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Unique spicules may confound species differentiation: Taxonomy and biogeography of *Melonanchora* Carter, 1874 and a new related genus (Myxillidae: Poecilosclerida) from the Okhotsk Sea

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Sponges are amongst the most difficult benthic taxa to properly identify, which has led to a prevalence of cryptic species in several sponge genera, especially in those with simple skeletons. This is particularly true for sponges living in remote or hardly accessible environments, such as the deep-sea, as the inaccessibility of their habitat and the lack of accurate descriptions usually leads to misclassifications. However, species can also remain hidden even when they belong to genera that have particularly characteristic features. In these cases, researchers inevitably pay attention to these peculiar features, sometimes disregarding small differences in the other "typical" spicules. The genus *Melonanchora* Carter 1874, is among those well suited for a revision, as their representatives possesses one of these unique, spicule types (spherancorae), which should ease their identification. Nevertheless, there are only five formally accepted species, with only two being commonly recorded over large geographical areas, while the three remaining species seem to be endemic to the Okhotsk Sea but present clear differences with their Atlantic counterparts. After a thorough review of the material available of this genus in several institutions, four new species of *Melonanchora*, *M. tumultuosa* sp. nov., *M. insulsa* sp. nov., *M. intermedia* sp. nov. and *M. maeli* sp. nov. are here formally described from different localities across the Atlanto-Mediterranean region. Additionally, two out of the three *Melonanchora* from the Okhotsk Sea are here reassigned to other genera, with *Melonanchora kobjakovae* being transferred to *Myxilla* (*Burtonanchora*) and the creation of a new genus, *Arhythmata* gen. nov. to allocate *Melonanchora tetradedritifera*. This new genus would be close to the

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Abstract

Sponges are amongst the most difficult benthic taxa to properly identify, which has led to a prevalence of cryptic species in several sponge genera, especially in those with simple skeletons. This is particularly true for sponges living in remote or hardly accessible environments, such as the deep-sea, as the inaccessibility of their habitat and the lack of accurate descriptions usually leads to misclassifications. However, species can also remain hidden even when they belong to genera that have particularly characteristic features. In these cases, researchers inevitably pay attention to these peculiar features, sometimes disregarding small differences in the other "typical" spicules.

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1. Introduction

Accurate species-level taxonomy is still nowadays a fundamental keystone for conservation assessment, planning, and management (Myers et al., 2000; Groves et al., 2017). As so, the differentiation between cryptic species (as in Knowlton, 1993), is of paramount importance for effective conservation policies (Lohman et al., 2010). While cryptic species are widespread phenomenon among both terrestrial and marine phyla (e.g. Baker, 1984; Mayer & Helversen, 2001; Concepción et al., 2008; Crespo & Pérez-Ortega, 2009; Dennis & Hellberg, 2010; Lohman et al., 2010; Payo et al., 2013), the assumed lack of barriers to gene flow in marine habitats (Hellberg, 2009) contributed to assumption that benthic organisms present wider distribution ranges and phenotypic plasticity than terrestrial organisms (Knowlton, 1993). As a result of this assumption, many benthic species were thought to be geographically widespread or even cosmopolitan (Klautau et al., 1999). Nevertheless, recent studies have generally demoted this idea (e. g. Klautau et al., 1999; van Soest et al., 1991; van Soest & Hooper, 1993). The dispersal capabilities greatly vary among benthic species even within the same phyla (Uriz et al., 1998) and they can be differentially reduced by natural barriers (Allcock et al., 1997; Waters & Roy, 2004). In this sense, some invertebrate Phyla, such as sponges and corals, produce short-life free larvae that cannot overpass apparently weak marine barriers such as littoral currents or substrate discontinuity, often resulting in extremely low dispersal capabilities (Hellberg, 2009). In sponges, for instance, genetically structured populations, even at short spatial scales, have been repeatedly reported (Duran et al., 2004a; 2004b; Calderón et al., 2007; Blanquer et al., 2009; Blanquer & Uriz, 2010; Guardiola et al., 2016), which favours speciation and makes unreliable the existence of widely distributed or cosmopolitan species.

Species complexes and cryptic species are particularly prevalent among sponges with few diagnostic characters (Klautau et al., 1999; Uriz et al., 2017a; 2017b), in particular when these characters are subjected to environmental plasticity (Maldonado et al., 1999; Xavier et al., 2010; De Paula et al., 2012). As examples, it can be mentioned the sponge complex *Chondrilla nucula* Schmidt, 1862, which was once believed to have a circumtropical distribution (Klautau et al., 1999), *Stylocordyla borealis* (Lovén, 1868), which had been reported to occur at both poles (Uriz et al., 2011), the Atlanto-Mediterranean *Scopalina lophyropoda* Schmidt, 1862 and *Hemimycale columella* (Bowerbank, 1874), which both hided several morphologically cryptic species that where revealed by molecular markers (Blanquer & Uriz, 2008; Uriz et al., 2017a, 2017b) or the excavating sponges *Cliona celata* Grant, 1826 and *Cliona viridis* (Schmidt, 1862), which are known to be "species complexes" which taxonomy is still partially unresolved (Xavier et al., 2010; De Paula et al., 2012; Escobar et al., 2012; Leal et al., 2016; Gastaldi et al., 2018). Cryptic species complexes are also prevalent in sponge genera without mineral (spicules) or organic skeletons (spongin fibres), such as *Hexadella* Topsent, 1896, where species are almost indistinguishable based solely on morphological or histological characteristics (Reveillaud et al., 2010; 2012). However, species can also remain hidden even when they belong to genera that have particularly characteristic spicules. In these cases, researchers inevitably pay attention to these peculiar spicules, sometimes disregarding small differences in the other "typical" spicules.

Some genera of Poecilosclerida, one of the most diverse orders in terms of spicule diversity (Hooper & van Soest, 2002), possess unique spicular types that greatly facilitate their identification. Examples include dianciastras in *Hamacantha* Gray, 1867 (Hajdu, 1994; Hajdu & Castello-Branco, 2014), clavidiscs in *Merlia* Kirkpatrick, 1908 (Vacelet, & Uriz, 1991), discorhabds in *Latrunculia* du Bocage, 1869 (Samaai et al., 2006) or thraustoxeas in *Rhabderemia* Topsent, 1890 (van Soest & Hooper, 1993). Nevertheless, because taxonomists historically have focused on these particular spicules (van Soest et al., 1991), differences in other apparently banal spicules have been disregarded so that some species might have been confounded and, as a result, considered to show a wide distribution. As a consequence, some of those genera (e.g. *Rhabderemia* van Soest & Hooper (1993), *Acarnus*, Gray, 1867, van Soest et al. (1991), *Merlia*, Vacelet, & Uriz (1991) or *Trachytedania* Ridley, 1881 (Cristobo & Urgorri (2001)) contain or contained until recently few formally described species. Moreover, only the thoroughly described species are usually recognised and reported in the literature (van Soest et al., 1991), while those with poor or imprecise descriptions remain forgotten, a trend which is aggravated for sponges living in remote or hardly accessible environments, such as the deep-sea (Reveillaud et al., 2010). For this reason, despite challenging and time consuming, comprehensive reviews of such genera are considered extremely useful for the discovery of cryptic species (Reveillaud et al., 2012) and to test biogeographical and evolutionary hypotheses (van Soest & Hooper, 1993; Cárdenas et al., 2007).

The genus *Melonanchora* Carter 1874, is among those well suited for such revisions, as (i) it possesses one of these unique, spicule types (spherancorae); (ii) contains only five formally accepted species (van Soest et al., 2021) (iii) only two out of the five species are commonly recorded over large geographical areas (Baker et al., 2018) and (iv) the three remaining species seem to be endemic to the Okhotsk Sea and nearby Pacific Islands (Koltun, 1958; 1970; Lehnert et al., 2006a) and present clear differences with their Atlantic counterparts (Lehnert et al., 2006a). Finally, *Melonanchora* representatives occur within Vulnerable Marine Ecosystems (VMEs) across the Atlanto-Mediterranean region, thus being in need of accurate identifications for the evaluation of the conservation status of the sponge grounds where they occur (Best et al., 2010; ICES, 2012).

In this context, this paper (1) reviews the status of all the species currently allocated to *Melonanchora* with particular emphasis in the Pacific species, apparently endemic to the Okhotsk Sea, and their relationships with other Myxillidae; (2) provides a reliable guide for their identification; (3) describes new species of the genus; (4) and discusses the biogeographical implications of the genus circumpolar distribution.

2. Material and Methods

2.1 Museum material and sample treatment

The materials for this study consisted of samples from natural history museums and other scientific institutions and unregistered individuals from surveys across the North Atlantic (Life+INDEMARES, NEREIDA and ABIDES) as well as specimens from authors' own collections. The institutions are abbreviated in the text as follow:
Canadian Museum of Nature, Canada (CMNI); Gothenburg Natural History Museum, Sweden (GNM); Museo Civico di Storia Naturale di Genova (MSNG); Museum of Biology of Lund, Sweden (MZLU); Naturalis Biodiversity Center, The Netherlands (NBC, previously ZMA); National Museum of Natural History, Smithsonian Institution, Unites States (NMNH); Musée Zoologique de la Ville de Strasbourg (MZS); National History Museum, United Kingdom (NHMUK); Swedish Museum of Natural History, Sweden (NRM); Yale Peabody Museum of Natural History, Unites States (YPM); Museum für Naturkunde, previously known as Zoologisches Museum Berlin, Germany (ZMB); Jean Vacelet's personal collections (JV); Manuel Solórzano's personal collections (MS). DNA was extracted from small pieces of tissue

of four samples (Vis4.7, CMNI-2980107, Por624, USNH.1082996) using QIAGEN's DNeasy Blood and Tissue kit, following the instructions of the manufacturer. Amplification and sequencing of the mitochondrial cytochrome c oxidase subunit I (COI) were attempted but proved unsuccessful, with only two samples yielding an amplicon but resulting in sequencing of non-target DNA (bacteria). This was likely due to the low quantity and integrity of the DNA in the samples, as assessed by spectrophotometry using a DeNovix DS-11 FX.

All known species of *Melonanchora* were represented in the studied material. Holotypes of all species but *Melonanchora tetradedritifera* Koltun, 1970 were examined. Spicule preparations for both optical and scanning electron microscopy (SEM) were performed according to Cristobo et al. (1993) and Uriz et al., (2017a). Optical observations were performed using a Leica DM IRB inverted microscope from the Instituto de Ciencias del Mar (ICM-CSIC), whereas SEM observation were conducted using an ITACHI TM3000 TableTop Scanning Electron Microscope from the Center for Advanced Studies of Blanes (CEAB-CSIC), Spain, a JEOL–6100 SEM from the University of Oviedo (UO), Spain, and a HITACHI S-3500 N scanning electron microscope from the Institut de Ciències del Mar (ICM-CSIC), Spain. Spicule sizes are given as ranges with average values (in italics) ± Standard Deviation (e.g. MIN. – *MEAN* ± SD – MAX.). Unless otherwise stated, spicule measurements were performed on 40 spicules per spicule type. The species classification adopted in the study follows that currently proposed by Morrow & Cárdenas (2015) and the World Porifera Database (van Soest et al., 2021). A key to *Melonanchora* can be found at the Supplementary material 1.

Finally, the electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: [urn:lsid:zoobank.org:pub:F1A22CAA-DE1F-434D-9A6B-

F00853C40FF5]. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central SCIE and CLOCKSS.

3. Results

3.1 Systematic Description

Phylum PORIFERA Grant, 1836

Class DEMOSPONGIAE Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order POECILOSCLERIDA Topsent, 1928

Family MYXILLIDAE Dendy, 1922

Genus *Melonanchora* Carter, 1874

Type species:

Melonanchora elliptica, Carter, 1874.

Diagnosis:

From encrusting to massive-globular growth form, with paper-like, easily detachable thin ectosome, bearing fistular processes. Ectosomal skeleton composed of smooth strongyles to tylotes with somewhat asymmetrical ends, whereas the choanosome is mainly composed of smooth strongyles or styles, the later either smooth or more rarely, acanthose. Microscleres include typically two categories of anchorate isochelae, rarely three, and spherancorae (amended from van Soest, 2002).

Remarks:

The genus *Melonanchora* was erected by Carter (1874) for *Melonanchora elliptica* on the account of the species singular anchorate-derived chelae (spherancoras), placing it tentatively on its "*Halichondria*" family concept built around *H*. (= *Myxilla*) *incrustans* (Johnston, 1842). The genus was later included in Desmacidonidae Schmidt (1880) until Lundbeck (1910), and later Topsent (1928), transferred it definitively to Myxillidae. Simultaneously, Hentschel assigned it to Dendoricellidae[1] (Hentschel, 1929), but this assignation had a limited acceptation (Alander, 1935) and was quickly disregarded.

The family Myxillidae has been redefined over the years (Hajdu et al., 1994; Desqueyroux-Faundez & Van Soest, 1996; van Soest, 2002) and the genus *Melonanchora* fits within the definition of Myxillidae currently established in the Systema Porifera (Hooper & van Soest, 2002), which is restricted to "those genera which combine the possession of anchorate chelae with diactinal ectosomal tornotes [oxeotes and tylotes] and choanosomal styles in a reticulate arrangement". Yet, after re-examination of all the available *Melonanchora* material, the current definition of the genus (van Soest, 2002) needs to be amended to better allocate the new species here described or re-described, including: presence of acanthostyles (*M. globigilva* Lehnert, Stone & Heimler, 2006a) or smooth strongyles (*Melonanchora emphysema* (Schmidt, 1875); *M. tumultuosa* sp. nov.) as choanosomal megascleres, the presence of anisochelae as microscleres (*M. indistinta* sp. nov.) and the possession of two to three chelae categories (*M. indistinta* sp. nov.; *M. maeli* sp. nov.).

Nevertheless, the main diagnostic character of the genus, the spherancoras, remains unaltered since Carter's original description (See Section 4.2). Aside from spherancoras, Carter also added the presence of a papillated paper-thin like ectosome (Figs.1A, C, and F) as an additional diagnostic character (Carter, 1874). Although this feature is shared with other deep-sea genera such as *Cornulum* Carter, 1876 or *Coelosphera* Thomson, 1873 (Lehnert & Stone, 2015; Schejter et al., 2019), *Melonanchora* differs from the later in its white-translucent ectosome, with brittle and loose appearance (Baker et al., 2018) and its characteristic wart-shaped papillae, which, altogether, makes external identification feasible at the genus level (Stone et al., 2011).

Subgenus *Melonanchora* Carter, 1874

Diagnosis and type species:

[1] While Hentschel assigned it to Dendoricellidae, he later wrongfully referred *Melonanchora* as part of Tedanidae within the text.

Melonanchora with smooth megascleres and complete spherancorae.

Type species:
Melonanchora elliptica Carter, 1874.
Remarks:
See remarks for *Melonanchora* (*Toretendalia*) subgen. nov.

Melonanchora (*Melonanchora*) *elliptica* Carter, 1874
(Figs. 1A, 2, 3)

Synonymy:
Melonanchora elliptica Carter, 1874a: 212, pI. XIII figs 6–12, pI. XV fig. 35a-b; Vosmaer, 1885: 31, pI. I fig. 14, pI. V figs 69–70 (*partim*); Topsent, 1892: 101–102; Fristedt, 1887: 454, pl. 25 fig. 5, 55 (*partim*); Arnesen, 1903: 15–16, pl. II fig. 4, pl. V fig. 4; Topsent, 1904: 144, pl. IV fig. 10; Lundbeck, 1905: 213–216, pl. VII figs. 4–6, pl. XX fig. 1 a–o; Lundbeck, 1909: 402–403; Arndt, 1913: 116; Topsent, 1913: 44; Topsent, 1928: 246; Hentschel, 1929: 966; Burton, 1931: 4; Alander, 1935: 5; Arndt, 1935: 71–73, Fig. 141; Koltun, 1959: 122–123, fig. 76; Baker et al., 2018: 20–25, fig. 5–7; Dinn & Leys, 2018: 63.
Not: *M. elliptica* Schmidt, 1880: 85, pl. IX fig. 8.

Material examined.
Holotype: NHMUK 1882.7.28.54a, between the north coast of Scotland and the Faroe Islands; 'HMS Porcupine', ca. 800 m depth, 1869. (two slides); NHMUK - Norman Coll. Nº50 10.1.1.1417, 'Porcupine' Expedition; NHMUK 1954.3.9.301 Nº50; NHMUK - Norman Coll. - H. J. Carter Slide Coll. 1954.3.9.301; ZMB Por 3042, between the North coast of Scotland and the Faroe Islands, North Atlantic Ocean (59°51'N 6° 01' 60"W).
Additional specimens examined:
CMNI 2018-0107, Saglek Bank, Labrador Sea, North Atlantic Ocean (60° 27' 7.69"N 61° 16' 8.19"W), 427 m depth, 2016-07-21, collected by Dinn, Curtis [Dinn & Leys, 2018]; MZLU L936/3483, Trondheim Fjord, Norway (63° 23' 25.99"N 10° 23' 08.98"E), 1936; NRM 113070, off Lindenows Fjord, Greenland, North Atlantic Ocean (60° 4'N 34° 15'E), 237.9 m depth, 1885 [Fristedt, 1887]; YPM IZ 006552.PR, Laurentian Channel, Nova Scotia, North Atlantic Ocean

(44° 34' 0.12"N 56° 41' 44.88"W), 'USFC Albatross', 218 m depth, 1885; NHMUK - Norman Collection 1910.1.1.588, Hardanger Fjord, ca. 180 m depth, 1882; NHMUK - Sott-Ryen Coll., 1931.6.1.19, Folden Fjord, Norway [Burton, 1931]; NHMUK Norman Coll. 1910.1.1.1418, Norway, 1882; NHMUK – Norman Coll. 1910.1.1.1419, Norway, 1882; NHMUK – Norman Coll. 1910.1.1.1420, Norway, 1882; NHMUK – Norman Coll. 1910.1.1.1421 [Fristedt, 1887]; NHMUK - Norwegian Coll. 1982.9.6.14.a., Norway, 1885; ZMA.POR.P.10797, North of Hammerfest, Norway, Artic Ocean (72° 9'N 22° 42'E), 'Willem Barents', 265 m depth, 1881 [Vosmaer, 1885]; ZMA.POR.1548, North of Hammerfest, Norway, Artic Ocean (72° 9'N 22° 42'E), 'Willem Barents', 265 m depth, 1881[Vosmaer, 1885].

Unregistered material:
NR0509_43, Flemish Cap, Tail Grand Bank, North Atlantic Ocean, 1554 m depth (NEREIDA Coll.); NR0509_49, Flemish Cap, Tail Grand Bank, North Atlantic Ocean, 1137 m depth (NEREIDA Coll.); NR0509_52, Flemish Cap, Tail Grand Bank, North Atlantic Ocean, 870 m depth (NEREIDA Coll.); NR0509_73, Flemish Cap, Tail Grand Bank, North Atlantic Ocean, 1122 m depth (NEREIDA Coll.); NR0509_82a, Flemish Cap, Tail Grand Bank, North Atlantic Ocean, 1127 m depth (NEREIDA Coll.); NR0610_21, Flemish Cap, Tail Grand Bank, North Atlantic Ocean, 1055 m depth (NEREIDA Coll.); NR0709_5, Flemish Cap, Tail Grand Bank, North Atlantic Ocean, 1248 m depth (NEREIDA Coll.).

Description:
Usually massive-globular sponge (Fig. 1A), more rarely encrusting (CMN 2018-0107), with an easily detachable paper-like thin ectosome bearing abundant fistular processes. The choanosome shows several scattered pores and channels. Colour whitish translucent outside, cream-orange in the choanosome.

Skeleton:
Ectosomal skeleton consists of tangential tylostrongyles with a criss-cross arrangement (Fig. 2C). Choanosomal skeleton with scattered poorly defined tracts (Fig. 2B) of styles to substyles and abundant organic content. Microscleres are distributed thorough the choanosome without any clear discernible patter, yet, in some individuals (including the holotype), spherancoras form

a dense palisade between the ectosome and the choanosome and might also cover the choanosomal tracts (Fig. 2D).

Spicular complement:
Styles, tylostrongyles, two categories of chelae, and spherancoras (Fig. 3A-G).

Ectosomal tylostrongyles (Fig. 3B): Unevenly, slightly flexuous unequally thinning towards both ends, with a more or less central swelling and, differentially inflated ends (strongyle to tylote appearance).
Size range: 560.3 – *624.3* ± 32.2 – 666.5 µm x 7.8 – *11.8* ± 3 – 17.3 µm

Choanosomal styles (Fig. 3A): Entirely smooth, slightly curved towards its distal end. In general, they have the point markedly acerate, but points can also be blunt to various degrees in some spicules (stylostrongyles) (Fig. 3F).
Size range: 782.5 – *830.8* ± 50 – 908.1 µm x 17.2 – *19.3* ± 1.1 – 20.5 µm

Isochelae I (Fig. 3E, c'): Small anchorate isochelae, with a straight shaft, well-developed fimbriae and spatulated alae. The distal alae slightly point outwards, giving a “V” lateral appearance to both ends.
Size range: 24.2 – *26.6* ± 3.4 – 29 µm

Isochelae II (Fig. 3D, b'): large isochelae with a straight shaft, well-developed fimbriae and spatulated alae. The distal alae slightly point outwards, giving a “V” lateral appearance to both ends.
Size range: 48.3 – *51.1* ± 3.8 – 58 µm

Spherancorae (Fig. 3C, a'): Unique to the genus, with an oval shape and slightly pointed ends, which might resemble a rugby ball. It possesses fimbriae on its internal face, which may be free or fused to various degrees.
Size range: 48.3 – *51.2* ± 2.7 – 53.1 x 23.1 – *28.3* ± 1.6 – 29.2 µm

Geographic distribution and ecological remarks:

M. elliptica is a common amphi-Atlantic species (Fig. 4) also occurring in Artic waters (Carter, 1877), as far as the Barents Sea (Koltun, 1959; Katckova et al., 2018). It has been recorded from the coasts of Norway (Vosmaer, 1885; Topsent, 1913), Faroe Plateau (Carter, 1874; Lundbeck, 1905), Porcupine Seamount (Könnecker, G., & Freiwald, 2005; van Soest & De Voogd, 2015) and Rockall Bank (van Soest, & Lavaleye, 2005), Greenland and Iceland (Lundbeck, 1905; Burton, 1959), the Azores archipelago (Topsent, 1892; 1904; 1928) and the area within the Labrador Peninsula and the Newfound Land Seas (Topsent, 1913; Michaud & Pelletier, 2006; Baker et al., 2018), from 80 to 1554 m depth. In the Canadian coasts and the Gulf of Maine, the species is commonly found on sponge grounds on trawlable areas (Maciolek et al., 2008; 2011) and it has been observed to be an occasional nursery ground for the octopus *Rossia palpebrosa Owen, 1935* (Wareham Hayes et al., 2017). Nevertheless, its role and ecological significance in Vulnerable Marine Ecosystems (VMEs) are still poorly understood and in need of further research.

Remarks:

Melonanchora elliptica is the type species of the genus, first described from a specimen collected during the 'Porcupine' expedition in the Northeast Atlantic (Carter, 1874). The holotype description referred to a soft roundish sponge with a thin paper like ectosome with papillate projections that lodge pores and oscula. However, while the pore areas are indeed located at the wart-like papillae, the oscula are not at their tip (Fig. 1C; F), as initially claimed (Carter, 1874; Vosmaer, 1885) but on the ectosome (Lundbeck, 1905), yet they are visible only after a careful examination. The conspicuous ectosome is loosely attached to the choanosome here and there, which, together with its fragility, might contribute to its rip off during trawl sampling (Vosmaer, 1885; Topsent, 1892). Collected individuals without ectosome, appear smooth, porous, and lack the characteristic papillae. However, the presence of spherancoras facilitates the species identification, even after the ectosome's detachment (Baker et al., 2018).

While Carter's original description was precise, its figures resulted insufficiently accurate. Thus, posterior authors (Vosmaer, 1885, Topsent, 1892; 1904) referred to Schmidt's species redescription on Caribbean individuals (Schmidt, 1880) instead of to the type description for their species identification. However, Schmidt's material (MZS Po165) was in fact another species (described below as *Melonanchora insulsa* sp. nov.) clearly differing from *M elliptica* in the shape of chelae and spherancorae. Finally, Topsent's individuals form the Azores are insufficiently described (Table 1) and were not available. While it is clear that they belong to *Melonanchora*, it is impossible to ascertain based on Topsent's descriptions that they unequivocally belong to *M. elliptica* and not to any other North Atlantic *Melonanchora* species.

Melonanchora (*Melonanchora*) *emphysema* (Schmidt, 1875)

(Figs. 1B; 5; 6)

Synonymy:

Desmacidon emphysema Schmidt, 1875: 118.

Melonanchora elliptica Alander, 1935: 5 (*partim*).

Melonanchora emphysema Vosmaer, 1885: 31, pI. I fig. 14, pI. V figs 69–70 (*partim*); Thiele, 1903: 393; Lundbeck, 1905: 213–216, pl. XX fig. 2a-d; Lundbeck, 1909: 402–403; Arndt, 1913: 116; Hentschel, 1929: 966 – 967; Arndt, 1935: 73, Fig. 142; Alander, 1942: 57 (*partim*); Vacelet, 1969: 200 – 201, fig. 38; *Melonanchora emphysema* Solórzano & Duran, 1982: 105 – 106, fig. 5c; Solórzano, 1990: 755 – 777, L. 92; Santín et al., 2021: Table 1.

Not *Melonanchora emphysema* van Soest, 1993: 210, Tab. 2; Pulitzer-Finali, 1983: 561.

Material examined.

Holotype:

ZMB Por 2680, North Sea, from a Fjord of the southern coasts of Norway; ZMB Por 6571, North Sea, from a Fjord of the southern coasts of Norway.

Additional specimens examined:

GNM Porifera 416, Skagerrak, Sweeden, 80 – 100 m depth, 1934, [Alander, 1935; 1942]; GNM Porifera 290, Norra Kosterområdet Säcken, Baltic Sea (59° 0' 51.89"N 11° 7' 11.2"W), 80 m depth, 1934, [Alander, 1935; 1942]; GNM Porifera 390, Norra Kosterområdet Säcken, Baltic Sea (59° 0' 51.89"N 11° 7' 11.2"W), 80 m depth, 1927, [Alander, 1935; 1942]; MZB 2019–1740 – Blanes Canyon, north-western Mediterranean Sea (41°30'26"N 2°56'02"E), 'ABIDES' survey, 684 m depth, 2018 [Santín et al., 2021]; ZMA.POR.P.10800 Outer Hebrides, Scotland, North-

East Atlantic (56°48'21.168"N 7°25'44.508"W), 2006; ZMA.POR.20192 Outer Hebrides, Scotland, North-East Atlantic (56° 48' 21.168"N 07° 25' 44.508"W), 2006; ZMA.POR.P.10799 West of Hvasser, Norway, Baltic Sea (59° 04' 42.06"N 10° 43' 55.379"E), 2006; ZMA.POR.20559.b West of Hvasser, Norway, Baltic Sea (59° 04' 42.06"N 10° 43' 55.379"E), 2006; ZMA.POR.20473.b West of Hvasser, Norway, Baltic Sea (59° 04' 42.06"N 10° 43' 55.379"E), 2006; ZMA.POR.20551 West of Hvasser, Norway, Baltic Sea (59° 04' 42.06"N 10° 43' 55.379"E), 2006; ZMA.POR.P.10798 Outer Hebrides, Scotland, North-East Atlantic (56° 48' 25.56"N 07° 25' 48.9"W), 2006; ZMA.POR.20353.a Outer Hebrides, Scotland, North-East Atlantic (56° 48' 25.56"N 07° 25' 48.9"W), 2006; ZMA.POR.P.10795 West of Ireland, North-East Atlantic (55° 30' 03.348"N 15° 47' 18.239"W), attached to *Madrepora* debris, 2005; ZMA.POR.P.20020 West of Ireland, North-East Atlantic (55° 30' 03.348"N 15° 47' 18.239"W), attached to *Madrepora* debris, 2005; ZMA.POR.20020 West of Ireland, North-East Atlantic (55° 30' 03.348"N 15° 47' 18.239"W), attached to *Madrepora* debris, 2005; ZMA.POR.P.10829 West of Hvasser, Norway, Baltic Sea (59° 04' 32.772"N 10° 44' 07.908"E), 2007; ZMA.POR.20467 West of Hvasser, Norway, Baltic Sea (59° 04' 32.772"N 10° 44' 07.908"E), 2007; ZMA.POR.P.10828 Outer Hebrides, Scotland, North-East Atlantic (56° 48' 21.24"N 07° 26' 30.588"W), 2006; ZMA.POR.20175.b Outer Hebrides, Scotland, North-East Atlantic (56° 48' 21.24"N 07° 26' 30.588"W), 2006; NBC ZMA.POR.P.10827 Outer Hebrides, Scotland, North-East Atlantic (56° 48' 20.268"N 07° 25' 33.707"W), 2006; ZMA.POR.20335 Outer Hebrides, Scotland, North-East Atlantic (56° 48' 20.268"N 07° 25' 33.707"W), 2006.

Unregistered material:
AVILES_0710 – 48DR5, Avilés Canyon System, Cantabrian Sea (43° 46' 132"N 05° 59' 621"E), 128 m depth (INTEMARES AVILES Coll.); MS, off Bares (44° 3' 18"N 07° 38' 47"W), Spanish coasts, 500 m depth; JV, Cassidaigne Canyon (42° 57'N 05° 23'E), 360 m depth [Vacelet, 1969]; Galician Bank, west of Galician coast, Spain (42° 34' 59"N 11° 34' 59"W) ca. 700 m depth; Baixo do Placer do Cabezo de Laxe (43°N 09° 2'E), Galicia Coast, Spain, Fishermen's by-catch, 58 m depth, 1981 [Duran & Solórzano, 1982].

Description:

Mostly encrusting, rarely massive-encrusting (GNM Porifera 416), with an easily detachable paper-like ectosome bearing fistular processes. Fistulae might be absent in small encrusting individuals. Colour whitish translucent in the ectosome, cream-orange in the choanosome while in alcohol.

Skeleton:

Ectosomal skeleton formed by intertwined tangential tylostrongyles. The choanosomal skeleton is ill defined, with scattered tracts of tylostrongyles identical to those conforming the ectosome. Microscleres mostly scattered thorough the choanosome without any clear discernible pattern.

Spicule complement:

Tylostrongyles, two categories of chelae, and spherancoras (Fig. 5A-E and Fig. 6A-F).

Ectosomal and choanosomal tylostrongyles (Fig. 5A; 6A): of similar shape to those of *M. elliptica*: they are unevenly and slightly flexuous, enlarged at the central zone and narrowing toward unequal tylotoid (Fig. 6F), giving them the appearance from strongyles to tylostrongyles.

Size range: 492.7 – *508.1* ± 13 – 521.6 µm x 9.7 – *10.6* ± 2.8 – 14.5 µm

Isochelae I (Fig. 5D, c'; 6E, c'): Small isochelae with a straight shaft, gently bending to its ends, with three spatulated alae and well-formed fimbriae.

Size range: 24.1 – *26.6* ± 2.8 – 28.9 µm

Isochelae II (Fig. 5C, b'; 6C, b'): very similar to isochelae I, but bigger in size.

Size range: 48.3 – *51.5* ± 5.5 – 58 µm

Spherancorae (Fig. 5B, a'; 6B, a'): Elongated-ovoid (Fig. 5B) to stadium shaped (Fig. 6B) with teeth-like fimbriae on its internal surface, which may be fused at various degrees.

Size range: 37.6 – *38.8* ± 1.1 – 40.5 x 25.1 – *27.6* ± 1.6 – 28.9 µm

Geographic distribution:

Originally described from the coasts of Norway (Schmidt, 1875), the species is known from deep Atlantic and Artic waters (Fig. 4), including Greenland and Iceland, (Lundbeck, 1905; 1909; 1910), Faroe Islands (Hentschel, 1929), Porcupine Bank (van Soest & De Voogd, 2015), Baltic Sea (Alander, 1935; 1942), the Spanish coasts (this paper), and the coasts of Norway (Vosmaer, 1885; Arndt, 1913) including the Svalbard archipelago (Gulliksen et al., 1999). The species had also been recorded from the Atlantic Canadian coast (Baker et al., 2018; Murillo et al., 2018), yet said records correspond to *Melonanchora tumultuosa* sp. nov., thus its presence remaining unconfirmed in the area. Additionally, the species has also been sparsely recorded from the Mediterranean Sea and nearby areas: the Gulf of Lyon (Vacelet, 1969; Santín et al., 2021) and the northern coasts of Spain (Durán & Solórzano, 1982; this study). The species usually grows with an encrusting habit on cold-water corals (Könnecker & Freiwald, 2005; van Soest & De Voogd, 2015) yet it might also occur attached to rocky substrates or debris.

Remarks:

Schmidt (1875) poorly described *Desmacidon emphysema* from the coast of Norway, a species characterized by the presence of a papillate ectosome and smooth megascleres enlarged at the middle, with unequally swelled ends. While Schmidt accurately reported spherancorae in his *M. emphysema* samples from the Caribbean (Schmidt, 1880), he missed these spicules in the Northern Sea samples, mistaking them with diatoms (Schmidt, 1875), which led to his misclassification of *M. emphysema* in the genus *Desmacidon*, until amended by Thiele (1903). Furthermore, Schmidt incomplete description (Table 1) led several authors to consider the species a synonym of *M. elliptica* (Vosmaer, 1885; Arnesen, 1903) while others claimed that a clear distinction existed (Thiele, 1903, Lundbeck, 1905). The problem mainly arose as the main distinguishing feature between both species relies on its choanosomal megascleres, with *M. elliptica* possessing styles and *M. emphysema* possessing strongyles (Lundbeck, 1905), yet several authors had described samples with blunt-ended styles (Vosmaer, 1885, Baker et al., 2018).

The re-examination of Schmidt holotype (ZMB Por 2680) however leaves no doubt about the validity of the species. As previously pointed out (Thiele, 1903; Lundbeck, 1905), *M. emphysema*'s choanosomal megascleres are exclusively tylostrongyles identical to its ectosomal ones while the spherancoras are smaller or equal in size than the large isochelae (Table 1).

Conversely, *M elliptica* there is a clear distinction between the choanosomal and ectosomal megascleres and, additionally, the spherancoras are within the size range of the large isochelae. Thus, individuals identified as *M. emphysema* with blunt-ended diactines in two clear categories do not correspond to this species, but to a new species, *Melonanchora tumultuosa* sp. nov. (here described). Finally, in the Mediterranean and nearby areas, *M. emphysema* tylostrongyles are half in size than those in the North Atlantic specimens (Table 1), and it had been suggested that they might correspond to a yet undescribed species (Vacelet, 1969). In this sense, reexamination of all known Mediterranean material did in fact reveal a new species *Melonanchora intermedia* sp. nov. (here described) from the Italian coasts, but no major differences could be observed for most other Mediterranean and nearby samples, other than the size of the tylostrongyles. In this sense, only two samples, one from the Galician coast, the other from the Cantabrian Sea, possess relatively smaller and thinner tylostrongyles, and, in the Galician sample, a category of chelae with reduced alae in very low numbers (Fig. 6D), absent from all other Iberian or Mediterranean *M. emphysema* samples, and most likely being a modification from chelae II or contamination. Yet, their spherancorae closely match the stadium-shaped definition of *M. emphysema* (Fig. 6). Given the high variability in megasclere size observed within all *Melonanchora* species and the poor conservation state of this deviant samples, it would be unwise to erect a new species based solely on the megascleres size, yet the possibility that those specimens corresponding to a cryptic species cannot be entirely ruled out, and its identity should be further clarified if more individuals with should characteristics should be discovered.

Melonanchora (*Melonanchora*) *tumultuosa* sp. nov.

(Figs.1C; 7)

Synonymy:

Melonanchora elliptica Vosmaer, 1885: 31, pI. I fig. 14, pI. V figs 69–70 (*partim*); Lundbeck, 1905: 213–216, pl. VII figs. 4–6, pl. XX fig. 1 a–o (*partim*); Lundbeck, 1909: 402–403 (*partim*); Alander, 1935: 5 (*partim*).

Melonanchora emphysema Alander, 1942: 57 (*partim*); Baker et al., 2018: 26–30, fig. 8–10.

Material examined.

Holotype (here designated): GNM Porifera 624, Kostergrundet, Sydkoster Island, Sweeden, 100 m depth.

Additional specimens examined:
NHMUK – Icelandic Coll. 1958.1.1.633, Iceland, North Atlantic Ocean (63° 33'N 11° 25'E), 1936; NHMUK Norman Coll. 1898.5.7.38, Norway, 1893; NHMUK, 83.12.13.70.89; MZLU L935/3858, Koster, Säcken, Swedeen, Baltic Sea (59° 0' 34.99"N 11° 6' 52.99"E), 1934, [Alander, 1935; 1942]; ZMA.POR.P.10796, Northwest of Tromsø, Norway, Artic Ocean (72° 36' 5"N 24° 57'E), 'Willem Barents', 256 m depth, 1881 [Vosmaer, 1885]; ZMA.POR.P.10825, Marsteinsboen, Norway, North East Atlantic (60° 07' 33"N 04° 59' 22"E), 130 – 150 m depth, on stone, 1982; ZMA.POR.P.10822, Marsteinsboen, Norway, North East Atlantic (60° 07' 33"N 04° 59' 22"E), 130 – 150 m depth, on stone, 1982; ZMA.POR.P.10824, Marsteinsboen, Norway, North East Atlantic (60° 07' 33"N 04° 59' 22"E), 130 – 150 m depth, on stone, 1982; ZMA.POR.4977, Marsteinsboen, Norway, North East Atlantic (60° 07' 33"N 04° 59' 22"E), 130 – 150 m depth, on stone, 1982; ZMA.POR.P.10823, off Saengsbokt, Bergen, Norway, North East Atlantic (60° 22'N 04° 49'E), 350 – 600 m depth, 1982; ZMA.POR.4976, off Saengsbokt, Bergen, Norway, North East Atlantic (60° 22'N 04° 49'E), 350 – 600 m depth, 1982.

Unregistered material:

NR0509_82b, Flemish Cap, Tail Grand Bank, North Atlantic Ocean, 1127 m depth (NEREIDA Coll.); NR0610_30a, Flemish Cap, Tail Grand Bank, North Atlantic Ocean, 613 m depth (NEREIDA Coll.).

Description:
Massive-globular sponge, with an easily detachable paper-like thin ectosome bearing abundant fistular processes (typical of the genus). The choanosome is orange-cream in colour and the ectosome results whitish, yet translucent, in alcohol.

Skeleton:

Spicule arrangement as in the other species of the genus (viz. *M. elliptica*), with its main distinguishing feature being the presence of strongyles as choanosomal megascleres.

Spicule complement:
Tylostrongyles, strongyles, two categories of isochelae, and spherancoras (Fig. 7A-F)

Ectosomal tylostrongyles (Fig. 7B): As in other *Melonanchora*, they are slightly flexuous, with a more or less central swelling. The tips can be strongyloid or slightly tylote often vaguely unequal.
Size range: 483 – *542.6* ± 38.3 – 600 µm x 10.6 – *12.9* ± 3.2 – 19.3 µm

Choanosomal strongyles (Fig. 7A): Entirely smooth, with asymmetrical ends (one clearly rounded and the other blunt but somewhat narrower. More or less curved throughout its entire length.
Size range: 627.9 – *802.3* ± 42.2 – 924.5 µm x 11.6 – 18.3 ± 1.5 – 24.4 µm

Isochelae I (Fig. 7E, c'): Anchorate, with a straight shaft, gently bending to its ends, with three-spatulated alae.
Size range: 21.2 – *26.5* ± 3.8 – 28.9 µm

Isochelae I (Fig. 7D, b'): Similar to isochelae I, but smaller in size.
Size range: 48.6 – *68.6* ± 8.1 – 72.9 µm

Spherancorae (Fig. 7C, a'): With a prolate-oval shape, and dentate fimbriae on its internal face, which might be free or fused at various degrees. The junction points of each couple of opposite alae can be observed in most spicules, with the resulting fused shaft being slightly asymmetrical.
Size range: 48.3 – *67.5* ± 6.8 – 78.62 x 18.9 – *22.3* ± 1.6 – 25.2 µm

Geographic distribution and type locality:
The species presents ~~and~~ amphi-Atlantic distribution (Fig. 4), being sympatric with *M. elliptica.* Its type locality is the Sydkoster Island, Sweden, yet, known records for the species also include

Iceland (NHMUK –1958.1.1.633) the Davis Strait (Baker et al., 2018) and Norwegian coasts (Vosmaer, 1885; this paper).

Etymology:
From the latin *tumultuosus*, meaning full of commotion. It refers to the confusion that samples of this species have caused between *M. elliptica* and *M. emphysema* during the past century.

Remarks:
Specimens of *M. tumultuosa* sp. nov. had been considered by several authors to be *M. emphysema* because of their possession of both ectosomal and choanosomal strongyles (Baker et al., 2018). Close re-examination of the *M. emphysema* ~~type~~ revealed only one type of megascleres, which is present in both ectosome and choanosome (Fig. 5A), whereas in *M. tumultuosa* sp. nov., two different types of strongyles characterise either the ectosome (Fig. 7B) or the choanosome (Fig. 7A).

Additionally, it had been suggested that those "*M.* cf. *emphysema*" could in fact be *M. elliptica* individuals (Baker et al., 2018) with styles modified to strongyles. In this regard, sponge spicules might vary in shape due to environmental conditions (Bell et al., 2002) and/or silica abundance (Uriz et al., 2003) even to the point not expressing one or more spicule types (Maldonado & Uriz, 1996; Maldonado et al., 1999). However, *M. elliptica* and *M. tumultuosa* sp. nov. co-occur in their areas of distribution, even at local scales (Baker et al., 2018), weakening such idea. In this sense, *M. tumultuosa* sp. nov., spherancorae shape is mostly prolate (Fig. 7C), commonly with asymmetrical shafts and rounded ends, whereas they are clearly spheroidal in *M. elliptica*, with slightly pointed ends (Fig. 3C), which is translated in an overall slender spherancorae for *M. tumultuosa* sp. nov, compared to *M. elliptica* (Table 1).

Melonanchora (*Melonanchora*) *intermedia* sp. nov.

(Figs. 8)

Synonymy:
Melonanchora emphysema Pulitzer-Finali, 1983: 561.

Material examined.

Holotype (here designated): MSNG – off Calvi, Corsica (42° 32'N 08° 36'E), depth 128 m, detrital, dredge, 18 July 1975. R.N. N IS.4.7 [Pulitzer-Finali, 1983].

Description:

Small subglobular individual attached to rocky debris. It possesses a paper-like ectosome with the warty-like papillae typical of the genus, yet with just a few papillae.

Skeleton:

Ill-defined paucispiculate tracts in the choanosomal area, and a clear crisscross pattern can be observed in the ectosome. Microscleres are abundantly scattered throughout the choanosome.

Spicule complement:

Tylostrongyles, three categories of chelae and spherancoras (Fig. 8A-F).

Ectosomal and choanosomal tylostrongyles (Fig. 8A): from more or less straight to entirely bent on its length. The show a wider central zone, narrowing asymmetrically toward differently marked tylotoid ends (Fig. 8F), giving the spicule a variable shape between strongyles to tylostrongyles.

Size range: 369.6 – *411.8* ± 14.5 – 475.3 µm x 7.2 – *9.7* ± 1.5 – 11 µm

Isochelae I (Fig. 8C, d'): anchorate, with a gently curved shaft and irregularly spatulated rounded alae, often with a malformed tooth in one or both of the extremes.

Size range: 19 – *21.5* ± 0.7 – 22.7 µm

Isochelae II (Fig. 8D, b'): With an almost straight shaft and three alae, presenting a prominent fusion between the lateral alae and the shaft.

Size range: 33.2 – *39.5* ± 5.1 – 47.8 µm

Isochelae III (Fig. 8E, c'): With a long, gently curved shaft and slightly asymmetrical ends, e.g. the alae of one extreme are ca. 1.5 longer that those of the opposite extreme (anisochelae appearance). Alae are usually flat and with and straight end, occupying ca. ¼ of the spicule size.

Size range: 30.1 – *35.2* ± 2.9 – 38.6 µm

Spherancorae (Fig. 8B, a’): with an elongated shape, and fimbriae on its internal face, which can be free or fused to varying degrees. Spherancorae with incompletely fused alae are present.
Size range: 38.9 – *44.4* ± 6.7 – 51.2 x 20 – *21.8* ± 1.9 – 24.2 µm

Geographic distribution and type locality:
The species seems to be endemic to the Mediterranean Sea (Fig. 4), only ~~been~~ known from its type locality off Calvi, at the Italian coasts (Pulitzer-Finali, 1983), growing on rocks at 128 m depth.

Etymology:
From the Latin *intermedia* (“in between”). The name refers to its unique possession of a third intermediate category of isochelae, contrary to almost all other *Melonanchora* species, which only possess two.

Remarks:
The species is easily distinguishable from all other *Melonanchora* by the presence of a third chelae category with slightly asymmetrical ends. The closest species to *M. intermedia* sp. nov. would be *M. emphysema*, a typical deep-sea species also recorded from the Mediterranean Sea. Both species share the presence of tylostrongyles as their only megascleres, yet their microscleres present clear divergences, with isochelae being smaller in size in *M. intermedia* sp. nov. compared to *M. emphysema*. Additionally, the smallest isochelae category in *M. intermedia* sp. nov. usually shows alae with aberrant morphologies whereas none of the examined *M. emphysema* individuals showed this trend.

Melonanchora (*Melonanchora*) *insulsa* sp. nov.
(Fig. 1E; 9)

Synonymy:
Melonanchora elliptica Schmidt, 1880: 85, pl. IX fig. 8.

Material examined.
Holotype (here designated): MZS Po165, Gulf of Mexico, 'USCSS Blake' expedition in the Gulf of Mexico, (24°N 86°W), deep-sea dredging, 1879.

Description:
A small (less than 1 cm$^{2)}$, thin fragment of choanosome, and some scrapped pieces of ectosome (Fig. 1E). Although we cannot report on the sponge's original shape, Schmidt 1(880) described the sample as a crust growing on an euplectellid glass sponge from the genus *Regadrella*.

Skeleton:
The ectosomal skeleton consists of tangential strongyles with a criss-cross arrangement, whereas the choanosomal skeleton is formed by ill-defined style-made tracts. Microscleres are widespread throughout the choanosome without a clear discernible pattern.

Spicule complement:
Styles, strongyles, two categories of chelae, spherancoras (Fig. 9A-F).

Ectosomal strongyles (Fig. 9B): slightly flexuous, with more or less unequal ends.
Size range: 593.6 – *656.7* ± 36.2 – 701 x 16.1 – *17.1* ± 1.2 – 19.5 µm

Choanosomal styles (Fig. 9A): entirely smooth, mostly straight, with acerate points (Fig. 9F), sometimes slightly curved towards its distal end.
Size range: 813.4 – *989* ± 41.2 – 1121.7 x 19.3 – *20.7* ± 1.4 – 22.5 µm

Isochelae I (Fig. 9E): Smaller in size, and with a more prominent fusion between the lateral alae and the shaft.
Size range: 27.2 – *30.9* ± 3.4 – 35.8 µm

Isochelae II (Fig. 9D): With a gently curved shaft, and spatulated alae.
Size range: 48.6 – *52.3* ± 5.1 – 68 µm

Spherancorae (Fig. 9C): with an elliptical slightly asymmetrical shape, and teeth-like fimbriae on its internal face, which might be free or fused to different extent. Ridges of the spherancorae are unequally, gently bent, giving its ellipsoid shape a slightly asymmetrical appearance.

Size range: 52.9 – *56.5* ± 4.2 – 62.1 x 22 – *24.3* ± 1.7 – 26.6 µm

Geographic distribution and type locality:

The species is so far only known from the Gulf of Mexico (East of the Campache Escarpment, 24.0°N 86.0°W), and was collected from deep waters (Fig. 4).

Etymology:

From the latin *in-* ("not") + *salsus* ("salted"), meaning insipid, tasteless. The name refers to the original description of the specimen made by Schmidt (1880), who regarded the sample as boring or "*uninteressanten*".

Remarks:

~~Schmidt'~~ unambiguously stated that this individual from the Gulf of Mexico belonged to *M. elliptica*. However, the two types of chelae in *M. elliptica*'s have a straight shaft with free alae pointing outwards, whereas in *M. insulsa* chelae show a slightly bent shaft and its alae are more parallel to the later. Moreover, *M. elliptica*'s spherancoras are regularly oval, whereas *M. insulsa*' spherancorae are irregular, somewhat asymmetrical ellipsoids. Differences in shape and size between microscleres of both species support that *M. insulsa* is a different species from *M. elliptica*.

Melonanchora (*Melonanchora*) *maeli* sp. nov.

(Fig. 1G; 10)

Synonymy:

Melonanchora emphysema van Soest, 1993: 210, Tab. 2.

Material examined.

Holotype (here designated): ZMA.POR.7269, Ponta Tremorosa, Ilha de Santiago, Cape Verde, (14° 52' 59.88" N 23° 31' 59.88" W), 1986; ZMA.POR.P. 10826, Ponta Tremorosa, Ilha de Santiago, Cape Verde, (14° 52' 59.88" N 23° 31' 59.88" W), 1986 (microscopic slide).

Description:

A small sub-globular sponge, covered with abundant, proportionally big, bulbous fistules which arise from a paper-thin like ectosome (Fig. 1G). The ectosome is only attached here and there to the cavernous choanosome, making the former easily detachable. The choanosome is beige-orange and the ectosome is somewhat whitish, yet translucid.

Skeleton:

The ectosomal skeleton consists of tangential tylotes with a more or less developed criss-cross arrangement, whereas the choanosomal skeleton is formed by ill-defined style-made tracts. Microscleres are widespread thorough the choanosome without a clear discernible pattern.

Spicule complement:

Styles, tylotes, three categories of chelae and spherancoras (Fig. 10A-H). The sample was contaminated with tetractinellid spicules from an unidentified specimen stored ~~altogether~~ with the holotype.

Ectosomal tylostrongyles (Fig. 10B): slightly flexuous, with clearly marked tyles at both ends. Very regular in size.

Size range: 531.3 – *590.9* ± 37.9 – 627.9 x 9.7 – *10.3* ± 0.5 – 10.6 µm

Choanosomal styles (Fig. 10A): entirely smooth and mostly straight to slightly bent, always with an acerate endings. The heads might vary between those of true styles to true tylostyles (Fig. 10G), albeit the later are rare.

Size range: 637.6 – *918.5* ± 75.6 – 1062.6 x 17.3 – *19.2* ± 1.3 – 21.3 µm

Isochelae I (Fig. 10F; d'): Small anchorate chelae, with a straight, short shaft, long fimbriae and spatulated alae.

Size range: 17.4 – *19.8* ± 1.7 – 23.2 µm

Isochelae II (Fig. 10E; c'): The least abundant of all three chelae categories, with a slightly bent shaft, in intermediate size between isochelae I and III, with short, slender alae. Only 29 spicules could be measured.
Size range: 27 – *29.3* ± 1.2 – 31.9 µm

Isochelae III (Fig. 10D; b'): The biggest of the three isochelae categories, it is strikingly similar to isochelae II, with a long, slightly bent shaft and reduced slim alae. Yet, the alae are more reduced in regards to the general size of the spicule, and they are widely opened in respect to each other, contrary to isochelae II, where the separation between alae isn't notorious.
Size range: 45.4 – *49.6* ± 2 – 53.1 µm

Spherancorae (Fig. 10C, H; a'): with an elongated oval shape, almost straight with just a subtle curvature near the tips, and teeth-like fimbriae on its internal face. It usually shows a slightly asymmetrical appearance.
Size range: 48.3 – *50.2* ± 1.7 – 53.2 x 17.4 – *19.2* ± 1.5 – 21.3 µm

Geographic distribution and type locality:
This is the southernmost species of *Melonanchora* known to date, and, the only species of the genus to occur in Cape Verde archipelago (14° 52' 59.88" N 23° 31' 59.88" W) (Fig. 4).

Etymology:
The species is dedicated to *Mael*, the Elder God of the Seas in the world of Malaz, co-created by Steven Erikson and Ian C. Esslemont, in recognition of the vast and unique universe of their novels.

Remarks:
Originally identified as *M. emphysema* ~~(van Soest, 1993),~~ the species appears to be nevertheless new to science. While the spicular set would place it close to *M. elliptica* and *M. insulsa* sp. nov. due to the possession of styles as choanosomal megascleres, the presence of three chelae

categories tells it apart from those. Additionally, the chelae's shape deviates from that of the abovementioned species, with considerably reduced alae in two of the said chelae categories, a feature which isn't shared by any other *Melonanchora* species. Furthermore, its spherancorae are almost straight, whereas in most *Melonanchora* species a clear oval morphology can be observed.

Subgenus *Toretendalia* subgen. nov.

Diagnosis:

Melonanchora with acanthoses-megascleres and incomplete spherancorae.

Type species:

Melonanchora globogilva Lehnert et al., 2006a.

Etymology:

The subgenus is dedicated to two much esteemed and dearly missed Nordic colleagues, Hans Tore Rapp (University of Bergen) and Ole Tendal (Natural History Museum of Denmark), in recognition of their exceptional contributions on taxonomy and ecology of deep-sea sponges of the boreal and Arctic regions.

Remarks:

Melonanchora globogilva is the only representative of the genus in the Pacific Ocean (Fig. 11), and shows some unique spicule types absent from their Atlantic counterparts (Lehnert et al., 2006a). The species resembles *M. elliptica* and *M. tumultuosa* sp. nov. externally, yet it shows acanthostyles (Fig. 12A) as choanosomal megascleres and particular isochelae with dentate fimbria (Fig. 12C) along the internal face of alae and shaft but with their alae free, different from the typical spherancorae.

The placement of this species within *Melonanchora* was initially based on its external morphology (Fig. 1F) and skeletal architecture (Lehnert et al., 2006a), under the consideration that another *Melonanchora* species (viz. *M. tetradedritifera* Koltun, 1970 and *M. kobjakovae* Koltun, 1958) had been previously described with incomplete "spherancorae" (Koltun, 1958;

1970). However, SEM observation of Koltun's species (this study, Figs. 14–15) proved that those species did not bear true spherancorae but more or less complete cleistochelae or asymmetrical chelae, and therefore both *M. tetradedritifera and M. kobjakovae* are here reassigned to different genera (See below).

Nevertheless, as suggested in its original description (Lehnert et al., 2006a), there is enough morphological support to say that *M. globogilva* "unique chelae" may represent ancestral spherancorae or, at least, that both spherancorae and *M. globogilva*'s unique chelae share a common origin (See Section 4.2). Similarly, the acanthose megascleres might also represent an ancestral character secondarily lost in all other *Melonanchora* species. While the dissimilarities between *M. globogilva* and other *Melonanchora* are quite clear (smooth vs. acanthose choanosomal megascleres, complete vs. incomplete spherancorae), they also share several traits (mainly two categories of smooth chelae, ectosomal tylostrongyles to strongyles, thin translucent paper-like ectosome and a more or less subspherical external morphology), thus, arguments both in favour and against erecting a new genus for *M. globogilva* could be made. Nevertheless, given the lack of molecular data, an intermediate is adopted here, with the creation of two subgenera within *Melonanchora*: *Melonanchora* (*Melonanchora*) Carter, 1874, for those species with similar characteristics as those of the type species, *M. elliptica*, and *Melonanchora* (*Toretendalia*) subgen. nov. for *Melonanchora globogilva*. Once molecular data and/or additional specimens can be obtained, it will be possible to properly assess whether or not *M. (Toretendalia) globogilva* represents a unique species within the genus *Melonanchora*, or if it should be allocated to a new one.

Melonanchora (*Toretendalia*) *globogilva* Lehnert, Stone & Heimler, 2006a

(Figs. 1F; 12)

Synonymy:

Melonanchora globogilva Lehnert et al., 2006a: 9–13, fig. 4 a–f, fig. 5 a–d; Stone et al., 2011: 88, Apendix IV. 168–169.

Melonanchora globoblanca Lehnert et al., 2006a: 12 (misspelling of the former).

Material examined.

Holotype: NMNH-USNM1082996, north of Amlia Island, Aleutian Islands (58°28'8.5N 173°35'52.9W), 190 m depth, 2006.

Description:
Sub-spherical shape, with an easily detachable paper-like thin ectosome bearing abundant bulbous fistules (Fig. 1F). The choanosome is light-yellow and the ectosome is somewhat translucent-whitish, in life.

Skeleton:
The ectosomal skeleton consists on a loose crisscross of spicules arranged perpendicularly to the surface here and there, yet for most of it no clear arrangement can be discerned. The choanosome consists of ill-arranged tracts of tylotes and acanthostyles, without a clear discernible orientation. Microscleres are abundant and concentrate towards the choanosomal tracts.

Spicule complement:
Tylotes, acanthostyles, and three chelae categories, one of them in the form of incomplete spherancoras (Fig. 12A-F).

Ectosomal tylotes (Fig. 12B): Unevenly flexuous, with a central thickening, unequally thinning towards both ends, which sow variable tyles with variable swellings.
Size range: 598.9 – *675* ± 22.5 – 724.5 x 9.7 – *10.9* ± 2.2 – 14.5 µm

Choanosomal acanthostyles (Fig. 12A): Slightly curved along its length, with an acerate point. Spines are short and stout, moderately abundant along the entire shaft but the tip.
Size range: 589.3 – *638.3* ± 30 – 677.3 x 27 – *28* ± 1.1 – 29 µm

Isochelae I (Fig. 12E): with a straight shaft, well-developed fimbriae and spatulated alae, the lateral ones largely fused with the shaft.
Size range: 23.1 – *26.2* ± 1.1 – 27 µm

Isochelae II (Fig. 12D): Almost identical to isochelae I, but bigger in size.

Size range: 48.3 – *64. 4* ± 6.8 – 67.6 µm

Spherancorae (Fig. 12C): Uncompleted, with free teeth, resembling chelae. As in all other *Melonanchora*, dentate fimbriae cover its internal face.
Size range: 77.3 – *86.9* ± 2.8 – 91.8 x 27 – *30* ± 2.3 – 33.8 µm

Geographic distribution:
The species appears to be rare, as it has only been seldomly recorded from deep bottoms around the Aleutian Archipelago (Lehnert et al., 2006a; Stone et al., 2011) (Fig. 11).

Remarks:
Further strengthening this view, the re-examination of the type material made it clear the existence of a second, larger, isochelae category identical to the smallest one, a common trait within *Melonanchora*. Finally, the original description mentions a second category of spherancorae-isochelae with outer dented margins which could not be found again upon re-examination of the type material. As they are similar in size with spherancoras, they are here regarded as likely to constitute aberrant modifications or developmental stages of *M. globogilva*'s unique spherancoras. The placement of the species in the genus *Melonanchora* is here validated, yet assigned its ~~on~~ subgenus, *Toretendalia* subgen. nov. (see rationale above), and the genus definition emended accordingly to encompass the peculiar spicule set of *M. globogilva*.

Genus *Myxilla* Schmidt, 1862

Subgenus (*Burtonanchora*) Laubenfels, 1936

Type species:
Myxilla (Burtonanchora) crucifera Wilson, 1925

Diagnosis:
Myxilla with smooth choanosomal styles. Chelae are three-teethed, with occasional polydentate modifications (amended from van Soest, 2002).

Myxilla (*Burtonanchora*) *kobjakovae* (Koltun, 1958)

(Fig. 13)

Synonymy:

Melonanchora kobjakovae Koltun, 1958: 58, fig. 13; Koltun, 1959: 122, fig. 75; pl. XVII, fig. 4; pl. XVIII, fig. 2; Javnov, 2012 (*partim*): 65–66.

Material examined:

Syntype (here designated): NHMUK 1963.7.29.23, Southern Kuril Islands, Pacific coast, 'Topokok expedition' (Stns 127, 128), Deep-sea dredging, 1949. Exchanged with Koltun in July 1963.

Description:

The sponge is tubular, digitate or funnel shaped, with a long stem. Its surface is smooth, with the oscules being located on the top of the finger-like processes in the digitate forms. Colour bright orange in life, and from ochre to dark-brown, in alcohol.

Skeleton:

Choanosomal skeleton consisting of a dense isodyctial reticulation of multispicular tracts embedded in spongin fibres without echinating spicules. Ectosomal skeleton formed by a tangential layer of more or less disarranged spicules.

Spicule complement:

Styles, strongyles, and two categories of chelae (Fig. 13A-E).

Ectosomal strongyles (Fig. 13B): Straight, short and stout, with a subtle swelling at each end (Fig. 13f', f''), finished in a ring of weak spines, typical of *Myxilla*. They can also be found scattered through the choanosome.

Size range: 140.3 – *190.3* – 323.8 ± 12.2 x 7.1 – *9.8* – 12.5 ± 2.1 µm

Choanosomal styles (Fig. 13B): slightly curved along its length, with and acerate distal end and a proximal end sometimes vaguely inflated.
Size range: 327.5 – 397.*5* – 567.3 ± 23.2 x 17.8 – *20.3* – 22.6 ± 1.9 µm

Isochelae I (Fig. 13D): Unusual small ancorate isochelae with three prominent alae ending in a double hook-like termination. The alae of both ends almost contact each other, somewhat resembling a cleistochelae. Fimbriae are well developed, and present and inner hook on its lower part which point towards the interior of the chelae.
Size range: 29.2 – *33.3* – 35.7 ± 2.8 µm

~~isochelae~~ II (Fig. 13C): Anchorated, three-teethed chelae, with spatulated alae. It has clear, well developed fimbriae, which expand from the shaft.
Size range: 60.1 – *79.7* – 87.6 ± 7.8 µm

Geographic distribution:
So far, the species has only been recorded from the Okhotsk Sea, at the Kuril, Iturup and Urup islands (Koltun, 1958; 1959; Javnov, 2012; Guzii et al., 2018) and the Kamchatka peninsula (Calkina, 1969) at depths ranging from 28 to 231 m (Fig. 11).

Remarks:
Myxilla (*B.*) *kobjakovae* was initially assigned to *Melonanchora* based on the presence of smooth choanosomal megascleres and spherancorae (Koltun, 1958). Yet, after re-examining the holotype, we verified that those supposed spherancoras were in fact cleistochelae derivatives (Fig. 13D). Additionally, *M. kobjakovae* clearly deviates from *Melanonchora* species in growth form, lack of a paper-like ectosome, and type of megascleres. Besides *Melonanchora*, just two other myxillidae genera possess smooth megascleres: *Myxilla* (*Burtonanchora*) Laubenfels, 1936 and *Stelodoryx* Topsent, 1904. Both genera resemble each other in most aspects (Lehnert & Stone, 2015), yet *Stelodoryx* is defined as possessing polydentate anchorate isochelae whereas *Myxilla* (*B.*) has exclusively three- teethed anchorate isochelae (van Soest, 2002). However, *Myxilla* (*B.*) *asigmata* Topsent, 1901 has been observed to possess chelae with 3–5 alae (Ríos & Cristobo, 2007), implying that *Myxilla* ~~definition~~ should be modified to include the eventual

possession of polydentate chelae. On the other hand, as a result of the inclusion of some other genera as synonyms of *Stelodoryx* by van Soest (2002), some of the current species of *Stelodoryx* possess three-teethed chelae (*viz*. *Stelodoryx lissostyla* (Koltun, 1959). As so, whether *Stelodoryx* and *Myxilla* are synonymous or two different genera is unclear and need revision.
The presence of polydentate chelae, while not specific enough, is still used as the main classifying feature to distinguish *Myxilla* and *Stelodoryx* (Bertolino et al., 2007, Lehnert & Stone, 2015). Thus, the new species is here referred to *Myxilla* (*Burtonanchora*) due to the possession of three-teethed anchorate chelae, yet it differs from most other *Myxilla* (*B.*) in the absence of sigmas, possession of two chelae categories, one of them in the form of cleistochelae, and its stalked growth form. Further reclassification of the species should not be ruled out in light of a broader myxillidae review.

Finally, the species description in the Russian Fauna of the East seas (Javnov, 2012) depicts varying morphologies for *M. kobjakovae.* While polymorphism is common in sponges, the huge variations depicted in the Russian individuals, which range from the typical digitate-branching orange sponge, to conical-shaped or tubular-rimmed, cream coloured individuals (Javnov, 2012) suggest they may represent a different related species.

Genus *Arhythmata* gen. nov.

Type species:

Arhythmata tetradedritifera (Koltun, 1970) (here designated).

Diagnosis:

Lamellate sponge, apparently resulting from coalescent digitations, with the surface slightly uneven. Ectosome thin, coriaceous, easy to detach, with subectosomal cavities. Oscula are large and unevenly spread. Choanosome crossed by numerous canals. The ectosomal skeleton is a tangential layer of strongyles perpendicular to the choanosomal spicule tracts. The choanosomal skeleton consists of a loose isodyctial reticulation of multispicular style tracts embedded in spongin. The spicule complement consists of smooth choanosomal styles, ectosomal tylotes with spiny heads and three categories of polydentate chelae, among which, at least one is asymmetrically modified. So far, monotypic genus restricted to the deep-sea areas around the Okhotsk Sea.

Etymology:

From the Latin *arhythmatus*, meaning "inharmonious" or "of unequal measure", referring to the asymmetry of the alae of *A. tetradedritifera*'s peculiar chelae.

Remarks:

Arhythmata tetradedritifera was originally described as *Melonanchora tetradedritifera* based on the possession of smooth choanosomal styles, two categories of chelae, and spherancoras (Koltun, 1970). However, Koltun misidentified unique, modified chelae as spherancorae (See Section 4.2), and described styles and tylostrongyles that highly differed in shape from those of other *Melonanchora* species. This spicule combination draws the species closer to *Myxilla (Burtonanchora)* and *Stelodoryx* as they are the only Myxillidae genera with smooth styles. However, in contrast to *M.* (*B.*) *kobjakovae, A. tetradedritifera* possesses polydentate (4–5) chelae, which will place the species closer to *Stelodoryx* than to *Myxilla.* However, while *Myxilla* (*Burtonanchora*) (13 accepted species; van Soest et al., 2021) represents a narrowed, well-defined, portion of *Myxilla* (91 accepted species; van Soest et al., 2021), *Stelodoryx* (18 accepted species; van Soest et al., 2021), represents an amalgam of spicule types on a rather small genus (Lehnert & Stone, 2015). Indeed, the actual concept of *Stelodoryx* is only distinguished from *Myxilla* by the presence of polydentate chelae, yet little attention has been paid to the other spicule complement (Lévi, 1993). Megascleres in *Stelodoryx* include both smooth (viz. *Stelodoryx flabellata* Koltun, 1959) or spiny (viz. *Stelodoryx mucosa* Lehnert & Stone, 2015) ectosomal tylotes or tornotes, or even styles (viz. *Stelodoryx* s*iphofuscus* Lehnert & Stone, 2015); with choanosomal acanthostyles (viz. *S. mucosa*), smooth styles (viz. *S.* s*iphofuscus* or *S. mucosa*), microspined styles (viz. *Stelodoryx lissostyla* (Koltun, 1959)), oxeas (viz. *Stelodoryx oxeata* Lehnert et al., 2006b) or even strongyles (viz. *S. flabellata*). Additionally, chelae may be three-teethed (viz. *S. lissostyla*) or polydentate, with teeth varying from four to seven, having from one (viz. *S. flabellata*) to three (viz. *S. oxeata*) chelae categories, with occasional accompanying sigmas (viz. *S. oxeata* or *S. mucosa*). Thus *Stelodoryx,* with just 18 species, harbours a spicule variability that might equal those of all 4 subgenera of *Myxilla* together (van Soest, 2002). With a combination of strongyles with microspined head and smooth styles, the closest relative to *A. tetradedritifera* within *Stelodoryx* would be *Stelodoryx jamesorri* Lehnert & Stone, 2020 which has already been signalled as of difficult allocation within the genus *Stelodoryx* (Lehnert & Stone, 2020). While both species share several common traits (stout choanosomal smooth styles, ectosomal tylotes to strongyles with microspined heads and the possession of two categories of peculiar polydentate chelae), both species differ in the possession of third, unique chelae category for *A. tetradedritifera* and in their skeletal organization, being plumoreticulate in S. jamesorri, as opposed to the isodyctial reticulation observed in *A. tetradedritifera.* Finally, *Stelodoryx pluridentata* (Lundbeck, 1905) and *Stelodoryx strongyloxeata* Lehnert & Stone, 2020, would also be arguably close to *A. tetradedritifera*, but they possess ectosomal styles instead of strongyles (Lévi, 1993; Lehnert & Stone, 2020) and sigmas in the former (Levi, 1993) and choanosomal strongyleoxeas in the later (Lehnert & Stone, 2020).

~~As so,~~ a new genus, *Arhythmata* gen. nov., is here erected to properly accommodate *Melanonchora tetradedritifera,* with a diagnosis based on the combination of ectosomal microspined strongyles, smooth choanosomal styles and 3 polydentate chelae categories, from which at least one is modified into asymmetrical chelae, a rare feature within Poecilosclerida, which has been considered of taxonomic value for other genera (e.g. *Echinostylnos* spp.; Lévi, 1993), and which are here termed *retortochelae* (Fig. 14C) and defined as "*asymmetrical chelae in which alae are not facing their direct opposite, but the space in-between opposing alae*". While currently the genus remains monotypic this might change in the future upon a proper re-examination of the genus *Stylodoryx*, which is on much need of a revision.

Arhythmata tetradedritifera (Koltun, 1970)

(Fig. 1D, 14)

Synonymy:

Melonanchora tetradedritifera Koltun, 1970: 209, fig. 22.

Material examined.

NMNH-USNM 148959, AB120069, South of Amlia Island, Central Aleutian Islands, Pacific coast, (51° 50' 21.12"N 173° 54' 21.6"E), 337m depth, July 2012; NMNH-USNM 1478958, AB120046, South of Kanaga Island, Central Aleutian Islands, Pacific coast, (51° 33' 31.32"N 177° 37' 19.2"E), 358m depth, July 2012.

Description:
As described in the genus definition (Fig. 1D). All the examined samples contained sand grains through the choanosome. Additionally, the colour when dry is dark brown, close to kobicha or tupe, whereas the ectosome is whitish with wheat-like shadings.

Skeleton:
Typical of the genus.

Spicule complement:
Styles, strongyles, three categories of chelae (Fig. 14A-D).

Ectosomal strongyles (Fig. 14B): Short, straight, with both ends slightly spinose and slight inflated somewhat unequally (Fig. 14f', f''); a distal thorn is present, which gives them the appearance of tornote-like strongyles.
Size range: 270.5 – *307.8* – 357.4 ± 24.3 x 9.6 – *10.3* – 14.5 ± 1 µm

Choanosomal styles (Fig. 14A): Entirely smooth, slightly curved along its length, almost doubling in width the tylostrongyles.
Size range: 521 – *608* – 685 ± 54.3 x 24.1 – *29.3* – 33.8 ± 2.3 µm

Isochelae I (Fig. 14E): Small ancorate pentadentate, with a short shaft.
Size range: 48.3 – *60.4* – 67.7 ± 7.3 µm

Isochelae II (Fig. 14D): ancorate pentadentate isochelae, with a comparatively large, almost straight shaft.
Size range: 67.7 – *70.6* – 87.3 ± 3.4 µm

Retortochelae (Fig. 14C): Asymmetrical, almost ovoid, ancorate isochelae with a curved, somewhat twisted shaft and four long teeth. The upper and lower teeth are not facing each other but slightly displaced, in such a way that each tooth occupies the space between two opposite teeth and ~~*viceversa*~~. This makes the chelae asymmetrical, with the alae looking as if they have been sculpted with notches and tips to accommodate the opposing alae.

Size range: 77.3 – *88.6* – 106 ± 2 x 48.3 – *49.1* – 53.1 ± 2 µm

Geographic distribution:

Currently, the species has only been located at the deep-sea waters (338 to 3335 m depth) of the Okhotsk Sea, mostly around the Simushir Islands (Koltun, 1970; Downey et al., 2018) and the Aleutian Islands (Fig. 11).

Remarks:

Although the ~~species~~ holotype could not be examined, the studied material fits well with Koltun's original description, in terms of spicule types and sizes (Koltun, 1970). However, the species has been observed to possess two different chelae categories, mainly distinguished by its size and shaft lengths, which were not described by Koltun, while the spherancoras mentioned in the original description are, in fact, modified chelae with a twisted shaft, long teeth and an ovoid contour (retortochelae; Fig. 14C).

Arhythmata tetradedritifera represents a new addition to the already diverse myxillidae fauna of the Okhotsk deep-sea and nearby areas. During the past years, several new species from the area have been included in Myxillidae (Lehnert et al., 2006a; 2006b; Lehnert & Stone, 2015, which might partially respond to a high abundance of endemic benthic fauna in the area (Downey et al., 2018). Although the genus stands monotypic for the time being, further exploration in the deep bottoms of the Okhotsk Sea and nearby areas might result in the discovery of additional species.

4. Discussion

4.1 Diversity and biogeography of the genus *Melonanchora*

In contrast to most sponge genera, *Melonanchora* shows a quite narrow distribution, restricted to the circumpolar Artic and some North Atlantic areas. Additionally, only one species, *M. elliptica* could be considered common across its distribution area (Fristedt, 1887; Lundbeck, 1905; Van Soest, & De Voogd, 2015; Baker et al., 2018). Despite initial misidentification of fossil spherancorae (Hinde & Holmes, 1892), there are no known fossil records for the genus, thus making discussion about its origin and radiation, tentative.

Contrary to biogeographic distributions of other sponge genera, which suggest they may have a Tethyan or Gondawanan origin (e.g. *Acarnus*, van Soest et al., 1991; *Rhabderemia*, van Soest & Hooper, 1993; Hajdu & Desqueyroux-Faúndez, 2008; *Hamigera*, Santín et al., 2020), the current distribution of *Melonanchora* might be better explained by trans-Artic exchanges. The opening of the Bering Strait during the late Pliocene (ca. 5.3 Ma; Vermeij, 1991), allowed a massive interchange of species among northern areas of the Atlantic and the Pacific (Vermeij, 1991), which is supported by both the fossil record (Reid, 1990) and molecular studies (Dodson et al., 2007; Coyer et al., 2011). This exchange did not just occur among vagile fauna (Dodson et al., 2007), but also among benthic species (Reid, 1990), including sponges (Ereskovsky, 1995). Benthic species are known to have crossed the strait, in the several opening and closing events of the strait during the glacial and interglacial periods (Coyer et al., 2011). Additionally, during these glacial and interglacial periods, species expanded or constrained their distribution areas as a result of climate changes and their associated biotic and abiotic factors, which provided new suitable habitats (Jansson & Dynesius, 2000). As such, ~~an~~ assuming a Pacific origin for the genus based on the "ancient" characteristics by *M. globogilva*, *Melonanchora* might have expanded from Pacific to Atlantic waters during one of the several events that opened the Bering Strait, and expanded further south towards the tropical regions during the glacial periods (Ereskovsky, 1995). Thus, *M. maeli* sp. nov. and *M. insulsa* sp. nov., the only representatives of the genus close to the equator, might be a legacy of this latitudinal migration, which are confined now to "deep-sea refugia" due to posterior climatic changes (Ereskovsky, 1995; Convey et al., 2009). Finally, the Mediterranean *M. indistinta* sp. nov. might represent a recent speciation process from *M. emphysema*. This might be supported by their similarities with the Atlanto-Mediterranean *M. emphysema*, which might have entered the Mediterranean after the Messinian Salinity Crisis, as hypothesized for other Mediterranean sponges (Boury-Esnault et al., 1992;

Xavier & van Soest, 2012). However, the lack of fossil records in their current distribution area (Ereskovsky, 1995) and the lack of phylogenetic data, paired with the scarcity of material of most *Melonanchora* species, makes it difficult to properly assess the vicariant events that led to its diversification, leaving it open future research efforts.

4.2 The origin of spherancoras

The order Poecilosclerida Topsent, 1928, build around the exclusive presence of chelae is, with over 2.500 formally described species (van Soest et al., 2021) possibly the most diverse group within Porifera (Hooper & van Soest, 2002). The high taxon diversity parallels that of its chelae, with basic chelae morphotypes (palmate, anchorate, and arcuate) described for the first time by Levinsen (1893) and Lundbeck (1905, 1910), and several modifications of the formers (Hajdu et al., 1994; Hooper & van Soest, 2002).

In its initial description of *Melonanchora,* Carter (1874) assumed that the two chelae categories present his specimen where in fact early developmental stages of the unique, "melon-shaped" chelae, which characterized the genus or even, the last developmental stage of anchorate chelae (Vosmaer, 1885). While this view was soon refuted, and the "melon-shaped" chelae was recognized as a separate chelae type (Schmidt, 1880), it was not until 1885 that they were given a specific designation, "*mel*", based on their unique shape (Vosmaer, 1885). However, the name would remain unsettled for the following years, with several authors following Vosmaer's proposal as *melonanchoras* (Fristedt, 1887; Levinsen, 1893; Arnesen, 1903), while others followed Topsent's proposed designation (Topsent, 1892) of *sphearancisters* (Thiele, 1903; Topsent, 1904). Topsent's proposal however, was based on his perception that each shaft of the chelae remembered a diancistra (Topsent, 1892). However, diancistras are sigmoid derivatives (Hajdu, 1994) whereas spherancoras are true chelae derivatives (Levinsen, 1893). Nevertheless, the term "*melonanchora*" was identical to that of the genus, which could lead to confusion. As so, Lundbeck settled the dispute in 1905, when he designated these unique chelae as spherancoras, highlighting its chelae nature and unique oval morphology (Lundbeck, 1905).

Regarding the spherancora's unique morphology, the common presence of developmental stages in several individuals has given a proper view of their chelae nature (Levinsen, 1893) as well of their developmental stages. As so, spherancoras start as slim ancorate chelae, with a thin shaft and three teeth (Fig. 15.1), of the same width. Later, those three teeth expand, until they coalesce (Fig. 15a), forming four indistinguishable shafts, all being at approximately right angles in respect to each other, and giving the spherancoras its characteristic oval shape (Fig. 15.2). While not usually visible as they occur on the internal shaft's view, the junction points of the alae usually develop into a swelling in adult spherancoras (Fig. 15c). Right after the arcs are formed, the spherancoras begin the development of its internal "teeth-brims" (Fig. 15.3), as in other teethed chelae, (e.g. *Guitarra solorzanoi*; Cristobo, 1998). The internal dentate fimbriae are regularly arranged along the internal surface of the *Melonanchora*'s shaft (Fig. 15.4; 15.5; 15.5'), yet the teeth are not fused to the shafts, but are free and protrude from a small ridge formed at side of the shafts (Fig. 15c). The length and a degree of fusion vary between individuals of the same species, ranging from the most common free teeth forms (Fig. 15b), to partially joined teeth, or even almost coalescent teeth. This intraspecific variability regarding the fusion degree of the alae might partially reflect silica availability at the time the spicules were formed (Uriz et al., 2003), as it has been reported for other sponge taxa (e.g Bavestrello et al., 1993; Cárdenas & Rapp, 2013).

While the spherancora's morphology seems to be rather conservative between *Melonanchora* species, *M. globogilva* poses a unique case within the genus, as it does not possess true spherancoras but a third chelae category (Fig. 12C), with non-coalescenting alae and internal teeth-brims, which loosely ~~remember~~ those in placochelae (Cristobo, 1998). Nevertheless, the architecture of this third chelae category is consistent with that of the developmental stages of true spherancoras, and its teeth-brims are not restricted to alae, but are present all along the shaft's internal surface, as in other *Melonanchora*. Thus, *M. globogilva* unique chelae might represent in fact ancestral, incomplete spherancoras (Lehnert et al., 2006a), further supporting its chelae ancestry.

Confusion between spherancoras and other spicular types is highly unlikely, yet there are a few spicular types that could, or have been, confused with spherancoras. Placochelae and derivatives (Fig. 16C) are a complex group of microscleres, synapomorphic for the family Guitarridae (Uriz & Carballo 2001; Hajdu & Lerner, 2002), which share with spherancoras the possession of teeth-brims along the shafts and ~~ale~~ (Hajdu et al., 1994). While the possible affinity of Guitarridae with Myxillidae was eventually proposed (van Soest, 1988), this was poorly supported, among others, by the likely palmate origin of placochelae (Hajdu et al., 1994), which are absent in

Myxillidae. As such, the development of teeth-brims among chelae, while not a common trait, should be regarded a homoplastic character acquired independently by several taxa. Apart from placochelae, both cleistochelae (*viz*. *M*. (*B*.) *kobjakovae*) and clavidiscs (Hinde & Holmes, 1892; Ivanik, 2003) have been interpreted at some point as spherancoras due to their ovoidal morphology. As ~~so,~~ fossil *Merlia* species (viz. *Merlia morlandi* (Hinde & Holmes, 1892); *Merlia* sp. Ivanik, 2003; Lukowiak et al., 2019) have been confused with *Melonanchora* due to the similarity between ~~clavidics~~ (Fig. 16D) and ~~spherancora's~~ (Fig. 16A) lateral view. Nevertheless, clavidiscs are synapomorphic for *Merlia* and believed to be sigmancistra derivatives (Hooper & van Soest, 2002), contrary to the spherancora's chelae origin. Coincidentally, the lateral view of cleistochelae (Fig. 16B) has also been misinterpreted as spherancoras. However, contrary to clavidiscs, cleistochelae are in fact true chelae, only sharing with spherancoras the presence of partially fused alae. Nevertheless, cleistochelae lack the inner teeth-brims and present a single arc (2D byplan), resulting from the fusion of all free alae in a single piece, whereas spherancoras present two arcs (3D byplan), as they result from the fusion of each one of the free alae with its opposing counterpart.

Finally, and despite their unique morphology amongst sponge microscleres, the function of spherancoras, as that of many other microscleres, remains unclear. In this sense, while megascleres possess a clear architectural role in the sponge skeleton, microscleres are mostly believed to play a consolidating or defensive role, if any (Uriz et al., 2003). In *M. elliptica* holotype, spherancoras were observed to concentrate and form a dense palisade on the outer layer of the choanosome as well as surrounding the aquiferous canals, which could imply towards such defensive role, or a possible role in the architecture of the aquiferous system, yet this was not observed in any other of the samples analysed, and remains purely speculative.

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Table 1(on next page)

Figure Caption for all figures

Figure Caption

Fig. 1 – A) External view of *Melonanchora elliptica* (MZLU L935/3858), *p* indicates some ectosomal papillae; B) Individual of *Melonanchora emphysema* (*Me*) attached to coral rubble (GNM Porifera 416); C) Holotype of *Melonanchora tumultuosa* sp. nov. (GNM Porifera 624), *Ect* indicates the ectosome, *Ch* indicates the choanosome, *Cha* indicates the choanosomal cavities, *Os* indicates the oscules; D) Individual of *Arythmata tetradentifera* (NMNH-USNM 148959); E) Holotype of *Melonanchora insulsa* sp. nov. (MZS Po165); F) Holotype of *Melonanchora globogilva* (USNM 1082996), *p* indicates some ectosomal papillae and *Os* indicates the oscules; G) Holotype of *Melonanchora maeli* sp. nov. (ZMA.POR.7269), *p* indicates some ectosomal papillae and *Ch* the choanosome.

Fig. 2 – A) General view of the spicules of *Melonanchora* (BMNH 1882.7.28.54a) ~~un~~ light microscopy. *Ch I* indicates the largest chelae category, *Ch II* indicates the smallest chelae category, and *Sph* indicates spherancoras; B) View of the loose choanosomal tracts ~~off~~ *Melonanchora elliptica* (BMNH 1882.7.28.54a) C) View of the characteristic criss-cross like pattern of the ectosome of *Melonanchora* (BMNH – Norman Coll. 1910.1.1.1421); D) Spherancoras covering the choanosomal tracts in *Melonanchora elliptica* (BMNH 1882.7.28.54a).

Fig. 3 – Spicular set for *Melonanchora elliptica* (sample BMNH 1882.7.28.54a., holotype). A) Choanosomal style; B) Ectosomal tylostrongyle; C) Spherancoras; D) Large chelae category (Chelae II); E) small chelae category (Chelae I); F) Detail of the styles' acerate end; G) General view of *M. elliptica*'s spicules by SEM imaging. a') Spherancora b') Chelae II and c') Chelae I relative sizes when compared with that of the megascleres. Scale bars for A), B), a'), b'), c') 300 µm; C) – F) 30 µm and G) 500 µm. Images A) to E) and G) were taken from sample BMNH 1882.7.28.54a (holotype). Images for F were taken from both BMNH 1882.7.28.54a (holotype) and CMN 2018-0107.

Fig. 4 – Distribution map for the North Atlantic *Melonanchora* species: *Melonanchora elliptica* (green circle), *Melonanchora emphysema* (orange square), *Melonanchora tumultuosa* sp. nov. (red triangle); *Melonanchora maeli* sp. nov. (dark green square); *Melonanchora intermedia* sp. nov. (purple square); *Melonanchora insulsa* sp. nov. (dark blue square). Projected view (UTM Zone 31N (WGS84)) with geographic (WGS84) coordinates indicated for reference. The 1000 m

depth isobaths is represented by a grey line. Geographic and bathymetric data used was obtained from http://www.naturalearthdata.com.

Fig. 5 – Spicular set for *Melonanchora emphysema* (sample ZMB Por 2680, holotype). A) Ectosomal and chonasomoal tylostrongyle; B) Spherancoras; C) Large chelae category (Chelae II); D) small chelae category (Chelae I); E) General view of *M. emphysema*'s spicules by SEM imaging. a') Spherancora b') Chelae II and c') Chelae I relative sizes when compared with that of the megascleres. Scale bars for A), a'), b'), c') 200 µm; B), C), D) 30 µm and E) 500 µm.

Fig. 6 – Spicular set for *Melonanchora* cf. *emphysema* from Laxe, Galicia coast, Spain. A) Ectosomal and chonasomoal tylostrongyle; B) Spherancoras; C) Large chelae category (Chelae II); D) Chelae II with reduced alae; E) small chelae category (Chelae I); F) Detail of the tyles. a') Spherancora b') Chelae II and c') Chelae I relative sizes when compared with that of the megascleres. Scale bars for A), a'), b'), c') 175 µm; B), C), D) 20 µm and F) 12 µm.

Fig. 7 – Spicular set for *Melonanchora tumultuosa* sp. nov. (sample GNM Por 624, holotype). A) Choanosomal strongyle; B) Ectosomal tylostrongyle; C) Spherancoras; D) Large chelae category (Chelae II); E) small chelae category (Chelae I), F) General view of *M. tumultuosa* sp. nov. spicules by SEM imaging. a') Spherancora b') Chelae II and c') Chelae I relative sizes when compared with that of the megascleres. Scale bars for A), B), a'), b'), c') 300 µm; C), D), E) 30 µm and F) 500 µm.

Fig. 8 – Spicular set for *Melonanchora intermedia* sp. nov. (sample MSNG – R.N. N IS.4.7., holotype). A) Ectosomal and chonasomoal tylostrongyle; B) Spherancoras; C) small chelae category (Chelae I); D) Large chelae category (Chelae II); E) Anisochelae; F) Detail of the tylostrongyle's ends. a') Spherancora b') Chelae II c') Anisochelae and d') Chelae I relative sizes when compared with that of the megascleres. Scale bars for A), a'), b'), c'), d') 200 µm; B), C), D), E), F) 20 µm.

Fig. 9 – Spicular set for *Melonanchora insulsa* sp. nov. (sample MZS Po165, holotype). A) Choanosomal style; B) Ectosomal tylostrongyle; C) Spherancoras; D) Large chelae category (Chelae II); E) small chelae category (Chelae I); F) Detail of the styles' acerate end as seen in SEM imaging. a') Spherancora b') Chelae II and c') Chelae I relative sizes when compared with that of the megascleres. Scale bars for A), B), a'), b'), c') 300 µm; C), D), E) 30 µm and F) 100 µm.

Fig. 10 – Spicular set for *Melonanchora maeli* sp. nov. (sample ZMA.POR.7269, holotype). A) Choanosomal style; B) Ectosomal tylostrongyle; C) Spherancoras; D) Large chelae category (Chelae III); E) Intermediate chelae category (Chelae II); F) Small chelae category (Chelae I); G) Head of a style modified into a tylostyle; H) Detail of a spherancora lateral view. a') Spherancorae b') Chelae III c') Chelae II and d') Chelae I relative sizes when compared with that of the megascleres. Scale bars for A), B), a'), b'), c'), d' 300 µm; C), D), E), F) 30 µm; G) 400 µm and H) 20 µm.

Fig. 11 – Distribution map for *Melonanchora globogilva* (red diamond)*, Myxilla (B.) kobjakovae* (green square) and *Arythmata tetradentifera* (purple circle). Projected view (UTM Zone 31N (WGS84)) with geographic (WGS84) coordinates indicated for reference. A grey line represents the 1000 m depth isobaths. Geographic and bathymetric data used was obtained from http://www.naturalearthdata.com.

Fig. 12 – Spicular set for *Melonanchora globogilva* (sample USNM1082996, holotype). A) Choanosomal acanthostyle; B) Ectosomal tylostrongyle; C) Spherancoras; D) Large chelae category (Chelae II); E) small chelae category (Chelae I); F) General view of *M. globogilva*'s spicules by SEM imaging. a') Spherancora b') Chelae II and c') Chelae I relative sizes when compared with that of the megascleres. Scale bars for A), B), a'), b'), c') 300 µm; C), D), E) 30 µm and F) 500 µm.

Fig. 13 – Spicular set for *Myxilla (B.) kobjakovae* (sample NHM 1963.7.29.23, holotype). A) Choanosomal style; B) Ectosomal strongyle; C) Large chelae category (Chelae I); D) Small chelae category (Chelae II); E) Style's aberrant end; f') close up view of the strongyles microspinned end; f'') close up view of the strongyles' microspinned other end. a') Chelae I b') Chelae II relative sizes when compared with that of the megascleres. Scale bars for A), B), a'), b') 150 µm; C), D), E) 30 µm and f'), f'') 10 µm.

Fig. 14 – Spicular set for *Arythmata tetradentifera* (sample NMNH-USNM 148959). A) Choanosomal style; B) Ectosomal strongyle; C) and C') Retortochelae; D) Large chelae category (Chelae II); E) Style's aberrant end; f') close up view of the strongyles microspinned end; f'') close up view of the strongyles' microspinned other end. a') Retortochelae b') Chelae II and c') Chelae I relative sizes when compared with that of the megascleres. Scale bars for A), B), a'), b'), c') 300 µm; C), D), E) 50 µm and f'), f'') 10 µm.

Fig. 15 – Formation process of a spherancora. 1. Initial stages of formation; the chelae origin can still be observed, with a full formed shaft (*s*) and free alae (*al*) still visible; 2. Fusion phase; the alae coalesce forming the four shafts; alae's junction points (*jp*) are visible (a.); 3. Thickening phase; the shafts start to thicken, and start forming the ridges (r) from which the fimbriae will later develop; 4. Fimbriae development phase; fimbriae start developing on the ridges, while the shafts continue thickening; 5. Fully formed spherancora, with complete, free fimbriae (*f*) clearly visible (b.); 5'. Internal view of a spherancora, visible due to the braking of a shaft; the junction point (*jp*) of the alae is still visible on the internal side of the shafts as a swelling (c.), while it is observable that fimbriae (*f*) are mostly free, only attached to the shafts (*s*) by its base. Scale bar for Figures 1–5 is 20 µm, whereas for figures a., b., and c. is 10 µm. All images were taken from *Melonanchora tumultuosa* sp. nov. (BMNH Norman Coll. 1898.5.7.38).

Fig. 16 – A.) Spherancorae from *Melonanchora elliptica* (BMNH 1882.7.28.54a); B.) cleistochelae from *Clathria* sp. (BMNH 1910.10.12.18); C.) placochelae from *Guitarra dendyi* (Kirkpatrick, 1907) (Ríos pers. Coll.); D.) Clavidisc from *Merlia normani* Kirkpatrick, 1908 (Uriz pers. Coll.).

Table 2(on next page)

Comparative table for all known *Melonanchora* records

Table 1. Comparative table between all known records of *Melonanchora*, including the locality (Loc.) and depth of the sample, as well as the measurement of their spicular complement. **(S)** indicates styles; **(St)** indicates strongyles; **(T)**; indicates tylostyles; **(Ac)** indicates acanthostyles; * indicates this is the holotype of the species; ***nm*** indicates a spicular type that was not mentioned on a description, yet it is assumed was present on the samples.

Author	Loc. / Depth	Ectosomal megascleres	Choanosomal megascleres	isochelae	Spherancorae
Melonanchora (*Melonanchora*) *elliptica* Carter, 1874					
Carter (1874)	Faroe Plateau * / 'deep-sea'	**(St)** ca. 750 µm	**(S)** ca. 495 µm	Present	Present
Reexamination van Soest (2002)	Faroe Plateau * / 'deep-sea'	**(St)** 450 – 650 x 13 – 15 µm	**(S)** 650 – 860 µm	**(I)** 22 – 44 µm **(II)** 60 µm	48 – 68 µm
Reexamination *This study*	Faroe Plateau * / 'deep-sea'	**(St)** 500 – *561.9* ± 34.4 – 611.2 x 14.7 – *15.9* ± 1.1 – 19.6 µm	**(S)** 730 – *804.3* ± 78.9 – 1176 x 14.7 – *19.2* ± 2.1 – 22.2 µm	**(I)** 22.8 – *25* ± 1.5 – 27.6 µm **(II)** 48.9– *61* ± 2.4 – 66.3 µm	58.8 – *62.4* ± 2.2 – 68.3 x 27.6 – *29.7* ± 1.8 – 31.3 µm
Vosmaer (1885)	Barents Sea	Present	Present	Present	Present
Reexamination *This study*	Barents Sea	**(St)** 584 – *678* ± 55.9 – 762 x 13.8 – *16.8* ± 1.7 – 18.6 µm	**(S)** 738 – *994.3* ± 89.9 – 1146 x 15 – *19.1* ± 2.7 – 23.7 µm	**(I)** 24 – *27.8* ± 1.5 – 31 µm **(II)** 63 – *71.8* ± 2.3 – 81 µm	63 – *67.5* ± 2.2 – 72 x 26 – *28.9* ± 1.7 – 30.5 µm
Fristedt (1887)	East Greenland / 580 m	**(St)** 500 µm	***nm***	**(I)** 15 µm **(II)** 60 µm	70 µm

Arnesen (1903)	Between Bergen and Trondheim / 100 – 180 m	***nm***	**(S)** ca. 1000 µm	**(I)** ***nm*** **(II)** 68 µm	60 µm
Lundbeck (1905)	North Atlantic / 105 – 1460 m	**(St)** 410 – 620 x 8 – 17 µm	**(S)** 680 – 860 x 14 – 21 µm	**(I)** 21 – 28 µm **(II)** 47 – 61 µm	54 – 68 x 24 – 38 µm
Arndt (1935)	North Atlantic / 'deep-sea'	**(St)** 410 – 620 µm	**(S)** 680 – 860 µm	**(I)** 21 – 28 µm **(II)** 47 – 75 µm	54 – 68 µm
Koltun (1959)	Barents Sea / 106 – 385 m	**(St)** 410 – 620 x 8 – 17 µm	**(S)** 680 – 904 x 14 – 27 µm	***nm***	***nm***
Baker et al. (2018)	Davis Strait / 537 – 1132 m	**(St)** 528.1 – *594.7* – 655.5 x 14.2 – *19.3* – 23.9 µm	**(S)** 689.7 – *842.8* – 902.8 x 11.1 – *15.1* – 21.1 µm	**(I)** 23.1 – *25.4* – 28.8 µm **(II)** 40.4 – *57.4* – 67.6 µm	48 – *57.2* – 65.7 x 24 – *29.7* – 35.9 µm
		(St) 575.9 – *618.6* – 661.5 x 18.3– *21.6* – 24.8 µm	**(S)** 730.2 – *778.4* – 822.4 x 13.3 – *15.5* – 17.9 µm	**(I)** 22.7 – *24.9* – 27 µm **(II)** 44.7 – *54.8* – 61.6 µm	54.1 – *62.8* – 68 x 26.9 – *31* – 36.9 µm
		(St) 497.4– *613.1* – 725.5 x 15.7 – *19.5* – 22.2 µm	**(S)** 701.8 – *759.8* – 827.4 x x 12 – *14.5* – 19 µm	**(I)** 21.4 – *25.1* – 29.1 µm **(II)** 50.9 –	51.2 – *57.9* – 63.4 x 23.7 – *30.1* – 37.5 µm

				56.9 – 60.8 µm	
		(St) 504.4– *568* – 629.1 x 16 – *19.2* – 22.7 µm	**(S)** 743.5 – *814.3* – 879.1 x 11.3 – *14.4* – 18.8 µm	**(I)** 23.2 – *26* – 27.2 µm **(II)** 48.2 – *52.5* – 57.7 µm	46.3 – *55.8* – 61.7 x 25.6 – *29* – 33.2 µm
		(St) 498.4 – *553* – 603 x 15.7 – *18.6* – 22.3 µm	**(S)** 682.2 – *758.4* – 835.4 x 13.5 – *17.4* – 20.5 µm	**(I)** 21.5 – *24.4* – 26.3 µm **(II)** 42.1 – *59* – 82.8 µm	41.5 – *49.5* – 57.5 x 27.8 – *31.8* – 37.9 µm
Dinn & Leys (2018)	Saglek Bank, Northern Labrador Sea / 427 m	**(T)** 554 – *623* – 693 x 12.6 – *15.5* – 18.6 µm.	**(S)** 749 – *833* – 923 x 18.5 – *23* – 26 µm	**(I)** 18 – *22* – 27.6 µm **(II)** 35 – *55* – 64 µm	43– *50* – 53 µm
Reexamination *This study*	Saglek Bank, Northern Labrador Sea / 427 m	**(St)** 560.3 – *624.3* ± 32.2 – 667.6 x 7.8 – *11.8* ± 3 – 17.3 µm.	**(S)** 782.5 – *830.7* ± 50 – 908 x 19.3 – *21.5* ± 1.2 – 23.1 µm	**(I)** 24.1 – *24.9* ± 1.2 – 29 µm **(II)** 48.3 – *51* ± 3.8 – 59 µm	48.3– *51.2* ± 2.6 – 53.1 x 26.5 – *29* ± 0.7 – 29.8 µm
This study	Flemish Cap, Tail Grand Bank / 1554 m	**(St)** 533 – 645 x 6 – 13 µm	**(S)** 619 – 803 x 14 – 18 µm	**(I)** 21 – 26 µm **(II)** 46 – 66 µm	48 – 64 x 20 – 33 µm
	Flemish Cap, Tail Grand Bank / 1137 m	**(St)** 488 – 610 x 8 – 17 µm	**(S)** 601 – 1000 x 15 – 27 µm	**(I)** 20 – 30 µm **(II)** 50 – 67 µm	52 – 61 x 19 – 28 µm
	Flemish Cap, Tail	**(St)** 504 – 598 x 12 –	**(S)** 751 – 1086 x 16 –	**(I)** 21 – 35	55 – 66 x 26 – 39 µm

	Grand Bank / 1122 m	16 µm	24 µm	µm **(II)** 55 – 77 µm	
	Flemish Cap, Tail Grand Bank / 870 m	**(St)** 555 – 625 x 11 – 17 µm	**(S)** 767 – 910 x 15 – 24 µm	**(I)** 25 – 29 µm **(II)** 39 – 70 µm	51 – 63 x 23 – 34 µm
	Flemish Cap, Tail Grand Bank / 1127 m	**(St)** 538 – 676 x 12 – 20 µm	**(S)** 637 – 867 x 17 – 20 µm	**(I)** 22 – 28 µm **(II)** 51 – 71 µm	58 – 68 x 27 – 39 µm
	Flemish Cap, Tail Grand Bank / 1248 m	**(St)** 532 – 842 x 10 – 19 µm	**(S)** 722 – 902 x 10 – 22 µm	**(I)** 19 – 27 µm **(II)** 38 – 52 µm	46 – 59 x 25 – 35 µm
	Flemish Cap, Tail Grand Bank / 1055 m	**(St)** 518 – 845 x 11 – 20 µm	**(S)** 705 – 833 x 13 – 22 µm	**(I)** 23 – 33 µm **(II)** 37 – 63 µm	50 – 62 x 26 – 35 µm
	Unknown	**(St)** 479.5 – *602.8* ± 24.1 – 673 x 14.3 – *16.4* ± 2.2 – 19.1 µm	**(S)** 765 – *863.8* ± 59.5 – 925.7 x 15.3 – *19.8* ± 1.5 – 21.7 µm	**(I)** 24.3 – *27.1* ± 2.4 – 33.3 µm **(II)** 61 – *72.6* ± 8 – 82 µm	67 – *75.6* ± 5.4 – 82.6 x 27.1 – *31.7* ± 4.3 – 35.4 µm
	Unknown	**(St)** 548 – *570.3* ± 10.3 – 628 x 13.7 – *15.8* ± 1.8 – 18.7 µm	**(S)** 745.6 – *880.1* ± 34.9 – 936 x 14.9 – *18.5* ± 1.3 – 23.5 µm	**(I)** 26 – *27.2* ± 0.8 – 28.5 µm **(II)** 67.3 – *75.5* ± 1.4 – 78 µm	67 – *75.2* ± 6.5– 83 x 23.7 – *33.1* ± 6.5 – 36 µm
Melonanchora (*Melonanchora*) cf. *elliptica* Carter 1874					

Topsent (1892)	Azores / 736 – 1267 m	**(St)** Present	**(S)** Present	**(I)** ***nm*** **(II)** 55 µm	70 µm
Topsent (1904)	Azores / 523 – 1360 m	***nm***	***nm***	**(I)** 18 – 21 µm **(II)** ***nm***	***nm***
Topsent (1913)	Norwegian coast / 440 m	***nm***	***nm***	***nm***	***nm***
Topsent (1928)	Azores / 650 – 950 m	***nm***	***nm***	**(I)** 19 – 23 µm **(II)** 40 – 41 µm	43 x 26 µm
	Azores / 1378 m	***nm***	***nm***	**(I)** 20 – 23 µm **(II)** 72 µm	72 x 35 µm
Melonanchora (*Melonanchora*) *emphysema* (Schmidt, 1875)					
Schmidt (1875)	Haugesund, Norway* / 193 m	**(St)** Present	***nm***	Present	***nm***
Reexamination *This study*	Haugesund, Norway* / 193 m	**(St)** 500 – *570* ± 15.9 – 627 x 10.9 – *15.8* ± 3.1 – 18.5 µm	Same as in ectosome	**(I)** 19.6 – *24.7* ± 2.7 – 29.4 µm **(II)** 55.3 – *60.2* ± 3.9 – 68.6 µm	40.4 – *44.3* ± 1.8 – 58 x 23.1 – *25.6* ± 1.3 – 28 µm
Thiele (1903)	North Atlantic	**(St)** ca. 650 µm	Same as in ectosome	**(I)** 21 µm **(II)** 60 µm	50 µm
Lundbeck (1905)	North Atlantic / 375	**(St)** 440 – 610 x 10 –	Same as in ectosome	**(I)** 24 – 30	50 – 56 x 28 µm

	– 1460 m	14 µm		µm **(II)** 57 – 71 µm	
Alander (1942)	Skandia, Sweden / 85 m	Present	Present	Present	Present
Reexamination *This study*	Skandia, Sweden / 85 m	**(St)** 492.7 – 508.*1* ± 13 – 521.7 x 9.7 – *10.6* ± 2.8 – 14.5 µm	Same as in ectosome	**(I)** 24.2 – *26.6* ± 2.7 – 29 µm **(II)** 48.3 – *51.5* ± 5.5 – 58 µm	37.6 – *38.9* ± 1 – 42.6 x 21.6 – *24.3* ± 1.6 – 29 µm
Vacelet (1969)	Mediterranean / 360 – 370 m	**(St)** 330 – 490 x 8.5 – 18 µm	Same as in ectosome	**(I)** 22 µm **(II)** 40 – 53 µm	40 – 45 x 20 µm
Rexamination *This study*	Mediterranean / 360 – 370 m	**(T)** 389.3 – *418.6* ± 11.7 – 477 x 12.2 – *14.6* ± 1.3 – 17.6 µm	Same as in ectosome	**(I)** 21.4 – *22.9* ± 0.9 – 25.3 µm **(II)** 41.2 – *45* ± 1.2 – 55.1 µm	38.4 – *41.3* ± 1.5 – 44.5 x 17.1 – *19.7* ± 2.3 – 22.7 µm
This study	Scotland / -	**(St)** 342 – *472.8* ± 61.8 – 540 x 5.4 – *6.9* ± 0.8 – 7.8 µm	Same as in ectosome	**(I)** 22.8 – *24.3* ± 1 – 25.8 µm **(II)** 48 – *52.5* ± 5.6 – 63 µm	37.8 – *41.7* ± 2.8 – 44.4 x 18 – *19.5* ± 1.3 – 21 µm
	Galicia Bank / 500 m	**(T)** 439.2 – *479.9* ± 30.4 – 537.6 x 12.2 – *15.5* ± 1.8 – 18.7 µm	Same as in ectosome	**(I)** 20.7 – *23.4* ± 1.5 – 25.4 µm **(II)** 42 – *51.2*	37.2 – *41.2* ± 2 – 44.6 x 17.3 – *20.6* ± 1.2 – 23.4 µm

				± 4.3 – 57.2 µm	
	Galicia Bank / 500 m	**(T)** 429.2 – _482.2_ ± 29.7 – 538.9 x 11.8 – _15_ ± 1.7 – 18.7 µm	Same as in ectosome	**(I)** 20.2 – _22.8_ ± 1.9 – 27.3 µm **(II)** 40.6 – _54_ ± 4.8 – 62.7 µm	34.7 – _41.2_ ± 4 – 54.5 x 17.2 – _20.2_ ± 2 – 23.5 µm
	Gulf of Lyon / 684 m	**(T)** 253.6 – _375.6_ ± 48.7 – 426.1 µm x 8.8 – _10.1_ ± 1.7 – 13.7 µm	Same as in ectosome	**(I)** 20.5 – _24.1_ ± 3.7 – 30.4 µm **(II)** 44.3 – _53_ ± 4.2 – 60 µm	41.2 – _43.7_ ± 2.1 – 46.6 x 18.3 – _20.5_ ± 2.7 – 26.3 µm
Melonanchora (*Melonanchora*) cf. *emphysema* (Schmidt, 1875)					
Solórzano & Duran (1981)	Galicia Coast, Spain* / 58 m	**(St)** 316 – 345 x 9 µm	Same as in ectosome	**(I)** 22– 26 µm **(II)** 44 –51 µm	27 – 40 µm
Reexamination Solórzano (1990)	Galicia Coast, Spain* / 58 m	**(St)** 316 – 345 x 8 – 9 µm	Same as in ectosome	**(I)** 22– 26 µm **(II)** 44 –51 µm	27 – 40 x 18 – 20 µm
Reexamination *This study*	Galicia Coast, Spain* / 58 m	**(T)** 302.6 – _345.8_ ± 24 – 384.5 x 4.9 – _6.83_ ± 0.8 – 8 µm	Same as in ectosome	**(I)** 16.5 – _20_ ± 1.4 – 22.2 µm **(II)** 35 – _44_ ± 3.9 – 50 µm	31.9 – _36.2_ ± 2.3 – 40.5 x 14.2 – _17.2_ ± 2.1 – 20.5 µm
This study	Cantabrian Sea /	**(T)** 274 – _329.6_ ± 30.6	Same as in ectosome	**(I)** 15.4 – _18_	34.7 – _37.2_ ± 1.2 –

	128 m	– 387.6 x 4.6 – _6.1_ ± 0.8 – 7.6 µm		± 1.3 – 20.7 µm **(II)** 33.6 – _44_ ± 3.8 – 48.9 µm	39.3 x 12.6 – _16_ ± 2 – 19.9 µm
Melonanchora (*Melonanchora*) *tumultuosa* sp. nov.					
Vosmaer (1885)	-	Present	Present	Present	Present
Reexamination *This study*	-	**(St)** 483 – _542.6_ ± 38.3 – 600 µm x 10.6 – _12.9_ ± 3.2 – 19.3 µm	**(St)** 627.9 – _802.3_ ± 42.2 – 924.5 µm x 11.6 – _18.3_ ± 1.5 – 24.4 µm	**(I)** 21.2 – _26.5_ ± 3.8 – 28.9 µm **(II)** 48.6 – _68.6_ ± 8.1 – 72.9 µm	48.3 – _67.5_ ± 6.8 – 78.62 x 18.9 – _22.3_ ± 1.6 – 25.2 µm
Baker et al. (2018)	Davis Strait / 537 – 1132 m	**(St)** 485.1 – _599.8_ – 673.3 x 12.7 – _15.6_ – 20 µm	**(St)** 831.1 – _913.6_ – 981.6 x 15.7 – _19.5_ – 22.7 µm	**(I)** 22.6 – _25.8_ – 32.2 µm **(II)** 43.3 – _59_ – 66.4 µm	53.2 – _57.5_ – 63.7 x 23.1 – _27.7_ – 35.3 µm
		(St) 537.5 – _582.6_ – 670.8 x 12.0 – _14.4_ – 17.4 µm	**(St)** 823.5 – _884.6_ – 957.8 x 13.5 – _19.2_ – 24 µm	**(I)** 22.2 – _24.3_ – 27.1 µm **(II)** 44 – _49.5_ – 56.8 µm	52.8 – _54.9_ – 59.3 x 24.9 – _30.4_ – 36.0 µm
		(St) 509.9 – _569.8_ – 611.6 x 11.3 – _14.7_ – 17.9 µm	**(St)** 672.6 – _770.9_ – 860.1 x 17.4 – _20_ – 23.9 µm	**(I)** 20.5 – _22.7_ – 25.4 µm **(II)** 49.5 – _52.3_ – 56.3 µm	57.5 – _61.7_ – 65.1 x 23.9 – _26.9_ – 28.8 µm

This study	Flemish Cap, Tail Grand Bank / 1027 m	**(St)** 548 – 657 x 11 – 17 µm	**(St)** 716 – 873 x 14 – 22 µm	**(I)** 22 – 26 µm **(II)** 49 – 68 µm	56 – 67 x 25 – 38 µm
	Flemish Cap, Tail Grand Bank / 613 m	**(St)** 544 – 657 x 8 – 18 µm	**(St)** 483 – 823 x 8 – 13 µm	**(I)** 24 – 32 µm **(II)** 38 – 67 µm	47 – 65 x 22 – 34 µm
	Sydkoster Island, Sweeden* / 100 m.	**(St)** 483 – *542.6* ± 38.3 – 600 x 10.6 – *12.9* ± 3.2 – 19.3 µm	**(St)** 627.9 – *802.3* ± 42.2 – 924.5 x 11.6 – *18.3* ± 1.5 – 24.4 µm	**(I)** 21.2 – *26.5* ± 3.8 – 28.9 µm **(II)** 48.6 – *68.6* ± 8.1 – 72.9 µm	48.3 – *67.5* ± 6.8 – 78.6 x 18.9 – *22.3* ± 1.6 – 25.2 µm
	Unknown	**(St)** 483 – *542.6* ± 38.3 – 600 x 10.6 – *12.9* ± 3.2 – 19.3 µm	**(St)** 768 – *895.7* ± 38.3 – 993 x 15.7 – *19.8* ± 1.6 – 24 µm	**(I)** 18.5 – *21* ± 2.6 – 25 µm **(II)** 55.7 – *76.1* ± 2.9 – 79 µm	62.8 – *70* ± 4.9 – 78 x 22.1 – *24.5* ± 1.9 – 29.3 µm
	Norway	**(St)** 490 – *550.4* ± 38.9 – 607.6 x 10.8 – *13.1* ± 3.3 – 19.6 µm	**(St)** 637 – *712.7* ± 31.3 – 813.5 x 11.8 – *14.7* ± 1.5 – 21.1 µm	**(I)** 21.3 – *26.5* ± 2.5 – 29 µm **(II)** 40.2 – *57.7* ± 8.2 – 69.6 µm	48.3 – *60* ± 4.2 – 67.6 x 25.1 – *27* ± 1.5 – 29 µm
	Norway / 130 – 150 m	**(St)** 528 – *617* ± 52.2 – 667 x 12.8 – *15* ± 2 – 18 µm	**(St)** 642 – *696* ± 58.8 – 804.3 x 14.7 – *18.6* ± 2.7 – 21.9 µm	**(I)** 24 – *28.9* ± 4.4 – 32 µm **(II)** 54 – *72.3* ± 8.7 – 81 µm	56.6 – *64.3* ± 6.4 – 72.3 x 18 – *23.8* ± 2.8 – 27.4 µm
	Norway / 130 – 150	**(St)** 402 – *499.5* ±	**(St)** 645 – *756* ± 88 –	**(I)** 24 – *28.9*	52.2 – *58.8* ± 7.9 – 74

	m	60.5 – 540 x 12 – *13.7* ± 1.8 – 16.1 µm	1026 x 12.5 – *19.3* ± 1.9 – 21 µm	± 4.4 – 32 µm **(II)** 54 – *72.3* ± 8.7 – 81 µm	x 23.4 – *25.9* ± 2.8 – 30 µm
	Norway / 130 – 150 m	**(St)** 462 – *515.5* ± 54.8 – 582 x 11.9 – *14.2* ± 1.6 – 16.5 µm	**(St)** 601.3 – *719.5* ± 79.3 – 1002 x 13.3 – *18.2* ± 2.7 – 22.7 µm	**(I)** 24 – *29* ± 2.6 – 33 µm **(II)** 60 – *71.5* ± 7.1 – 84 µm	48 – *55.6* ± 6.2 – 72 x 24 – *25.9* ± 2.4 – 30 µm
Melonanchora (*Melonanchora*) *intermedia* sp. nov.					
Pulitzer-Finali (1983)	Corsica, Mediterranean Sea* / 128 m	**(St)** 380 – 490 x 6 – 11 µm	Same as in ectosome	**(I)** 19 – 21 µm **(II)** 32 – 49 µm	37 – 43 µm
Reexamination *This study*	Corsica, Mediterranean Sea* / 128 m	**(St)** 369 – *411.8* ± 14.5 – 475.3 x 7.2 – *9.7* ± 1.5 – 11 µm	Same as in ectosome	**(I)** 19 – *21.5* ± 0.7 – 22.7 µm **(II)** 33.2 – *39.5* ± 5.1 – 47.8 µm **(III)** 30.1 – *35.2* ± 2.9 – 38.6 µm	38.9 – *44.4* ± 6.7 – 51.2 x 20 – *21.8* ± 1.9 – 24.2 µm
Melonanchora (*Melonanchora*) *insulsa* sp. nov.					
Schmidt (1880)	Gulf of Mexico* / ‘deep-sea’	-	-	**(I)** 23 µm **(II)** 68 µm	60 µm
Reexamination *This study*	Gulf of Mexico* / ‘deep-sea’	**(St)** 593.6 – *656.7* ± 36.2 – 701 x 16.1 –	**(S)** 813.4 – *989* ± 41.2 – 1121.7 x 19.3 – *20.7* ±	**(I)** 27.2 – *30.9* ± 3.4 –	52.9 – *56.5* ± 4.2 – 62.1 x 22 – *24.3* ± 1.7

		17.*1* ± 1.2 – 19.5 µm	1.4 – 22.5 µm	35.8 µm **(II)** 48.6 – *52.3* ± 5.1 – 68 µm	– 26.6 µm
Melonanchora (*Melonanchora*) *maeli* sp. nov.					
This study	Cape Verde* / 'deep-sea'	**(T)** 531.6 – *590.9* ± 37.9 – 627.9 x 9.7 – *10.3* ± 0.5 – 10.6 µm	**(S)** 637.6 – *918.5* ± 75.6 – 1062.6 x 17.3 – *19.2* ± 1.3 – 21.3 µm	**(I)** 17.4 – *19.8* ± 1.7 – 23.2 µm **(II)** 27 – *29.3* ± 1.2 – 31.9 µm **(III)** 45.4 – *49.6* ± 2 – 53.1 µm	48.3 – *50.2* ± 1.7 – 53.2 x 17.4 – *19.2* ± 1.5 – 21.3 µm
Melonanchora (*Toretendalia*) *globogilva* Lehnert, Stone & Heimler, 2006a					
Lehnert et al. (2006a)	Aleutian Islands* / 190 m	**(T)** 640 – 680 x 10 – 12 µm	**(Ac)** 660 – 670 x 20 – 30 µm	**(I)** 23 – 25 µm **(II)** -	**(I)** 65 – 93 µm **(II)** 65 – 93 µm
Reexamination *This study*	Aleutian Islands* / 190 m	**(T)** 598.9 – *675* ± 22.5 – 724.5 x 9.7 – *10.9* ± 2.2 – 14.5 µm	**(Ac)** 589.3 – *638.3* ± 30 – 677.3 x 27 – *28* ± 1.1 – 29 µm	**(I)** 23.1 – *25.2* ± 1.1 – 27 µm **(II)** 48 – *64.4* ± 6.8 – 67.6 µm	77.3 – *86.9* ± 2.8 – 91.8 x 27 – *30* ± 2.3 – 33.8 µm

3

Figure 1

External view of most *Melonanchora* species

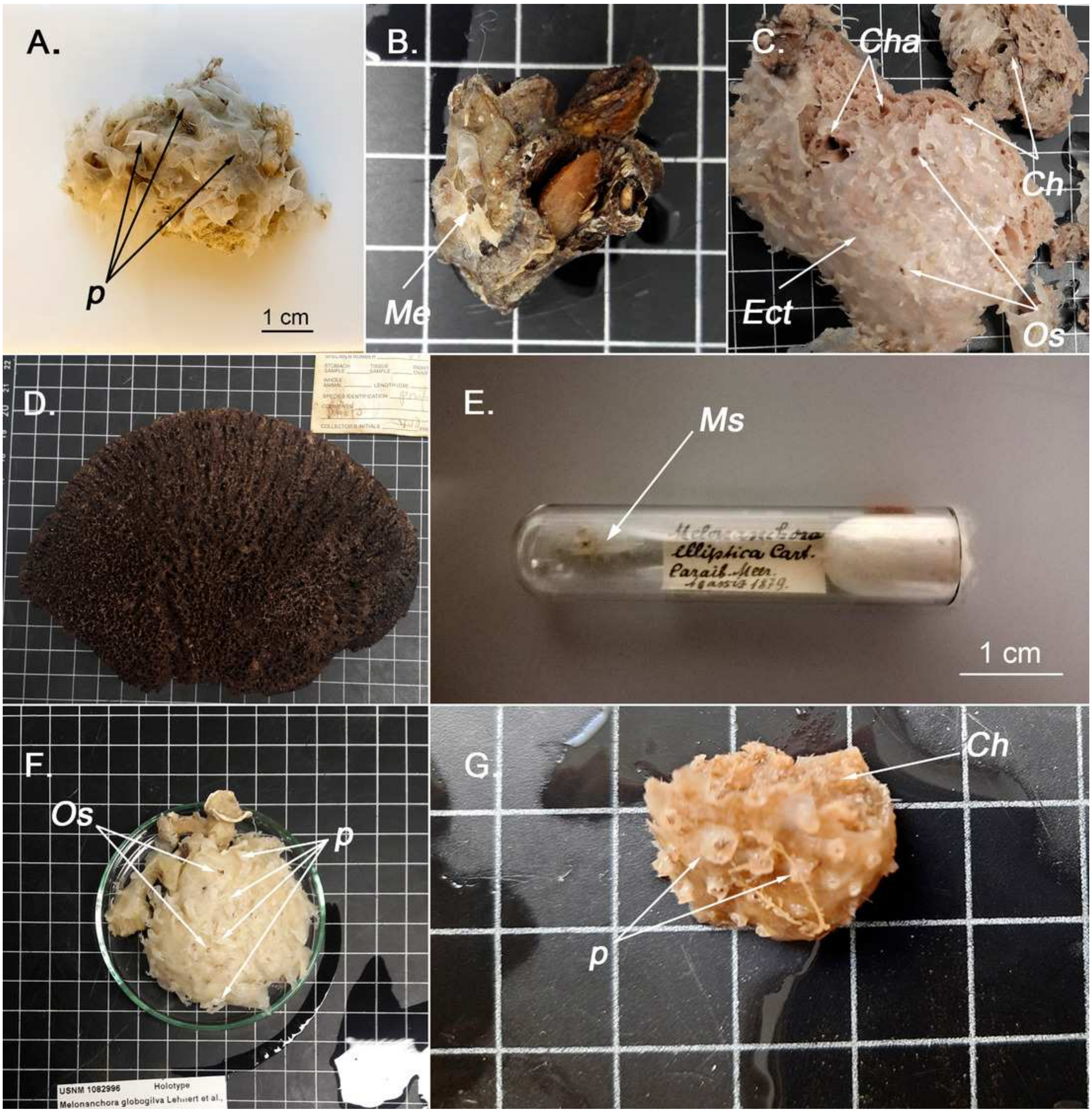

Figure 2

Optical imaging for *Melonanchora* general skeletal features

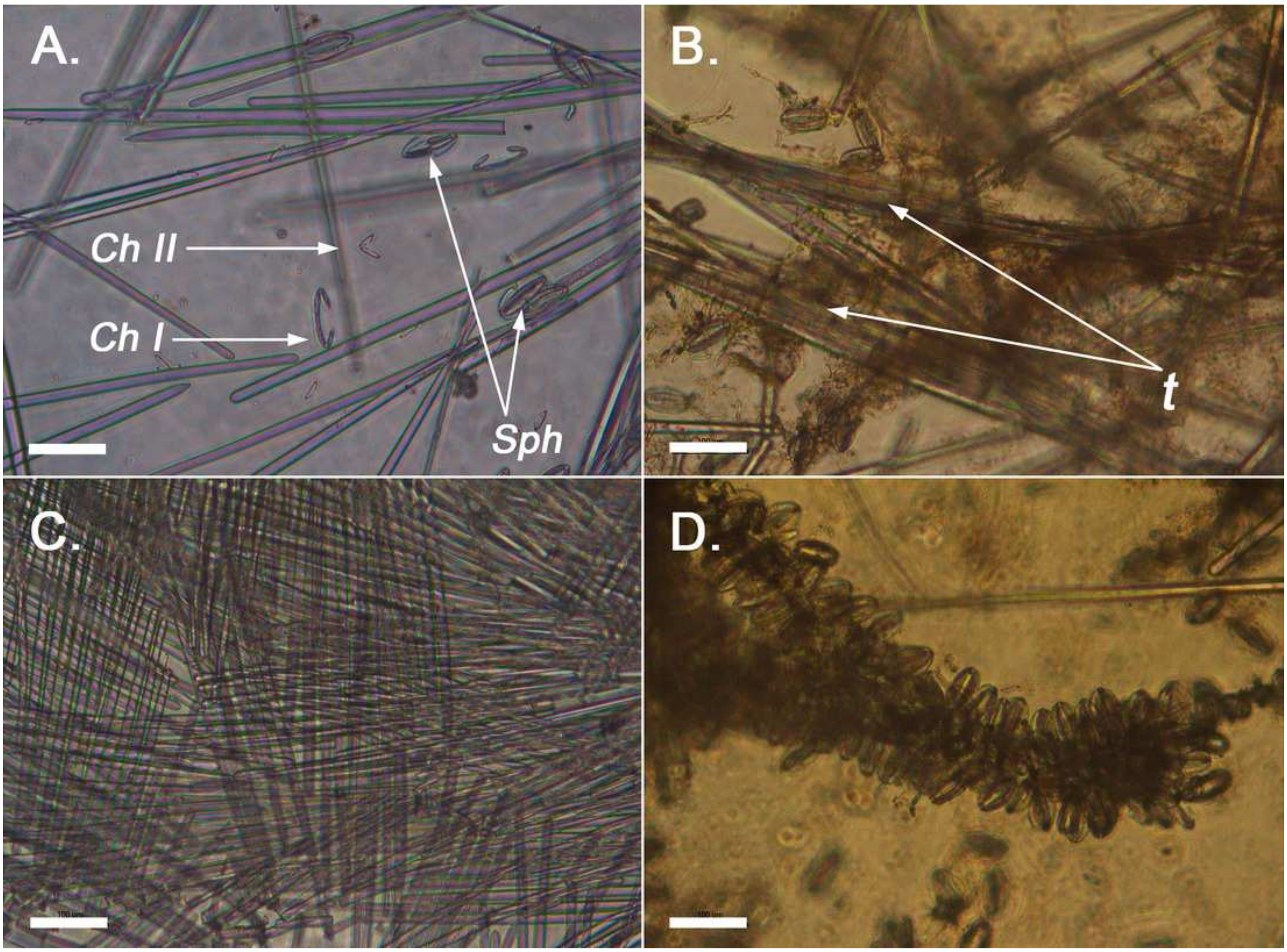

Figure 3

Melonanchora elliptica spicule plate

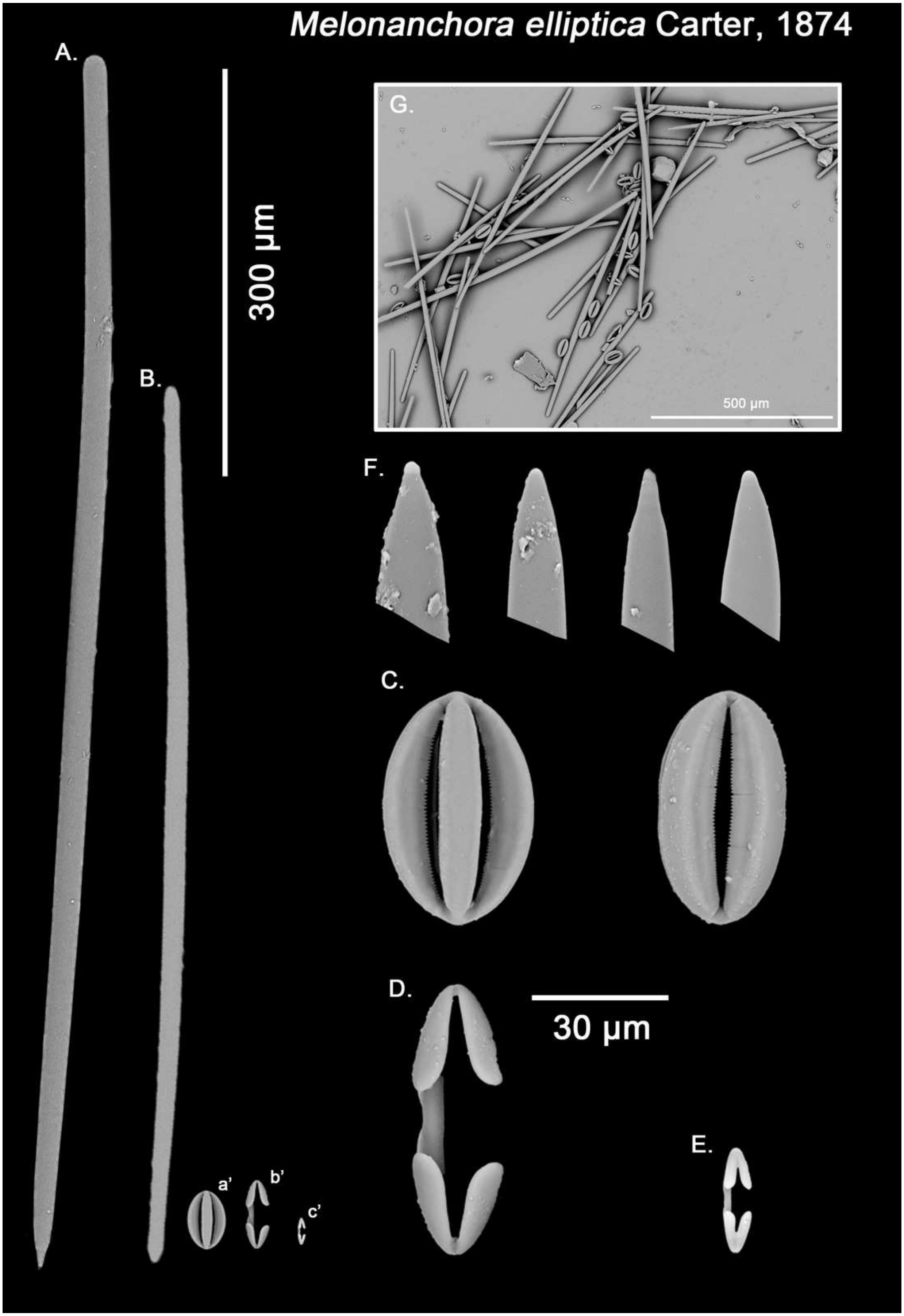
Melonanchora elliptica Carter, 1874
A.
B.
300 µm
G.
500 µm
F.
C.
D.
30 µm
E.
a'
b'
c'

Figure 4

Distribution map for North Atlantic *Melonanchora*

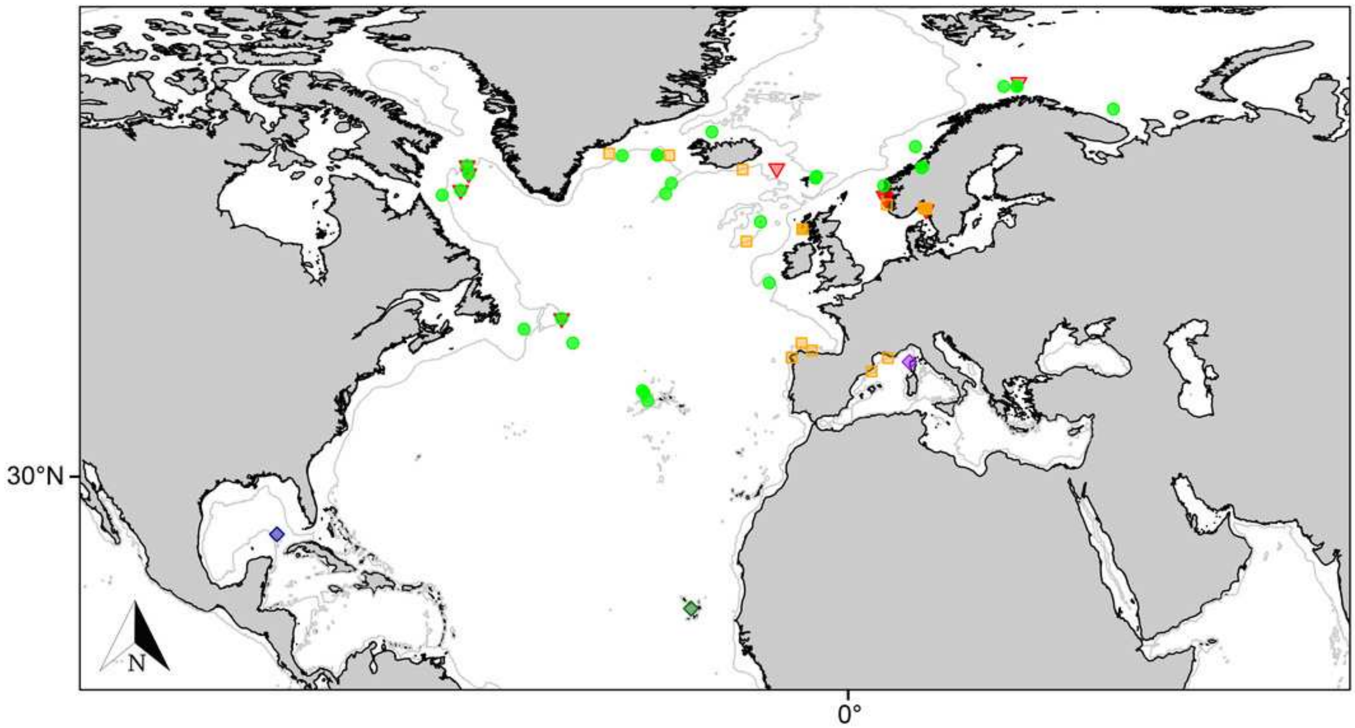

Figure 5

Melonanchora emphysema spicule plate

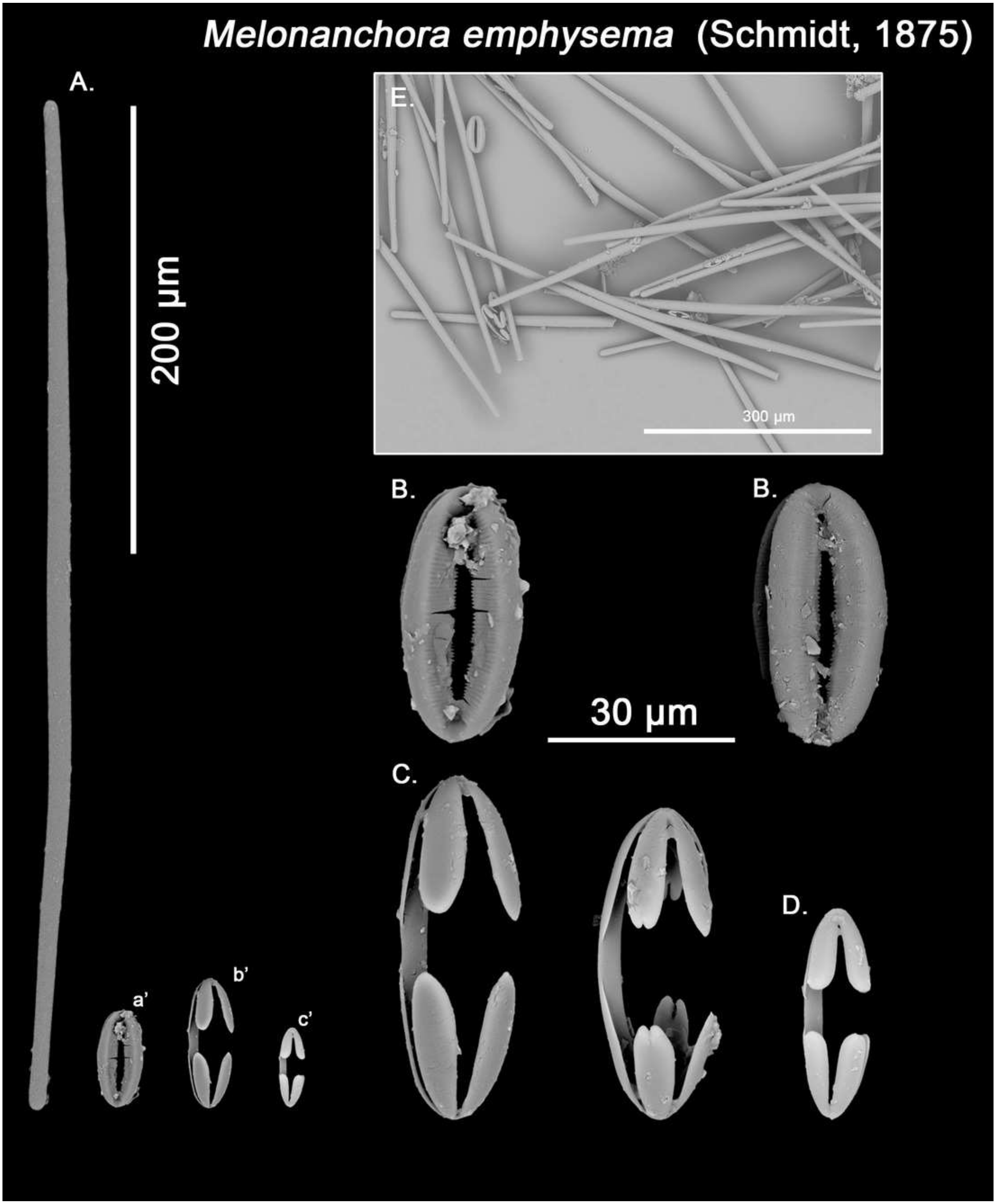
Melonanchora emphysema (Schmidt, 1875)
A.
200 µm
E.
300 µm
B.
B.
30 µm
C.
D.
a'
b'
c'

Figure 6

Melonanchora emphysema spicule plate

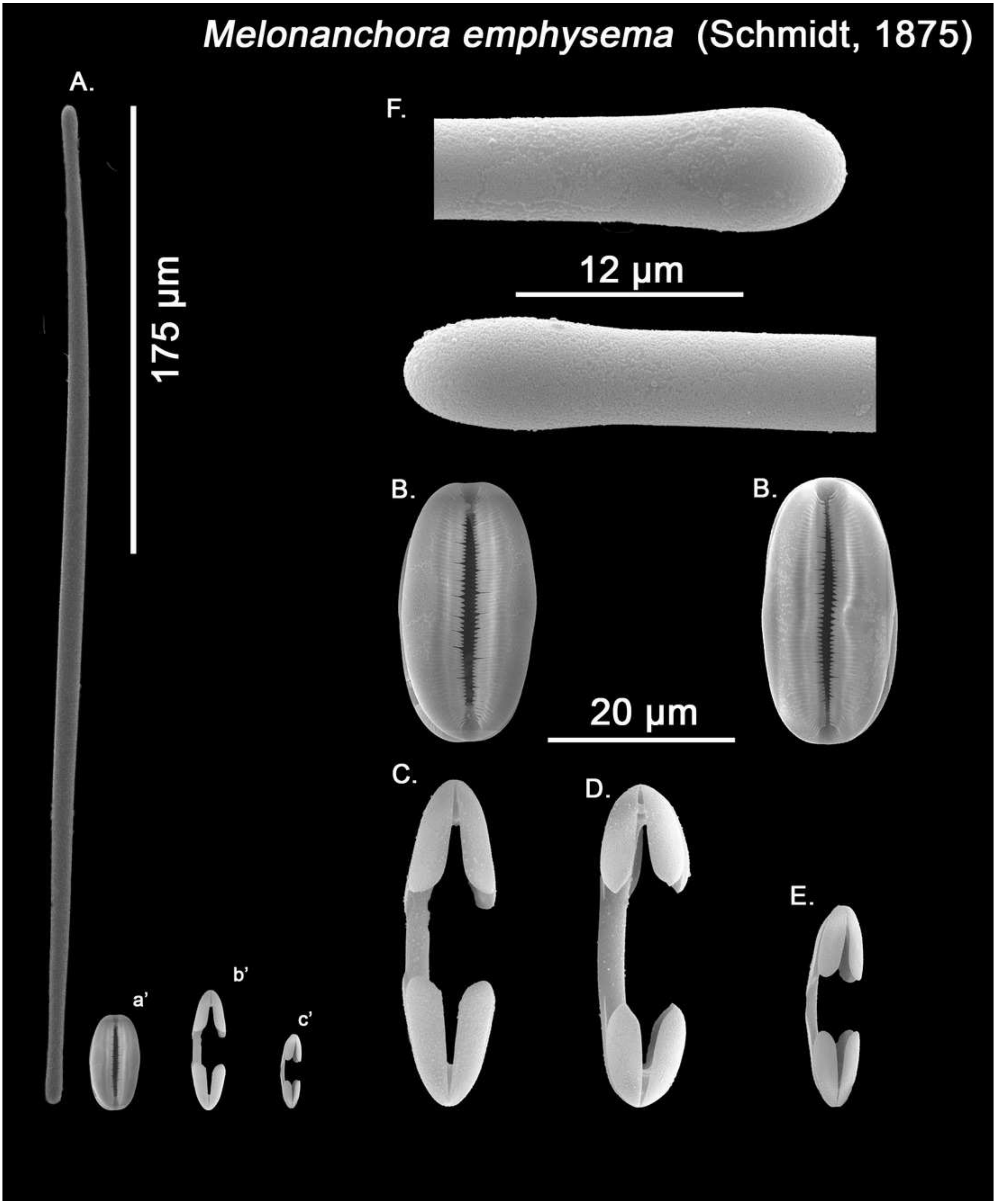
Melonanchora emphysema (Schmidt, 1875)
A.
175 µm
F.
12 µm
B.
B.
20 µm
C.
D.
E.
a'
b'
c'

Figure 7

Melonanchora tumultuosa sp. nov. spicule plate

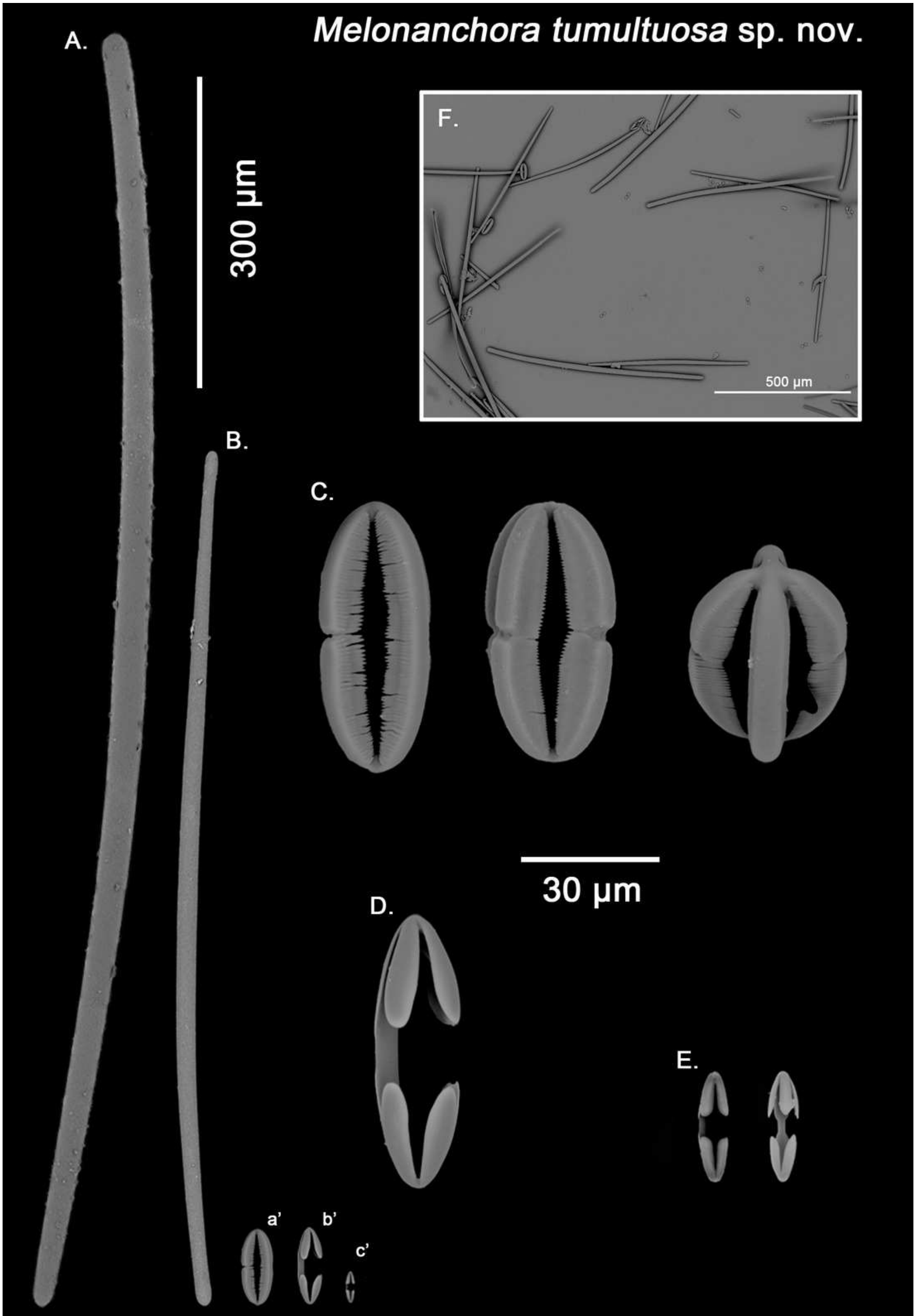
Melonanchora tumultuosa sp. nov.
A.
300 µm
F.
500 µm
B.
C.
30 µm
D.
E.
a'
b'
c'

Figure 8

Melonanchora intermedia sp. nov. spicule plate

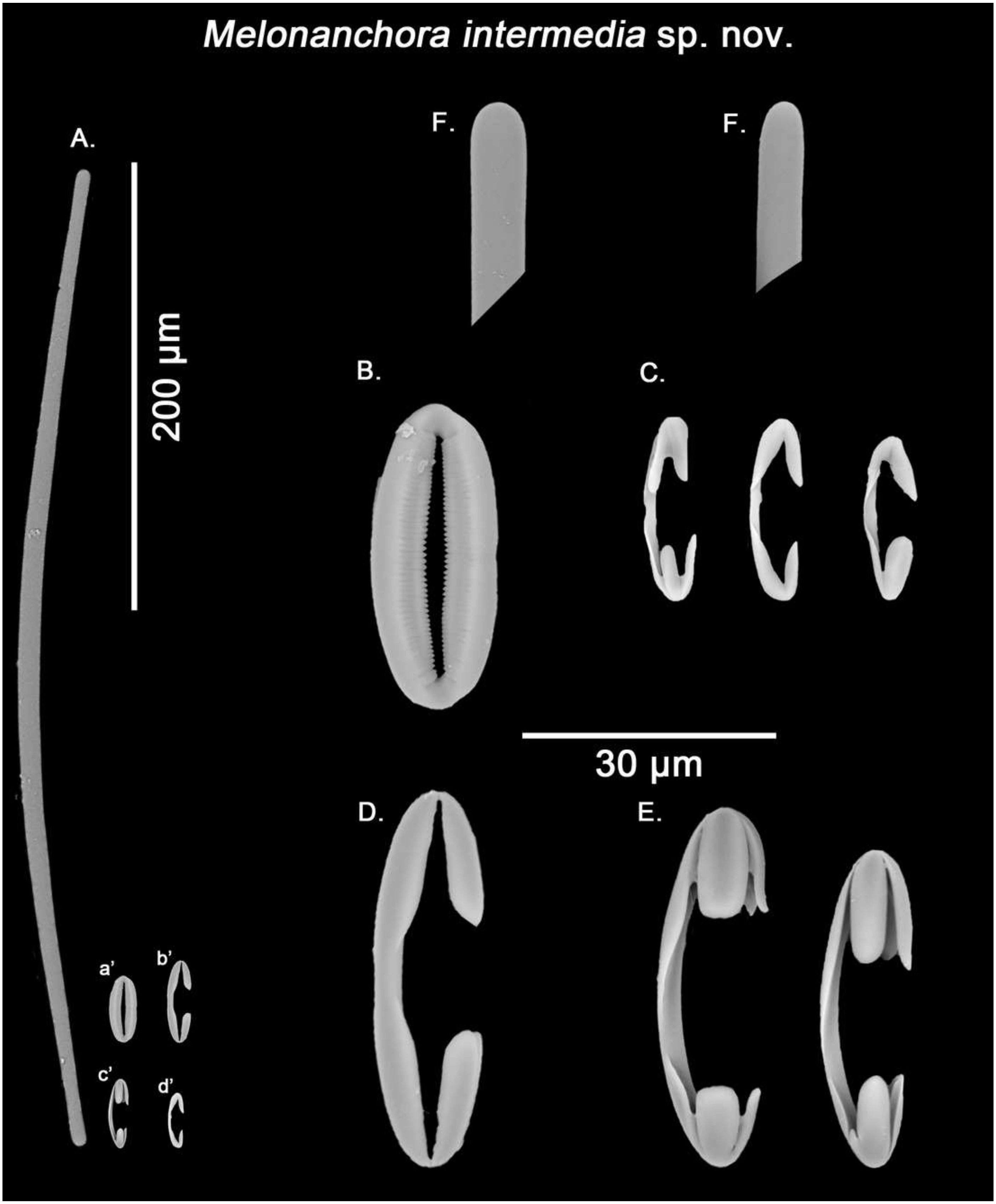
Melonanchora intermedia sp. nov.
A.
200 µm
F.
F.
B.
C.
30 µm
D.
E.
a'
b'
c'
d'

Figure 9

Melonanchora insulsa sp. nov. spicule plate

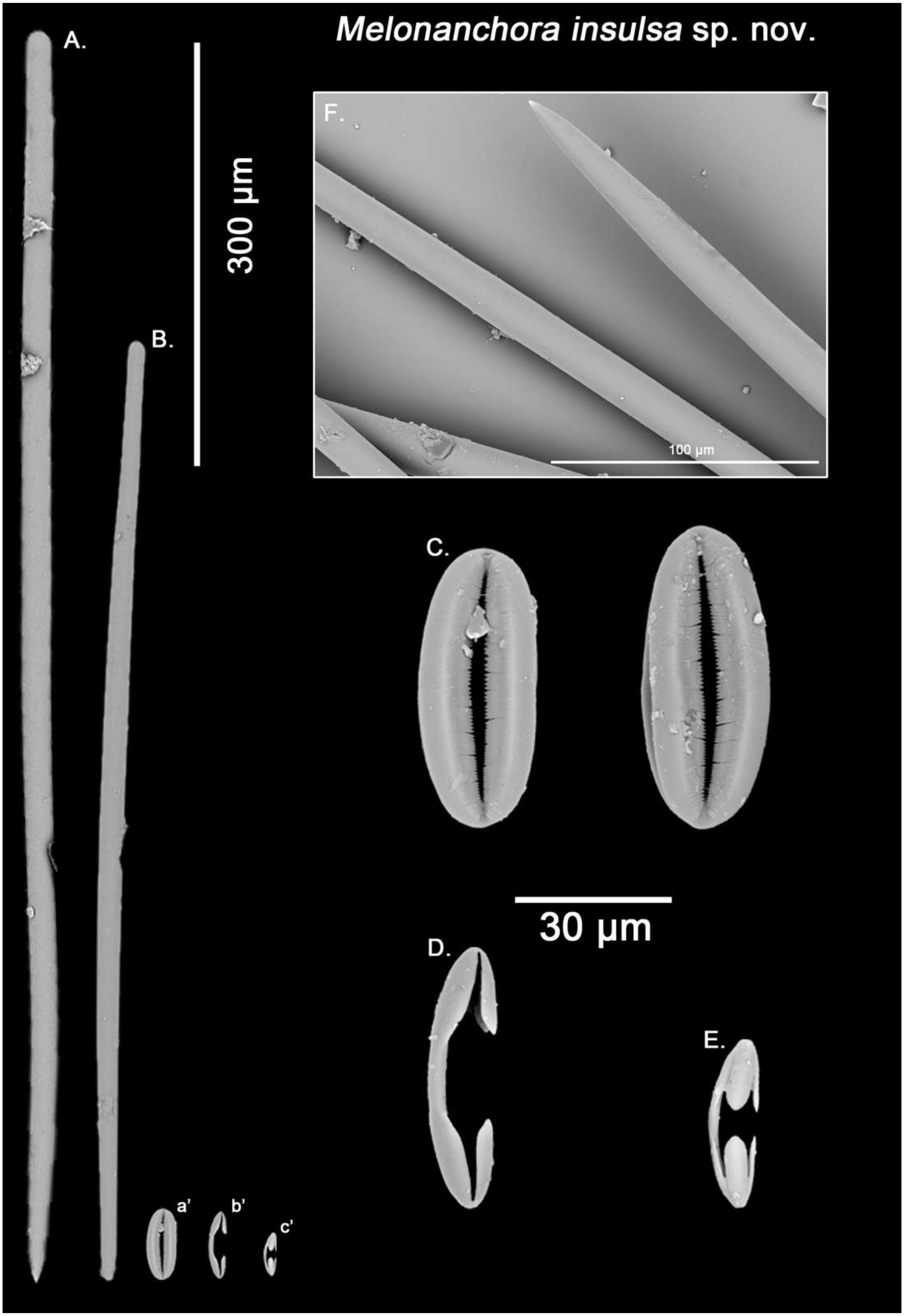
Melonanchora insulsa sp. nov.
A.
B.
300 µm
F.
100 µm
C.
30 µm
D.
E.
a'
b'
c'

Figure 10

Melonanchora maeli sp. nov. spicule plate

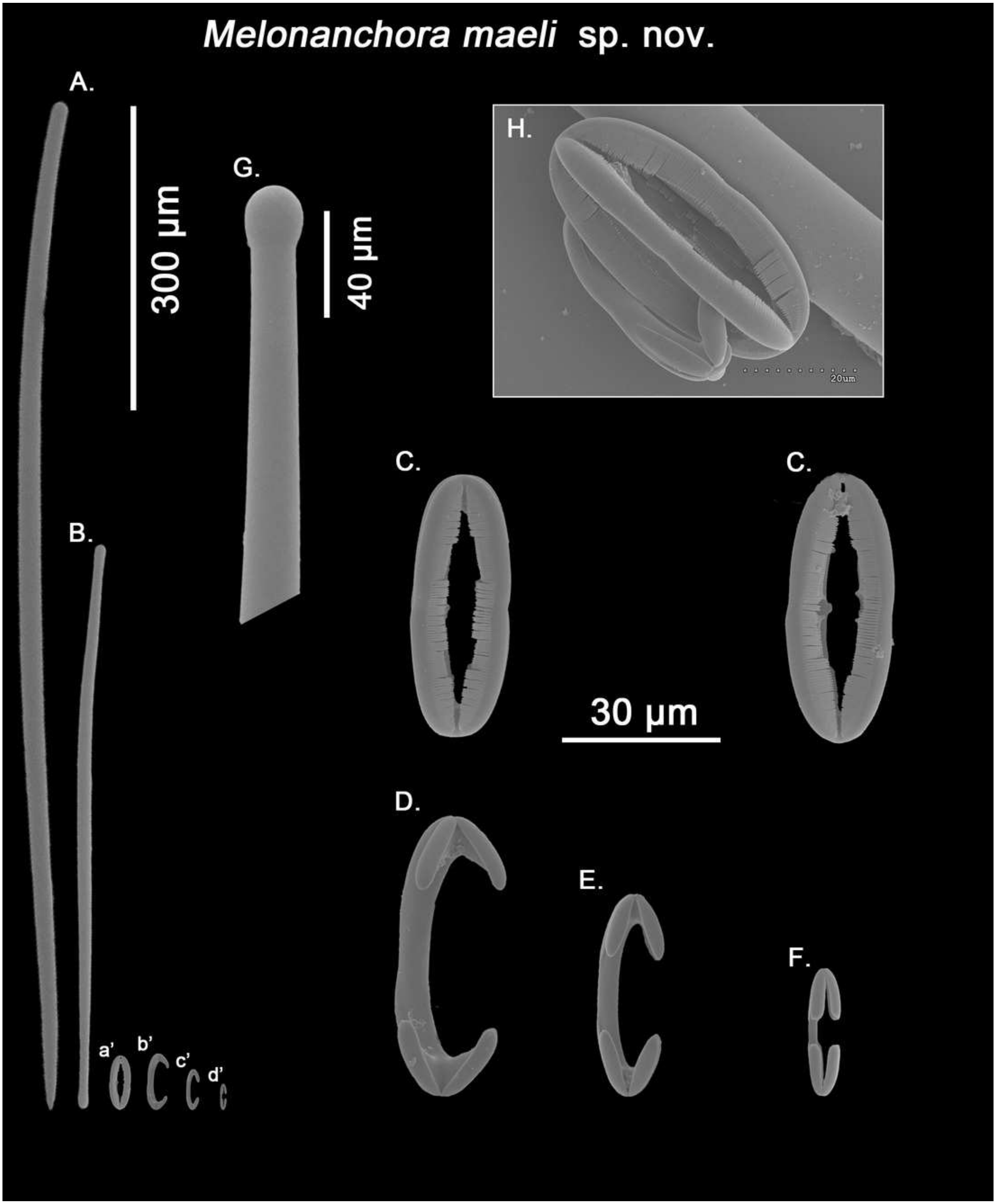
Melonanchora maeli sp. nov.
A.
300 µm
G.
40 µm
H.
20um
B.
C.
C.
30 µm
D.
E.
F.
a'
b'
c'
d'

Figure 11

Distribution map for Pacific *Melonanchora*

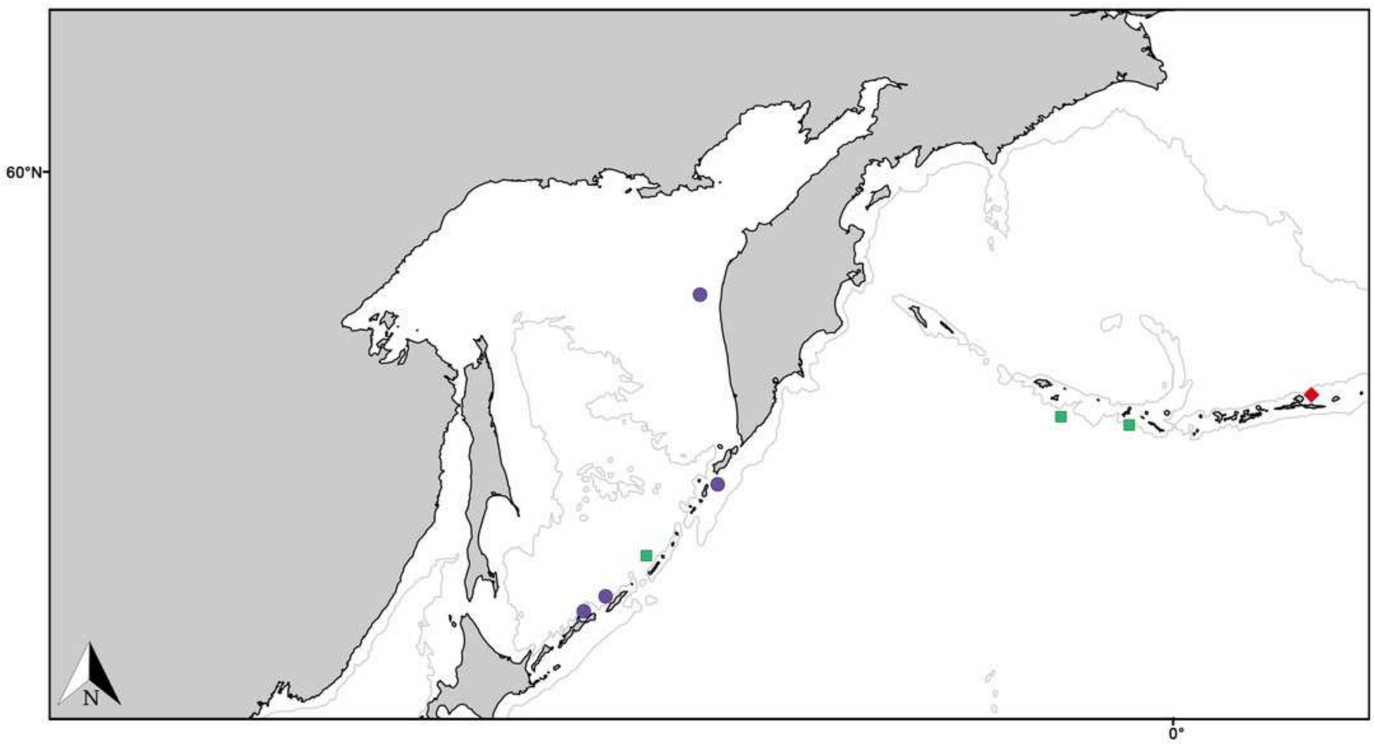

Figure 12

Melonanchora globogilva spicule plate

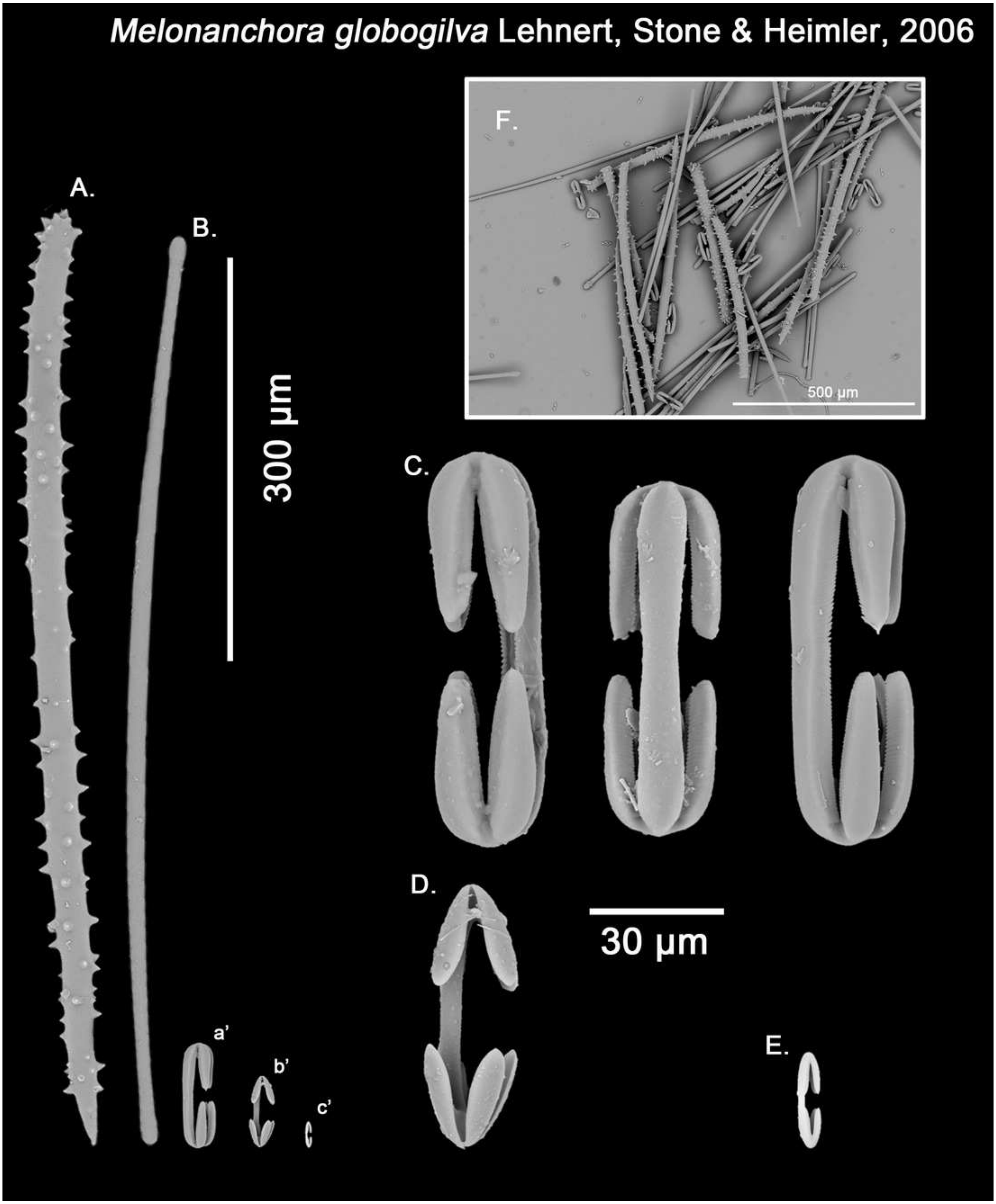
Melonanchora globogilva Lehnert, Stone & Heimler, 2006
F.
500 µm
A.
B.
300 µm
C.
D.
30 µm
a'
b'
c'
E.

Figure 13

Myxilla kobjakovae spicule plate

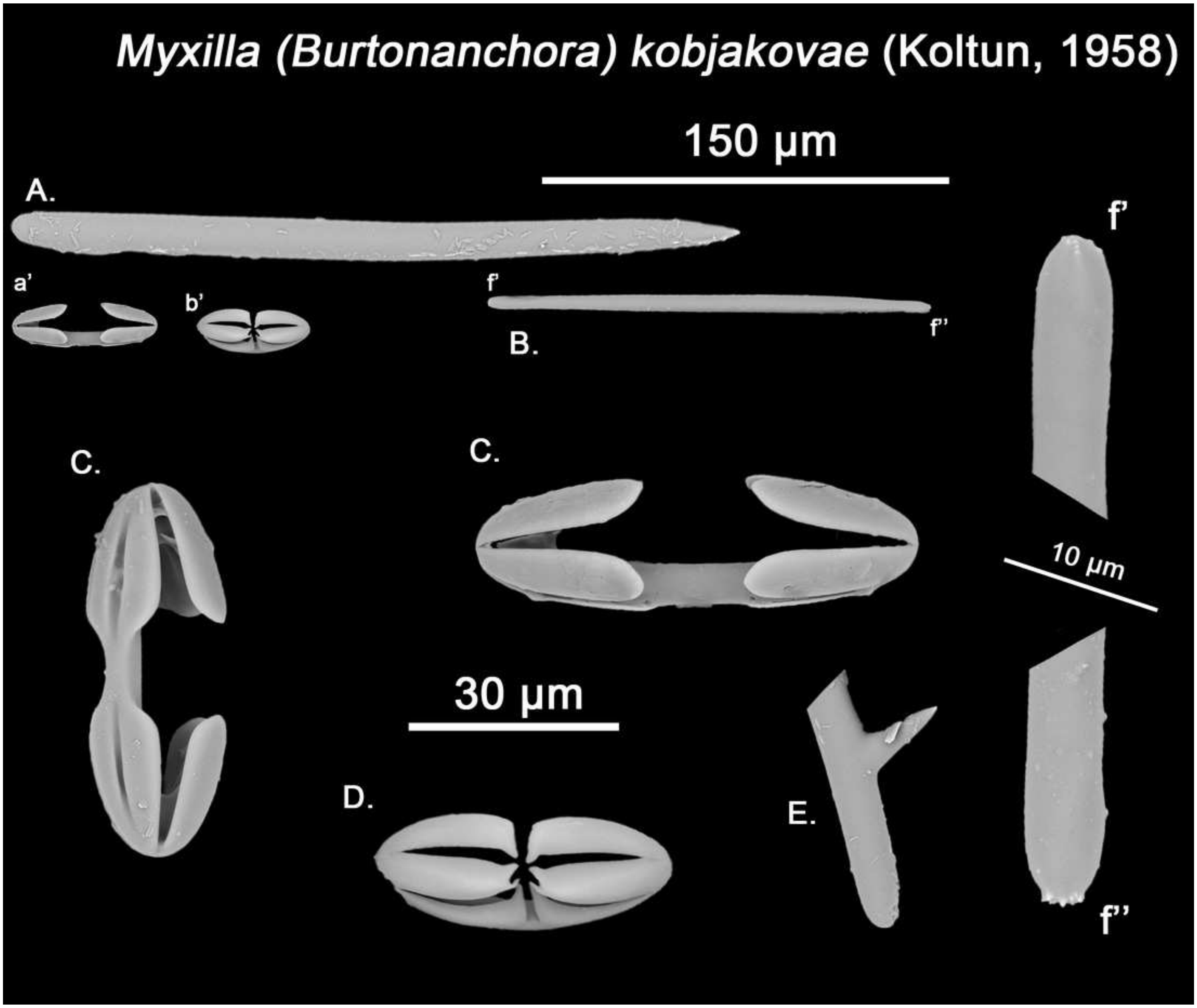

Figure 14

Arhythmata tetradentifera spicule plate

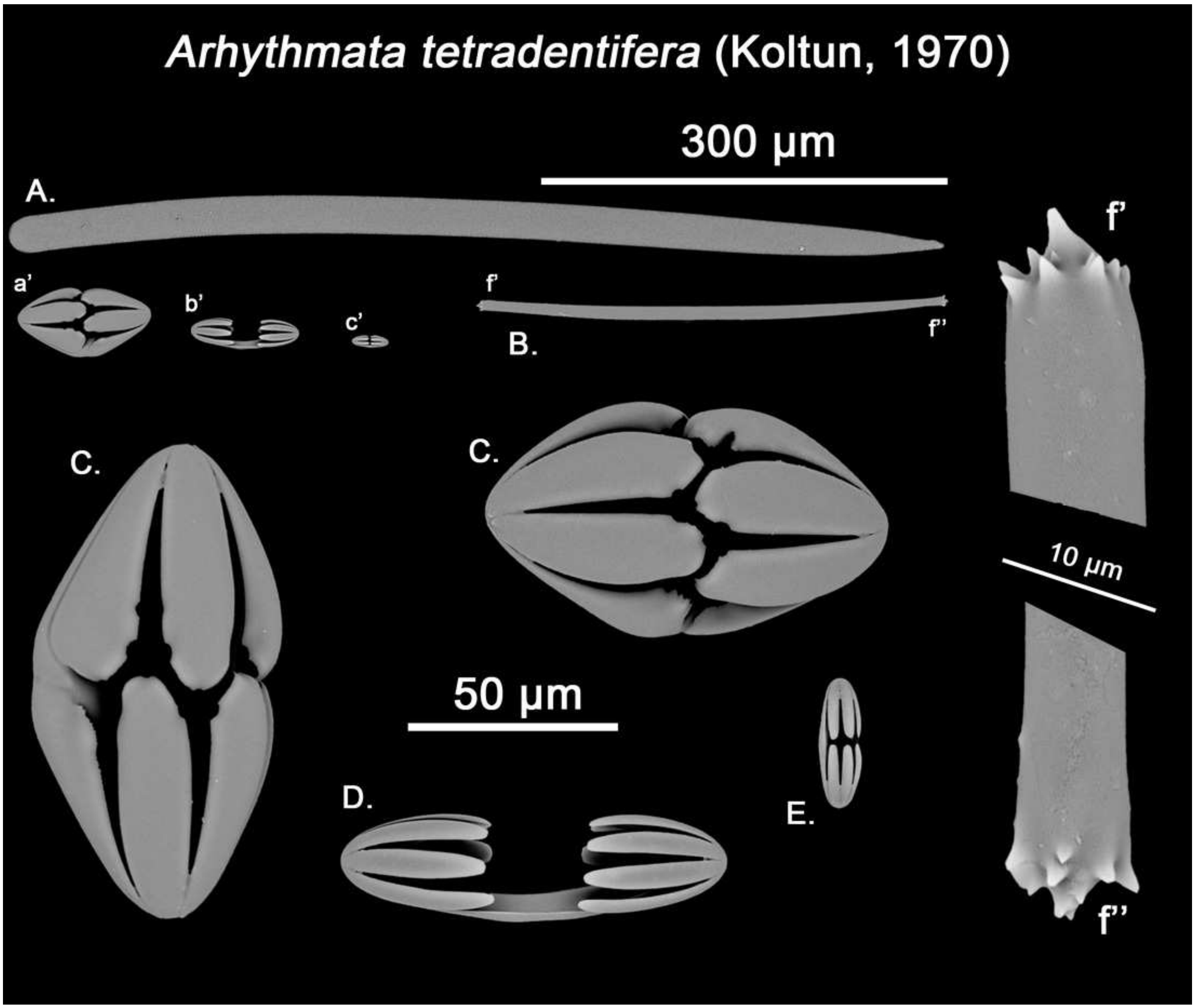

Figure 15

Development stages of spherancorae

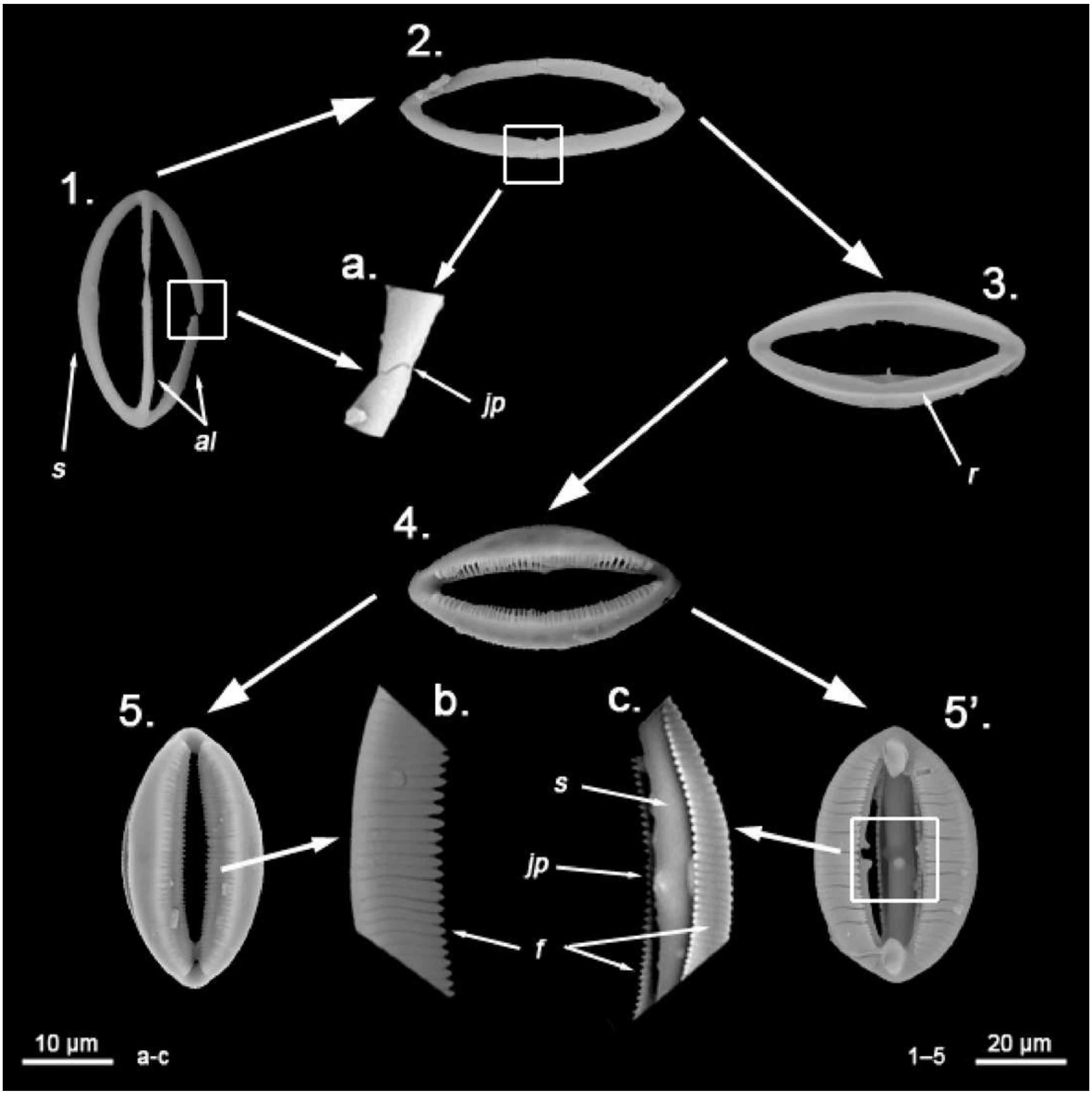

Figure 16

Comparison between spherancorae and other similar chelae derivatives