman, 1893: p. 349; Lundbeck, 1909: p. 455; Burton, 1930: p. 490; 1959: p. 9; Filatova, 1938: p. 28; Alander, 1942: p. 73; Blacker, 1957: p. 27; Burdon-Jones & Tambs-Lyche, 1960: p. 6; Koltun, 1964: p. 147; 1966: p. 54; Dyer *et al.*, 1984: p. 669; Boury-Esnault *et al.*, 1994: p. 38; Klitgaard, 1995: p. 2; Klitgaard & Tendal, 2004: p. 57; Nichols, 2005: appendix A; Cárdenas *et al.*, 2010: p. 89; Cárdenas *et al.*, 2011: table S1; Murillo *et al.*, 2012: p. 842; Guihen *et al.*, 2012: p. 1; Schöttner *et al.*, 2013: p. 2;
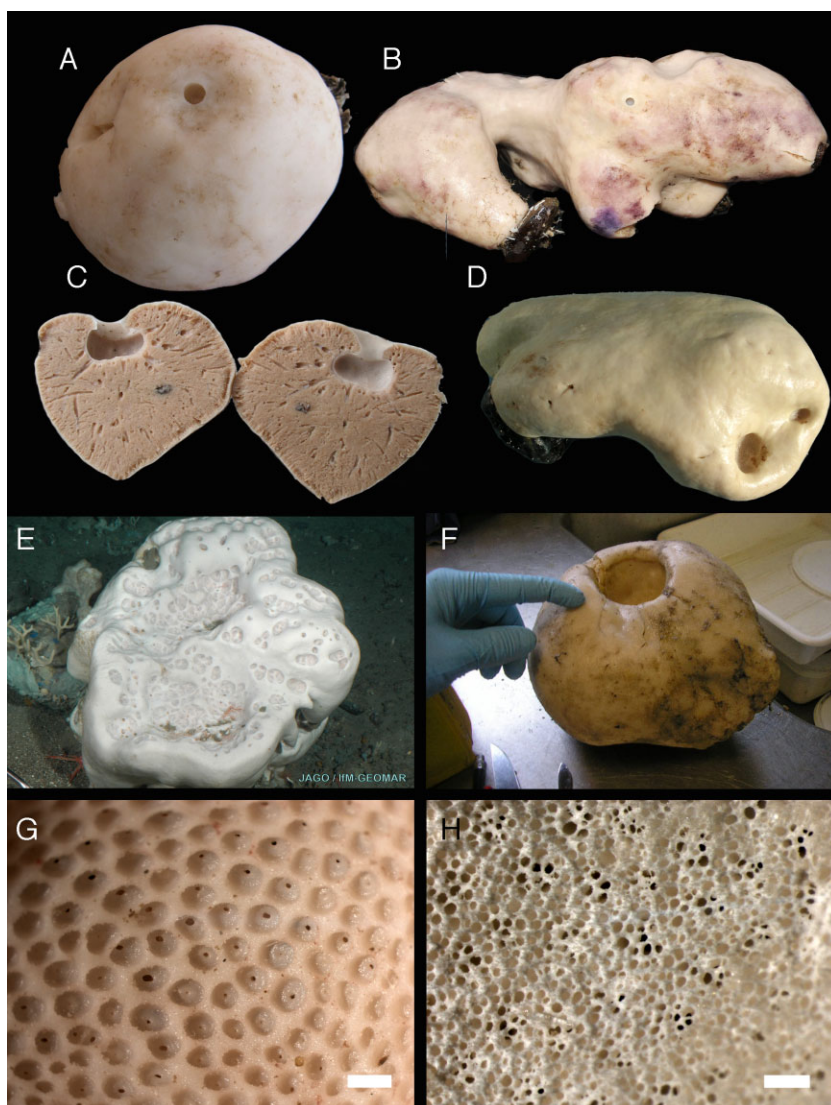

Figure 7. External morphology of *Geodia barretti* Bowerbank, 1858. A, specimen PC10 (fixed in ethanol) from Korsfjord, Norway; specimen is 10 cm large. B, specimen ZMBN 89716 just after dredging from north of Spitsbergen, 215 m depth; specimen is 30 cm long. C, specimen cut in half just after dredging from the Polarstern ARK-XXII/1a, 2007, field# 40-4(3); specimen is 14 cm large. D, specimen PC72 just after dredging from Korsfjord, Norway, at 200–400 m depth; specimen is 30 cm long. E, specimen *in situ* at Trænadjupet, northern Norway, 66°58′N, 11°7′E, 292 m depth, later collected under field# 27-1(11) (picture taken by J. Schauer, Polarstern ARK-XXII/1a, 2007). F, specimen PC359 just after dredging at 1818 m depth off western Ireland; specimen is 16 cm large. G, uniporal oscules inside the preoscule of ZMBN 89722 (from Spitsbergen); each oscule has a separate sphincter. Scale bar: 1 mm. H, cribriporal pores of ZMBN 89715 (from Spitsbergen). Scale bar: 1 mm.
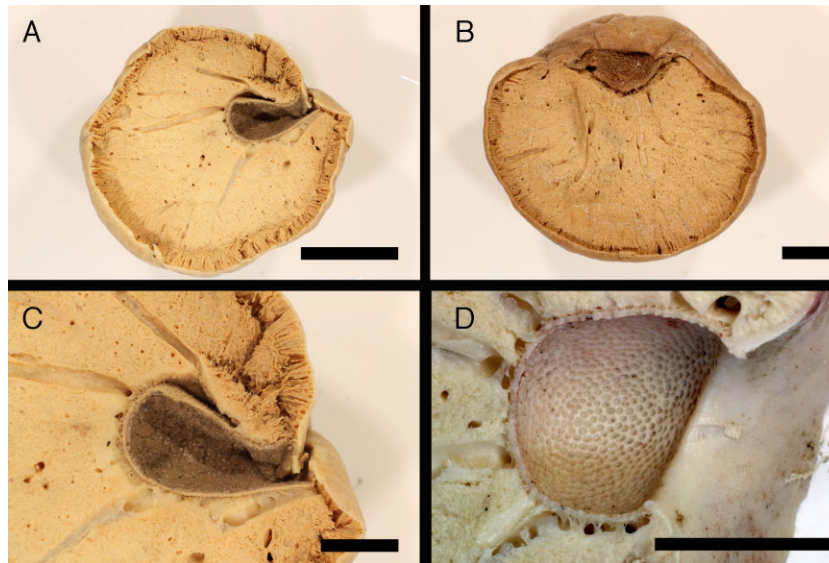
Figure 8. External morphology of *Geodia barretti* BOWERBANK, 1858. A. Balgim specimen CP63-22 cut in half, showing the preoscule full of sediments. B. Balgim specimen CP98-47 cut in half, showing the preoscule. C. Close-up of preoscule full of sediments (CP63-22). D. Close-up of preoscule (ZMBN 89722 from Spitsbergen). Scales: A: 5 cm; B-D: 2 cm.

Cárdenas & Rapp, 2013. *Geodia baretti* (misspelling), Schmidt, 1866: p. 11–12; Fristedt, 1885: p. 43; 1887: p. 463; Breitfuss, 1911: p. 213; Brøndsted, 1914: p. 526; Lidgren *et al.*, 1986: p. 3283; Warén & Klitgaard, 1991: p. 52; Reitner & Hoffmann, 2003: table 1; Rosenberg *et al.*, 2005: p. 45; Purser *et al.*, 2013: p. 37. *Geodia barreti* (misspelling), Rezvoj, 1928: table 1.

Cydonium barretti, Gray, 1867: p. 548.

Sidonops barretti, von Lendenfeld, 1903: p. 101; Hentschel, 1929: p. 919. *Sidonops baretti* (misspelling), Breitfuss, 1930: p. 277.

Sidonops sp., Hentschel, 1929: p. 867 (synonymy by this study).

Geodia simplicissima, Burton, 1931: p. 2; Oug & Rapp, 2010: p. 189; Cárdenas & Rapp, 2013 (synonymy by Cárdenas & Rapp (2013)).

Not:

Geodia barretti, Boury-Esnault *et al.*, 1994 (in part): p. 38 (CP63-E5 = *Geodia megastrella*); Voultsiadou & Vafidis, 2004: p. 593 (= *Geodia conchilega*); van Soest *et al.*, 2007 (in part?): table 2 (= *Geodia atlantica*).

Geodia barretti var. *nodastrella* Carter, 1876: p. 397; Sollas, 1888: p. 247; Topsent, 1892: p. 48 (= *Geodia nodastrella*).

Geodia barretti var. senegalensis Topsent, 1891: p. 15 (= *Geodia barretti* var. *senegalensis*).

Geodia barretti var. *divaricans* Topsent, 1928: p. 110 (= *Geodia divaricans*).

Misidentification:

Geodia cydonium, Burton, 1959: p. 9.

Type locality and deposition of holotype
Geodia barretti, collected by Robert McAndrew (1802–1873). South side of Vikna Island (formerly called Vigten or Vikten Island), North-Trøndelag, Norway, 183 m, BNHM 1877.5.21.1399 (dry specimen), BNHM 1877.5.21.1400 (one slide of surface and one spicule preparation), BNHM 1877.5.21.1401 (slide of section).

Geodia simplicissima, Foldenfjord, northern Norway, 10–75 m, TSZY 10 (wet specimen). Spicule preparations made during this study are now stored at TSZY.

External morphology and cortex: Irregularly massive, up to at least 80 cm in diameter, and up to a weight of *c.* 38 kg (wet); young specimens are usually spherical to subspherical. Mostly with an obvious attachment area, sometimes formed as several stilt-like projections each attached to a piece of gravel. The surface colour (alive) is usually white (Fig. 7A-C, E), but with sometimes various shades of light yellow (Fig. 7D) or light brown (Figs 7F, 8). The choanosome alive is light brown (Fig. 7C) and becomes whitish in ethanol. The surface is usually clean and smooth but shallow specimens (30–50 m) can be slightly dirty and hispid. Some NWA specimens were very hispid over their entire surface. One to many (more than 30) preoscules (i.e. a depression protecting the true oscules), more or less deep, more or less narrow, with a circular to irregular opening (up to several cm wide)
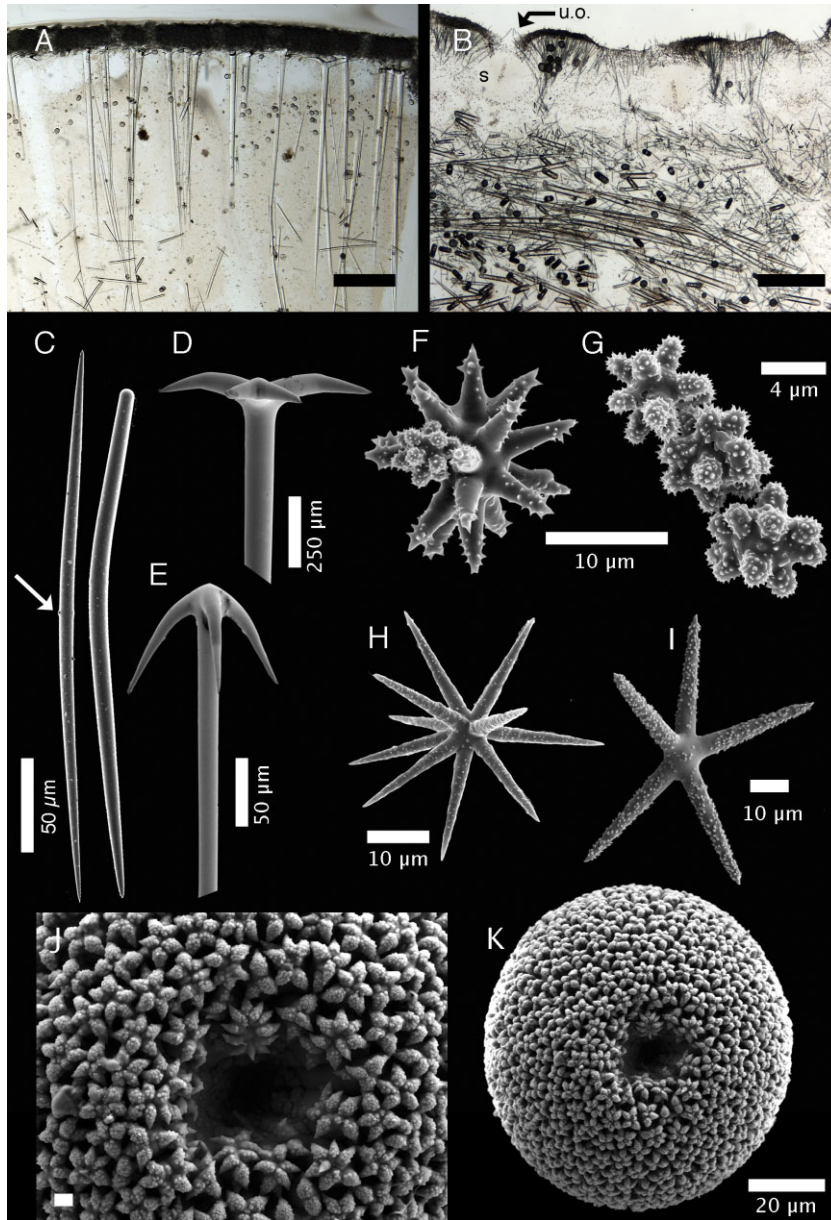
Figure 9. Sections and spicules of *Geodia barretti* Bowerbank, 1858. A, thick section showing the cortex essentially made of sterrasters, and underlying large dichotriaenes. Scale bar: 1 mm. B, thick section in a preoscule showing the uniporal oscules (u.o.) with a single sphincter (s). Between the oscules, bundles of microxeas and strongylasters. Note the near absence of sterrasters. Scale bar: 500 μm. C, microxeas, rarely modified to microstyles (ZMBN 77922, Korsfjord). Arrow points at centrotylote portion. D, dichotriaene (UPSZMC 78260, Davis Strait). E, anatriaene (UPSZMC 78260, Davis Strait). F, oxyaster II (ZMBN 77922, Korsfjord). G, strongylasters (ZMBN 77922, Korsfjord). H, oxyasters I (PC359, western Ireland). I, oxyasters I (Balgim CP98-47). J, close-up on the hilum of a sterraster. Notice the warty rosettes (ZMBN 77922, Korsfjord). Scale bar: 2 μm. K, sterraster (ZMBN 77922, Korsfjord).

(Fig. 7A–F). Preoscules are generally on top. The preoscule contains uniporal oscules (Fig. 7G). Each oscule (1 mm in diameter) has a sphincter. Cribriporal pores are scattered over the entire body surface (Fig. 7H); single pores are 50–80 μm, and poral sieves are *c.* 0.5 mm. The cortex is 0.4–0.6 mm (ectocortex: *c.* 250 μm, endocortex: *c.* 750 μm) (Fig. 9A). In the preoscule, the cortex is without sterrasters and triaenes (Fig. 9B), and ridges of microxeas and strongylasters surround the uniporal oscules (Figs 7G, 9B).
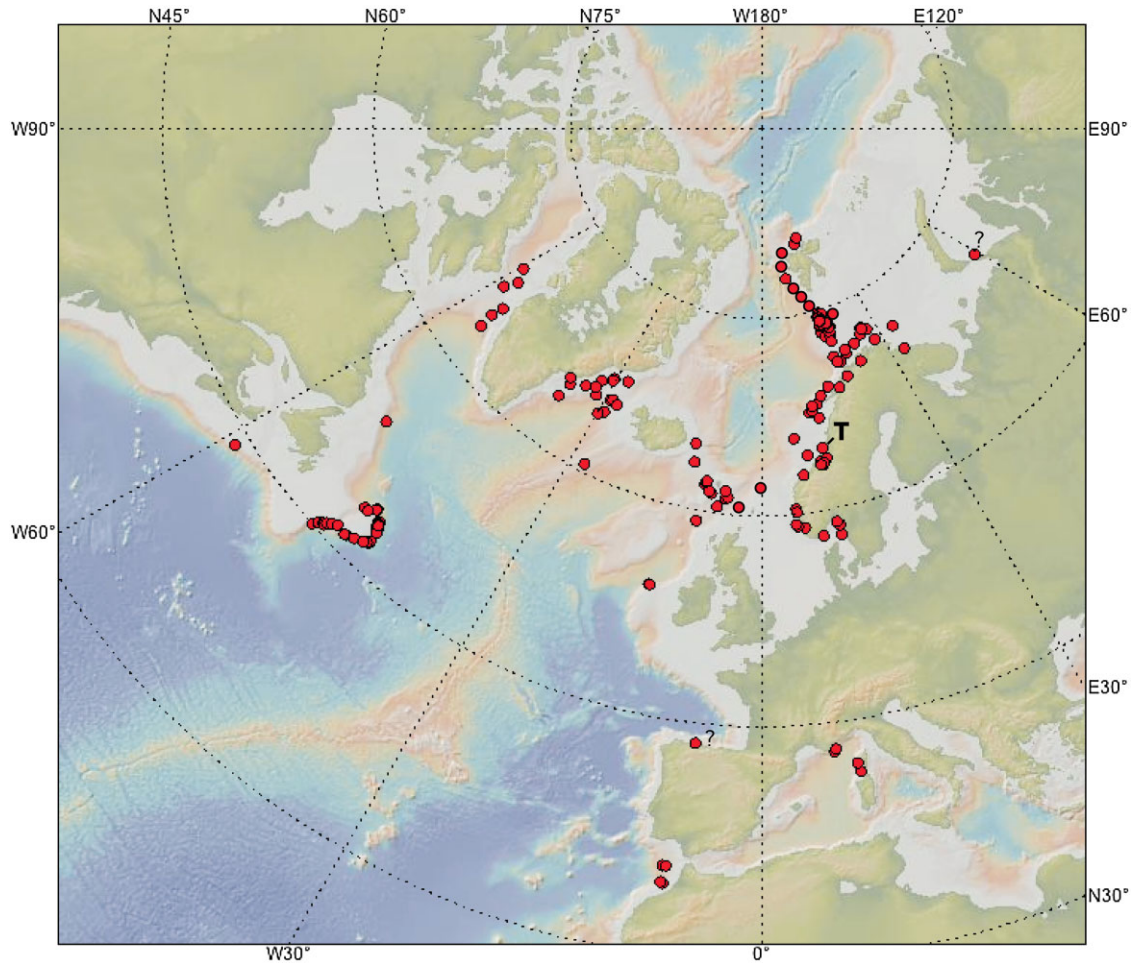
Figure 10. Distribution of *Geodia barretti* Bowerbank, 1858 (map made with GeoMapApp, http://www.geomapapp.org). T, type locality; ?, dubious records.

Description of type material: Medium-sized oval specimen (length: 12 cm, width: 8 cm) from Bowerbank (1872a: plate XI) which has been cut into five pieces (the main specimen and four smaller pieces); three Bowerbank slides including spicule preparation, section, and cortex surface.

Spicules (Fig. 9, Table 2): Megascleres: (a) oxeas I, straight or bent, length: 1075–4450 μm; width: 15–75 μm. (b) Oxeas II, straight or bent, rarely modified to styles, sometimes slightly centrotylote, length: 190–900 μm; width: 4–16 μm. (c) Dichotriaenes, rare orthotriaenes, rhabdome length: 620–4600 μm; width: 20–150 μm; orthotriaene clad length: 240–500 μm; protoclad length: 100–400 μm; deuteroclad length: 45–450 μm. (d) Anatriaenes, rhabdome length: more than 7.4 mm; width: 9–40 μm; clad length: 50–250 μm. (e) Meso/protriaenes (rare), rhabdome length: up to 2640 μm; width: 7.5–15 μm; clad length: 25–115 μm; central clad length: 25–98 μm. Microscle-

res: (f) sterrasters, spherical to elongated, length: 65–130 μm, width: 51–105 μm, thickness: 60–80 μm; hilum diameter: 12–23 μm. Rosettes are made of 3–7 rays, covered with warts; rosette diameter: 4–7 μm. (g) Strongylasters, rough actines, 3–11 μm in diameter. (h) Oxyasters I (only in very deep specimens > 1000 m), rough actines, diameter: 30–80 μm. (i) Oxyasters II, rough actines, diameter: 6–32.5 μm.

The spiculogenesis of shallow specimens (30–50 m depth) being somewhat disrupted, their spicule measurements have not been included here but they are shown in Table 2 and discussed in Cárdenas & Rapp (2013).

DNA barcodes: We found two haplotypes for the COI Folmer marker. GenBank accession nos. HM592679, HM592695, and EU442195: haplotype 1 from Spitsbergen (5), southern, western, and northern Norway (12), Sweden (1), off western Ireland

Table 2. Individual spicule dimensions and cortex thickness for specimens of *Geodia barretti* (in μm) collected at different depths

Material	Depth (m)	Cortex thickness (mm)	Strongylasters (diameter)	Sterrasters (diameter)	Oxyasters I (diameter)	Oxyasters II (diameter)	Ortho-dichotriaenes (rhabdome: length/width)	Ortho-dichotriaenes (ortho/proto/deuteroclads)
Trollholmflua MNHN-DCL4098	31	0.5	3.9–**5.6**–7.5*	26.9–**40.1**–51.9*	n.f.	7.8–**11.7**–15*(18)	260–**1044.5**–2175/ 5–**19.9**–40	70–**207.0**–300/ –/ –
Søndre Brevik ZMO B1375	40–80	n.o.	5–**7.5**–11	85–**98.9**–115	n.f	10–**19.1**–32.5	620–**2606.1**–3500(24)/ 28–**98.6**–150	150–**201.1**–260/ 65–**193**–300
Skagerrak ZMBN 85201	137–149	0.48–0.55	3.5–**5.7**–8	65–**74.2**–83	n.f.	10.5–**13.0**–15.5	1225–**2020.8**–2350(6)/ 25–**69.4**–90(17)	100–**209.3**–270 (24)/ 45–**145.0**–250 (28)
Korsfjord ZMBN 77922	200–400	0.55–0.65	4.5–**6.8**–10.1*	66.5–**79.3**–90.1*	n.f.	9.9–**15.3**–22*	3000–**3200**–3480(3)/ 50–**80**–100(11)	120–**194.8**–250/ 40–**195.9**–300 (27)
Spitsbergen ZMBN 89716	215	0.45	5–**7.3**–10	68–**89.0**–99/ 70–**78.0**–90	n.f.	6–**11.4**–16	1020–**2478**–3200/ 20–**79.5**–100	240–**385.6**–500(16)/ 200–**268**–400/ 60–**170.3**–300
Davis Strait UPSZMC 78260 (PA2010-set 141)	410	0.6	5–**7.2**–10	85–**104.6**–117/ 51–**81**–92	n.f.	9–**13.7**–20	2589–**2994.4**–3496/ 104–**120.9**–135	189–**228.4**–358/ 82–**160.8**–261
Flemish Cap UPSZMC 78268 (BC89)	1574	0.5	4–**6.4**–9	100–**112.2**–125	12.5–**24.9**–42.5		1850–**2562.5**–3000/ 90–**114**–130 (20)	–/ 150–**193.4**–250/ 130–**260.4**–400 (26)
Porcupine Bank ZMBN 85202	1818	<1	3.8–**5.1**–6.6*	84–**90.7**–101/ 75–**81.9**–92	31.5–**43.7**–58.8*	11–**17.3**–25.6*	n.o.	n.o.
Ibero-Moroccan gulf BalgimCP98-47	1747	0.45	3–**4.6**–7.5	92–**105.8**–130/ 70–**81.2**–105	30–**50.4**–80	10–**16.8**–25	3100–**4007.4**–4600(27)/ 70–**107.8**–120	–/ 170–**216**–290/ 175–**283**–450 (15)

Table 2. *Continued*

Material	Oxeas I (length/width)	Oxeas II (length/width)	Anatriaenes I (rhabdome: length/width)	Anatriaenes I (clad)	Anatriaenes II (rhabdome: length/width)	Anatriaenes II (clad)	Pro(meso)triaenes (rhabdome: length/width)	Pro(meso)triaenes (clad/central clad)
Trollholmflua MNHN-DCL4098	720–**1656.7**–2275/ 4–**20**–28	178–**299.9**–560/ 2.5–**4.2**–7	1375–**1790**–2475/ 3–**6.3**–10(5)	0–5–**31**–50 (5)	n.f.	n.f.	n.f.	n.f.
Søndre Brevik ZMO B1375	2050–**2743.5**–3400/ 25–**56.1**–73	235–**302.2**–375/ 5–**10.7**–14	n.f./ 20	150	n.f.	n.f.	n.f./ 10–15(2)	25–40(2)/ 25–50(2)
Skagerrak ZMBN 85201	1650–**2390.5**–3025/ 23–**44.5**–75	290–**371.6**–460/ 6.5–**8.6**–12	2800–**2987.5**–3525(4)/ 9–**14.2**–23	60–**132**–170	n.f.	n.f.	n.f.	n.f.
Korsfjord ZMBN 77922	2125–**3166**–3575/ 50–**58.6**–75 (20)	250–**302.5**–350/ 6.5–**8.3**–10	2250–**2947.7**–3440(11)/ 10–**19**–30	60–**122.4**–160	n.f.	n.f.	n.f.	n.f.
Spitsbergen ZMBN 89716	1580–**2774.5**–3520/ 15–**45.6**–70	260–**311.2**–375/ 4–**8.6**–12	1925–**3115.2**–4880(22)/ 10–**14**–20	90–**128**–200	n.f.	n.f.	2640/ 10(2)	50–100(2)/ 50–60(2)
Davis Strait UPSZMC 78260 (PA2010-set 141)	2419–**2646.8**–3194/ 44–**54.9**–68	242–**331.1**–396/ 6–**13.6**–16	1573–**3016**–391/ 10–**21**–29	34–**113**–158	n.f.	n.f.	n.f.	n.f.
Flemish Cap UPSZMC 78268 (BC89)	1825–**3798.2**–4440/ 22–**51.4**–65 (20)	205–**261**–410/ 4–**10.5**–17.5	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.
Porcupine Bank ZMBN 85202	1525–**2566.3**–4300/ 25–**43.4**–75	220–**381.3**–630/ 7–**8.9**–13	n.o.	n.o.	n.o.	n.o.	n.o.	n.o.
Ibero-Moroccan gulf BalgimCP98-47	2127–**3415.7**–4450/ 30–**50.4**–61	275–**388.2**–900/ 7–**8.5**–12	>7400/ 15–**30.6**–40 (14)	50–**157**–250 (13)	580–**1104**–1950/ 4–**6.6**–14	35–**73.2**–130	>1900/ 10(2)	120–130(2)/ 40

Means are in bold; other values are ranges; $N = 30$ unless stated otherwise in parentheses, or unless measurements come from other studies. A dash indicates that this measurement is not given in the literature. n.f., not found; n.o., not observed in the specimen in our possession (usually because the sample was too small).
*SEM measurements.

(2), Davis Strait (1), Flemish Cap (1), and the Mediterranean Sea (1). No. KC574389: haplotype 2 (1-bp difference with haplotype 1 in position 382: 'A' instead of 'T') was found in two specimens from the Flemish Cap (UPSZMC 78262, UPSZMC 78268). Nos. EU552080, HM592809 (28S, C1-D2 domains): we have sequenced 28S (C1-D2) from specimens from Spitsbergen (1), western Norway (2), and off Ireland (1): we did not observe genetic differences in this marker among NEA specimens. No. KC481224 (18S), obtained from ZMBN 77922 (Korsfjord, Norway) and ZMBN 89722 (Spitsbergen): no variation was observed.

Distribution (Fig. 10): Geodia atlantica, G. barretti, and *G. hentscheli* may have been confused in the past, especially until the description of *G. atlantica* by Stephens (1915) and *G. hentscheli* by Hentschel (1929), and above all when juveniles were found (e.g. Burton, 1949). This should be kept in mind when examining the *G. barretti* distribution map that includes a few records not verified by us. However, we did check specimens from Fristedt (1887) (SMNH), Lundbeck (1909) (ZMUC), Boury-Esnault *et al.* (1994) (MNHN), Voultsiadou & Vafidis (2004), Nichols (2005), and van Soest *et al.* (2007) (ZMAPOR). Specimens from Voultsiadou & Vafidis (2004) and van Soest *et al.* (2007) were mis-identifications (cf. Discussion). The record in the Asturias (Spain) given by Ferrer-Hernández (1918) at 150–300 m depth is based on slides, and it is dubious as it seems too shallow for this species at this latitude, but he unfortunately gives no description. Other identifications could be confirmed by accurate descriptions and plates (e.g. Vosmaer, 1882). *Geodia barretti* has been found at depths from 30 to 2000 m. Most NEA records are from between 200 and 500 m, at temperatures of 4–8 °C; Grand Banks, Flemish Cap, Nova Scotia, and Davis Strait specimens were found at 410–1852 m, at temperatures of 3–5 °C. Shallow specimens from the western Norwegian coast have been collected at temperatures of 3–9 °C, and possibly experience up to 14–15 °C in September–October (Cárdenas & Rapp, 2013). The only specimen we identified from the Mediterranean Sea was collected at 167 m where the water temperature is around 13 °C and the salinity usually more than 38 p.p.m. Localities where the species occurs at lower temperatures, down to 0.4 °C, were only found in the Denmark Strait. Breitfuss (1930) reports *G. barretti* in the southern part of the Kara Sea at –1.75 °C but we have not examined this specimen, and because no other records exist of this species in this area, this record needs to be confirmed and is here considered dubious.

Blacker (1957) only gives the coordinates for his 1949 and 1950 trawls; we could not find coordinates for the 1951, 1952, 1954, and 1955 trawls. Likewise, Dyer *et al.* (1984) do not give coordinates for their 1978–81 trawls. We therefore manually copied on Figure 10 the *G. barretti* records between northern Norway and Spitsbergen from figure 3c in Dyer *et al.* (1984), which also integrates the Blacker (1957) localities.

Biology: Gametogenesis has been well studied as well as the annual reproductive cycle (Spetland *et al.*, 2007). This study on Scandinavian fjord populations shows that *G. barretti* is (1) gonochoric and oviparous and that (2) reproduction coincides with phytoplankton blooms. Gametogenesis usually takes place from February to May with a gamete release in early summer; sometimes a second gametogenesis/spawning event takes place later in the summer (Spetland *et al.*, 2007). In our only specimen from the Mediterranean Sea, collected on 22 August 2010, spermatogenesis was observed. We found no indications of asexual reproduction in this species.

Geodia barretti survives well in tanks in open circulation systems. Specimens at Tjärnö Marine Biological Laboratory (University of Gothenburg) and High-Technology Center (University of Bergen) have been kept in tanks for two years and we have even observed release of sperm cells (Rapp & Cárdenas, unpublished results). Cultivation of explants has also been successful, and has led to studies on growth and regeneration (Hoffmann *et al.*, 2003), stability of the microbial community (Hoffmann, Rapp & Reitner, 2006), as well as oxygen dynamics (Hoffmann *et al.*, 2005), the last showing the importance of anaerobic processes within this species. Actually, both aerobic (nitrification) and anaerobic (denitrification) microbial processes were later detected in *G. barretti* (Hoffmann *et al.*, 2009; Radax *et al.*, 2012a, b), thus suggesting the complexity of the nitrogen cycle in *G. barretti*. The microbial community was further studied and understood using conventional bacterial cultivation and 16S rDNA clone libraries (Graeber *et al.*, 2004) or using a metatranscriptomic approach (Radax *et al.*, 2012a). In *G. barretti*, this community seems to be dominated by three prokaryotic groups: phylum *Chloroflexi* (SAR202 cluster), the candidate phylum *Poribacteria*, and *Acidobacteria*; potential eukaryotic symbionts were poorly represented (< 1%) (Radax *et al.*, 2012a).

The sponge-feeding chiton *H. nagelfar* and the parasitic foraminiferan *H. sarcophaga* have been found living on *G. barretti* in the NEA (Warén & Klitgaard, 1991; Cedhagen, 1994; Todt *et al.*, 2009). Predators such as the aforementioned chiton may cause surface injuries which are later filled with sediments and spicules, and encapsulated in new sponge tissue, thus forming large inclusions (Hoffmann *et al.*, 2004). Klitgaard (1995) shows that, overall, this species has less associated macrofauna

than any of the other boreo-arctic *Geodia* species: only ten different species of epibionts were recorded vs. 62 for *G. macandrewii*. The chemistry (elemental analysis, amino acids, sterols and quaternary ammonium compounds) has been investigated by Hougaard *et al*. (1991a, b). Brominated cyclodipeptides have been particularly studied in *G. barretti*. Three structurally similar brominated cyclodipeptides (barettin, 8,9-dihydrobarettin, and bromobenzisoxazolone barettin) were isolated and described (Lidgren *et al*., 1986; Sölter *et al*., 2002; Sjögren *et al*., 2004; Hedner *et al*., 2008). Experiments have shown that these three cyclodipeptides inhibit settlement of barnacle larvae [*Amphibalanus improvisus* (Darwin, 1854)] in a dose-dependent manner (Sjögren *et al*., 2004; Hedner *et al*., 2008), thus suggesting that these chemicals may play a role in preventing fouling of the sponge surface. It has further been shown that barettin and 8,9-dihydrobarettin act in synergy against foulers (Sjögren *et al*., 2011). These compounds may also be involved in defence against grazers or predators [deterrence experiments with the hermit crab *Pagurus bernhardus* (L., 1758)] (Sjögren *et al*., 2011). The spelling of 'barettin' with only one 'r' is due to a misspelling of *G. barretti* with one 'r' in the original paper describing this molecule (Lidgren *et al*., 1986).

Distinctive characters: External morphology: the generally smooth surface (absence of hispidity and epibionts) and white colour. The irregular form, especially in specimens larger than about 15 cm in diameter. The clearly visible sieves in the sometimes numerous preoscular cavities. Spicules: usually dichotriaenes and strongylasters (but these characters are not sufficient as *G. hentscheli* can also have both).

Remarks: As explained before (Cárdenas *et al*., 2010), we stress that *G. barretti*'s oscules are not covered by a sieve. There is a depression called a preoscule, in which we find single uniporal oscules (without any kind of sieve). Every oscule has its own unique sphincter, and this is clearly visible with the naked eye (Fig. 7G) or in a thick section (Fig. 9B). We find the same arrangement in *G. hentscheli* (cf. below).

Burton (1949) identified some very small *Geodia* specimens as *G. barretti*; this identification is probably wrong, as the specimens seem to have been buds, and came from 'an unspecified point in the Arctic and from an unknown depth'. But he pointed out the similarity of some of his specimens to *G. parva*. Indeed, what he had in front of him must have been buds from *G. hentscheli* or *G. parva*.

Sidonops sp. (ZMB Por 7552) described by Hentschel (1929) has cribriporal pores and uniporal oscules in large preoscules (7–3.5 cm in diameter), and has microxeas and strongylasters. According to these characters and pictures of the specimen (courtesy of C. Lueter, ZMB), we can be sure that this is *G. barretti*. Of the two *G. barretti* specimens reported by van Soest *et al*. (2007) from Rockall Bank, only one was found in the collection (ZMAPOR 19647) and it turned out to be *G. atlantica*.

We examined a spicule slide of the specimen identified as *G. barretti* from the Mediterranean Sea (specimen A183), collected at a surprising 4–6 m depth in the Aegean Sea (Voultsiadou & Vafidis, 2004). In our opinion, this is a misidentification; the dichotriaenes and oxyasters are typical of *Geodia conchilega* Schmidt, 1862, a common Mediterranean shallow species for which we had comparative material (e.g. MNHN DNBE-846, *G. conchilega* from Banyuls, France, collected and identified by N. Boury-Esnault). But we did identify a *G. barretti* specimen collected in the 'Canyon des Moines' (south Corsica) at 167 m depth ('CorSeaCan' campaign with the ROV *Achille*). The spicule morphologies match those of our other specimens: there are only oxyasters II (10–35 μm); microxeas can be slightly bent and are occasionally centrotylote; the cortex thickness is standard (0.5–0.6 μm). The main and only difference we could find is that the spherical sterrasters are smaller (56–59.9–65 μm) than in the Atlantic *G. barretti* (Table 2), except those from shallow waters. It had the same COI Folmer haplotype 1 as all the NEA and most of the NWA specimens. This is the first true record of this species in the Mediterranean Sea. At least six additional sightings between 167 and 199 m depth (without collection) of *G. barretti*-like specimens were made during the 'MedSeaCan' and 'CorSeaCan' campaigns: in the 'Banc de Magaud', 'Banc de Niou-large' (both off the Côte d'Azur), and 'Canyon de Cargèse' (western Corsica) (J. Vacelet & M. Fourt, pers. comm.). Overall, these *G. barretti*-like specimens seem less smooth than northern ones, with regular small bumps on their surface (where megascleres cross the cortex and retain sediments); unlike the NEA specimens, they always had a single deep, wide preoscule (*c*. 3 cm in diameter). We cannot be completely sure they are all *G. barretti* because *Geodia megastrella* Carter, 1876 can have a very similar external morphology, although it has never been observed in the Mediterranean (although we have found it in the Balgim material collected off Morocco, along with *G. barretti*).

The spiculogenesis of shallow specimens (30–50 m) is disrupted so that spicule morphologies are somewhat different (Cárdenas & Rapp, 2013). Thus, it has been shown that *G. simplicissima* from northern Norway is actually a *G. barretti* growing in shallow waters. *G. simplicissima* has therefore been put in synonymy with *G. barretti* (Cárdenas & Rapp, 2013).

We examined the holotype of *Geodia barretti divaricans* [MOM 04-1333 (wet specimen) and MNHN DT-1299 (type slide)]. In the choanosome, it has slightly spined oxyasters which can reach a very large size (25–70 μm in diameter) and just under the cortex strongly spined oxyspherasters (17–22 μm in diameter), which are different from the oxyasters II of *G. barretti*. *Geodia divaricans* is clearly different from *G. barretti*.

Geodia barretti senegalensis was elevated to the species rank by Burton (1956) without any explanation. We therefore examined the holotype of *G. barretti senegalensis* (MNHN DT-3241, dry specimen). This shallow *Geodia* does not have a preoscule so it is certainly not *G. barretti* and *G. senegalensis* is a valid species. The external morphology looks more similar to some specimens of *Geodia gibberosa* Lamarck, 1815 from the Caribbean reefs.

Specimens from the Ibero-Moroccan Gulf (Fig. 8A–C) collected during the 'Balgim' campaign (CP63-E2, CP98-47) have a few differences from the rest of the specimens (Boury-Esnault *et al.*, 1994). The preoscules are covered with sediment and the preoscule cortex is loosely attached to the underlying choanosome (Fig. 8B, C). Small anatriaenes II have been found in the preoscule, along with a few pro(meso)triaenes. Their presence may be due to the large amount of sediments in the preoscule, a condition seldom observed in boreo-arctic specimens where preoscules are usually clean of sediments and usually more firmly attached to the choanosome in northern specimens (Fig. 8D). We decided to consider these anatriaenes as a second size category as such smaller anatriaenes were never observed in other specimens. The microxeas are essentially straight, usually slightly thicker on one half, and never centrotylote, but the straightness seems to be a common feature of all NEA and NWA specimens collected at more than 1000 m depth (e.g. ZMBN 85202 from Ireland, UPSZMC 78259 from the Flemish Cap). When spicules of Balgim specimen CP98-47 were examined by SEM, we could not find any other differences with our SEM observations of Norwegian and deep Ireland specimens. Together, these differences (dirty preoscule and anatriaenes II, slightly asymmetrical microxeas never centrotylote) do not justify a new species for the time being. More specimens and genetic data would be necessary to understand the status of this southern population, probably related to the Mediterranean Sea populations (Fig. 10). Specimen CP63-E5 had unusually large sterrasters (125–155 μm), orthotriaenes, and a fairly thick cortex (1 mm thick), so we re-identified it as *G. megastrella*.

No morphological differences were found between specimens from the NWA (Flemish Cap, Nova Scotia, Davis Strait) and specimens from the NEA. We just note that some NWA specimens were very hispid (e.g. UPSZMC 78268–78269), a feature never observed in NEA specimens. NWA Specimens deeper than 1000 m depth do have oxyasters I but they are much smaller (*c.* 32–42 μm) than in NEA specimens deeper than 1000 m (up to 58–80 μm), and more difficult to consider as a separate size category. Also, NWA specimens deeper than 1000 m have subspherical sterrasters, not elongated like in NEA specimens collected at the same depths. No morphological differences were observed between the two haplotypes (Table 2: UPSZMC 78269 vs. other specimens). Interestingly, haplotype 2 is closer by 1 bp to the sequence of *G. hentscheli* than haplotype 1: it is therefore closer to the common ancestor of these sister-species, which would suggest that the common ancestor lived in the NWA. It so happens that UPSZMC 78268 (haplotype 2) was initially identified as *G. hentscheli* due to its important hispidity, spherical shape, and narrow unique preoscule (see a complete description of UPSZMC 78268 on the Sponge Barcoding Project, http://www.spongebarcoding.org). Further work is needed to see if haplotype 2 has a consistently *G. hentscheli*-like morphology (as in Fig. 7A).

Blacker (1957) and Dyer *et al*. (1984) sampled extensively between northern Norway and Spitsbergen between 1949 and 1981 and found extensive sponge grounds. But when O.S.T. participated in the Meteor 1990 cruise in the same area, very few *Geodia* were collected (Barthel, Tendal & Witte, 1991). Eight triangular dredges were made in the southern area off Bear Island, and only one small *Geodia* was collected. In the northern area off Spitzbergen numerous triangular dredges were made and no *Geodia* were collected; a single large specimen of *G. macandrewii* was taken by a hyperbenthic sledge. There is a possibility that the reason for this sampling discrepancy is the sampling method – Blacker (1957) and Dyer *et al*. (1984) used a trawl while a large triangle-dredge was essentially used on the Meteor – but this does not seem very likely. Alternatively, the large masses of sponges earlier reported may have disappeared since 1981 due to an inflow of very cold water from the north, intensive trawling activity in the area, or disease, although it is difficult to believe that any of these would hit such a large area. It is also possible that the Meteor cruise was rather unlucky in finding sponge grounds. The 'Ecosystem Barents Sea' cruise in 2007 collected tonnes of *Geodia* in station 2562, but this was much closer to the Norwegian coast (*c.* 80 km).

Mass mortality of *G. barretti* was actually observed in the Kosterfjord area (southern Norwegian and western Swedish waters) and started in the winter of 2006/07; this may be due to unusually high

temperature and a deepening of the thermocline in 2006 and 2008 in this region (Guihen *et al*., 2012). Maximum temperatures in the autumn 2006/08 at Tisler reef were 12.5 °C instead of 9 °C in other years. However, shallow specimens at 30 m depth on the western Norwegian coast seem to experience up to 14–15 °C in September–October (Cárdenas & Rapp, 2013). So the dramatic rate of change in temperature in the Kosterfjord (4 °C in less than 24 h) is more likely to be one of the causes of this mass mortality. The population still suffers from the incident and the mortality is still high (P.C. & M.T., ROV observations at *c*. 80 m depth in Swedish waters of the Kosterfjord in May 2012).

GEODIA HENTSCHELI CÁRDENAS *ET AL*., 2010

DEPRESSIOGEODIA^P HENTSCHELI

(*PhyloCode* SPECIES NAME)

(FIGS 11–14, TABLE 3)

Sidonops mesotriaena, Hentschel, 1929: p. 865 (junior homonym by Cárdenas *et al*., (2010)).

Geodia mesotriaena, Burton, 1934: p. 6; Koltun, 1964: p. 147; 1966: p. 52; Barthel & Brandt, 1995: p. 223; Klitgaard & Tendal, 2004: p. 57.

Geodia hentscheli, Cárdenas *et al*., 2010: p. 89; Cárdenas *et al*., 2011: table S1; Tangen, 2011: p. 47.

Misidentification:

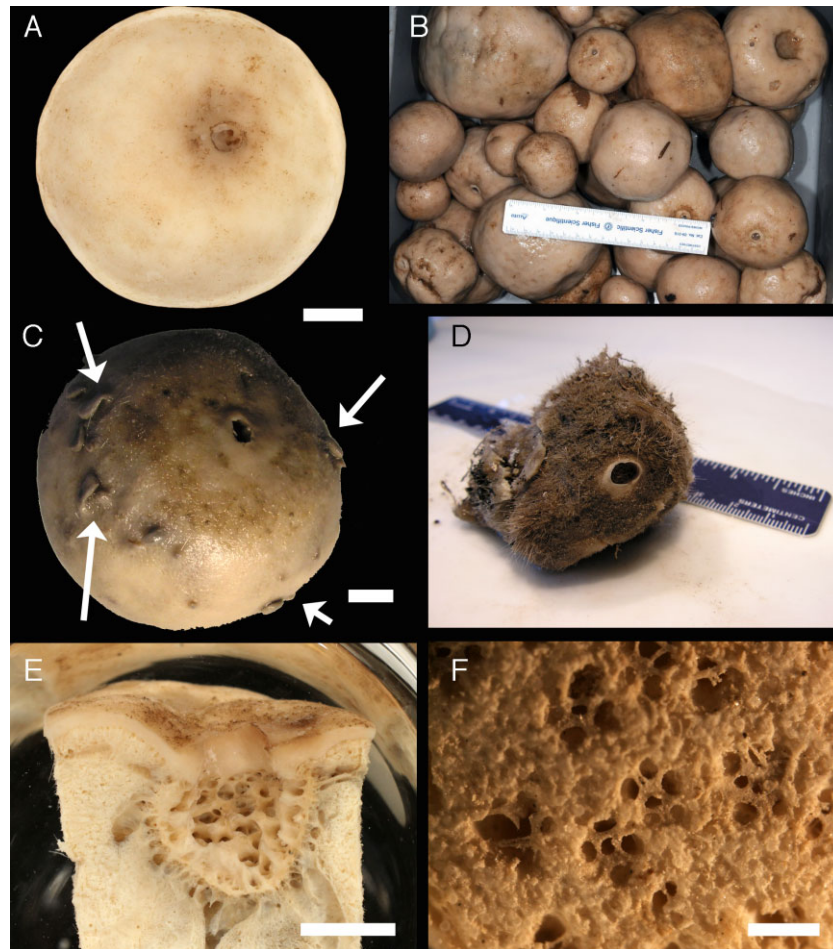*Geodia nodastrella*, Burton, 1934: p. 6.

Figure 11. External morphology of *Geodia hentscheli* Cárdenas *et al*., 2010. A, specimen UPSZMC 78266 (fixed in ethanol) from Davis Strait, 847 m depth. B, specimens just dredged in the Davis Strait at 847 m depth (photo courtesy of DFO Canada Central and Arctic Region). C, specimen from Ingolf Exp., st. 78, south of Iceland, 1462 m depth (fixed in ethanol). The arrows point at the buds. D, specimen PC221 (fixed in ethanol) from the Schultz Massif, 1262 m depth. E, cross-section in the preoscule of specimen UPSZMC 78266 (Davis Strait, 847 m). Note the massive and irregular ridges between the oscules. F, cribriporal pores of PC16 (northern Iceland, 604 m). Scale bars: A: 5 mm; C, E: 1 cm; F: 0.2 mm.
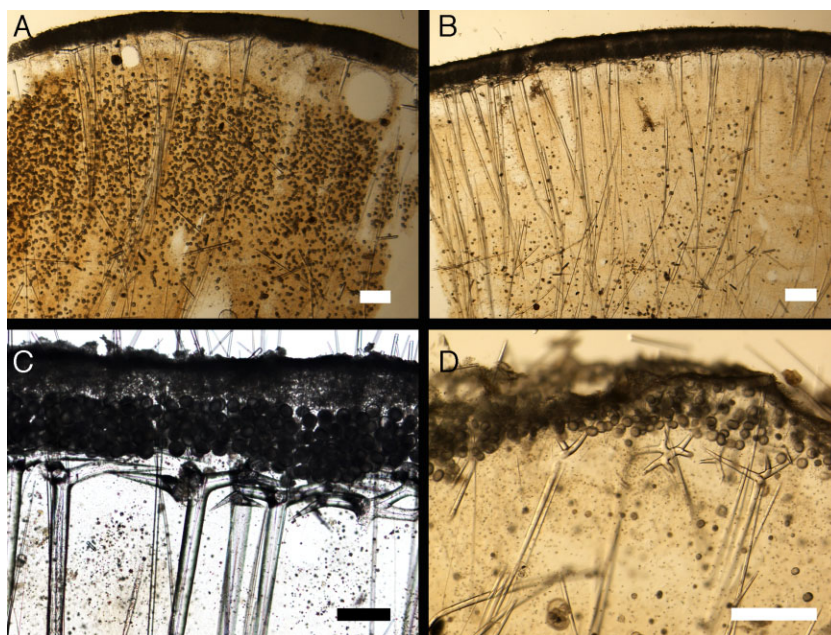
Figure 12. Thick sections of *Geodia hentscheli* Cárdenas *et al.*, 2010. A, paratype ZMB Por 7551. B and C, Ingolf Exp., st. 78, south of Iceland, 1462 m depth. D, ZMBN 77925, lower slope of the Schultz Massive Seamount, 1997 m. Scale bars: A, B and D: 500 μm; C: 300 μm.

Type locality and deposition of types: Hentschel (1929) explicitly designated a holotype (ZMB Por 7549 has an old label saying 'Sidonops mesotriaena n. sp. Typ') from north of Spitsbergen, station 41, 81°20′N, 20°30′E, 1000 m, 11ᵗʰ of August 1898. Paratypes are ZMB Por 7545–7546, 7548, 7550–7551, 8421, all from st. 41 and st. 40 (81°22′N, 21°21′E, 650–1000 m).

External morphology and cortex: The body is spherical (Fig. 11A–D), up to about 15 cm in diameter. The colour alive is white to light yellow or brownish. With the use of ROVs, we found that this species can be entirely covered with long spicules, making them look very fury (Fig. 11D), which may be lost when dredged, and specimens then seem completely smooth (Fig. 11A–C). Some specimens are budding (Fig. 11C), and buds are usually columnar with sometimes a small peduncle. A preoscule opening, usually narrow (up to 1.8 cm in diameter), occasionally up to three, is found on the top side. This preoscule is even observed in young specimens (8 mm in diameter). These preoscule openings are often surrounded by a narrow elevated ring with a thickened cortex. Sometimes, in large specimens, the preoscule opening 'sinks' in the sponge body (one such specimen can be seen in the upper right corner of Fig. 11B). As in *G. barretti*, uniporal oscules are concentrated in the preoscule (Fig. 11E); the cortex there is without sterrasters, and ridges of microxeas and strongylasters surround oscules. These ridges can be much more developed

than in *G. barretti*. The cribriporal pores are scattered over the sides of the body (total diameter of the sieve: 0.1–0.2 mm) (Fig. 11F). The sterraster layer is elastic, 0.25–1.4 mm thick (Fig. 12), with the ectocortex poorly developed (0.1 mm thick, in holotype) (Fig. 12B) to well developed (0.3 mm thick) (Fig. 12C).

Description of type material: The holotype ZMB Por 7549 is cut into four pieces. For this study, we have examined only a small slice of the paratype ZMB Por 7551. Thick sections of ZMB Por 7551 made during this study (Fig. 12A) are now stored at the ZMB. Figure 13 shows SEM pictures of the spicules of the paratype ZMB Por 7551.

Spicules (Fig. 13, Table 3): Megascleres: (a) oxeas I, straight or bent, length: 1200–5175 μm; width: 29–82 μm. (b) Oxeas II, usually straight (sometimes slightly bent), sometimes slightly centrotylote, length: 142–610 μm; width: 5–23 μm. (c) Ortho- to dichotriaenes, rhabdome length: 252–4060 μm (maximum length was measured by Hentschel, 1929); width: 22–145 μm; orthotriaene clad length: 196–835 μm; protoclad length: 60–520 μm; deuteroclad length: 96–492 μm. (d) Anatriaenes, rhabdome length: more than 6000 μm; width: 17–43 μm; clad length: 90–308 μm. (e) Meso/protriaenes, rhabdome length: up to 4185 μm; width: 17–36 μm; clad length: 87–224 μm; central clad length: 98–196 μm. Microscleres: (f) sterrasters, usually spherical, some are very
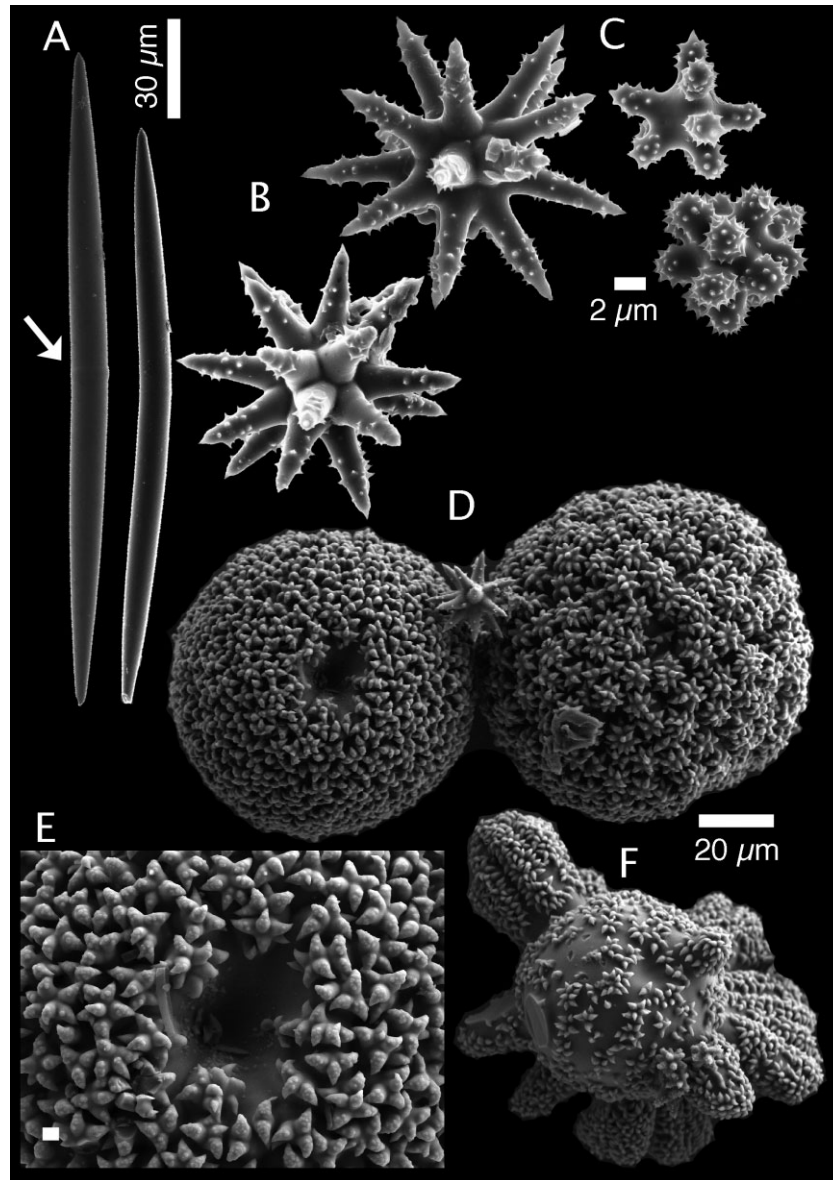
Figure 13. Spicules of the paratype ZMB Por 7551 of *Geodia hentscheli* Cárdenas *et al*., 2010. A, microxeas. Arrow points at centrotylote portion. B, oxyasters. C, strongylasters. D, sterrasters and oxyaster. E, close-up on the hilum of a sterraster. Notice the warty rosettes. Scale bar: 2 μm. F, irregular sterraster.

irregular, 56–102 μm in diameter; thickness: 55–80 μm; hilum: 12–20 μm. Rosettes are made of 3–7 rays, covered with warts. Rosette diameter: 5–6 μm. (g) Strongylasters to sphero-strongylasters, spiny, 4–22 μm in diameter. (h) Oxyasters, spiny, with a more or less inflated centrum, with 4–20 rays, diameter: 10–62 μm.

DNA barcodes: GenBank accession nos. HM592671, EU442197 (Folmer COI): we have sequenced COI from specimens from northern Iceland (1), the Schultz Massive Seamount in the Greenland Sea (4), and the Davis strait (1): the Folmer COI is identical in all these specimens. No. EU552083 (28S, C1-D2 domains): we have sequenced 28S from two specimens from the Schultz Massive Seamount in the Greenland Sea, and no variation was observed. No. KC481226 (18S), obtained from UPSZMC 78042 (Schultz Massive Seamount).

Distribution (Fig. 14): Geodia hentscheli is an Arctic species. The species has been recorded at depths of 130–2000 m, at temperatures of –1.76 (eastern Greenland) to 4.5 °C (west of Iceland and Reykjanes
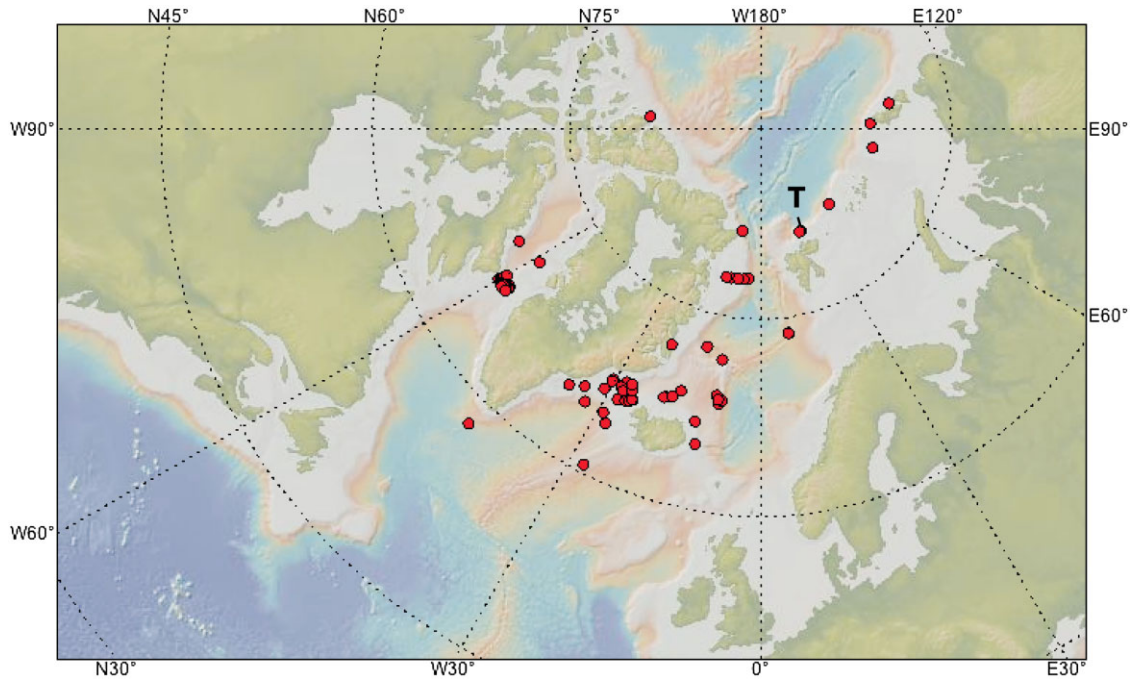
Figure 14. Distribution of *Geodia hentscheli* Cárdenas *et al*., 2010 (map made with GeoMapApp, http://www .geomapapp.org). T, type locality.

Ridge). The shallowest records (less than 200 m deep) come from the Canadian Ice Island at 81°N (Wagoner *et al*., 1989) and eastern Greenland (Burton, 1934; Koltun, 1964), the deepest records being off eastern Greenland, at temperatures of –1.76 to 0.4 °C. This species has not been found off Newfoundland.

Biology: Budding seems to be fairly common in this species (Fig. 11C). The isopod *Caecognathia robusta* (G. O. Sars, 1879) is a common epibiont living in the preoscule of this species (Barthel & Brandt, 1995). We have observed very few sponges living on the fur of *G. hentscheli* (e.g. Calcarea spp.).

Distinctive characters: External morphology: the almost spherical form with one narrow preoscular cavity on top. Also, usually there is a thickening of the cortex just around the oscule, and there might be more or less high ridges between the small oscules (inside the preoscule). Spicules: on average, small size and 'bumpiness' of the sterrasters, some sterrasters are very irregular, short and thick microxeas, large and sometimes irregular strongylasters. But one or all of these characters may be absent.

Remarks: We examined specimen B331 (ZMO) from East Greenland (137 m depth), identified as *G. nodastrella* by Burton (1934). A misidentification was suspected as *G. nodastrella* is a typical Lusitanian

deep-sea species, never formerly described from arctic waters. B331 (ZMO) is a small spherical specimen (8 mm in diameter) with two bundles of long spicules (mainly mesoprotriaenes) sticking out from it and a 0.5-cm-thick cortex. The presence of one very small preoscule opening already suggests that this is not *G. nodastrella* (which has cribriporal pores and oscules, no preoscules). Furthermore, the spicules clearly match those of *G. hentscheli*. Burton (1934) was probably misled by the strongylasters which, in Greenland and Icelandic specimens, can become large sphero-strongylasters (up to 22 µm in diameter in this specimen, larger than those measured in Table 3). We also examined the larger specimen B330 (ZMO) from the same catch and identified by Burton (1934) as *G. mesotriaena* (now *hentscheli*); this identification is correct.

In Table 3, the maximum size of oxyasters measured is 38 µm. But we also examined more specimens and we found that oxyasters could reach sizes of 48 µm (ZMBN 85205, Iceland, 604 m depth), 55 µm (UPSZMC 78266, Davis Strait, 847 m depth) or even 62 µm (PC18, Iceland, 800 m depth). These large sizes of oxyasters are not mentioned by Koltun (1966). We also noted that the NEA specimens have oxyasters with fairly thin actines (2 µm thick) whereas the three specimens from Davis Strait (PA2010-set 155) we examined have oxyasters with less numerous, thicker actines (up to 5 µm thick). There is also quite

Table 3. Individual spicule dimensions and cortex thickness for specimens of *Geodia hentscheli* (in μm) collected at different depths

Material	Depth (m)	Cortex thickness (mm)	Strongylasters (diameter)	Sterrasters (length/width)	Oxyasters (diameter)	Ortho/dichotriaenes (rhabdome: length/width)	Ortho/dichotriaenes (ortho/proto/ deuteroclads)
G. hentscheli Spitsbergen holotype (Hentschel, 1929)	650–1000	0.4–0.5	6–9.5	65–84/ 60–69	16–19	4060/ 70–90	560–840/ 98–210/ 336–378
Spitsbergen paratype ZMB Por 7551 (this study)	650–1000	0.4–0.5	6.5–**9.3**–13.9*	58.3–**79.2**–89.5*	14–**19.9**–25.9*	1200–**2347.2**–3250(9)/ 50–**82.2**–100	550–**684.3**–770(7)/ 190–**352**–520(5)/ 160–**242**–380(5)
Schultz Massive Seamount ZMBN 77925	1997	0.25–0.5	6–**8.8**–11	64–**69.2**–79	12.5–**21.3**–30	252–**1159.6**–1650(9)/ 22–**47.5**–74(25)	244–**360.8**–470(15)/ 60–**140**–300(7)/ 96–**156.6**–240(8)
Schultz Massive Seamount GS08-3e1 (Tangen, 2011)	1860–2560	0.3–0.7	n.f.	**63.5**	**19.9**	584–**1112.4**–1900/ **65** (7)	434–835(2)/ 133–**225.9**–367(7)/ 200–**320.4**–492(7)
South of Iceland Ingolf Exp., St. 78	1462	0.4–0.5	4–**6.6**–8	56–**67.3**–72	10–**20.7**–38	1575–**2560.3**–3080(14)/ 45–**77**–90	–/ 140–**175.5**–270/ 112–**218**–350
Davis Strait PA2010-09, set 155	847	1.1	9–**11**–14	73–**93.9**–102	16–**21**–28	1073–**2594**–3194/ 42–**102**–145	196–**507**–820/ 226–**262**–305(5)/ 172–**218**–279(5)

Table 3. *Continued*

Material	Oxeas I (length/width)	Oxeas II (length/width)	Anatriaenes (rhabdome: length/width)	Anatriaenes (clad)	Pro(meso)triaenes (rhabdome: length/width)	Pro(meso)triaenes (clad/central clad)
G. hentscheli holotype (Hentschel, 1929)	3642/ 42	168–336/ 9	–	308	3640/ 24	140–224/ 98–196
paratype ZMB Por 7551	1200–**2293.8**–3450/ 35–**46.4**–60 (25)	170–**216.8**–420/ 7–**10.4**–15	>3500/ 17–**28.9**–43 (15)	90–**155.3**–210 (15)	n.o.	n.o.
Schultz Massive Seamount ZMBN 77925	2575–5175/ 30 (2)	142–**187**–225/ 5–**8.9**–12 (3)	>2575/ 20–30 (4)	115–176 (3)	>1950/ 17	87/ 148
Schultz Massive Seamount GS08-3e1 (Tangen, 2011)	2240–**3753.3**–4900/ **29.7** (3)	400–**426.7**–480/ **11** (3)	n.o.	n.o.	n.f.	n.f.
South of Iceland Ingolf Exp., St. 78	2200–**3401.6**–4480/ 35–**44.3**–60 (13)	152–**236**–610/ 6–**8.2**–12	>6040/ 20–**25**–30(4)	90–**110**–120 (4)	n.f.	n.f.
Davis Strait PA2010-09, set 155	1815–**2638**–3726/ 29–**51**–82	174–**208**–247/ 13–**16**–23	n.f.	n.f.	3895–4185/ 21–36 (2)	107–119/ 161–177 (2)

Means are in bold; other values are ranges; $N = 30$ unless stated otherwise in parentheses, or unless measurements come from other studies. A dash indicates that this measurement is not given in the literature. n.f., not found; n.o., present but not observed in the sample in our possession, or broken. *SEM measurements.

a lot of variation of the strongylasters (more so than in *G. barretti*). As we noted earlier, they can be fairly large and fairly irregular, and their actines can also be so small that they look like irregular spheres. We also noted that some specimens from Davis Strait (e.g. UPSZMC 78266) have particularly large spicules overall and a much thicker cortex (1–1.4 mm) than other specimens we examined (Table 3), probably because they are larger specimens (> 10 cm). The smaller specimen UPSZMC 78267 (Fig. 11A), *c.* 3 cm in diameter, from the same station has a cortex of 0.55 mm. So cortex thickness may increase with size of specimens.

Based on their morphology, *G. barretti* and *G. hentscheli* have previously been considered sister species (Koltun, 1966): their spicule and external morphologies are very similar so that they can be easily confused. But spicule measurements suggest that, on average, *G. hentscheli* has smaller sterrasters, thicker and shorter oxeas II, and larger somewhat more irregular strongylasters than *G. barretti*, but their ranges overlap so that these characters are not sufficient. Orthotriaenes are more common in *G. hentscheli* than in *G. barretti*. At all depths, *G. hentscheli* sterrasters are usually spherical whereas *G. barretti* sterrasters tend to become elongated in the NEA below 1000 m depth (but not in the NWA). Also, *G. hentscheli* sterrasters may have a bumpier surface than in *G. barretti*, due to slightly larger rosettes with more spines, but again, this character is not always present or easy to distinguish for a non-specialist. On the other hand, *G. hentscheli* sterrasters can often be irregularly developed (Fig. 13F), and this is never observed in *G. barretti*. As for external morphology, confusion is still possible because *G. barretti* can sometimes have a subspherical shape with a narrow preoscule as well (Fig. 7A). Genetically *G. barretti* and *G. hentscheli* are clearly different: 6–7 bp difference in the COI Folmer fragment, 8 bp difference in the 28S (C1-D2) fragment, and even 1 bp difference with 18S.

GEODIA MACANDREWII BOWERBANK, 1858

CYDONIUM[P] *MACANDREWII*
(*PhyloCode* SPECIES NAME)
(FIGS 15–17, TABLE 4)

Geodia macandrewii, Bowerbank, 1858: p. 284; 1872a: p. 196; Schmidt, 1866: p. 11–12; Koltun, 1966: p. 50; Barthel *et al.*, 1991: p. 40; Hougaard *et al.*, 1991a: p. 225, b: p. 469; Warén & Klitgaard, 1991: p. 52; Ereskovsky, 1993: p. 23; Klitgaard 1995: p. 2; Reitner & Hoffmann, 2003: table 1; Murillo *et al.*, 2012: p. 842; Schöttner *et al.*, 2013: p. 2. *Geodia macandrewia* (misspelling), Cedhagen, 1994: p. 67.

Geodia macandrewi (misspelling), Klitgaard & Tendal, 2004: p. 57; Cárdenas *et al.*, 2010: p. 91; Cárdenas *et al.*, 2011: table S1.

Cydonium normani, Sollas, 1888: p. 263; Norman, 1893: p. 347; Vosmaer, 1933: p. 102 (synonymy by this study).

Synops macandrewii, Sollas, 1888: p. 265.

Sidonops macandrewii, Sollas, 1889: p. 277; von Lendenfeld, 1903: p. 100. *Sidonops macandrewi* (misspelling), Brøndsted, 1932: p. 5.

Geodia normani, Burton, 1930: p. 490 (synonymy by this study).

Misidentification:

Geodia megastrella, Kingston *et al.*, 1979: p. 528.

Type locality and deposition of holotype: Collected by Robert McAndrew. Vikna Island (formerly called Vigten or Vikten Island), North Trøndelag, Norway, 183 m. The holotype specimen was not found (E. Sherlock, BNHM, pers. comm.); only type slides were examined: BNHM 1877.5.21.1396 (surface and two spicule preparations) and BNHM 1877.5.21.1398 (one section, one spicule preparation).

External morphology and cortex: Young specimens are spherical (Fig. 15E). The regular spherical body form persists during growth until the body reaches a size of about 10 cm in diameter; from that on the diameter is larger than the height, and our largest specimens are somewhat flattened, measuring 35–42 cm in maximum diameter and 20–24 cm in height (Fig. 15A–C). Some mid-sized specimens from eastern Greenland and the Flemish Cap (Fig. 15D) are unusually flat, the diameter measuring more than twice the height. The colour alive is whitish yellow to light grey; whitish in ethanol. The choanosome is yellowish in live specimens (Fig. 15B); whitish in ethanol. Small specimens have smooth surfaces; larger ones develop a fur of long spicules, essentially on the sides (Fig. 15A), which is frequently damaged during the catching procedure, so that large surface areas appear smooth. Cribriporal oscules (Fig. 15F) are regularly scattered over the upper surface; each sieve is 0.5–1 mm in diameter. Cribriporal pores (Fig. 15G) are scattered over the sides of the body; sieves are also 0.5–1 mm in diameter. The sterraster layer is very strong and tough, and usually 1–2 mm thick (occasionally up to 4 mm thick) (Fig. 15H, I). The ectocortex with spheroxyasters and microxeas is very thin (45–100 μm thick) compared with the endocortex (Fig. 15H, I).

Spicules (Fig. 16, Table 4): Megascleres: (a) oxeas, straight or bent, length: up to 14 mm; width: 5–106 μm. (b) Microxeas, straight or slightly bent, rarely centrotylote, length: 220–445 μm; width: 3–13 μm. (c) Ortho- to dichotriaenes, orthotriaenes
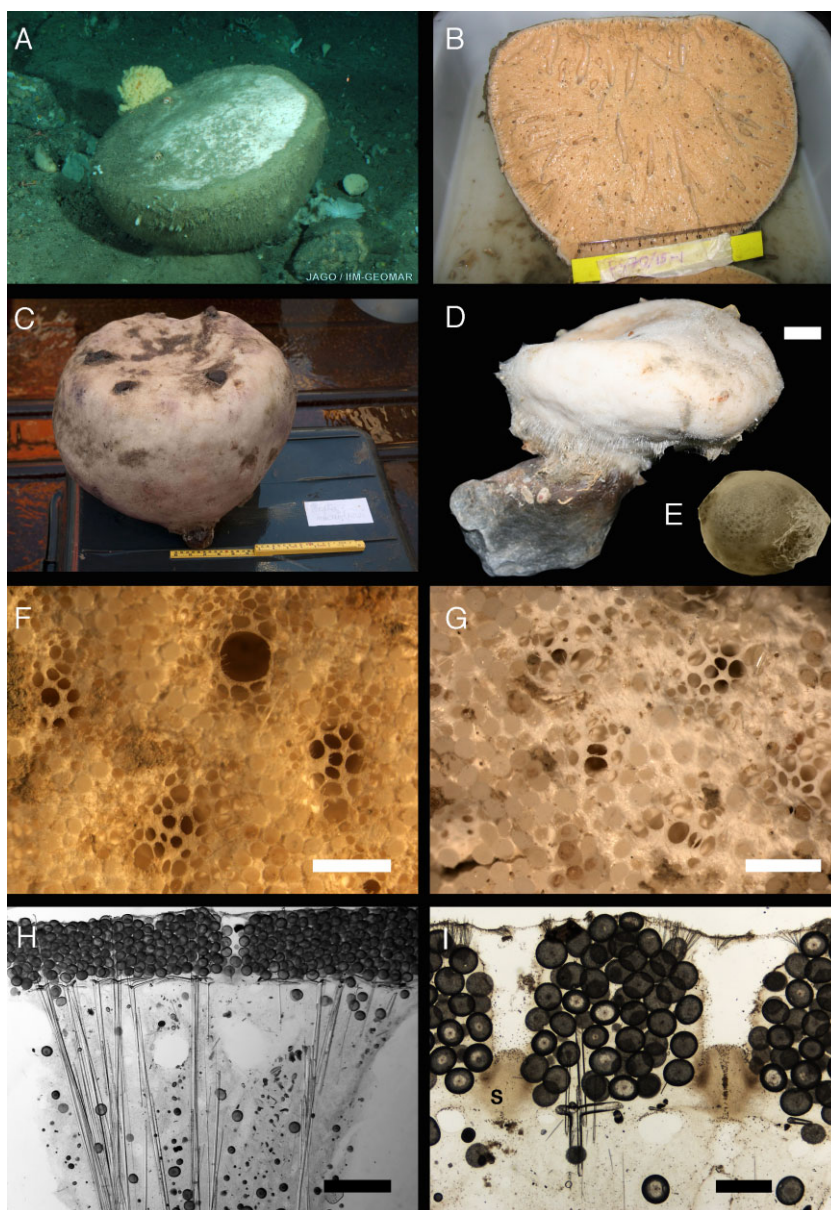
Figure 15. External morphology and thick sections of *Geodia macandrewii* Bowerbank, 1858. A, specimen *in situ* at Trænadjupet, northern Norway, 66°58′N, 11°7′E, 293 m depth, not collected, specimen is *c.* 35 cm large. Notice two hermit-crabs on the top surface (picture taken by J. Schauer, Polarstern ARK-XXII/1a, 2007). B, specimen ZMBN 85207 cut in half just after collecting from the Røst reef, 312 m depth (Polarstern ARK-XXII/1a, 2007); specimen is 27 cm large. C, specimen ZMBN 89718 just after dredging from north of Spitsbergen, 215 m depth; specimen is 25 cm large (photo: A. Plotkin). D, flattened specimen UPSZMC 78254 from Flemish Cap, just after dredging at 1079 m depth (photo courtesy of NEREIDA Project). E, young specimen from the Labrador coast, SMNH-474. F, cribriporal oscules of ZMBN 85207. Scale bar: 1 mm. G, cribriporal pores of ZMBN 89717 (Spitsbergen, 215 m). H, thick section of ZMBN 77924 (Korsfjord, 200–400 m). Scale bar: 1 mm. I, close-up of cribriporal oscules (ZMBN 77924), a single sphincter (s) sits at the bottom of the oscule. Scale bars: D and E: 1 cm; F–H: 1 mm; I: 500 μm.

are more common, straight rhabdome, rhabdome length: 1650–9625 μm (maximum from Brøndsted, 1932); width: 40–165 μm. Clads can often end with a small downward bend, orthotriaene clad length: 210–1125 μm; protoclad length: 220–500 μm; deuteroclad length: 70–450 μm. (d) Anatriaenes, common swelling on top of the cladome, rhabdome length up to 22 mm; width: 3.5–63 μm; clad length: 24–285 μm. (e) Meso/
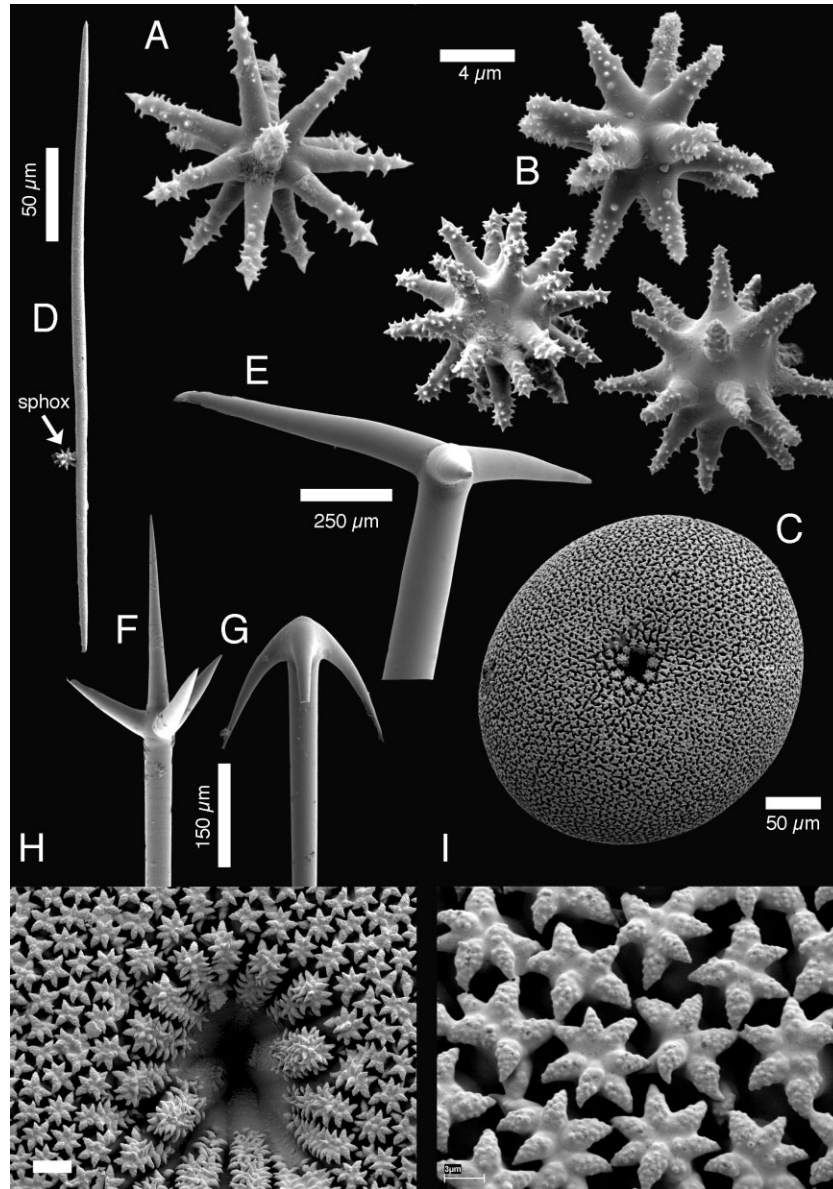
Figure 16. Spicules of *Geodia macandrewii* Bowerbank, 1858. A–D, H and I, ZMBN 89717, Spitsbergen, 215 m depth. E–G, UPSZMC 78255, Davis Strait, 564 m. A, oxyaster. B, cortical spheroxyasters. A and B have the same scale. C, sterraster. D, microxea. E, orthotriaene. F, mesoprotriaene. G, anatriaene. H, close-up on the hilum of a sterraster. Scale bar: 10 μm. I, close-up on the warty rosettes of a sterraster. Scale bar: 3 μm.

protriaenes, rhabdome length: up to 12 mm; width: 5–79 μm; clad length: 32–330 μm; central clad length: 49–685 μm. Microscleres: (f) sterrasters, spherical to subspherical, 124–360 μm in diameter; thickness: 128–230 μm; hilum diameter: 20–30 μm. Rosettes are made of 5–7 warty rays; rosette diameter: 6–10 μm. (g) Spheroxyasters, rough actines (difficult to see with the optical microscope), with centrum more or less developed, diameter: 4–18 μm. (h) Oxyasters, thin rough actines, diameter: 10–88 μm.

DNA barcodes: GenBank accession nos. EU442198, HM592689, HM592696 (Folmer COI): we have sequenced COI from specimens from western and northern Norway (4), Spitsbergen (2), Davis Strait (1), and Flemish Cap (1): the Folmer COI is identical in all these specimens. No. EU552082 (28S, C1-D2 domains): we have sequenced 28S from the Bergen area (2), and Spitsbergen (1), 1-bp difference was observed between the two Bergen specimens. No. KC481225 (18S), obtained from ZMBN 89717
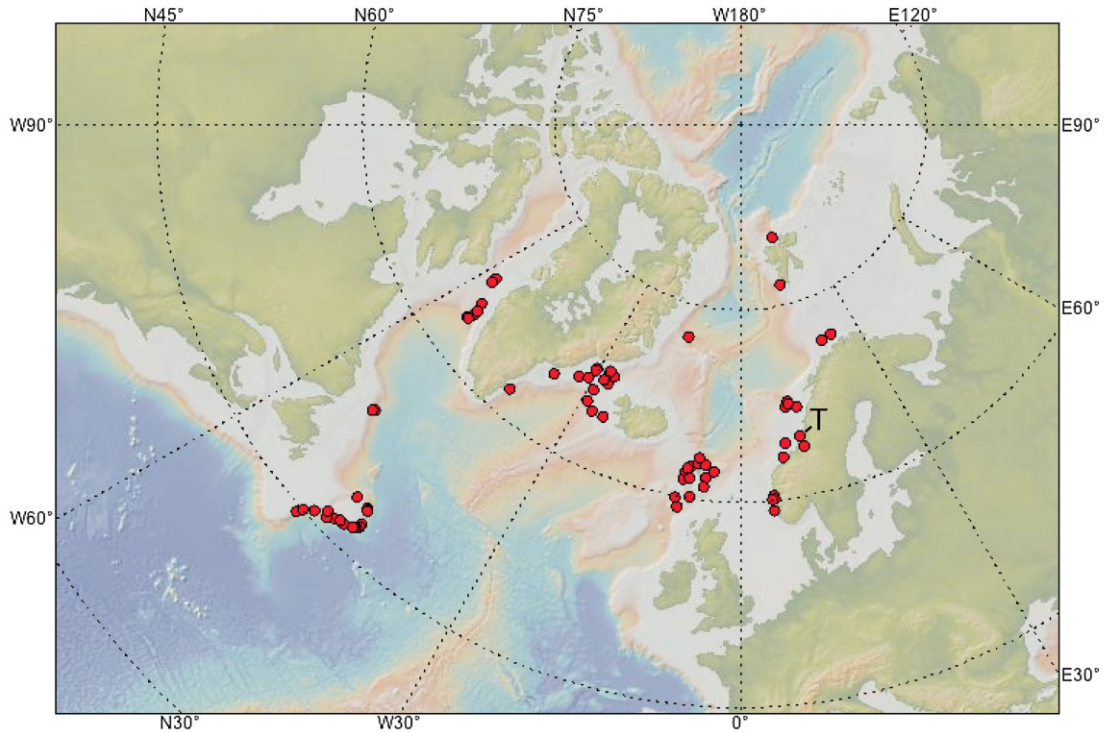
Figure 17. Distribution of *Geodia macandrewii* Bowerbank, 1858 (map made with GeoMapApp, http://www .geomapapp.org). T, type locality.

(Spitsbergen). Two specimens from Spitsbergen sequenced: no variation was observed.

Distribution (Fig. 17): We characterize the species as northern boreal, with the ability to invade some neighbouring cold-water areas, but not penetrating into real Arctic conditions. It has been recorded at depths from 157 m (Trondheimsfjord) to 1900 m (eastern Greenland). The temperature range is –0.82 °C (north of the Faroe Islands, BIOFAR st. 901) to 8.3 °C (south-west of the Faroe Islands, BIOFAR st. 69). Most eastern records are from between 230 and 400 m, at temperatures of 5–8 °C. Occurrences at temperatures below 2 °C were essentially found in the Denmark Strait (282–467 m depth). The records on the southern flanks of the Bill Bailey and Faroe Banks came from rather deep water, 1140 and 650 m, respectively. They hardly represent the southern distribution limit of the species but could indicate that off the Shetland Isles and Scotland it can be expected to occur on the upper slope. Brøndsted (1932) and Koltun (1966) mentioned the Shetlands as part of the distribution area; although this is to be expected, there is so far no proof, the record being a mistake by Brøndsted for the Norwegian record of the type specimen. Koltun (1966) mentioned occurrences in the south-western Barents Sea and the Denmark Strait, but gave no detailed information.

Biology: We found no indications of asexual reproduction. The predator chiton *H. nagelfar* and the parasitic foraminiferan *H. sarcophaga* have been found living on *G. macandrewii* (Warén & Klitgaard, 1991; Cedhagen, 1994; Todt *et al.*, 2009). More associated fauna has been investigated by Klitgaard (1995). The chemistry (elemental analysis, amino acids, sterols, and quaternary ammonium compounds) has been investigated (Kingston *et al.*, 1979; Hougaard *et al.*, 1991a, b). Note that *G. macandrewii* off the Labrador coast (Canada) and from the Faroe Islands have very similar sterol composition (Kingston *et al.*, 1979; Hougaard *et al.*, 1991b).

Distinctive characters: External morphology: the regularly round, almost spherical form with no conspicuous openings, the hard consistency, the uniform distribution on the top side of cribriporal oscules, and the very thick cortex. Spicules: very large sterrasters (124–360 μm in diameter).

Remarks: It was named after Robert MacAndrew who collected this species. Spicule measurements of this species are scarce apart from Sollas (1888), Brøndsted (1932), and Koltun (1966). Although this is a fairly common species in some areas, it is rarely mentioned in the literature compared with *G. barretti* or *G. phlegraei*, perhaps because it is often confused

Table 4. Individual spicule dimensions and cortex thickness for specimens of *Geodia macandrewii* (in µm) collected at different depths

Material	Depth (m)	Cortex thickness (mm)	Spheroxyasters (diameter)	Oxyasters (diameter)	Sterrasters (length/width)	Ortho/dichotriaenes (rhabdome: length/width)	Ortho/dichotriaenes (ortho/proto/deuteroclads)
Vikna Isl., Norway holotype (Sollas, 1888)	183	3.26	6.5	25	270	7300/110	–/500/320
BMNH 1877.5.21.1396–1398 holotype (this study)	183	3.7	5-**6.8**-10	10-**16.7**-25	220-**252.2**-290	3800-**5872.2**-7500 (9)/60-**90.4**-110 (23)	340-**502.7**-710 (11)/220-**296**-430(3)/170-**196**-230(3)
Faeroes (Brøndsted, 1932)	240	1-1.5	8	15	216-300	up to 9625/120	–/220/375
Korsfjord, Norway ZMBN 77924	200–400	1.5	6-**8.4**-11	10-**14.3**-17.5	235-**260**-290	3500-**5200**-6750(3)/40-**74.4**-110	210-**511.9**-850(26)/280-**421**-500(5)/70-**226**-450(5)
Spitsbergen ZMBN 89718	215	1.7	8-**11.7**-15	15-**16**-28	250-**286.6**-340	1650-**4708.3**-6600 (6)/50-**88.7**-110 (14)	250-**536.2**-660(8)/n.f./n.f.
Flemish Cap UPSZMC 78254 (DR18-57)	1079	1.5–2	4-**8.6**-12.5	12-**34**-88	124-**180.8**-200	>4400/40-**89.8**-116	300-**631.3**-1125/n.f./n.f.
Davis Strait UPSZMC 78255 (PA2010, set 167)	564	1.2–2	8-**12**-18	12-**17**-29	165-**212.9**-285	2668-**5787**-8274/68-**130**-165	212-**598**-1042/–/–
G. normani holotype Vikna Isl. (Sollas, 1888)	–	1.6	12	40	320	7150/110	1000/–/–

Table 4. *Continued*

Material	Oxeas I (length/width)	Oxeas II (length/width)	Anatriaenes (rhabdome: length/width)	Anatriaenes (clad)	Promesotriaenes (rhabdome: length/width)	Promesotriaenes (clad/middle clad)
Vikna Isl., Norway holotype (Sollas, 1888)	–	350/–	>8920/–	–	–/37	167
BMNH 1877.5.21.1396–1398 holotype	>7500/ 80	220–**343.8**–445/ 6–**9.5**–13	>5500/ 20–**26**–35 (5)	130–**168.3**–200 (6)	>5450/ 21–**35.7**–55 (27)	80–**190.2**–330(18)/ 115–**232.5**–410(10)
Faroes (Brøndsted, 1932)	2000–3000/ –	300–400/ –	yes	yes	yes	yes
Korsfjord, Norway ZMBN 77924	>6500/ 70	295–**364.2**–445/ 4–**5.8**–7.5	>3550/ 3.5–**14.8**–22 (12)	50–**141.5**–210 (11)	>2075/ 5–**24.1**–45 (6)	42–**131.4**–210(5)/ 65–**228.3**–520(6)
Spitsbergen ZMBN 89718	2150 to >6650/ 30–**46.2**–60(9)	240–**339.2**–442/ 3–**6.5**–12.5	>8250/ 16–**19.7**–23(6)	80–**150**–250 (6)	5100/ 15	105/ n.f.
Flemish Cap UPSZMC 78254 (DR18-57)	1550–**3276**–5280/ 8–**37.3**–80(3)	212–**318.6**–410/ 4–**8.5**–12	>1600/ 4–**39.5**–60(11)	24–**117.1**–172 (11)	>1750/ 20–**33.6**–48(5)	60–**92**–120/ 170–**197.3**–230 (5)
Davis Strait UPSZMC 78255 (PA2010, set 167)	2371–**6296**–14661/ 5–**75**–106	285–**341**–426/ 6–**7**–9	12266–**12862**–13960(4)/ 24–**43**–63(9)	49–**199**–285 (9)	8540–12339(2)/ 22–**36**–48 (6)	32–**148**–242/ 49–**341**–685 (6)
G. normani holotype Vikna Isl. (Sollas, 1888)	6100/ 64	–	22500/ 40	180	11780/ 79	250/ 280

Means are in bold; other values are ranges; $N = 30$ unless stated otherwise in parentheses, or unless measurements come from other studies. A dash indicates that this measurement is not given in the literature. n.f., not found.

with these species. In spicule preparations, it can be difficult to separate the largest ectocortical spheroxyasters from the smallest choanosomal oxyasters as there is no clear transition from one form to the other, so we recommend measuring them on a section, to ensure not to mix both categories (this was done for the holotype and ZMBN 77924). There is some variation within oxyasters: small (up to 25–28 µm) with thin actines (1–2 µm thick) usually in specimens from shallower depths (183–600 m), to very large oxyasters (40–88 µm) with thick actines (4–7 µm thick) in specimens living deeper than 1000 m. The large sizes are not mentioned by Koltun (1966). The large dichotriaenes with atypical forward orientated cladomes represented by Bowerbank (1872a: plate X, fig. 4) were indeed observed on the type slide number 'Bk.1398'. However, in our opinion, they result from a contamination from another Astrophorina (probably *Stelletta normani* Sollas, 1880a, a common species on the Norwegian coast at these same depths).

Molecular phylogenetic studies suggest that *G. macandrewii* belongs to *Cydonium*^{p} along with *G. cydonium*, *G. conchilega*, and *Geodia papyracea* Hechtel, 1965 (Fig. 2). *G. macandrewii* shares the possession of identical cribriporal oscules and pores with *G. cydonium* and *G. conchilega*; *G. papyracea*, by contrast, has uniporal oscules (Cárdenas *et al.*, 2009). We could nonetheless suggest that the association of cribriporal oscules and oscules could be an autapomorphy of the clade, and that the cribriporal oscules were later modified and lost in *G. papyracea*. These four species also share spiny euasters but spiny euasters are also present in the neighbouring *Geodia* clades (*Depressiogeodia*^{p} and *Geodia*^{p}) (Fig. 2). *Geodia macandrewii*, *G. cydonium*, and *G. papyracea* share orthotriaenes but *G. conchilega* has dichotriaenes. So additional sampling is needed to better understand the *Cydonium*^{p} clade and find morphological apomorphies that would support it.

No spicule differences were observed between NWA and NEA specimens. Sterrasters are usually subspherical but we noted that one specimen from Davis Strait (UPSZMC 78255) had some atypically shaped sterrasters, most of them 'lemon-shaped', but other specimens from the same locality had 'normal' sterrasters.

Geodia normani (Sollas, 1888) is known only from the original description. The single specimen was collected by Rev. Canon A. M. Norman at Vikna Island, which is also the type locality for *G. macandrewii*. Burton (1930) worked on the Norman collection, but indicated that the single specimen was not at his disposal. Accordingly the specimen may have been untraceable even at that time. New searches in the BMNH collection for the present study have not

been successful (E. Sherlock, BMNH, pers. comm., September 2012) so the type is presumably lost. We may suppose that Sollas (1888) did not examine the type specimen of *G. macandrewii* while describing *G. normani*, and misinterpreted Bowerbank's description of *G. macandrewii*. Indeed, Sollas (1888) moved *G. macandrewii* to the genus *Synops* Vosmaer, 1882 and therefore did not think of comparing it with *G. normani* that he had placed in *Cydonium* Fleming, 1828 (because of the presence of cribriporal pores and oscules). However, the description of *G. normani*, notably concerning the fairly thick cortex, the cribriporal openings, and the spicule morphologies (large spherical sterrasters, common promesotriaenes, and anatriaenes with swollen cladomes), matches that of *G. macandrewii*. *Geodia normani* only differs from *G. macandrewii* by the absence of microxeas and we can suppose that these may have been overlooked or Sollas more likely thought they were a contamination. To conclude, because *G. normani* and *G. macandrewii* come from the same type locality and share so many characters (external morphology and spicules), we formally propose to consider *G. normani* as a junior synonym of *G. macandrewii*.

We examined slides (74-8-27.1) made by H. M. Reiswig from material published under the name *Geodia megastrella* and collected off the Labrador coast (53°24′50″N, 52°15′00″W) at 732 m depth (Kingston *et al.*, 1979). We observed a thick cortex (2 mm thick), orthotriaenes, common ana/protriaenes, very large sterrasters (up to 360 µm), and spiny oxyasters with thin actines (10–30 µm). This leaves no doubt that this is in fact *G. macandrewii*.

GEODIA PHLEGRAEI (SOLLAS, 1880b)
GEODIINAE^p PHLEGRAEI (*PhyloCode* SPECIES NAME)
(FIGS 18–20, 23, TABLE 5)

Isops phlegraei, Sollas, 1880b: p. 397; 1888: p. 267; von Lendenfeld, 1903: p. 95; Hentschel, 1929: p. 919; Burton, 1930: p. 498; Vosmaer, 1933: p. 141; Alander, 1942: p. 73; Warén & Klitgaard, 1991: p. 52; Klitgaard, 1995: p. 2; Reitner & Hoffmann, 2003: table 1; Klitgaard & Tendal, 2004: p. 57; Cárdenas *et al.*, 2010: p. 91.

Synops pyriformis, Vosmaer, 1882: p. 20; 1885: p. 10 (synonymy by Burton, 1930).

Isops sphaeroides, Vosmaer, 1882: p. 13 (synonymy by Burton, 1930).

Isops pallida, Vosmaer, 1882: p. 16 (in part); Rezvoj, 1928: table 1 (synonymy by Burton, 1930).

Isops pyriformis, von Lendenfeld, 1903: p. 95.

Geodia phlegraei, Koltun, 1964 (in part): p. 148; Koltun, 1966 (in part): p. 55; Cárdenas *et al.*, 2011 (in part): table S1; Murillo *et al.*, 2012 (in part): p. 842; Schöttner *et al.*, 2013: p. 2.
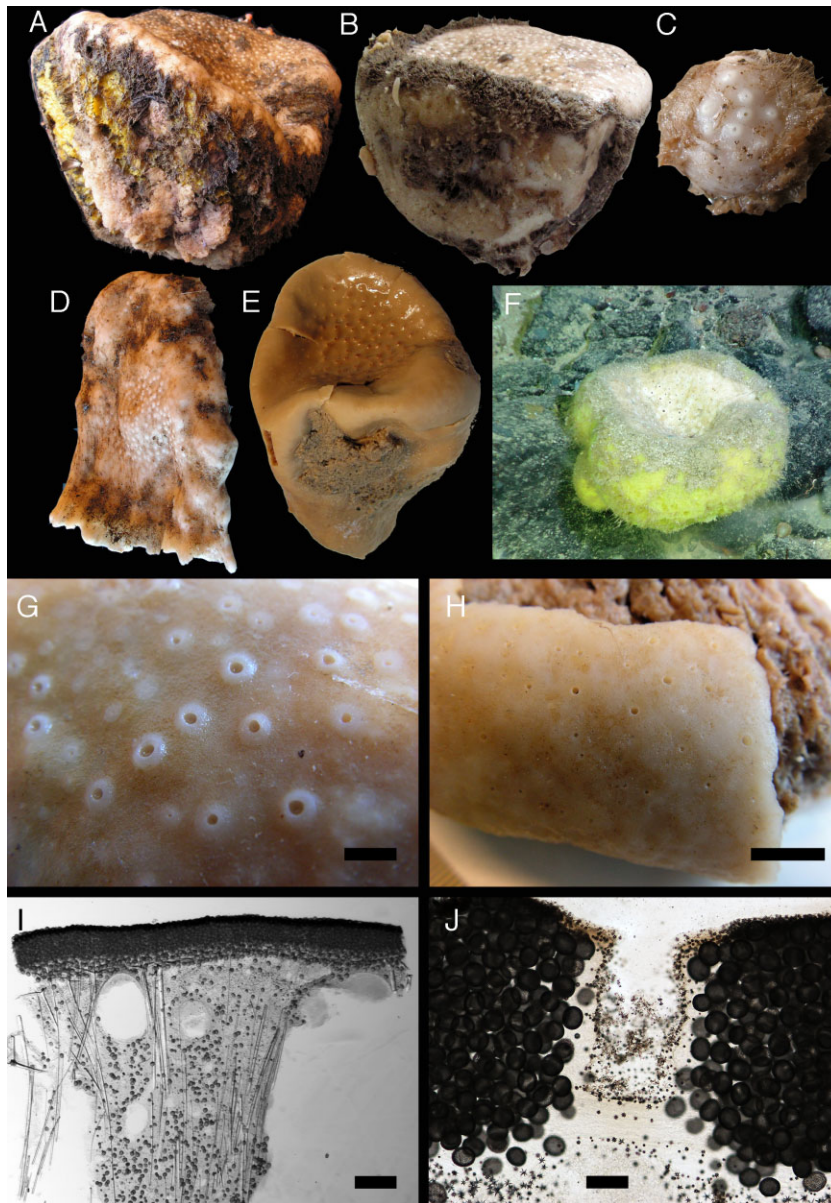
Figure 18. External morphology and thick sections of *Geodia phlegraei* Sollas, 1880b. A, specimen PC124 just after dredging from the Korsfjord, Norway, 200–400 m depth; specimen is 20 cm in diameter. B, specimen ZMBN 85211 just after collecting from Trænadjupet, northern Norway, 290 m depth: specimen is 20 cm in diameter. C, specimen PC68 just after dredging from the Korsfjord, Norway, 200–400 m depth; specimen is 4 cm in diameter. D, specimen PC191 just after dredging from the Korsfjord, Norway, 200–400 m depth; specimen is 20 cm in length. E, specimen from Ingolf Exp., st. 90, Denmark Strait, 1039 m depth (fixed in ethanol); specimen is 15 cm high and 8 cm in diameter. F, specimen R1341-18 *in situ*, collected at 2347 m depth, Orphan Knoll (50.05894, 45.60638); specimen is 20 cm in length and covered with the yellow encrusting sponge *Hexadella dedritifera* (Canadian DFO/ROPOS 2010). G, uniporal oscules (specimen from Shinkai Maru Exp., st. 32). H, uniporal pores (specimen from Shinkai Maru Exp., st. 32). I, thick section from ZMBN 77929 (Korsfjord, 200–400 m). J, uniporal pore with sphincter. Scale bars: G: 5 mm; H: 1 cm; I: 1 mm; J: 200 μm.
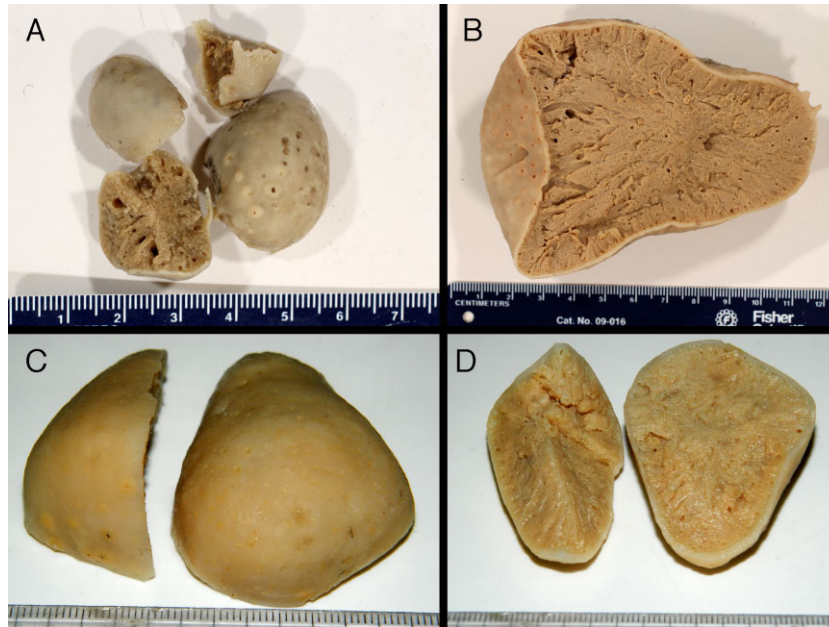
Figure 19. A, holotype of *Geodia phlegraei* SOLLAS, 1880b, BMNH 1910.1.1.840. B, holotype of *Synops pyriformis* Vosmaer, 1882, RMNH Por. 660. C, lectotype of *Isops pallida* Vosmaer, 1882, RMNH Por. 652, external appearance (picture: R. van Soest). D, lectotype of *I. pallida*, RMNH Por. 652, internal appearance (picture: R. van Soest).

Not:

Isops pyriformis, Hentschel, 1929: p. 865 (= *G. parva*).

Geodia cf. *phlegraei*, Wagoner *et al*., 1989: p. 2344 (= *G. parva*).

Isops phlegraei pyriformis, Klitgaard & Tendal, 2004: p. 57 (= *G. parva*).

Isops phlegraei, van Soest *et al*., 2007: p. 129 (= *G.* cf. *nodastrella*).

Geodia phlegraei, Koltun, 1966 (in part): p. 55; Cárdenas *et al*., 2011 (in part): table S1; Murillo *et al*., 2012 (in part): p. 842 (= *G. parva*).

Misidentifications:

Pachymatisma johnstonia, Hansen, 1885: p. 17.

Cydonium mülleri, Breitfuss, 1912: p. 62 (according to Koltun, 1966).

Geodia cydonium, Gorbunov, 1946: p. 37 (according to Koltun, 1966).

Type locality and type material examined
Isops phlegraei, Korsfjord near Bergen, Norway. 60°10′N, 05°10′E, 330 m. Collected by Rev. A. M. Norman in 1878, BNHM 1910.1.1.840.

Synops pyriformis, near Hammerfest, Norway, 71°12′5″N, 20°30′5″E, 247 m, Willem Barents Exp. 1878–79, RMNH Por. 660 (wet specimen); MNHN-DN23, Norman Collection, spicule preparation and section; BMNH 10.1.1.1147–1148, Norman Collection, spicule preparation and section (not seen).

Isops sphaeroides, near Hammerfest, Norway, 71°12′5″N, 20°30′5″E, 247 m, Willem Barents Exp. 1878–79, MNHN-DN24, syntype 1, Norman Collection, spicule preparation and section; RMNH, Vosmaer slide collection, box number 37, syntype 2, two spicule preparations and one stained thin section; BMNH 10.1.1.1158–1159, Norman Collection, two slides (not seen).

Isops pallida, near Hammerfest, Norway, 71°12′5″N, 20°30′5″E, 247 m, Willem Barents Exp. 1878–79, RMNH Por. 652, wet specimen (seen only from pictures); RMNH, Vosmaer slide collection, box number 37, two spicule preparations with number 62.

External morphology and cortex: More or less spherical, the largest specimens somewhat flattened on the top, cup-shaped, generally up to 20 cm in diameter, and 15 cm high (Fig. 18A, B, E); our largest specimen measures 43 cm in maximum dimension. Juveniles are spherical (Fig. 18C). Specimens growing on vertical cliffs (i.e. fjords) can be flattened or more irregular (Fig. 18D). Lower part sometimes formed as a base, with root-like outgrowths (Fig. 19B). The colour alive usually varies from whitish grey to light brown, to slightly rose. One shallow fjord specimen (PC111, shallower than 175 m) was faintly purple in ethanol, like shallow *G. barretti* and *Pachymatisma normani* Sollas, 1888 (a NEA boreal Geodiidae) (Cárdenas & Rapp, 2013). Other specimens fixed in ethanol seemed to be reddish, although this staining comes from the
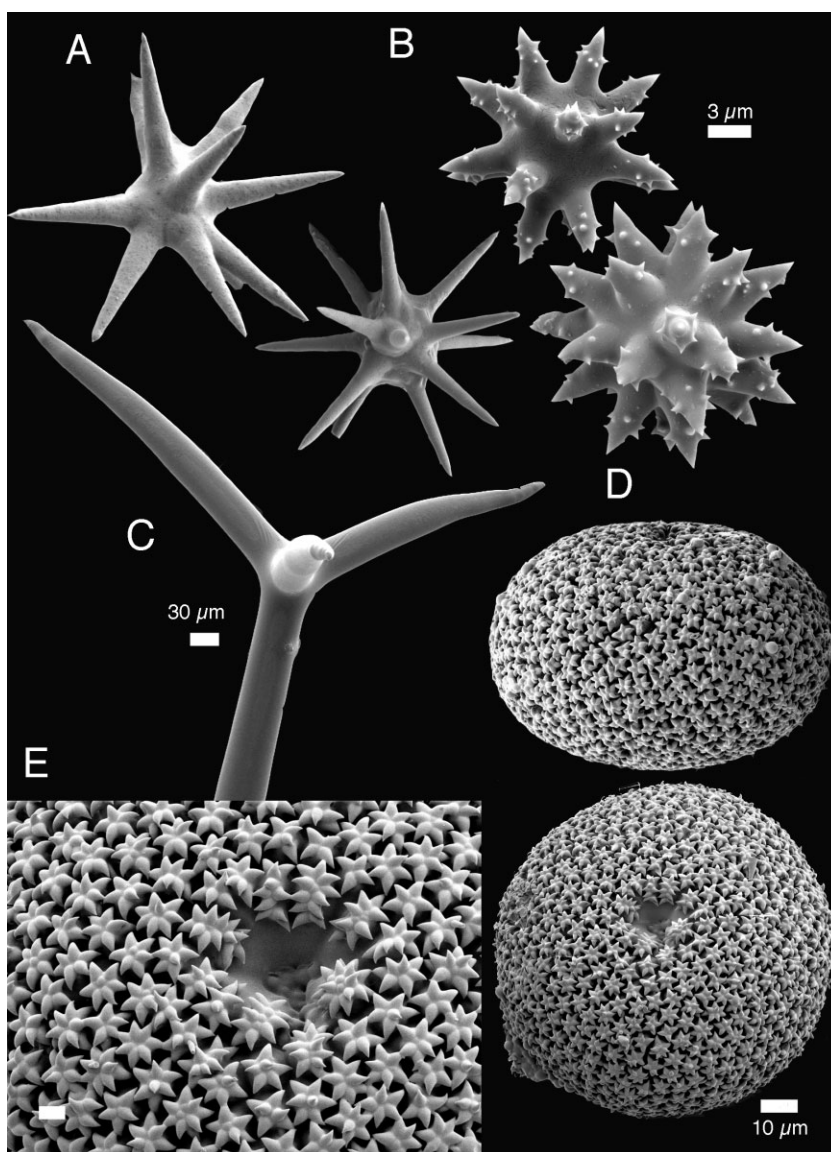
Figure 20. Spicules of the holotype (BMNH 1910.1.1.840) of *Geodia phlegraei* Sollas, 1880b. A, oxyasters. B, spherasters. A and B have the same scale. C, orthotriaene. D, sterrasters. E, close-up on the hilum of a sterraster. Note the smooth rosettes. Scale bar: 3 μm.

epibiont yellow sponge *Hexadella dedritifera* Topsent, 1913 (Fig. 18A, F) which turns dark red during the fixation. Many specimens are very hispid on the sides, but never on the top surface (Fig. 18A–C). The fur can be up to 10 mm long, but is not a regularly occurring feature in dredged specimens as it may be easily lost during the collection. The cortex (Fig. 18I) is thin to fairly thick (0.7–2 mm thick); it is usually difficult to cut and tends to break in pieces. Many epibionts (especially sponges) are present in this hispid part. Uniporal oscular openings are up to 1 mm in diameter, and are found mainly on the upper surface (Fig. 18A–F). Oscular openings may be at the tip of thick conical elevations, more or less pointy, which can be lighter-coloured (Fig. 18G) (but not always) and which gave the name to this species: Campi phlegraei is a local name of the Naples volcanic area (Sollas, 1880b). Uniporal pores (*c.* 300–400 μm in diameter) (Fig. 18H–-J) are scattered on the sides and partly on the underside of the body. Pores are usually not elevated but can also be surrounded by a white margin.

Description of type material: The holotype of *G. phlegraei* is a small subspherical specimen (diameter: 2.5 cm) cut up into four parts (Fig. 19A); it has conical-shaped oscules. There is also one BMNH slide

Table 5. Individual spicule dimensions and cortex thickness for specimens of *Geodia phlegraei* and *Geodia parva* (in μm) collected at different depths

Material	Depth (m)	Cortex thickness (mm)	Spherasters (diameter)	Sterrasters (length/width)	Oxyasters (diameter)	Orthotriaenes (rhabdome: length/width)	Ortho/dichotriaenes (ortho/proto/ deuteroclads)	Oxeas (length/width)
G. phlegraei holotype Korsfjord, N. (Sollas, 1888)	330	0.64	12	90	20–70	4000/ 42	300/ – –	6000/ 63
BMNH 1910.1.1.840 holotype (this study)	330	0.64	11.6–**17**–23.5*	82–**93.3**–102*/ 76–**85.7**–95*	17–**23.5**–40.8*	586–**2129.3**–3640(10)/ 12–**50.1**–72	80–**415.5**–660/ 220–250(2)/ 100–250(2)	1825–**3292.6**–4480/ 20–**41.1**–60 (27)
Isops pallida slides 62, specimen α lectotype Barents Sea	247	n.o.	14–**16.5**–20	93–**103.2**–110/ 80–**88**–95	17–**22.3**–35 (11)	1400–**3595**–4800/ 30–**77**–90 (10)	165–**527**–800/ n.o./ n.o.	2490–**4293.5**–5450/ 25–**54**–70 (17)
Isops sphaeroides [1]MNHN-DN24 [2]slides 63 and 101 types Barents Sea	247	1[1] 0.5–0.7[2]	13–**15.7**–23[1]	105–**113.8**–130[1]/ 75–**89.6**–110[1] 98–**104.6**–115[2]/ 75–**84.7**–95[2]	15–**29.3**–60[1]	1975–**4525**–5600/ 50–**66.8**–75 (9)[2]	250–**862.5**–1950(8)[2]/ 190[2]/ 190[2]	3250–**4910**–6650/ 30–**60.4**–80 (20)[2]
Synops pyriformis RMNH-Por660 holotype Barents Sea	247	1.1–1.3	10–**14.2**–20	100–**115.7**–125/ 70–**93.7**–105	10–**30.5**–60	2125–**4418.3**–6655(15)/ 40–**81.2**–150	250–**611.6**–890/ – –	2600–**4875.6**–7040/ 14–**45.2**–85
Korsfjord, N. ZMBN 77929	200–400	1	8–**14.3**–17.5	97–**106.9**–120/ 88–**94.5**–104	15–**27.3**–58	1175–**3461.6**–4600(12)/ 20–**59.8**–100	170–**545.3**–1000/ – –	1625–**4190**–6000/ 10–**40.6**–65
Kosterfjord, S. UPSZMC 75157	200	1–2	12.5–**16.5**–22.5	95–**112.3**–125/ 85–**96.2**–105	18–**30.8**–60	2600–>4050/ 50–**97.8**–120	240–**694.8**–1125/ – –	1925–**5274**–7600/ 25–**78.2**–100
Spitsbergen ZMBN 89719	215	1.8	10–**17.6**–22.5	100–**111.5**–120/ 85–**92.4**–103	14–**22.8**–40	3400–**4095**–4440(8)/ 45–**69.4**–90	320–**726**–960/ – –	2960–**4560**–5400/ 35–**55.4**–65 (7)
Orphan Knoll UPSZMC 78308 (R1340-04)	3000	0.5–0.8	11–**18**–26	88–**100**–107/ 83–**90**–105	24–**38**–65	801–**2238**–2960/ 19–**62**–90 (20)	116–**519.2**–950/ – –	1173–**3333**–5782/ 10–**51.4**–68

Table 5. *Continued*

Material	Anatriaenes (rhabdome: length/width)	Anatriaenes (clad)	Protriaenes (rhabdome: length/width)	Protriaenes (clad)
G. phlegraei holotype Korsfjord, N. (Sollas, 1888)	yes	yes	n.f.	n.f.
BMNH 1910.1.1.840 holotype (this study)	>3760/ 8–**18.5**–25 (6)	48–**71.6**–130 (6)	n.f.	n.f.
Isops pallida slides 62, specimen α lectotype Barents Sea	n.f.	n.f.	n.f.	n.f.
Isops sphaeroides MNHN-DN24 holotype Barents Sea	>15000/ 20–**28.3**–35 (12)	70–**102.1**–150 (12)	11600–12750(2)/ 25–**27.3**–30(3)	190–**196.6**–200 (3)
Synops pyriformis RMNH-Por660 holotype Barents Sea	11000/ 22	70	n.f.	n.f.
Korsfjord, N. ZMBN 77929	n.f.	n.f.	n.f.	n.f.
Kosterfjord, S. UPSZMC 75157	n.f.	n.f.	n.f.	n.f.
Spitsbergen ZMBN 89719	n.f.	n.f.	n.f.	n.f.
Orphan Knoll UPSZMC 78308 (R1340-04)	n.f.	n.f.	n.f.	n.f.

Table 5. *Continued*

Material	Depth (m)	Cortex thickness (mm)	Spherasters (diameter)	Sterrasters (diameter)	Oxyaster (diameter)	Orthotriaenes: (rhabdome: length/width)	Ortho/dichotriaenes (ortho/proto/ deuteroclads)	Oxeas (length/width)
G. parva ZMBN 100 holotype	–	–	13.1–**16.1**–21*	75–**84.9**–93*	19–**41.7**–64 (spiny)	360–**697.1**–1000/ 20–**26.3**–33 (8)	102–**161.3**–232(7)/ 56/ 44	773–**1193.6**–1625/ 14–**21**–34 (6)
Schultz Massive Seamount (bottom), Greenland Sea ZMBN 85210	1997	0.15–0.4	12.5–**15.5**–18	56–**67.2**–75	10–**14.6**–25 (rare)	2225/ 60–70	420–**539.4**–640 (9)	2700–3200/ 60–70
Schultz Massive Seamount (top), Greenland Sea PC553	688	0.5–0.7	12–**14.5**–18	67–**77.1**–87	15–**29.7**–55	>2700/ 60–**70**–85 (12)	500–**680**–920 (4)	> 7500/ 50
Spitsbergen Hentschel (1929)	1000	–	12.5–19	81–91	31–56	–	–	–
Boreas Basin ZMAPOR16755	1000	n.o.	10–**14.9**–22.5	75–**80.8**–90	17–**36.6**–72	n.o./ 70	975	n.o.
Greenland Sea UPSZMC 76801	1900	<1	12.5–**19**–30	68–**83.6**–92	20–**40**–65	1125–**3056.6**–5120(10)/ 24–**72.6**–108	120–**477.3**–960/ 100–**144.4**–128(5)/ 84–**137.2**–270(5)	1521–**3723.8**–5000/ 17–**59.1**–75 (8)
Davis Strait UPSZMC 78275 (PA2010-Set 161)	787	0.7	8–**17.1**–25	68–**77.1**–90	16–**30.4**–52	1669–**4103**–5395/ 97–**108**–131 (16)	106–**352.1**–642 (25)	4403–**5659.7**–7524/ 53–**80.7**–102
Flemish Cap NEREIDA DR07-43	1339	0.5–0.65	15–**17.4**–23	61–**80.2**–90	19–**39.9**–67	2565–**3919**–5202/ 36–**86**–102 (17)	232–**644**–1008(17)/ 203–**313.5**–405(4)/ 203–**398**–521(4)	2940–**6100**–7935/ 58–**72**–87

Table 5. *Continued*

Material	Anatriaenes (rhabdome: length/width)	Anatriaenes (clad)	Pro(meso)triaenes (rhabdome: length/width)	Pro(meso)triaenes (clade/central clade)
G. parva ZMBN 100 holotype	n.f.	n.f.	840/9	36/60
Schultz Massive Seamount (bottom), Greenland Sea ZMBN 85210	n.f.	n.f.	n.f.	n.f.
Schultz Massive Seamount (top), Greenland Sea PC553	n.f.	n.f.	>500/25	100/ n.f.
Spitsbergen Hentschel (1929)	1000/ –	–	n.f.	n.f.
Boreas Basin ZMAPOR16755	n.f.	n.f.	n.f.	n.f.
Greenland Sea UPSZMC 76801	>1000/ 20–28	116–173	n.f.	n.f.
Davis Strait UPSZMC 78275 (PA2010-Set 161)	n.f.	n.f.	6073–**7113**–8371/ 24–**45**–68 (3)	119–**134**–161(3)/ 334
Flemish Cap NEREIDA DR07-43	10367–**13997**–16016/ 15–**28**–34 (9)	29–**53**–78 (9)	n.f.	n.f.

Means are in bold; other values are ranges; $N = 30$ unless stated otherwise in parentheses, or unless measurements come from other studies. A dash indicates that this measurement is not given in the literature. n.f., not found; n.o., not observed in the specimen in our possession. N, Norway; S, Sweden.
*SEM measurements.

of the type but it is damaged and the embedding medium has blackened. Figure 20 shows SEM pictures of the spicules from the holotype. The type of *S. pyriformis* is a medium-sized specimen (length: 10 cm, width: 8 cm) cut into five pieces. The main piece (Fig. 19B) is the elongated cup-shaped half represented by Vosmaer (1882: plate IV). We have only seen pictures of the wet specimen of the lectotype (specimen α) of *I. pallida* (Fig. 19C, D): the pear-shaped specimen is cut into two fragments (one-half and one-third of a single specimen). The half fragment is about 6 × 4 cm with a thick cortex (1–2 mm thick), uniporal oscules, and uniporal pores. There are also two spicule preparations of the lectotype (slide 62: α) of *I. pallida* (Fig. 4A). One slide is broken so the label is gone but the spicules are identical to those of slide 62.

Spicules (Fig. 20, Table 5): Megascleres: (a) oxeas, length: 1173–7600 μm; width: 10–100 μm. (b) Orthotriaenes, rare dichotriaenes, rhabdome length: 586–6655 μm; width: 12–150 μm; orthotriaene clad length: 80–1125 μm; protoclad length: 220–250 μm; deuteroclad length: 100–250 μm. (c) Anatriaenes, rare (some clads were dichotomized in the type of *I. sphaeroides*) rhabdome length: up to 11 mm; width: 8–25 μm; clad length: 30–130 μm (minimum according to Koltun, 1966). (d) Protriaenes, very rare, rhabdome length: 11 600–12 750 μm; width: 25–30 μm; clad length: 190–200 μm. Microscleres: (e) sterrasters, subspherical (NEA specimens) or spherical (in some NWA specimens), length: 82–144 μm; width: 70–124 μm; thickness: 65–80 μm; hilum: 12–15 μm. Rosettes are made of 4–12 smooth rays; rosette diameter: 6–8 μm. (f) Spherasters with spiny conical actines (more rarely with blunt ends), 8–26 μm in diameter. (g) Oxyasters, smooth (rough actines were rarely observed in very large oxyasters), 10–70 μm in diameter (maximum is from measurements of the type by Sollas, 1888).

DNA barcodes: GenBank accession nos. EU442196, HM592701 (Folmer COI). We have sequenced COI from specimens from Spitsbergen (1), western and northern Norway (10), Mingulay Reef (1), and Orphan Knoll (1): the Folmer COI is identical in all these specimens. No. KC481222 (18S), obtained from ZMBN 77929 (Korsfjord, Norway). 18S of ZMBN 89719 (Spitsbergen) was also sequenced: no variation was observed.

Distribution (Fig. 23): Geodia phlegraei has a boreal distribution and seems to avoid arctic waters; it can be found from 40 m (Trondheimsfjord) to 3000 m (Orphan Knoll). It is commonly found at depths from 100–300 m (Norwegian continental shelf) to 725 m (Faeroes), at temperatures of 0.3 °C (BIOICE, st. 2926) to 7.9 °C

(BIOFAR, st. 297). It has also been recorded by divers in Norwegian fjords at shallower depths: for example, it has been photographed by A. Salesjö in the Trondheimsfjord at only 40–50 m depth (http://www.anderssalesjo.com/?id=3306&lang=42, accessed 7 May 2013). We also identified it in material collected in Mingulay Reef (western Scotland) at 128–139 m depth. In Mingulay reef (R. van Soest, pers. comm.) and Norwegian fjords at shallow depths, temperatures can reach 10.5 °C. The specimen identified as *G. phlegraei* from Rockall Bank (van Soest *et al.*, 2007) was actually a *Geodia* cf. *nodastrella*. Interestingly, all but one of the NWA specimens from the Flemish Cap that we examined (a total of eight specimens) collected during NEREIDA 2009–10 and originally identified as *G. phlegraei* were in fact *G. parva*. The only specimen from the Flemish Cap that we identified as *G. phlegraei* (DR24-69d = UPSZMC 78280) has an external morphology similar to *G. phlegraei* and large elongated sterrasters (*c.* 132–136 μm in diameter). Unfortunately, we could not get a COI sequence from it to confirm this identification. However, we did get a COI sequence for R1340-04 (= UPSZMC 78308) confirming it was *G. phlegraei*: it has large spherical sterrasters (88–107 μm in length) and it was collected at 3000 m depth at Orphan Knoll, where the temperature was 2.4 °C (Fig. 18F shows R1341-18 collected at 2347 m in the same area). The most western specimen of *G. phlegraei* found is from western Greenland ('Shinkai Maru', st. 32, 64°13.5′N, 54°42.1′W. 970 m) (Fig. 18G, H), but this material was not suited for molecular studies.

Biology: When he described this species, Sollas (1880) immediately noticed that it was 'covered by various foreign bodies'. Indeed, *G. phlegraei* is the boreo-arctic *Geodia* which is most often found covered with epifauna, especially sponges and including individuals of its own species. Here are a few sponges found on *G. phlegraei*: *Craniella* sp., *Cyamon spinispinosum* (Topsent, 1904), *Hexadella dedritifera* (mis-identified as *Aplysilla sulphurea* in Klitgaard (1995)), *Leucandra* spp., *Lissodendoryx (L.) fragilis* Fristedt, 1885, *Polymastia grimaldii* (Topsent, 1913), *Stelletta normani*, *Ute gladiata* Borojevic, 1966, etc. *G. phlegraei* can settle on other sponges as well such as other large Astrophorina [*S. normani*, *Stryphnus fortis* (Vosmaer, 1885)]. The predator chiton *H. nagelfar* and the parasitic foraminiferan *H. sarcophaga* have been found living on *G. phlegraei* (Warén & Klitgaard, 1991; Cedhagen, 1994; Todt *et al.*, 2009). More associated fauna has been investigated by Klitgaard (1995). The chemistry (elemental analysis, amino acids, sterols, and quaternary ammonium compounds) has been investigated by Hougaard *et al.* (1991a, b).

The associated microsymbionts of *G. phlegraei* collected in the Sula Ridge reef (Norway) have been studied (Graeber *et al.*, 2004; Dieckmann *et al.*, 2005) and led to the isolation and description of a new gammaproteobacterium (*Oceanospirillales* group): *Spongiispira norvegica* (Kaesler *et al.*, 2008).

We observed on the type section of *I. sphaeroides* made by Vosmaer many subglobular oocytes without pseudopodes. This specimen has been collected in the Barents Sea on 2 July 1879.

In the NEA, *G. phlegraei* can easily be confused with another Geodiidae, *Pachymatisma normani*, which also has raised white-rimmed uniporal oscules, but *P. normani* has microrhabds in the cortex, instead of spheroxyasters. *Geodia phlegraei* can also be easily confused with its sister species *G. parva*, and in that case only spicule and genetic characters can differentiate them (cf. below).

Distinctive characters: External morphology: round to sometimes cup-shaped, with only uniporal openings (i.e. no sieve). The numerous small oscules on the top of specimen, each with a whitish rim making it look like a little wart. Often overgrown with other sponges, hydrozoa, bryozoa, etc. Spicules: large spherasters, smooth oxyasters along with fairly large sterrasters (70–144 µm).

Remarks: Choanosomal oxyasters can sometimes be separated into two size categories (10–25 and 45–60 µm) but in some specimens we have more of a continuum of sizes so we decided to treat oxyasters as one category (Table 5). Koltun (1966) notes the presence of rare small slightly curved oxeas (230–420 × 8–10 µm); we never observed those and wonder whether these could have been contamination. Dichotriaenes have been reported by Koltun (1966) and Vosmaer (1882), but it should be stressed here that they are fairly rare as we only found a few (notably in the holotype). Anatriaenes are rare and we report for the first time the presence of protriaenes in this species (found in the type of *I. sphaeroides*), but they seem to be very rare.

Geodia phlegraei is the type species of *Isops* Sollas, 1880b, a genus synonymized with *Geodia* based on molecular results (Cárdenas *et al.*, 2010). *Synops pyriformis* is the type species of *Synops*, a genus later synonymized with *Isops* (Sollas, 1889). Vosmaer's (1882) species (*Isops sphaeroides*, *Isops pallida*, *Synops pyriformis*) were all described from the same station near Hammerfest (71°12′5″N, 20°30′5″E) and collected on the same day (2 July 1879). Burton (1930: 498) writes: 'Examinations of the preparations in the Norman Collection, made from the type-specimens of these species, show conclusively that *Geodia parva* Hansen, *Isops pallida* Vosmaer, *I. sphaeroides*

Vosmaer, and *Synops pyriformis* Vosmaer are synonymous with *Isops phlegraei* Sollas.' We stated earlier that Burton did not look at the type of *I. pallida*, and that a lectotype (Fig. 19C, D) was designated to keep the synonymy with *G. phlegraei*. On the other hand, Burton did look at the BMNH type slides of *I. sphaeroides* and *S. pyriformis*.

Isops sphaeroides was described from two globular syntypes (both presumably lost, R. van Soest & N. de Voogd, pers. comm.): one larger specimen was hispid, whereas the smaller was not. All type slides we examined were identified as *G. phlegraei* (Table 5). However, we found differences between the MNHN type slides (Norman Collection) and those from the Vosmaer slide collection, namely differences in cortex thickness and sterraster sizes (Table 5), so these may represent the two syntypes. The Vosmaer slides include a section from half of a smooth specimen with an estimated total diameter of 2–2.5 cm, which must be the smaller syntype. To conclude, we presume that the Vosmaer slides correspond to the smaller syntype so the MNHN slides correspond to the larger syntype.

We also compared type specimen and type slides of *S. pyriformis* with our material. The cortex thickness of *S. pyriformis* (1.1–1.3 mm) agrees well with *G. phlegraei* (Table 5). Spicule measurements also match those of *G. phlegraei* (Table 5). Finally, observation of the external morphology (Fig. 19B) and new spicule preparations from the wet type of *S. pyriformis* further confirmed this. All in all, we therefore follow Burton (1930) and confirm the synonymy for *S. pyriformis*, *I. pallida*, and *I. sphaeroides*.

Koltun (1966) had already underlined the morphological variability of *G. phlegraei*. He notably states that in deeper and colder waters the morphology of *G. phlegraei* is somewhat different. Klitgaard & Tendal (2004) also noticed this arctic water morphotype and considered it as a subspecies of *G. phlegraei*: *G. phlegraei pyriformis*. After having examined many specimens from the whole boreo-arctic area, we confirm the existence of different morphotypes, and, after incorporating additional morphological data as well as molecular data, it was decided that the arctic morphotype represented a valid species which had in fact been previously described under the name *Geodia parva* Hansen, 1885, before being synonymized with *G. phlegraei* (Burton, 1930). Below, we resurrect and redescribe *G. parva*.

GEODIA PARVA HANSEN, 1885
GEODIINAE[P] PARVA (*PhyloCode* SPECIES NAME)
(FIGS 21–23, TABLE 5)

Geodia parva, Hansen, 1885, p. 17.
Isops phlegraei pyriformis, Klitgaard & Tendal, 2004: p. 57 (synonymy by this study).
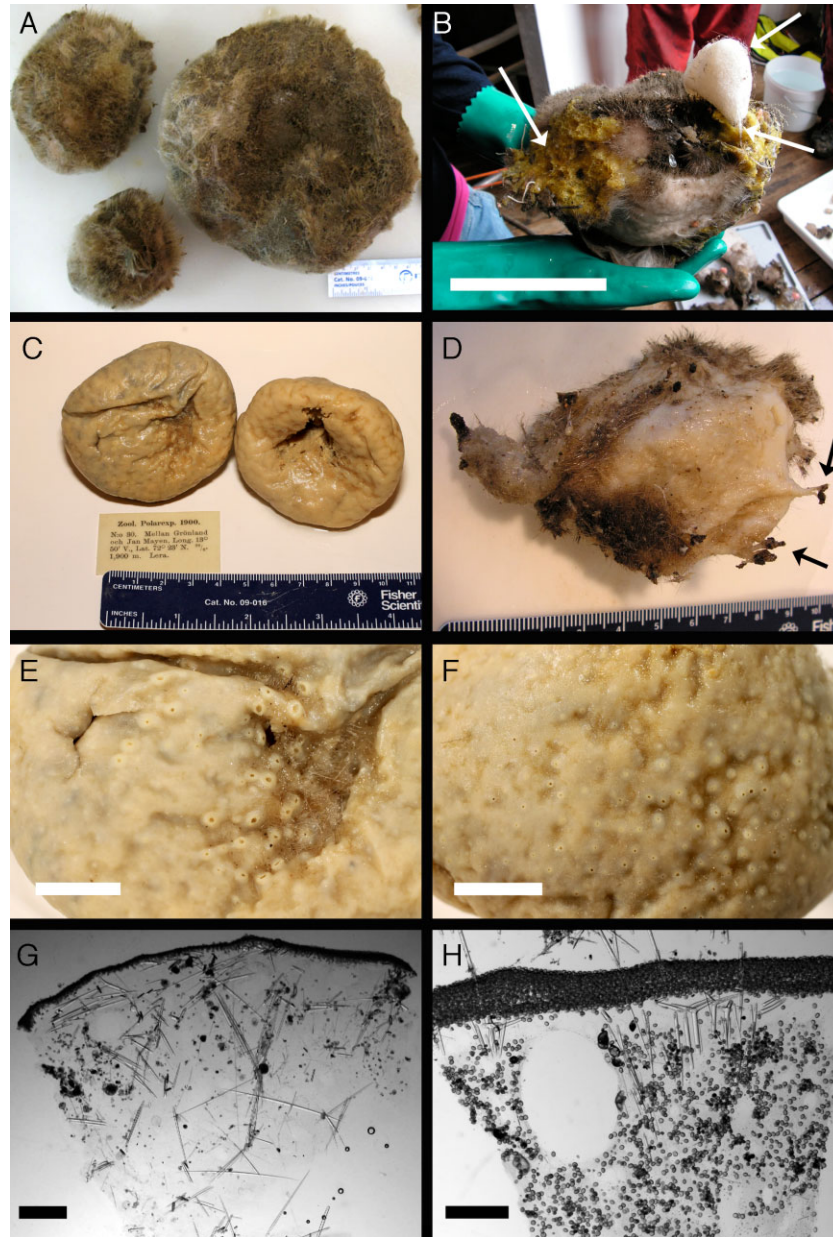
Figure 21. External morphology and thick sections of *Geodia parva* Hansen, 1885. A, specimens from Canadian Ice Island at 81°N, 130 m depth (Wagoner *et al.*, 1989). B, specimen collected on the Schultz Massive Seamount (H2DEEP Exp. 2008). The three arrows point to other sponges living on the specimen: *Hexadella dedritifera*, *Asbestopluma* (*A.*) *lycopodium* and a large white hexactinellid. C, UPSZMC 76801 (left) and 76802 (right) from eastern Greenland, 1900 m depth (Swedish Polar Exp. 1900). D, specimen ZMBN 85210, budding (arrows point to the buds), from the lower slope of the Schultz Massive Seamount, 1997 m depth (BIODEEP Exp. 2007). E, uniporal oscules (UPSZMC 76802). F, uniporal pores (UPSZMC 76802). G, thick section (ZMBN 85210, Schultz Massive Seamount, 1997 m depth). H, thick section (PC553, Schultz Massive Seamount, 688 m depth). Scale bars: B: 10 cm; E and F: 1 cm; G and H: 1 mm.

Misidentifications:
Isops pyriformis, Hentschel, 1929: p. 865.
Geodia phlegraei, Koltun, 1964 (in part?): p. 148; Koltun, 1966 (in part): p. 55; Cárdenas *et al.*, 2011 (in part): table S1; Murillo *et al.*, 2012 (in part?): p. 842.

Geodia cf. *phlegraei*, Wagoner *et al.*, 1989: p. 2344.

Type material examined
Geodia parva, unknown station, Norwegian North Sea Exp. 1876–78, ZMBN 100 (wet specimen).
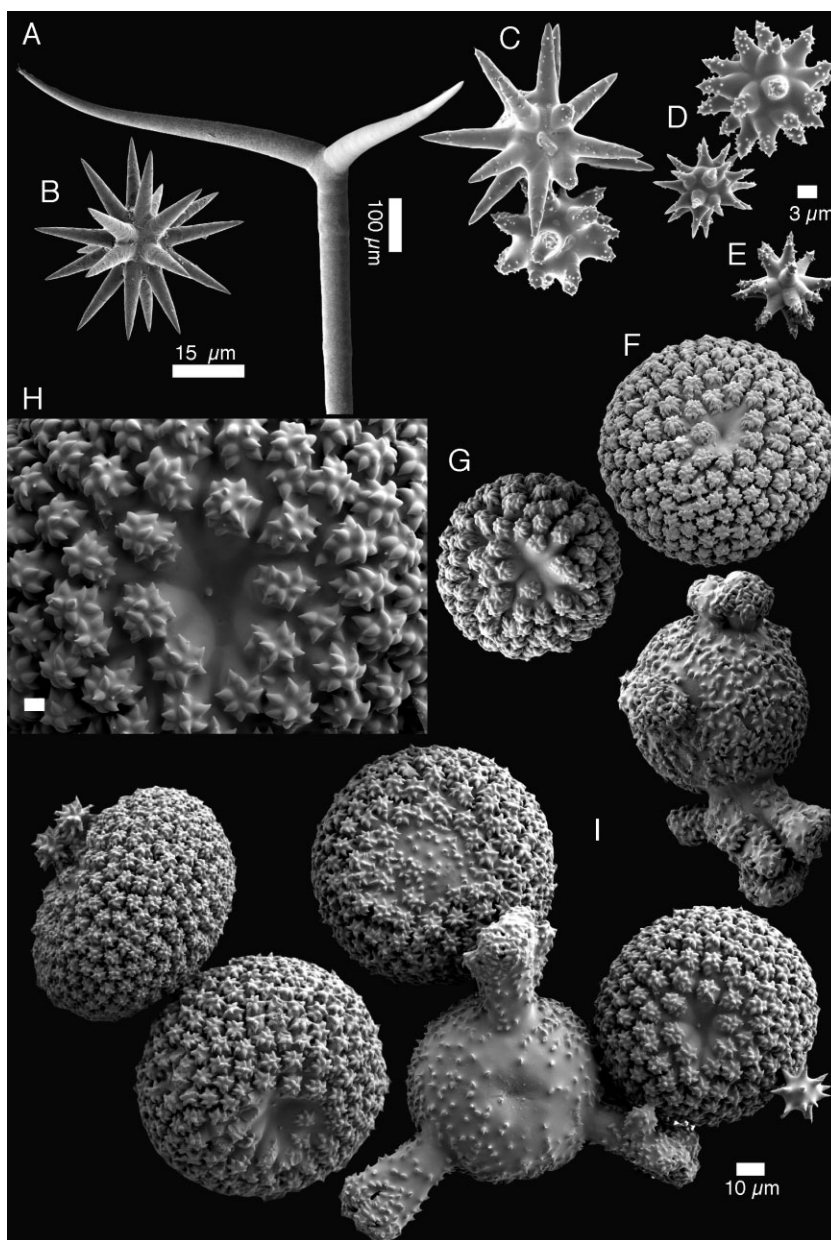
Figure 22. Spicules of *Geodia parva* Hansen, 1885. A, orthotriaene (UPSZMC 76801, eastern Greenland). B, oxyaster (UPSZMC 78273, Flemish Cap). C, oxyaster and spheraster (UPSZMC 76801). D, two spherasters (UPSZMC 76801). E, spheraster (ZMBN 100, holotype). F, sterraster (ZMBN 100, holotype). G, sterraster (ZMBN 85210, Schultz Massive seamount). H, close-up on the hilum of a sterraster. Note the smooth rosettes (UPSZMC 76801). Scale bar: 3 µm. I, sterrasters (regular and irregular) (UPSZMC 76801). All sterrasters of this plate are at the same scale (10 µm). C and D are at the same scale (3 µm).

External morphology and cortex: It seems there are two morphotypes for this species. The first morphotype can be found in true Arctic waters (Norwegian Sea, Greenland Sea, Davis Strait) – it is very characteristic and different from *G. phlegraei*; this morphotype is the one described below. The second morphotype, henceforth called the mixed-water mor- photype, is found in areas where Arctic and Atlantic waters mix (Denmark Strait, Flemish Cap) and has a mix of characters of the Arctic morphotype and *G. phlegraei* (cf. Discussion for its description). *Arctic morphotype:* Juveniles are spherical. Larger speci- mens are more or less spherical, flattened and cup- shaped (Fig. 21A–C); the largest specimens are 26 cm
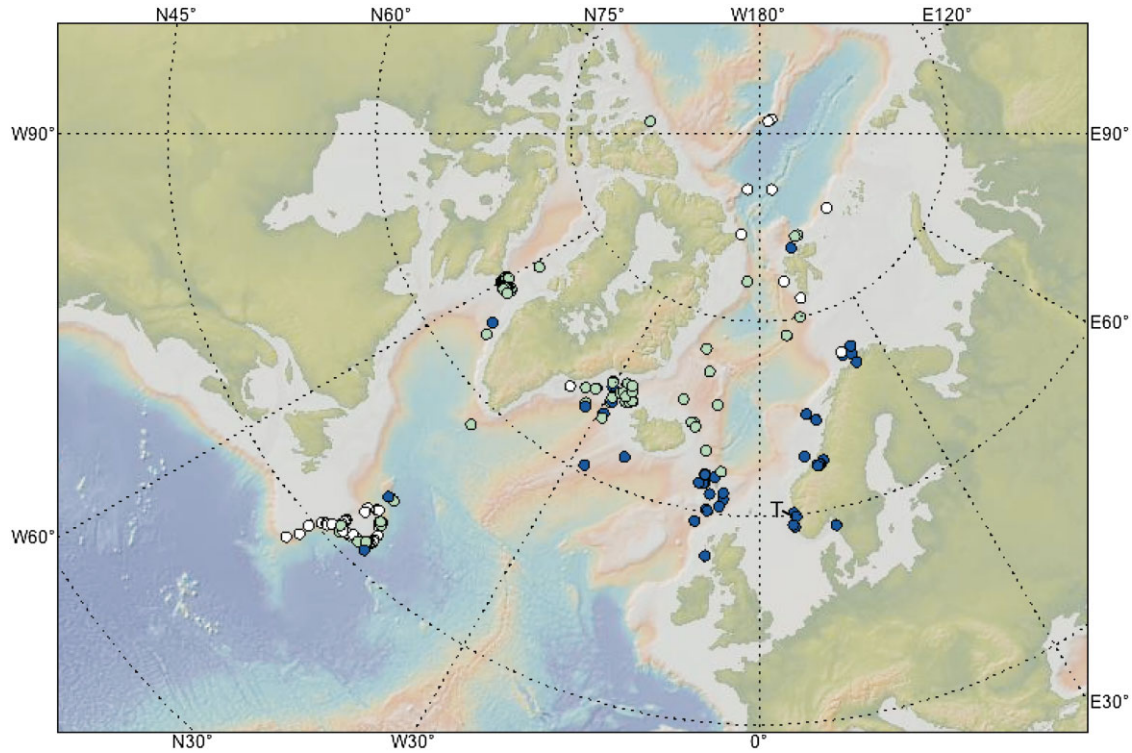
Figure 23. Distribution of *Geodia phlegraei* Sollas, 1880b (dark dots) and *Geodia parva* Hansen, 1885 (light dots). White dots represent specimens of *G. phlegraei* or *G. parva* but that we could not assign to the proper species for various reasons (map made with GeoMapApp, http://www.geomapapp.org). T, type locality.

in diameter (Klitgaard & Tendal, 2004), so *G. parva* reaches smaller sizes than *G. phlegraei*. Specimens from the Schultz Massive Seamount (Biodeep and H2deep Expeditions) can be fairly irregular (Fig. 21D). Root-like structures at the base are fairly common. Budding is commonly observed, and the buds are string like (Fig. 21D) to more massive (e.g. club-shaped). Most specimens have a dense fur covering the whole body, even the top surface where the oscules are found (Fig. 21A, B). In dredged specimens, this fur is often lost except in sheltered folds (Fig. 21E). Colour alive is whitish to light brownish. With the openings usually lighter-coloured this gives the sponge a characteristic mottled appearance. The cortex is very thin to thin (0.15–0.7 mm thick) (Fig. 21G, H), flexible, and easily cut (no breakage in large pieces as in *G. phlegraei*). Many epibionts (e.g. sponges) are present in this hispid part (Fig. 21B). Uniporal oscular openings are up to 1 mm in diameter, and are found mainly on the upper surface (Fig. 21E). Oscular openings are often wide and surrounded by a white rim (more rarely conical elevations), as in many specimens of *G. phlegraei*. Uniporal pores (up to 1 mm in diameter) (Fig. 21F) are scattered on the sides and partly on the underside of the body. Pores can be very slightly elevated and are usually surrounded by a white margin.

Description of holotype: The type material of *G. parva* is composed of one very small spherical sponge (4 mm in diameter) and a small piece of cortex of another specimen (3 mm). This explains the name given to this species: 'parva' means 'small' in Latin. The small piece of cortex has been completely used for spicule and SEM preparation (Fig. 22E, F), and the resulting slides and SEM stub are now stored at the ZMBN under the same number.

Spicules (Fig. 22, Table 5): Megascleres: (a) oxeas, sometimes modified to styles, length: 773–7935 µm; width: 14–102 µm. (b) Orthotriaenes, dichotriaenes are fairly rare, rhabdome length: 360–5395 µm; width: 20–108 µm; orthotriaene clad length: 102–1008 µm; protoclad length: 56–405 µm; deuteroclad length: 44–521 µm. (c) Anatriaenes are fairly rare, rhabdome length: 1–16 mm (minimum length measured by Hentschel, 1929); width: 15–34 µm; clad length: 29–78 µm. (d) Meso/protriaenes, very rare, clades are slightly forward or even slightly backward, with or without a central clad, rhabdome length:

840–8371 µm; width: 9–68 µm; clad length: 36–161 µm; central clad length: 60–334 µm. Microscleres: (e) sterrasters, spherical with a 'bumpy' appearance and commonly irregular (Arctic morphotype), usually spherical, but also sometimes elongated, similar to the sterrasters of *G. phlegraei* (mixed-water morphotype), 56–104 µm in diameter (Arctic morphotype); length: 68–124 µm (mixed-water morphotype); thickness: 52–56 µm; shallow and large hilum: 16–25 µm. Rosettes are made of 10–15 piled smooth rays. Rosette diameter: 6–8 µm. (f) Spherasters with fairly spiny actines which look almost blunt under an optical microscope and commonly irregular (Arctic morphotype), spherasters with less spiny actines, which look more conical and pointy under an optical microscope as in *G. phlegraei* (mixed-water morphotype), 10–30 µm in diameter. (g) Oxyasters, smooth or more rarely slightly rough actines, 10–72 µm in diameter.

DNA barcodes: GenBank accession no. HM592690 (Folmer COI). We have sequenced COI from specimens from Spitsbergen (1), the Schultz Massive Seamount in the Greenland Sea (3), the Davis Strait (1), the Flemish Cap (2), and Orphan Knoll (1): the Folmer COI is identical in all these specimens. No. KC481223 (18S), obtained from ZMBN 85210 (Schultz Massive Seamount).

Distribution (Fig. 23): Arctic distribution. It has been found at depths from 100 m [Canadian Ice Island (Wagoner *et al.*, 1989)] to 2747 m (Orphan Knoll), at temperatures of –1.5 °C (Wagoner *et al.*, 1989) to 4.4 °C (Ingolf Exp. st. 90).

Biology: Associated fauna has never been closely investigated but, as in *G. phlegraei*, our observations suggest that many macrosymbionts grow on its fur, especially sponges (Fig. 20B): Hexactinellida, *Hexadella dedritifera*, *Asbestopluma* (*A.*) *lycopodium* (Levinsen, 1887), *Craniella infrequens* (Carter, 1876), etc. *H. nagelfar* (chiton) and the parasitic foraminiferan *H. sarcophaga* have not been observed on *G. parva*, but these two species do not actually thrive in cold waters.

Distinctive characters: External morphology (Arctic morphotype): bumpy/wrinkled surface and thin flexible cortex (*c.* 0.5 mm). Budding. Hispidity all over the sponge and overgrown with other sponges, etc. Spicules: spherical small sterrasters (56–92 µm), some irregular sterrasters.

Remarks: Koltun (1966) noted a different *G. phlegraei* morphotype of the Norwegian Sea, the Greenland Sea, and the central part of the Arctic Ocean. They

are smaller, brighter in colour, with a thinner cortex (0.5–0.9 mm) and their spherasters have blunt rays (instead of being pointy). Klitgaard & Tendal (2004) also recognize this morph and consider the boreal and arctic form to be subspecies by calling them *Isops phlegraei phlegraei* and *I. phlegraei pyriformis* (arctic subspecies). They in fact sometimes occur in the same catch, in the hydrographically mixed regions of the Denmark Strait (Stations 78, 90, and 92 of Ingolf Exp.), the south-western Barents Sea, and at Orphan Knoll (Fig. 23). As we have shown above, *I. pyriformis* is a synonym of *I. phlegraei* and is therefore not an available name. On the other hand, a re-examination of the type material of *G. parva* (Table 5, Fig. 22) showed that it belonged to the arctic population.

The most obvious differences between *G. phlegraei* and *G. parva* are that *G. parva* show budding and have a thin flexible cortex which gives a characteristic bumpy wrinkled surface appearance. We have never seen buds in *G. phlegraei*, and its cortex is thick and stiff. Koltun (1966) also notes that oxeas are often modified to styles in *G. phlegraei*; we have observed this, but only in *G. parva*. The presence of irregular sterrasters is fairly common in *G. parva* (Fig. 22F) but never observed in *G. phlegraei*. Furthermore, the 1-bp difference (position 370, A in *G. phlegraei*, C in *G. parva*) between the COI of the two species is consistent. It reflects the close phylogenetic relationship of these species but also suggests that they may have completely diverged. 18S being far more conserved than the Folmer COI marker, we observed no differences between the 18S of *G. phlegraei* and *G. parva*. We therefore gather here enough morphological and molecular evidence to upgrade these two subspecies to two sister species: *G. phlegraei* and *G. parva* (here officially resurrected).

We remain troubled by the specimens collected in areas where Atlantic and Arctic waters mix (Denmark Strait, Flemish Cap), which essentially includes specimens from St. 90 (Ingolf Exp.) and from the NEREIDA campaign off Newfoundland. Using the COI marker, specimens from the Flemish Cap were identified as *G. parva*. However, their external morphology may in some occasions be closer to *G. phlegraei* [thicker cortex, up to 1.8 mm (UPSZMC 78279), oscules with conical elevations, smooth surface]. Their spicules make us also think of *G. phlegraei* (larger sterrasters and regular less spiny spherasters). Without a molecular marker they are almost impossible to identify for some of them. The status of these populations is therefore questioned: these could be *G. parva* populations in different environmental conditions (mixing of waters) or *G. phlegraei/parva* hybrids. Faster evolving genetic markers are clearly needed to settle this matter.

The specimens identified by Hentschel (1929) as *I. pyriformis* were collected in arctic deep waters (1000 m depth) along with typical arctic species (e.g. *G. hentscheli*, *Stelletta rhaphidiophora* Hentschel, 1929). Furthermore, sterraster measurements (81–91 μm) fit well with those of *G. parva* (Table 5). Pictures of the specimens described by Hentschel (ZMB Por 7542, 7543, 7544, and 8420, courtesy of C. Lueter) confirm that these are *G. parva*. Also, Koltun (1964) records *G. phlegraei* from the Greenland Sea (Obb, 1956, st. 7, 1441 m, −0.4 °C), south-west of Spitsbergen (Lena, 1958, st. 2, 759 m, ca 0.65 °C) and north-west of Franz Josef Land (F. Litke, 1955, st. 26, 415 m, 0.4 °C). We suppose that *G. phlegraei* specimens from station 7 (Obb, 1956) are *G. parva* because only typical Arctic species were collected at this deep station with negative temperature: *Craniella infrequens*, *Stelletta rhaphidiophora,* and *Thenea abyssorum* Koltun, 1964. Concerning stations 26 and 2, we cannot be sure.

The phylogenetic position of the *G. phlegraei*+ *G. parva* clade in the Geodiinae is still very uncertain, except that it does not belong to the three well-supported clades *Cydonium^p*, *Depressiogeodia^p*, or *Geodia^p* (Fig. 2). Contrary to the *Cydonium^p* and *Depressiogeodia^p* clades which, for the time being, only include Atlantic species, the *G. phlegraei*+ *G. parva* clade forms a well-supported clade with *Geodia intermedia* (Wiedenmayer, 1989) from Southern Australia.

DOUBTFUL SAMPLES AND SPECIES
Geodia cydonium (Jameson, 1811)

Records in the boreo-arctic region
North-eastern Kara Sea: Off Sewernaja Semlja (Gorbunov, 1946: p. 37).

South-western Barents Sea: Kola Fjord (Breitfuss, 1912: p. 62, as *Cydonium mülleri*; also referred to by Hentschel, 1929: p. 920, as *Geodia mülleri*).

Norway: Off Vadsø, Varanger Fjord (Burton, 1930: p. 490, *G. mülleri*); Røberg, Trondheim Fjord (Arndt, 1913: p. 112, *G. mülleri*); Korsfjord near Bergen (Norman, 1879: p. 13, *Geodia* sp.; Brunchorst, 1891: p. 31, *Geodia* sp., according to Arndt, 1935: p. 30, both *G. cydonium*); off Haugesund (Schmidt, 1875: p. 120, *Geodia gigas*, according to Arndt, 1935: p. 30, *G. cydonium*); off Stavanger (Burton, 1930: p. 490, *G. mülleri*).

Iceland: 64°56′N, 11°48′W, 216 m, 25.08.1902 (Burton, 1959: p. 9); Faxa Bay (Einarsson, 1941: p. 23, as *G. mülleri*).

Discussion: Koltun (1966) reinvestigated the specimens of Gorbunov (1946) and Breitfuss (1912) and found that they are *G. phlegraei*. The specimen of Arndt (1913) could not be traced. A.B.K. and H.T.R. have sampled intensively on the same locality, Røberg in the Trondheimsfjord, and found many specimens of *G. barretti* and *G. phlegraei*, but not a single specimen referable to *G. cydonium*; note that the specimen of Arndt was probably about 15 cm in diameter. We conclude that Arndt's specimen must have been misidentified. Arndt (1935) referred to some *Geodia* 'sp.'s in the literature as *G. cydonium*. Nothing indicates that Arndt ever saw any of these specimens, rather he just felt certain that *G. cydonium* was an inhabitant of Norwegian waters. We have worked along most of the Norwegian coast and we have not found specimens that could be referred to *G. cydonium*. Probably all those referred to above represent *G. barretti*, which is very common along the entire Norwegian coastline.

The Icelandic records are doubtful, too. We reinvestigated the specimen of Burton (1959) stored at ZMUC; in our opinion it is a fragment of *G. barretti*. Einarsson (1941) wrote '. . . enormous masses of sponges (*G. mülleri*?) are encountered . . .' Unfortunately we have no other samples from the same area, but everything considered, if it is a *Geodia* at all, it is presumably *G. barretti*.

Our conclusion is that there are no certain records of *G. cydonium* north of the line Shetland Islands–Lousy Bank, west of the Faroe Islands. The last mentioned locality is listed by Burton (1959), and no description or further reference is given; accordingly, it may also be considered doubtful until a control is possible.

Geodia simplex Schmidt, 1870

Geodia simplex, Schmidt, 1870: p. 70; Arndt, 1913: p. 112; Burton, 1930: p. 490; 1946: p. 856.

Type locality and deposition of holotype: Egedesminde, West Greenland, 50–90 m, ZMUC-DEM-319 (wet specimen). Burton (1946) also speaks of a Schmidt spicule preparation from the type, still in the BMNH collection today (BMNH 70.5.3.79).

Discussion: Arndt (1913) identified with hesitation a small specimen from Norway as *G. simplex*; the specimen has not been located. Burton (1946), after an examination of spicule preparations from the type material from Greenland, concluded that *G. simplex* is probably identical to *G. cydonium*, which explains why Burton (1959) later mentioned *G. cydonium* as occurring in Greenland and Norway. Also, Koltun (1966: 57) doubted the existence of *G. simplex* as an

independent species. We have inspected the holotype, a whole specimen cut in two. It is a rounded lump, measuring *c*. 7 cm in diameter and 3 cm in height; the surface is damaged in some areas, and algae are growing on it. The cortex is 1 mm thick. The spicule repertoire is clearly that of *G. cydonium* from the Mediterranean Sea. However, there must be a mistake, most likely from Schmidt's side, as the label is in his handwriting. The algae growing on the specimen do not occur in Greenland; on the contrary, one of the species is Mediterranean, another one Mediterranean–southern boreal (Dr Poul Møller Pedersen, pers. comm.). We therefore confirm that *G. simplex* is a junior synonym of *G. cydonium*. As molecular results suggest that *G. cydonium* is a species complex (Cárdenas *et al*., 2011), only a thorough morphological revision of this complex will tell us to which species group *G. simplex* belongs.

GENERAL DISCUSSION AND CONCLUSION
BIOLOGY

Overall, the biology of boreo-arctic *Geodia* species is poorly known. They are supposed to be gonochoric and oviparous, as shown for *Geodia barretti* (Spetland *et al*., 2007) and other *Geodia* species (Mercurio, Corriero & Gaino, 2007), but the larval stages have never been observed. Asexual reproduction was only observed in Arctic species: *G. hentscheli* and *G. parva*. As these two species are phylogenetically quite distant (Fig. 2), this may suggest a relationship between the Arctic water environment and the asexual reproduction strategy. We have no measurement of the longevity of these animals but based on their very slow growth rate in tanks (H.T.R., unpublished results) and in the wild (Guihen *et al*., 2012: fig. 8) and the large sizes they can reach, we suppose they could become fairly old (at least several decades).

Geodia species are in terms of size and biomass the dominating species in north Atlantic sponge grounds (Klitgaard & Tendal, 2004; Murillo *et al*., 2012). A very large number of associated fauna (> 242 species) use these sponges as a substratum (Klitgaard, 1995) so *Geodia* are of paramount importance for the conservation of deep-sea north Atlantic macrofauna biodiversity. However, they may also significantly contribute to enhance bacterial diversity by harbouring rich microbial communities (Schöttner *et al*., 2013). Indeed, *Geodia* species are high-microbial abundance (HMA) sponges hosting more than 10^{10} microbes cm^{-3} (Hoffmann *et al*., 2006), but contrary to the macrofauna which is considered facultative (Klitgaard, 1995), a small portion of these numerous associated microbes may be specific to the boreal *Geodia* species. The four boreal species of *Geodia* investigated by Schöttner *et al*. (2013) (*G. atlantica*, *G. barretti*, *G. macandrewii*, *G. phlegraei*) share similar but clearly distinct bacterial communities. In the future, it may be interesting to investigate how different microbial communities could be in phylogenetically closer species, such as sister species (*G. barretti*/ *hentscheli* and *G. phlegraei*/*parva*).

Usually boreo-arctic *Geodia* species do not settle to grow on other sponges. An exception is *G. phlegraei*, which has been occasionally found growing on other large Astrophorina sponges (*Stelletta normani* and *Stryphnus fortis*). As *G. parva* and *G. phlegraei* are sister species, we assume that *G. parva* can also settle on other sponges, but this has not yet been recorded. Interestingly, *G. phlegraei* and *G. parva* are also the two species most tolerant to sponge epibionts, while *G. barretti* is rarely associated with them. Since it has been shown that *G. barretti* produces brominated cyclodipeptides against foulers (Sjögren *et al*., 2011), we can hypothesize that these may be absent, or produced in lower quantities, in *G. phlegraei* and *G. parva*. Of interest is the yellow encrusting sponge *Hexadella dedritifera*, commonly found on *G. phlegraei*, *G. parva*, and other large Astrophorina such as *S. fortis*, *S. normani*, and *Characella pachastrelloides* (Carter, 1876) (Cárdenas & Rapp, 2012). The fact that it is never found on nearby *G. barretti*/*macandrewii*/ *hentscheli*/*atlantica* strongly suggests that *H. dedritifera* may carefully choose its hosts.

BIOCHEMISTRY

The sterol composition of *G. barretti*, *G. atlantica* (identified as *Geodia* sp.), *G. macandrewii*, and *G. phlegraei* has been analysed by Hougaard *et al*. (1991b), from specimens collected during the BIOFAR project. They show that *G. barretti*, *G. atlantica*, and *G. macandrewii* share similar arrays of sterols, with 24-methylenecholesterol as the major component. *Geodia barretti* and *G. macandrewii* further share the same proportion (*c*. 76%) of 24-methylenecholesterol while *G. atlantica* has *c*. 58% 24-methylenecholesterol and *c*. 20% of fucosterol. *Geodia phlegraei* shares some of these sterols but in minute quantities and instead more than 95% of its sterol profile is dominated by aplysterol. This is in reasonable accordance with the *Geodia* molecular phylogeny (Fig. 2) (Cárdenas *et al*., 2011) where *G. barretti* and *G. macandrewii* are closest. The sterol composition further suggests that *G. atlantica* is closer to *G. barretti*/ *hentscheli*/*macandrewii* than *G. phlegraei*, which is in contradiction to the molecular phylogeny (Fig. 2), but this topology is very poorly supported. To conclude, sterol composition may be a biochemical dataset worth completing and investigating to bring new phylogenetic characters to this group.

SPICULE MORPHOLOGY

The fact that microxeas are often centrotylote in *G. barretti*, *G. hentscheli* and more rarely in *G. macandrewii* had never been pointed out before this study. This may suggest that these microxeas evolved from asters.

Cardenas & Rapp (2013) showed that very large oxyasters may appear in *G. barretti* in specimens living deeper than 1000 m. Our measurements suggest similar trends of size of oxyasters I vs. depth in *G. atlantica* (Table 1) and *G. macandrewii* (Table 4). Furthermore, large oxyasters were also observed in some *G. hentscheli* but this was not related to depth (these were found in shallower specimens than the specimens measured in Table 3). This particular case and the overview given by our measurements (Tables 1–5) show that depth per se is probably not influencing spicule size but rather it is a combination of environmental parameters such as water temperature and/or silica concentration. These large oxyaster size categories in *G. macandrewii* and *G. hentscheli* had not been reported by Koltun (1966) so it is important to take them into consideration to avoid mis-identifications (with the Lusitanian *G. megastrella* for instance, which is characterized by very large oxyasters).

We investigated in this study new sterraster characters (rosette diameter, number of rays of rosettes, hilum size) but most of them failed to help in species identification. Rosette diameter and hilum size were very similar in all boreo-arctic *Geodia* species. It is, however, interesting to note that some species have smooth rosettes while others have warty rosettes, as observed previously in the Caribbean *Geodia papyracea* and *Geodia tumulosa* Bowerbank, 1872b (Cárdenas *et al.*, 2009). We further note that all the species examined so far with SEM from the two sister clades *Depressiogeodia*[p] (*G. barretti*, *G. hentscheli*) and *Cydonium*[p] (*G. macandrewii*, *G. papyracea*) have warty rosettes, whereas the more basally branched *G. tumulosa*, *G. atlantica*, *G. phlegraei*, and *G. parva* have smooth rosettes. Rosette morphology could therefore potentially be a good phylogenetic character and we therefore recommend including SEM observation of rosette appearance in future revisions or new species descriptions of *Geodia*. The number of rays of these rosettes is fairly similar (3–7) in all species except in *G. phlegraei* and *G. parva* where it can reach up to 15 rays per rosette. In *G. hentscheli* and *G. parva*, these rays tend to pile up on one another. Actually, the Arctic species, *G. hentscheli* and *G. parva*, share two other spicule characters: occasional irregular sterrasters and irregular cortical euasters. As these two species are not closely related, we can consider that these spicule modifications may somehow be related to the Arctic water habitat.

Megasclere sizes are definitely not good characters for species identification, and sizes are roughly the same in all boreo-arctic *Geodia* species (Tables 1–5). A similar conclusion was made with respect to boreo-arctic *Thenea* species (Cárdenas & Rapp, 2012). On the other hand, presence of orthotriaene and/or dichotriaene is fairly consistent and may help in the identification (although there are exceptions): *G. barretti* is the only species that usually has dichotriaenes, whereas *G. atlantica*, *G. macandrewii*, *G. phlegraei*, and *G. parva* usually have orthotriaenes. *Geodia hentscheli* can often have both orthotriaenes and dichotriaenes.

BIOGEOGRAPHY

All six species have deep-sea amphi-Atlantic distributions. Water temperature is clearly the limiting factor of the distribution of these species. Some are arctic species (*G. hentscheli*, *G. parva*), while others are typically boreal (*G. atlantica*, *G. barretti*, *G. phlegraei*, *G. macandrewii*) but are occasionally found in the Arctic (*G. macandrewii*), the Lusitanian (*G. atlantica*, *G. barretti*), and the Mediterranean Sea (*G. barretti*) provinces. The arctic species are sympatric in the Norwegian and Greenland Sea, the Denmark Strait, and the Davis Strait where temperatures can be negative. The boreal species are sympatric on the Norwegian coast, Faroe Islands, Denmark Strait, and Davis Strait, where temperatures are usually above 3 °C. These two groups of *Geodia* correspond to the boreal and Arctic sponge ground assemblages defined by Klitgaard & Tendal (2004: 89). However, in areas where Atlantic and Arctic waters mix or areas where Arctic waters are not too cold (i.e. above 0 °C), these two groups of *Geodia* can be brought together. In the Denmark Strait (area of mixture) and Davis Strait (Arctic water) all six species of *Geodia* can be found. Likewise in the Grand Banks off Newfoundland and the Flemish Cap (area of mixture), all species were identified, except for *G. hentscheli*. We find a similar bi-partition in the amphi-Atlantic boreo-arctic species of *Thenea*: Arctic species [*Thenea abyssorum*, *Thenea valdiviae* von Lendenfeld, 1907 (arctic COI haplotype)] and boreo-arctic species [*Thenea levis* von Lendenfeld, 1907, *Thenea muricata* Bowerbank, 1858, *Thenea valdiviae* (boreal COI haplotype)] (Steenstrup & Tendal, 1982; Cárdenas & Rapp, 2012).

The amphi-atlantic distributions of these boreo-arctic *Geodia* species is not surprising as amphi-Atlantic distributions have been previously reported for other boreo-arctic deep-sea sponges such as *Thenea* (Cárdenas & Rapp, 2012), Calcarea (Rapp, 2013), Cladorhizidae (Hestetun *et al.*, 2013), and *Asconema* species (Tabachnick & Menshenina, 2007). While examining the *Geodia* in the NEREIDA

material, more deep-sea sponge species were found which are fairly common in the boreal NEA: *Hexadella dedritifera*, *Craniella* spp., *Stelletta normani*, and *Stryphnus fortis* [mistakenly identified as *Stryphnus ponderosus* (Bowerbank, 1866) in Murillo *et al*. (2012)]. In addition, many more typical NEA sponge species are now recorded from Newfoundland and the Labrador region (Hentschel, 1929; Fuller, 2011; Murillo *et al*., 2012) [e.g. *Stylocordyla borealis* (Lovén, 1868), *Tentorium semisuberites* (Schmidt, 1870), *Mycale* (*Mycale*) *lingua* (Bowerbank, 1866), *Phakellia ventilabrum* (L., 1767)]. Likewise for other benthic invertebrates such as boreal deep-sea corals [e.g. *Lophelia pertusa* (L., 1758), *Paragorgia arborea* (L., 1758) (Fig. 1), *Primnoa resedaeformis* (Gunnerus, 1763)] (Tendal, 1992; Mortensen & Buhl-Mortensen, 2004; Gass & Willison, 2005; Wareham & Edinger, 2007). Interestingly, these same coral species are found more south on the US north-eastern coast (Packer *et al*., 2007) so we can suspect *Geodia* species to be present there too, at least the boreal ones. The absence of significant and consistent morphological and genetic differences between *Geodia* sp. populations across their geographical range suggests that gene flow is ongoing and/or that these areas were very recently colonized (i.e. after the Late Glacial Maximum *c*. 10 000 years ago). Ongoing gene flow would not be too surprising since our distribution maps show that all the *Geodia* species have fairly continuous distributions, and the few gaps observed are in our opinion due to a sampling bias. Indeed, due to their wide bathymetric ranges, there is virtually no geographical barrier restricting dispersal and connectivity of the different populations, and water temperature seems to be the main environmental barrier. Our distribution maps confirm that these species are not restricted to sponge grounds (i.e. the densest most noticeable populations) but can be found throughout the north Atlantic, thus forming more or less dense populations, perhaps depending on food availability, currents, and suitable substrates. So if there were intra-specific variation, it should be between the peripheral populations (i.e. found on the edge of a species range): for instance, Flemish Cap populations vs. Norwegian populations. However, no clear intra-specific spicule morphological patterns were observed; the variations observed rather seemed to be the result of the environment (water temperature, silica concentration). However, more variable molecular markers are needed to investigate any kind of geographical structure at the population level.

We note that some of these species have Lusitanian and Mediterranean populations (*G. barretti*, *G. atlantica*) but we have no or too few genetic data to assess the status of these southern populations. It is not too surprising to find *G. barretti* at 167 m depth in the Mediterranean Sea as it was recorded near the Gibraltar Strait (Balgim specimens) and because it can withstand rather high temperatures. Other deep-sea boreal benthic invertebrates also have wide geographical ranges between Norway and the deep Mediterranean Sea: the corals *L. pertusa* and *Madrepora oculata* (L. 1758) (e.g. Mastrototaro *et al*., 2010), or other large Astrophorina [*T. muricata*, *C. pachastrelloides*, *Peocillastra compressa* (Bowerbank, 1866)] (Cárdenas & Rapp, 2012). Note that no mass occurrences of *Geodia* have been observed in the Mediterranean Sea, and other large Astrophorina such as *P. compressa* and *Pachastrella monilifera* Schmidt, 1868 seem to dominate Mediterranean sponge grounds instead (Bo *et al*., 2012).

All the boreo-arctic *Geodia* species have fairly wide bathymetric ranges, especially the boreal ones (*G. atlantica*, *G. barretti*, *G. phlegraei*) which can be found at fairly shallow depths (30–65 m depth) in Norwegian fjords. No specimens were found deeper than 3000 m (record for *G. phlegraei* at Orphan Knoll) but they may be present in the poorly accessible and poorly explored north Atlantic basins (Greenland basin, Norwegian and Lofoten basin, Iceland basin, Irminger basin, Labrador basin) and/or mid-Atlantic ridges. *Geodia barretti* has the widest range of temperature tolerance and depth, which may explain why it is the most common *Geodia* species in this part of the north Atlantic. Another good illustration of this tolerance and resistance is also visible in large fjords: extensive sampling in the Trondheimfjord showed that *G. barretti* was present in the three successive basins of the fjord, whereas *G. atlantica* and *G. macandrewii* were very rare in the innermost basin (270 m maximum depth) while *G. phlegraei* was absent in the innermost basin (Klitgaard & Tendal, 2004). *Geodia atlantica* seems to be the least tolerant to cold waters; it has not been found in waters colder than 1.4 °C (south of Denmark Strait, Ingolf Exp., st. 92), and it prefers warmer waters which explains it being the only boreo-arctic *Geodia* to be present in Rockall Bank and Porcupine Bank.

It is interesting to note that although *Geodia* species thrive and dominate in Arctic waters, they are nearly absent in sponge grounds of the Antarctic, often dominated instead by large Tetillidae or Hexactinellida.

KEYS AND DNA BARCODING

Being the dominant species in long-overlooked deep-sea sponge grounds of the north Atlantic, *Geodia* species are a key component of deep-sea ecosystems, notably due to the macro- and microbiodiversity that they host. We therefore expect that ecologists, microbiologists, and conservationists will need to study the

biology of these sponges in order to grasp this complex habitat. To facilitate their identification, we have compiled important characters of these six species in Table 6. We have also produced two different keys (see below), one based on external characters of adult specimens, the other based only on spicules. Many deep-sea habitat and ecological studies are today based on identification from underwater observations (Howell *et al*., 2010; Purser *et al*., 2013). Therefore, the first key that we present below is based as much as possible on external characters visible on pictures. However, some characters may still be difficult to use in low-resolution pictures (e.g. nature of the openings) or clearly not accessible (cortex thickness to distinguish *G. phlegraei* and *G. parva*). Also, all *Geodia* juveniles being subglobular are nearly impossible to identify on pictures. Other studies are based on sampling (e.g. Klitgaard & Tendal, 2004) where fragments are often collected, and then the second key using spicule characters can be used. However, using spicule morphology can still be challenging to discriminate sister species such as *G. barretti*/*G. hentscheli* or *G. phlegraei*/*G. parva*, especially for specimens from the Flemish Cap for which the key might fail to discriminate between those sister species pairs. Molecular identification of *Geodia* species using the DNA barcoding tool can therefore be of great help. The species of *Geodia* revised here have unique COI (obtained for the six species) and 28S (obtained only for *G. barretti*, *G. hentscheli*, and *G. macandrewii*) barcodes which can enable unambiguous identification.

18S is known to be fairly conserved and used so far for class (Borchiellini *et al*., 2004), order (Redmond *et al*., 2007) or family phylogenies (Schmitt *et al*., 2005), so it is obviously not a good candidate for DNA barcoding. Before this study there were only two *Geodia* species with 18S sequences in GenBank (*G. neptuni*, *G. cydonium*), so the variability of this marker within *Geodia* was poorly known. We found that 18S was only unique for four species (*G. barretti*, *G. hentscheli* and *G. macandrewii*, *G. atlantica*), but could not discriminate *G. phlegraei* from *G. parva*. However, it seems 18S is variable enough to be used for *Geodia* phylogeny in the future, even though the number of informative characters may be low compared with the fragment length (1708 bp). For instance, there is a 19-bp difference between the 18S of *G. barretti* and *G. phlegraei* (two phylogenetically very distant species; Fig. 2) vs. the 38-bp difference in the Folmer COI marker. There is an 11-bp difference between the 18S of *G. barretti* and *G. atlantica* vs. the 34-bp difference in the Folmer COI marker. There is only 1-bp difference between the 18S of the sister species *G. barretti* and *G. hentscheli* vs. the 6–7-bp difference in Folmer COI marker. 18S sequences of

Geodia species are furthermore easy to align; no indels were found apart from one insertion of 2 bp in *G. macandrewii*.

COI and 28S sequences, chromatograms, and detailed descriptions of the barcoded specimens were earlier submitted to the Sponge Barcoding Project (http://www.spongebarcoding.org) (Cárdenas *et al*., 2010). Thanks to the present revision, we have completed these records, and added the 18S sequences as well as the new COI Folmer haplotype of *G. barretti* (UPSZMC 78268). These *submitted* records have now been shifted to *reference* records, which can be used for boreo-arctic *Geodia* species routine identification.

Geodia nodastrella has been included in both keys as it was found in the NEREIDA material from Flemish Cap and west of the Faroe Islands (type locality of *G. nodastrella*). However, this species has not been revised here as it is more of a typical Lusitanian species.

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Table 6. Comparative table of boreo-arctic *Geodia* spp.; spicule measurements are given in μm (unless otherwise stated)

Species	Depth (m)	Temperature range (°C)	Shape of large specimens	Epi-macrobionts	Budding	Oscules (diameter in mm)	Pores	Cortex thickness (mm)	Triaene types
G. atlantica	65–2338	1.4–10.5	Flat, convoluted or cup with flattened sides	*H. sarcophaga* *H. nagelfar*	no	uniporal (0.3–0.5)	cribriporal	c.. 0.5	Orthotriaenes (rarely dichotriaenes)
G. barretti	31–2000	0.4–15	Subspherical to irregular	*H. sarcophaga* (rare) *H. nagelfar*	no	uniporal in 1–30 preoscule(s) (1)	cribriporal	c.. 0.5	Dichotriaenes (rarely orthotriaenes)
G. hentscheli	130–2000	−1.76–4.5	Subspherical, very hispid	–	yes	uniporal in 1–3 preoscule(s) (1)	cribriporal	0.5–1	Orthotriaenes and dichotriaenes
G. macandrewii	157–1900	−0.82–8.3	Subspherical to massive cup sometimes flattened	*H. sarcophaga* (rare) *H. nagelfar*	no	cribriporal	cribriporal	1–4	Orthotriaenes (sometimes dichotriaenes)
G. phlegraei	40–3000	0.3–10.5	Subspherical to cup-shaped, hispid on the sides	*H. sarcophaga* *H. nagelfar* many sponges	no	uniporal (1)	uniporal	0.7–2	Orthotriaenes (rarely dichotriaenes)
G. parva	130–2747	−1.5–4.4	Subspherical to cup-shaped, very hispid	many sponges	yes	uniporal (1)	uniporal	0.15–0.7[a]	Orthotriaenes (rarely dichotriaenes)

Table 6. *Continued*

Species	Triaene (rhabdome length/width; orthotriaene clad; proto+deutero clad)	Oxeas I (length/width)	Anatriaenes	Anatriaenes (rhabdome: length/width; clad)	Pro/mesotriaenes	Pro/mesotriaenes (rhabdome: length/width;clad; central clad)	Ectocortical euasters (diameter)	Sterrasters (diameter)	Sterraster rosettes (diameter in μm)
G. atlantica	630–4400/ 18–125/ 95–750/ 140–430+90–300	1275–4440/ 11–68	very common	376–5200/ 2–32/ 9–300	protriaenes, very rare	3000/ 8–15/ 96–130/ no	spheroxyaster spiny 5–16	elongate 75–125	smooth 4–7
G. barretti	620–4600/ 20–150/ 70–500/ 100–310+45–450	1075–4450/ 15–75	common	>7400/ 9–40/ 50–250	pro/mesotriaenes, rare	>2300/ 7.5–15/ 25–130/ 25–98	strongylaster spiny 3–11	spherical /elongate 65–130	warty 4–7
G. hentscheli	252–4060/ 22–145/ 244–835/ 60–520+96–492	1200–5175/ 35–60	rare	>6040/ 17–43/ 90–308	pro/mesotriaenes, rare (common in fur)	>4000/ 17–24/ 87–224/ 98–196	strongylaster spiny 4–22	spherical /elongate 56–89.5	warty 5–6
G. macandrewii	1650–9625/ 40–165/ 210–1125/ 220–500+70–450	2150–7000/ 30–80	common	up to 22 mm/ 3.5–40/ 24–250	pro/mesotriaenes, common	up to 11 mm/ 5–79/ 32–330/ 49–685	spheroxyasterspiny 4–15	spherical 124–360	warty 6–10
G. phlegraei	586–6655/ 12–150/ 80–1125/ 220–250+100+250	1173–7600/ 10–100	rare	up to 15 mm/ 8–35/ 30–150	protriaenes, very rare	11600–12750/ 25–30/ 190–200/ no	spherasters spiny 8–26	usually elongate 70–144	smooth 6–8
G. parva	360–5395/ 20–108/ 102–1008/ 56–405+44–521	773–7935/ 14–102	rare	1–16 mm/ 15–34/ 29–78	pro/mesotriaenes, very rare	840–8371/ 9–68/ 36–161/ 60–334	spherasters 10–30	usually spherical 56–116	smooth 6–8

Table 6. *Continued*

Species	Oxyasters I (diameter)	Oxyasters II (diameter)	Oxeas II (length/width)
G. atlantica	spiny 22–104	spiny 12–35	no
G. barretti	spiny 30–80 (only specimens > 1000 m)	spiny 6–32.5	sometimes centrotylote 205–630/ 4–17.5
G. hentscheli	–	spiny 10–62	sometimes centrotylote 142–610/ 5–15
G. macandrewii	–	spiny 10–88	rarely centrotylote 220–445/ 3–13
G. phlegraei	–	smooth (rarely spiny) 10–70	no
G. parva	–	smooth or spiny 10–72	no

[a]Up to 1.8 mm in NWA specimens.

KEY FOR THE ATLANTIC BOREO-ARCTIC *GEODIA* SPECIES (BASED ON EXTERNAL MORPHOLOGY OF ADULT SPECIMENS)

1. Preoscule(s) (= large opening(s))..2
   No preoscules..3
2. Preoscule(s) (one to more than 30) very variable, shallow to deep, narrow to large. Naked surface....*Geodia barretti*
   Preoscule(s) (one to three) are usually narrow and deep. Hispid surface.................................*Geodia hentscheli*
3. No visible openings...4
   Visible small openings (uniporal = no sieve)..5
4. Hispid sides, thick cortex (1–4 mm)...*Geodia macandrewii*
   Globular shaped, thin cortex (*c.* 0.5 mm)..*Geodia nodastrella*
5. Uniporal oscules grouped on top of the specimen look like (white) warts. Hispid surface, often with sponge epibionts...6
   Uniporal oscules never surrounded by a white edge; cribriporal pores. Naked surface..............*Geodia atlantica*
6. Bumpy, wrinkled surface, thin cortex (0.15–0.7 mm)..*Geodia parva*
   Smooth surface, thick cortex (0.7–2 mm)...*Geodia phlegraei*

KEY FOR THE ATLANTIC BOREO-ARCTIC *GEODIA* SPECIES (BASED ON SPICULE MORPHOLOGY)

1. Smooth choanosomal oxyasters, no microxeas..2
   Spiny choanosomal oxyasters...3
2. Spherical sterraster with 'bumby' surface, diameter: 56–116 μm, common irregular sterrasters, shallow hilum (SEM)..*Geodia parva*
   Elongated sterrasters (usually), diameter: 70–144 μm, deep hilum (SEM).............................*Geodia phlegraei*
3. Cortical strongylasters...4
   Cortical spheroxyasters..5
4. Sterraster with 'bumpy' surface, diameter: 56–89.5 μm, common irregular sterrasters..............*Geodia hentscheli*
   Sterraster diameter: 65–130 μm ....*Geodia barretti*
5. No microxeas ....*Geodia atlantica*
   Microxeas present 6
6. Ectocortical spheroxyasters (4–15 μm), orthotriaenes..*Geodia mancandrewii*
   Large spherasters (14–40 μm), dichotriaenes..*Geodia nodastrella*

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