

New observations on the rare physonect *Melophysa melo* (Siphonophora; Agalmatidae) from the northern Gulf of Mexico

GILL MAPSTONE^{1,3} & MARSH YOUNGBLUTH²

¹The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

²Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, FL 34946, US.

³Corresponding author: E-mail: g.mapstone@nhm.ac.uk

Abstract

The rare short-stemmed physonect *Melophysa melo* typically lives above the thermocline in warm waters of the world's oceans. In the past this species has been described from fragmented or distorted material, with the last two accounts being published in 1931 and 1954. A new description is given herein with pertinent figures based on nine samples recently collected in the Gulf of Mexico (GoM), including the first detailed illustrations of mature nectophores, and of a well-developed corm. The corm comprises a prominent pneumatophore, a narrow nectosome bearing small attachment lamellae for four nectophores and a much larger short, swollen spiral siphosome bearing eight cormidia. The last five cormidia of this corm are still attached to the pneumatophore, while the oldest three are free, with cormidium one being the oldest and eight the youngest. Two rings of bracteal muscular lamellae occur on the siphosome of this corm, one on the upper surface of each cormidium and a second on the lower surface. Laterally each cormidium supports an upper gonodendron, a zooid meridian bearing palpons and a lower gonodendron. Cormidium one has the most mature gonodendra, and all cormidia have palpons on the zooid meridian, which become progressively mature towards the base. Differences in corm structure from previously described corms are attributed to the younger age of the present two corms. Bracts are re-described from photographic images of both young and mature bracts.

Key words: *Melophysa*, Gulf of Mexico, short-stemmed, siphonophore

Introduction

Mostly a rare species and limited to tropical latitudes, *Melophysa melo* is a short-stemmed physonect of the family Agalmatidae (WoRMS database). This species has typical agalmatid tricornuate tentilla, similar to those of long-stemmed agalmatids and the better known short-stemmed species *Athorybia rosacea*. In the latter species, the nectosome has been lost (Dunn *et al.* 2015), but in *Melophysa* this structure is present, albeit much reduced. The few nectophores that develop in *Melophysa* arise from the dorsal side of the nectosomal stem (Pugh 2006), and typically only a single nectophore is likely to be functional (Grossmann *et al.* 2015). Intact specimens are rarely, if ever collected, and there is currently no photographic image of a living colony of *Melophysa melo*.

The body form of *Melophysa melo* appears to be intermediate between that of *Physophora hydrostatica*, with a fully developed nectosome and reduced corm-like siphosome, and *Athorybia rosacea*, which has only a corm-like siphosome. All three species have a pneumatophore. In *Melophysa* the nectophores arise from the dorsal meridian. In *Physophora* the nectophores protrude from the ventral meridian of the nectosome and its tentilla are distinctive. These two characters place *P. hydrostatica* in the family Physophoridae whilst *Athorybia* and *Melophysa* are members of the Agalmatidae *sensu stricto* (see Mapstone 2014). Bracts on the siphosome of *Melophysa* are heavy and ribbed, whilst in *Athorybia* they are delicate and striated (Totton 1954).

In *Melophysa melo*, as in *Athorybia rosacea*, most tentilla are 'tricornuate' and 'involucrate' with two distal terminal filaments flanking a central ampulla at the distal end of the cnidoband; when mature, the cnidoband becomes relatively elongate, coiled, and eventually should become completely covered by a transparent sheath termed the involucrum. However, these details are unknown for *Melophysa*, and in *Athorybia* a second type of tentillum forms,

which is known as ‘dendritic’. The tricornuate involucrate type of tentillum is diagnostic for the family Agalmatidae (see Mapstone 2014 Fig.13A–C), and, according to a recently published maximum likelihood phylogram for 1,423 sequenced genes (Munro *et al.* 2018), *Athorybia* falls within Clade A of a new clade Euphysonectae, in the physonect family Agalmatidae (together with *Halistemma rubrum* and *Nanomia bijuga*) and is sister to the long-stemmed species *Agalma elegans* (see Munro *et al.* 2018, fig.3A). Characters of this clade include the presence of an involucrum on the tentilla, a descending mantle canal in the nectophores (when present) and monoecious sexual reproduction. *Melophysa* has yet to be sequenced and has been assigned to the Agalmatidae based on shared morphological characters, as noted above (Dunn *et al.* 2005, Pugh 2006, Munro *et al.* 2018).

Material and methods

All collections were conducted with a 10-m² Multiple Opening Closing Net and Environmental Sensing System (MOCNESS) fitted with 6 nets of circular 3 mm mesh. Consecutive oblique tows passed through five nominal depth intervals (ca. 200–400 m ranging from 15 to 75 min duration, sampling 10,000 to 50,000 m³ per interval) from 1500 m to the surface during day (1300–2000 h) and night (2200–0500 h) periods (net 0 from the surface to 1500 m, net 1 from 1500–1200m, net 2 from 1200–1000 m, net 3 from 1000–600 m, net 4 from 600–200 m, and net 5 from 200 m to the surface).

Samples were initially examined under a Zeiss ZD1302 binocular microscope and then imaged using a Leica MZ16 Stereomicroscope. NHM registration numbers for deposited samples are: 2019.20 to 2019.28. Images in Figures 1–3 and 6–9 were adjusted for brightness and contrast; blemishes in Figures 1–2 removed with Spot Healing Brush Tool and Clone Stamp Tool; larger labels were superimposed over the original labels in Fig. 11 for clarity.

Results

Nine samples of *Melophysa melo* were collected from 1482 trawls during the period of sampling, and are listed in Table 1. Four samples which contained bracts that were not retained are listed in Table 2. Trawls were conducted in the area located around the Deepwater Horizon oil spill, samples identified in the National Oceanic and Atmospheric Administration (NOAA) National Resource Damage Assessment (NRDA) samples from April to June 2011 and Deep Pelagic Nekton Dynamics Consortium (DEEPEND) Cruises in May and August 2015 and 2016, April–May 2017 and July–August 2018.

Table 1 indicates that samples 5, 6 and 9 were collected in nets towed in the mesopelagic and bathypelagic realms, respectively. However, these MOCNESS samples contained epipelagic and mesopelagic gelata and fishes (T. Sutton, pers.comm.). This contamination with shallower living species, as discussed by Angel (2012), suggests that the *M. melo* zooids, especially in sample 6, probably leaked in whilst the nets were passing through the epipelagic zone.

Colonies: Bigelow (1931), reiterated by Totton (1965), concluded from his *Arcturus* specimens (and estimates by previous authors) that each corm could bear from 27 to 36 or more bracts. If this is the case, then the nine samples described here could each represent one colony, or more, especially if the colonies were immature. However, this estimate is tentative since some bracts and/or nectophores are likely to have been lost during sampling. Similarly, determinations from preserved material as to whether the nectophores listed in Table 1 were mature or still developing were impossible, since in many siphonophores, maturity can vary with food availability.

Pneumatophore: *Melophysa melo* colony fragments identified from Sample 6 included a single pneumatophore with attached swollen siphosome and from Sample 7 included a smaller pneumatophore with attached siphosome. These two structures comprise the ‘corm’ as defined by Mapstone & Ljubenkov (2013) in rhodaliids, although in *Melophysa* very few nectophores form, and are not arrayed in a corona. The length of the pneumatophore in the larger corm was 5.5 mm, in the smaller corm 5 mm. The pneumatophore is described below in the subsection ‘corm’.

Nectophores: 37 nectophores were identified in seven of the nine samples studied (Table 1); they ranged in maximum length from ca. 10 mm to 18 mm. The former length is corrected for distortion of a ‘basal process’, which projects from the proximal end of the nectosac and is reflexed underneath in several of the smaller preserved nectophores (Samples 2 and 7). In all studied nectophores this basal process was more turgid than the main nectophore

TABLE 1. Summary of collection data for *Melophysa melo* zooids retained, identified and imaged. DP=DEEPEND cruises, MS=Meg Skansi NRDA cruises, N=Night, D=Day

Sample ID

Sample ID	Coordinates [N/W]	Towing times	Depth interval [m]	Volume filtered [m ³]
DP02-16Aug15-B080N-026-Net4	28.54901/87.0295	0158–0223	209–100	21370
DP03-01May16-B082D-036-Net3	28.0037/88.0062	1648–1703	249–150	13305
DP03-06May16-B079D-044-Net5	27.4912/86.9618	1544–1625	201–10	32390
DP03-10May16-B252D-052-Net5	28.5053/87.5220	1534–1607	198–11	25370
MS8-29Jul11-SW7D-154-Net4	27.0005/90.3296	1511–1628	600–201	57337
MS6-13Mar11-B254D-Y6-Net2	27.9641/86.44632	1227–1303	1200–1001	22725
DP05-02May17-B082N-0-Net5	26.0098/88.029	0250–0316	220–0	25043
MS6-20Feb11-B022-SW6N-Net5	26.1298/89.1564	0256–0338	202–0	31467
MS6-20Mar11-B0320-B079N-Net4	27.8234/87.1852	0130–0246	600–200	55623

TABLE 1. (Continued)

Sample ID

Sample ID	Temperature [°C]	Salinity [PSU]	Sample No.	NHM Reg. No.	Corm	Nectophores	Bracts
DP02-16Aug15-B080N-026-Net4	15–19.6	35.93–36.48	1	2019.20	-	3	16
DP03-01May16-B082D-036-Net3	11.5–15.9	35.26–36.13	2	2019.21	-	7	24
DP03-06May16-B079D-044-Net5	13.7–24.6	35.7–36.5	3	2019.22	-	7	20
DP03-10May16-B252D-052-Net5	12.8–24.7	35.6–36.5	4	2019.23	-	4	23
MS8-29Jul11-SW7D-154-Net4	9.9–21.1	-	5	2019.24	-	-	19
MS6-13Mar11-B254D-Y6-Net2	4.4–4.8	34.18–34.91	6	2019.25	1	8	32
DP05-02May17-B082N-0-Net5	16.3–24.9	36.13–36.49	7	2019.26	1	7	22
MS6-20Feb11-B022-SW6N-Net5	14.8–19.6	-	8	2019.27	-	-	7
MS6-20Mar11-B0320-B079N-Net4	7.3–16.7	-	9	2019.28	-	2	12

body, resulting in deformation of the delicate nectosac at preservation with either lateral or upper-lower compression, almost occluding the cavity within in some nectophores, and typically deforming the ostium. Representative nectophores (Fig. 1) all seem mature. The angle at which the basal process projects from the nectophore body is either orthogonal, giving the nectophore an inverted L-shape in lateral view (Fig. 1E), or obtuse, giving the nectophore a flatter appearance in lateral view (Fig. 1F). The ostium is typically directed towards the lower surface, and in many nectophores has an inverted triangular shape (Fig. 1C, G), but in a few is less distorted and broader across the right-left axis (Fig. 1D). The widest part of the nectophore is the ‘girdle’, which circumscribes the nectophore (Figs. 1A, E, G, H). This structure is discontinuous in the upper mid-line (Figs. 1A, H), and is interrupted by the ostium distally, terminating close to the lateral borders of the latter on each side (Fig. 1G). The girdle delimits a distal nectophore surface including the ostium, and typically three longitudinal ridges, which pass from the upper side of the ostium, over onto the upper distal facet of the nectophore and terminate close to the girdle on the upper (or distal) side, depending on nectophore shape. These ridges, labelled ‘a’, ‘b’ and ‘c’ (Figs. G, H), are more developed in some nectophores, and are separated by two longitudinal furrows. In elongate nectophores (Fig. 1F), the three ridges are discernible in both upper and lower views (Figs. 1A, C, G, H), but in orthogonal nectophores (lateral view, Fig. 1E), they are not visible in upper view. Two more ridges are identifiable in the orthogonal nectophore, which is shown in Fig. 1E; each ridge passes from the upper-lateral region of the girdle to the end of the basal process, delimiting the proximal surface with the two mantle canals (‘amc’ and ‘dmc’) in the mid-line. Only the ridge nearest to the viewer appears in Fig. 1E, labelled ‘x’. Equivalent longitudinal ridges were not identified in any other nectophores, perhaps due to their fragility (Fig. 1F).

TABLE 2. Samples containing identified *Melophysa melo* bracts which were not retained. Abbreviations as for Table 1.
Sample ID

	Coordinates [N/W]	Towing times	Depth interval [m]	Volume filtered [m ³]	Temperature [°C]	Salinity [PSU]
DP01-03May15-B252N-006-N5	28.66/87.55	1509–0551	198–0	4007	15.3–25.1	27.41–36.54
DP03-04May16-B003N-042-N5	27.891/86.8787	0249–0349	193–10	52576	11.8–24.8	35.43–36.39
DP03-06May16-B079N-045-N5	27.4613/86.8992	0222–0253	198–19	27568	14.6–25.1	35.85–36.55
DP03-12May16-B081D-054-N4	28.505/88.0134	1517–1558	593–203	35553	7.2–14.5	34.87–35.85

The nectophore attaches to the nectosome via a muscular lamella in all codonophorans, and this lamella inserts onto the nectophore along the line of the ascending and descending mantle canals (‘amc’ and ‘dmc’, see Figs. 1E, F, H). An external pedicular canal passes from the stem canal to the nectophore, and onto the internal pedicular canal (‘pi’) on the proximal surface of the basal process (Figs. 1E, F, H). The internal pedicular canal is long and prominent in *Melophysa melo*, and inserts onto the four radial canals at the proximal end of the nectosac (Figs. 1A, B, C, E, F, H). These radial canals continue to the ostial ring canal as a sinuous upper radial canal, two looped lateral radial canals and a straight lower radial canal (see ‘urc’, ‘lrc’, ‘loc’ in Figs. 1E, F, G, H, and unlabelled in Figs. 1A, B, C).

A pronounced velum borders the ostium in all nectophores examined, and from the upper and lateral ostial borders a thick sheet of surface mesogloea arises and bulges out distally beyond the ostium in lateral view (Figs. 1E, F). An ostial ‘chromatophore’ (no pigment remaining in present material) arises just distal of the ostial ring canal on each side of the ostium, and from each a narrow and deep furrow extends out at 45° (Figs. 1D, G). The mesogloal sheet is typically characterized by three low ridges and two furrows above the ostium in mature nectophores, as described above, and these furrows may or may not extend as far as the transverse girdle on the distal/upper surface. On the lower nectophore surface the two lateral mesogloal sheets merge to form a thick sheet on the underside of the nectophore that continues proximally to the angle in the lower nectophore surface (Figs. 1E, H), beyond which the sheet merges with the lower side of the basal process (Figs. 1E, F).

Bracts: 173 bracts were collected during the nine cruises and ranged in length from 8.5 to 33 mm. The large bracts of Sample 6 suggest that colonies in this collection were the most mature. A few large bracts were also

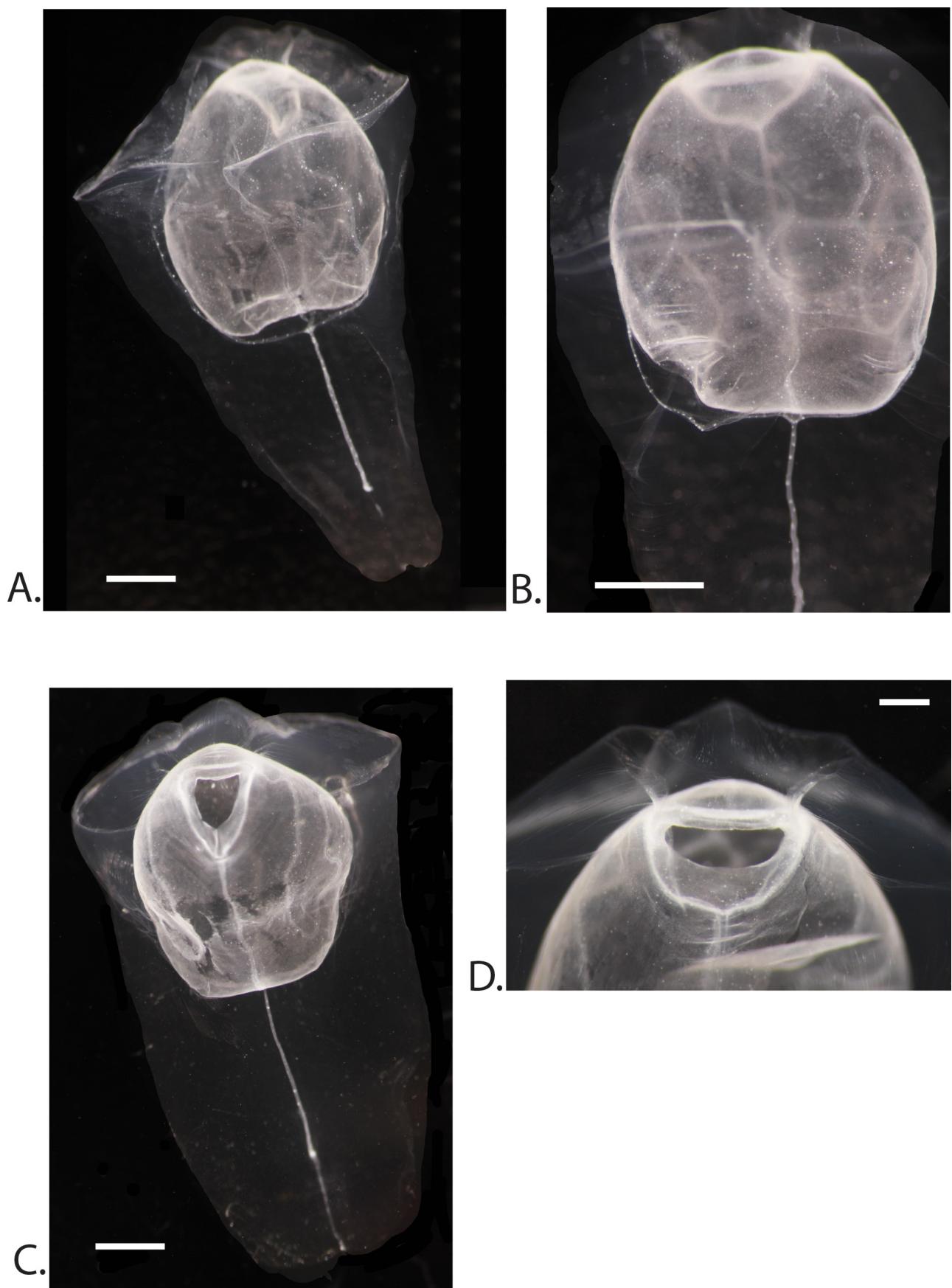


FIGURE 1 A–D. *Melophysa melo*. Images of mature nectophores from Sample 6. A, B: Upper views of two mature nectophores showing girdle and sinuous upper radial canal; C: lower view of a mature nectophore; D: detail of ostium. Scale bars A–C represent 2mm; D represents 1mm.

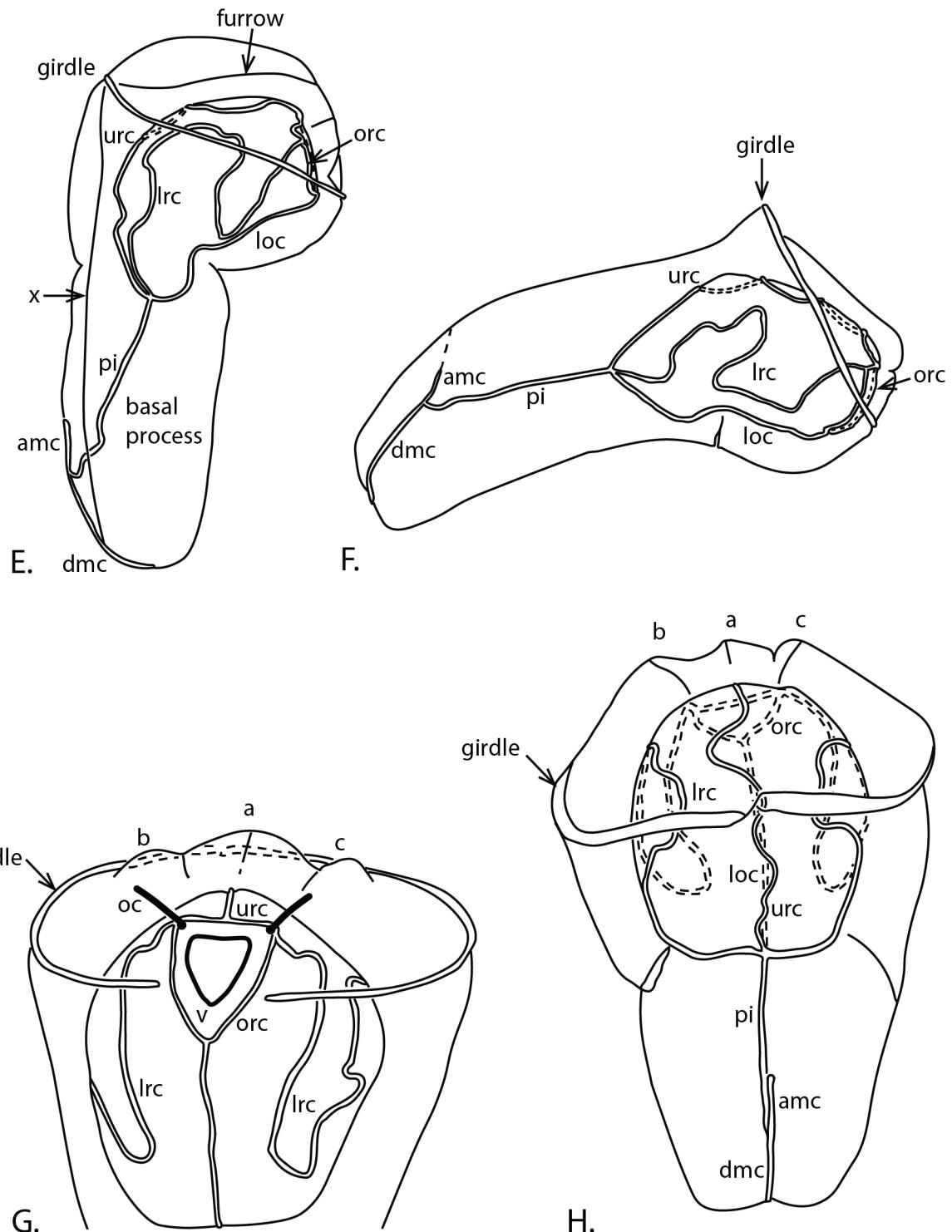


FIGURE 1 E–H. *Melophysa melo*. Figures of mature nectophores from Sample 6. E: Lateral drawing of orthogonal nectophore (Sample 6 Nectophore 7); F: Composite lateral drawing of obtuse nectophore (Sample 6 Nectophore 6 and Sample 6 Nectophore 4); G: Drawing of ostial view to complement Fig. 1D (from Sample 6 Nectophore 7); H: Drawing of a mature nectophore in upper view (Sample 6, Nectophore 4). Abbreviations: amc—ascending mantle canal; dmc—descending mantle canal; loc—lower radial canal; lrc—lateral radial canal; oc—presumed ostial chromatophore; orc—ostial ring canal; pi—internal pedicular canal; urc—upper radial canal; v—velum.

present in Sample 3 (Fig. 2F). Small and immature bracts are identifiable by a thick and particularly opaque bracteal canal and, generally, small size (Fig. 2A). The bracteal canal diminishes in diameter with bract enlargement (Fig. 2B) and becomes very thin in mature bracts (Fig. 2C, D, F). A diverticulum may develop halfway (or further) along the length of the bracteal canal (Fig. 2C); bract attachment is via a broader gutter on the base of the keel known as the bracteal canal scar (Fig. 2D). The keel is delimited somewhat from the bract body by a ‘collar’ or ‘groove’ (Fig. 2F).

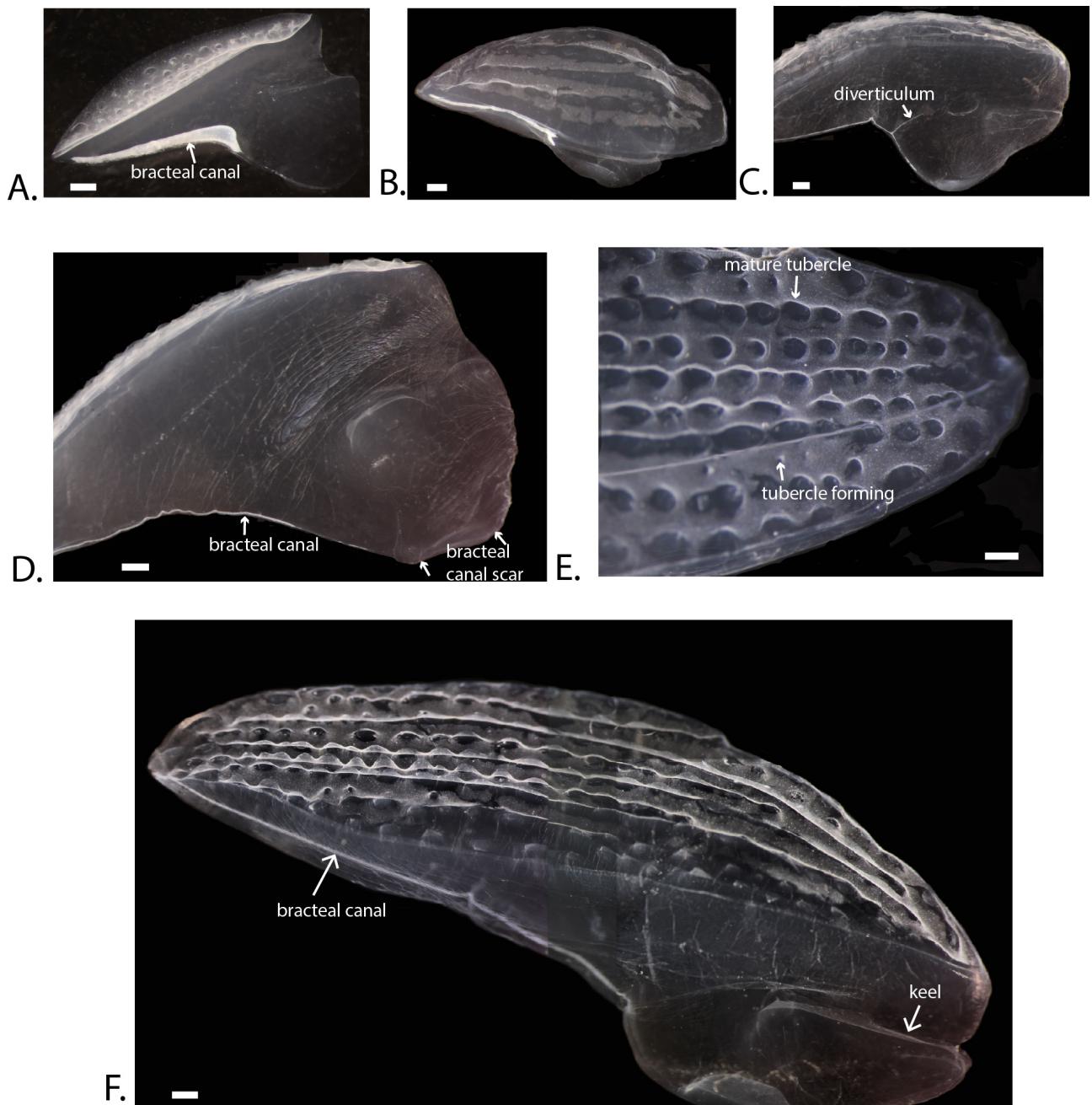


FIGURE 2. Images of immature and mature bracts from a range of *Melophysa melo* colonies (Samples 2–4). A: Immature bract; B: Slightly older bract; C: part of a bract showing diverticulum from the bracteal canal; D: Bract displaying bracteal canal scar along lower side of keel; E: Upper surface of a mature bract showing newly forming tubercles; F: Montage of a mature bract, lateral view. Scale bars all 1 mm.

The upper surface of all bracts bears rows of tubercles separated by strips of epidermis, which were not abraded during collection. The smallest number of tubercle rows is found in immature bracts, with a minimum of 6 (Fig. 2A, B). A thin, opaque line of epidermis delimits the upper surface, which is typically rounded proximally and pointed distally (Fig. 2B, F). The upper surface in some less turgid and relatively small bracts (from Samples 1, 2, 4 and 5)

is broader and more rounded than in turgid bracts, with the rows of tubercles clearly separated by strips of intact epidermis (Fig. 2B). Larger bracts usually bear 8–9 rows of tubercles at mid-length (Fig. 2E), with fewer at both ends, and, at the proximal end, an outer lateral row of tubercles may continue around to form an equivalent lateral row on the other side of the upper surface (Fig. 2F). At the distal end of larger bracts, rows of large tubercles are interspersed with newly forming small tubercles (Fig. 2E).

Corm: Only two recognizable corms were identified in the GoM collection, in Samples 6 and 7, as noted above (Table 1). The larger corm (6) will be described in detail first as it is more developed than the smaller corm (7), comprising a pneumatophore firmly attached to the siphosomal corm, which had a maximum diameter of 12 mm (Fig. 3). The collection of just two corms suggests that zooid attachment is fragile, and must frequently result in loss of the corm and more delicate zooids (such as gastrozooids) during net collection, retaining only the large and robust bracts. In the larger corm, the pneumatophore is relatively enlarged and short, 5.5 mm length, with a much contracted nectosome hidden beneath; four small nectosomal buds are identifiable on the nectosome, together with small nectophoral muscular lamellae, which are occluded by the large pneumatophore (in Fig. 3).

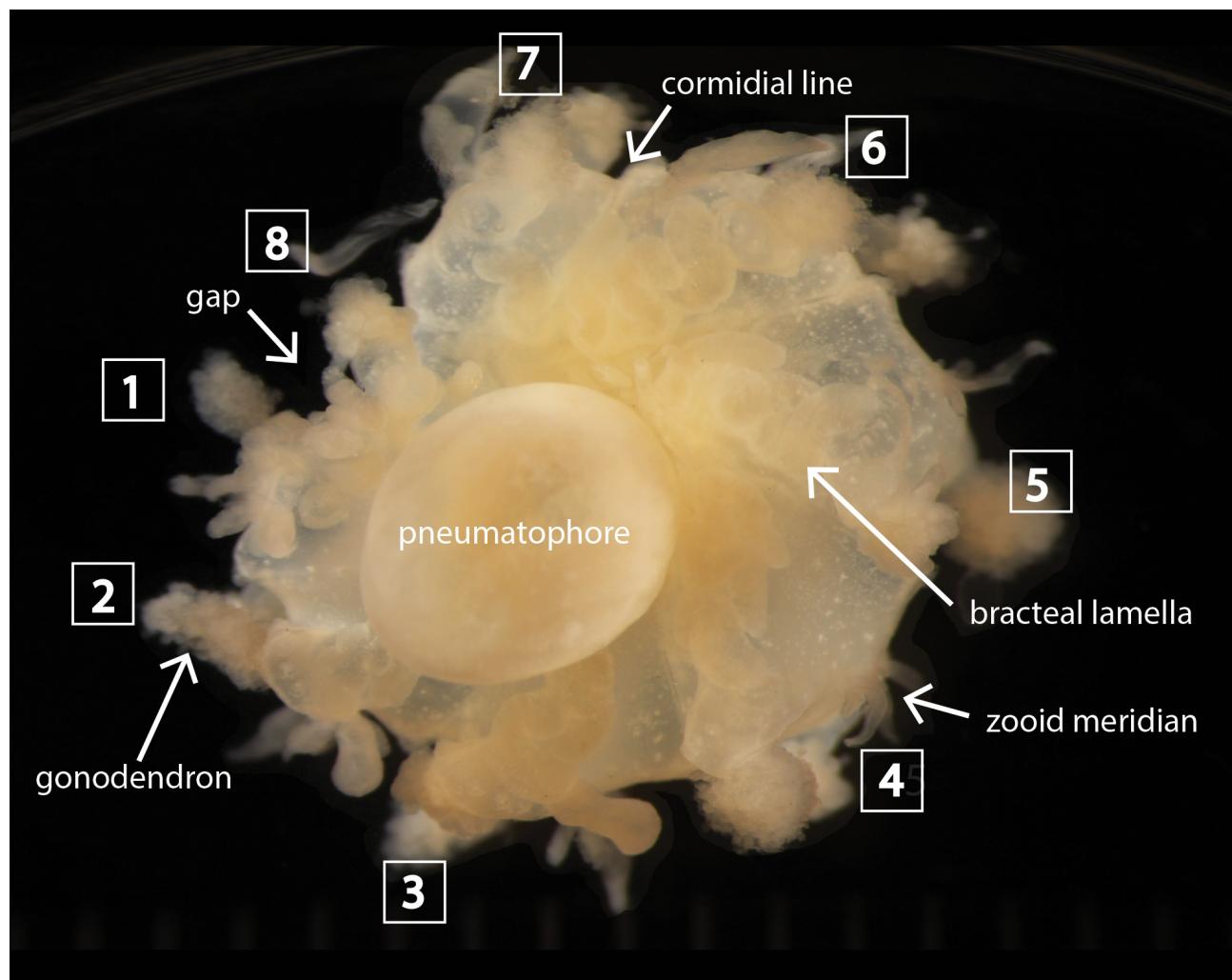


FIGURE 3. *Melophysa melo* pneumatophore and siphosomal corm from above (Sample 6) showing sequential cormidia and zooid characters. Note corm divided into 8 cormidia (delineated by white lines) each displaying a bracteal lamella, gonodendron and zooid meridian in this view. Maximum diameter of corm 12mm. Image adjusted for brightness and contrast.

The siphosome is swollen and forms a short, inflated spiral beneath the pneumatophore/nectosome. The siphosome is subdivided into ca. 8 segments by obvious divisions on the surface (Fig. 3, ‘cormidal lines’); these delimiting lines are more prominent on the lateral and lower surfaces of the corm (Figs. 6–7), and extend from the upper corm surface around to the lower corm surface, often at a slightly oblique angle. Each cormidium comprises a bracteal lamella on the upper side of the corm, an upper gonodendron at the upper distal end of this lamella, a zooid meridian, which extends down the lateral surface of the corm to a lower gonodendron, and a second bracteal

muscular lamella, extending from the lower gonodendron on the lower surface to the inner face of the corm. This arrangement is shown diagrammatically in Fig. 4, for cormidia 4–8, where the inner surface of the corm is attached to the pneumatophore/nectosome. Cormidia 1–3 are free on their inner edges, representing the free end of the spiral, and there is some evidence that extra zooids are present in this region. This supposition was not investigated because the corm would have had to be dissected.

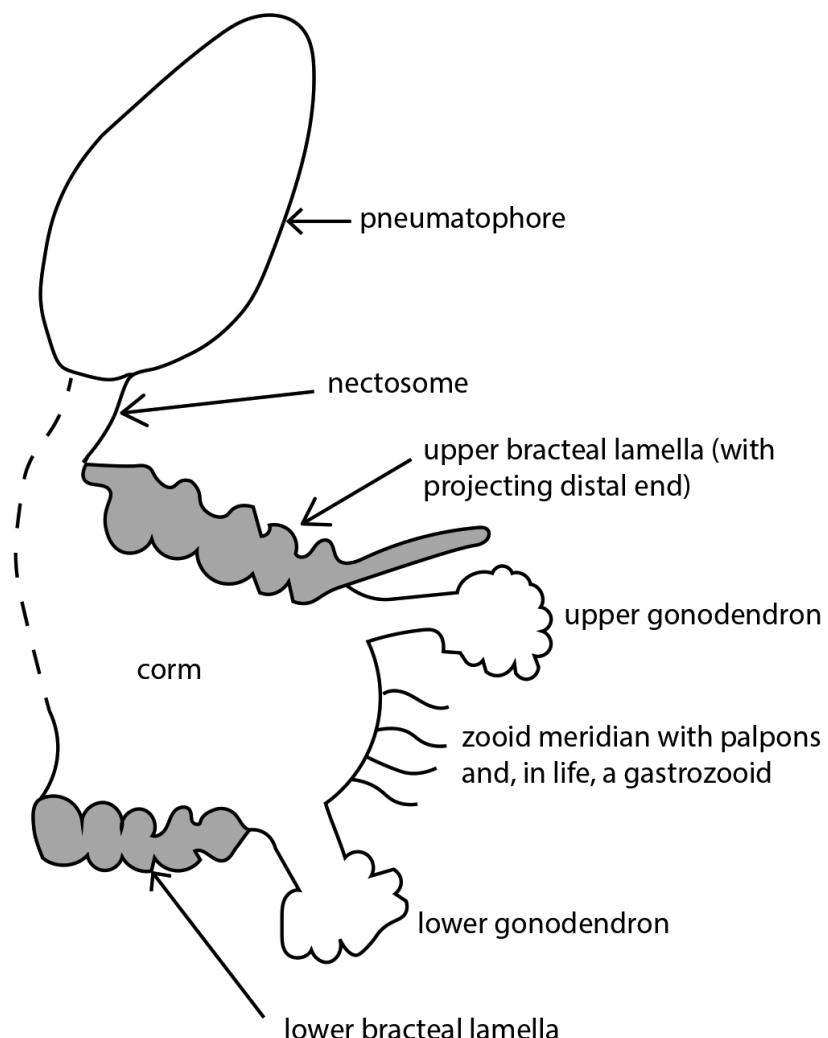


FIGURE 4. *Melophysa melo* diagrammatic longitudinal section through the Sample 6 corm, showing arrangement of structures within a typical cormidium.

All cormidia have an upper bracteal lamella, except cormidium 8, and a lower bracteal lamella, except cormidium 1. The latter could be missing either because it never developed or because the protozooid was originally attached here and later dropped off. The gonodendra each arise on a thick stalk, and all bear a number of gonophores. These gonophores are insufficiently developed in the present larger corm to determine the sex, even on the largest gonodendra of cormidia 1 and 2. A line of chevrons passes down the stalk of the upper gonodendron, connects to a zooid meridian on the lateral surface, and the lower end of this meridian joins a second line of chevrons on the stalk of the lower gonodendron. These chevrons may represent developing zooid buds, but this possibility seems unlikely because the largest zooids on each meridian were at the lower end. A zooid meridian is clear on every cormidium, and often projects outward beyond the other zooids, bearing palpons, with a deep furrow adjacent, above the white cormidial line. This line is particularly prominent between cormidia 3 and 4 in Fig. 5, but the line between cormidia 4 and 5 is only apparent in Fig. 6, because in Figs 5 and 7 it is occluded by the gonodendra. Unfortunately, no gastrozooids remained on the zooid meridian in any cormidium, although a single large detached gastrozooid was identified, assumed to be from *Melophysa melo* (Fig. 8), and is described below.

The disposition of all structures described on the larger GoM corm is shown in detail in Figs. 5 to 7, from three different views. The spiral nature of the siphosomal corm is illustrated in lateral and lower views (Figs 6–7).

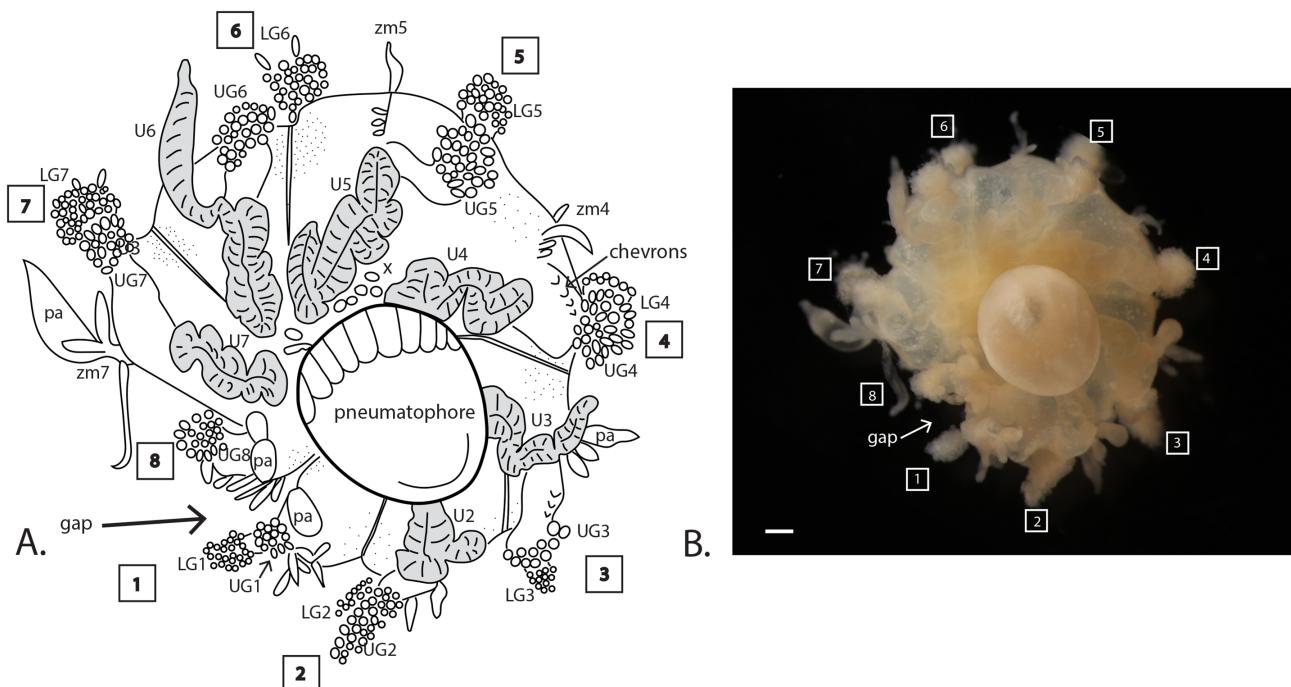


FIGURE 5. Gulf of Mexico *Melophysa melo* corm, from above (upper view) (Sample 6, Table 1). A: drawing; B: image, scale bar 1 mm. Abbreviations: LG—lower gonodendron; pa—palpon; U—upper bracteal lamella (shaded in grey); UG—upper gonodendron; x—nectosomal zooids; zm—zooid meridian.

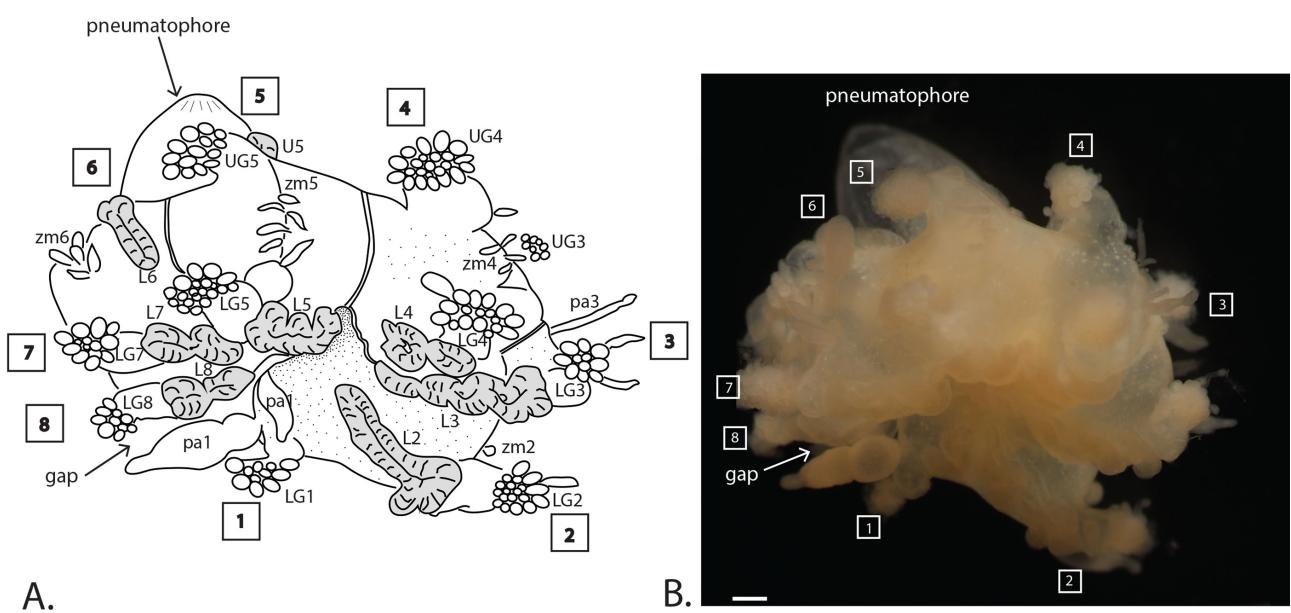


FIGURE 6. Gulf of Mexico *Melophysa melo* corm, lateral view (Sample 6, Table 1). A: drawing; B: image, scale bar 1 mm. Abbreviations: L—lower bracteal lamella (shaded in grey); LG—lower gonodendron; pa—palpon; U—upper bracteal lamella (one small part of one showing); UG—upper gonodendron; zm—zooid meridian.

The smaller corm has a smaller pneumatophore, as already noted, which still bears a number of thin red lines extending over the upper half to the apex (Fig. 8C), and below a ring of ca. 12 white septa (Figs 8A, B). The reduced nectosome bears a line of small nectophore buds, although only 7 nectophores were found in Sample 7. Maximum dimensions of the corm below the pneumatophore are 5 mm length by width. Below the nectosome are the proximal

ends of ca. 6 quite prominent bracteal lamellae, on each side of the flattened siphosome (Figs 8A, B). At the distal end of each bracteal lamella is a gonodendron (Figs 8A, B, 'GD'). A number of palpons are also present, with two particularly long ones arising from near the proximal ends of two of the bracteal lamellae. A number of smaller palpons arise distally, between the gonodendra, with a single zooid meridian identified on the 'left' side of the flattened siphosome in the Sample 7 corm (Fig. 8A). A gastrozoooid arises from the distal end of the siphosome, with a developing tentacle on the 'right' side, and a prominent palpon nearby (Fig. 8B). It seems likely that this small corm has six cormidia, though only a single white line delimiting one cormidium from the next was discernible, on the right side of the corm, adjacent to 'X' a region of bare siphosome (Fig. 8B). By comparing the two GoM corms, it is concluded that as growth proceeds in *Melophysa melo*, the diameter of the siphosome increases and it becomes more spiralled, with the 'dorsal' surface forming the inside of the spiral, and the 'ventral' surface becoming the lateral surface of the corm, delimited by both an upper and a lower gonodendron (Fig. 4).

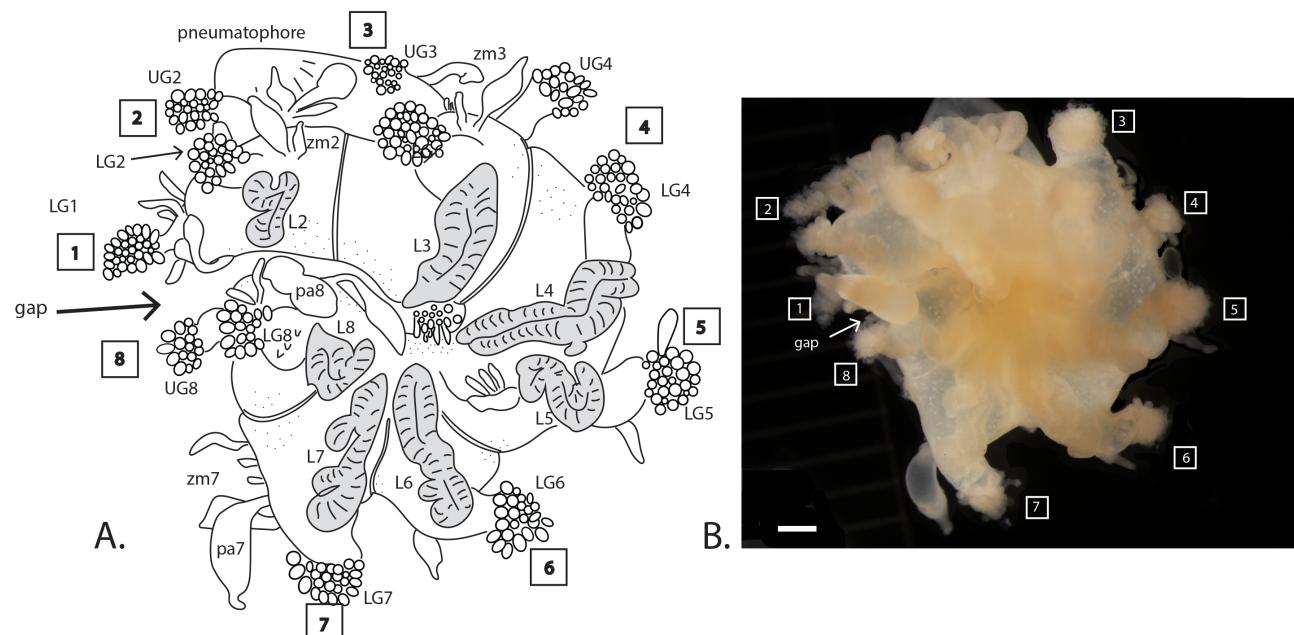


FIGURE 7. Gulf of Mexico *Melophysa melo* corm, lower view (Sample 6, Table 1). A: drawing; B: image, scale bar 1 mm. Abbreviations, as for Figs 5 and 6.

Gastrozooids, palpons and gonodendra: The single gastrozoooid identified from the larger *Melophysa melo* corm (Fig. 9A) is loose, 8 mm long, with a mouth at the distal end, and a basigaster proximally, where new tentilla are being formed on a tentacle. A much smaller and still attached gastrozoooid present on corm 7 was 2.5 mm long, with the tentacle just starting to form (Fig. 8A–C). A large palpon still attached to corm 6 is shown in Fig. 9B, with the proximal region delimited from the remainder of the palpon by a constriction. However, this proximal region is not a site of nematocyst production, and other large palpons on the corm lacked this constriction. All palpons had a ring of nematocysts around the mouth. Palpons on corm 7 were smaller and displayed no specific regions.

Two gonodendra were identified in all 8 cormidia of corm 6, an upper and a lower one, as described above. 12 gonodendra were identified in the smaller corm 7. Gonophores were immature in all gonodendra (as in *Erenna*, see Pugh 2001), so sex could not be determined.

Historical Summary and Synonymy. The colony was first described by Quoy and Gaimard (1827) from a specimen collected at the entrance to the Strait of Gibraltar (North Atlantic), and illustrated in the plate reproduced below.

These authors described the colony as comprising an upstanding red-tipped pneumatophore, greenish below (as in their F.1), in life typically almost sunk down and partially obscured by a corona of thick bracts (as in their F.2). The bracts are heavy, transparent and resemble the ribs of a melon, with six to seven parallel ridges on the outer side and a keel ('bulge') on the inner side for attachment to the corm. The tentacles bear side branches (tentilla) with corkscrew (coiled) cnidobands having trifid tips and elongated suckers (gastrozooids). The ovaries (female gonophores) are pigmented yellow and carmine.

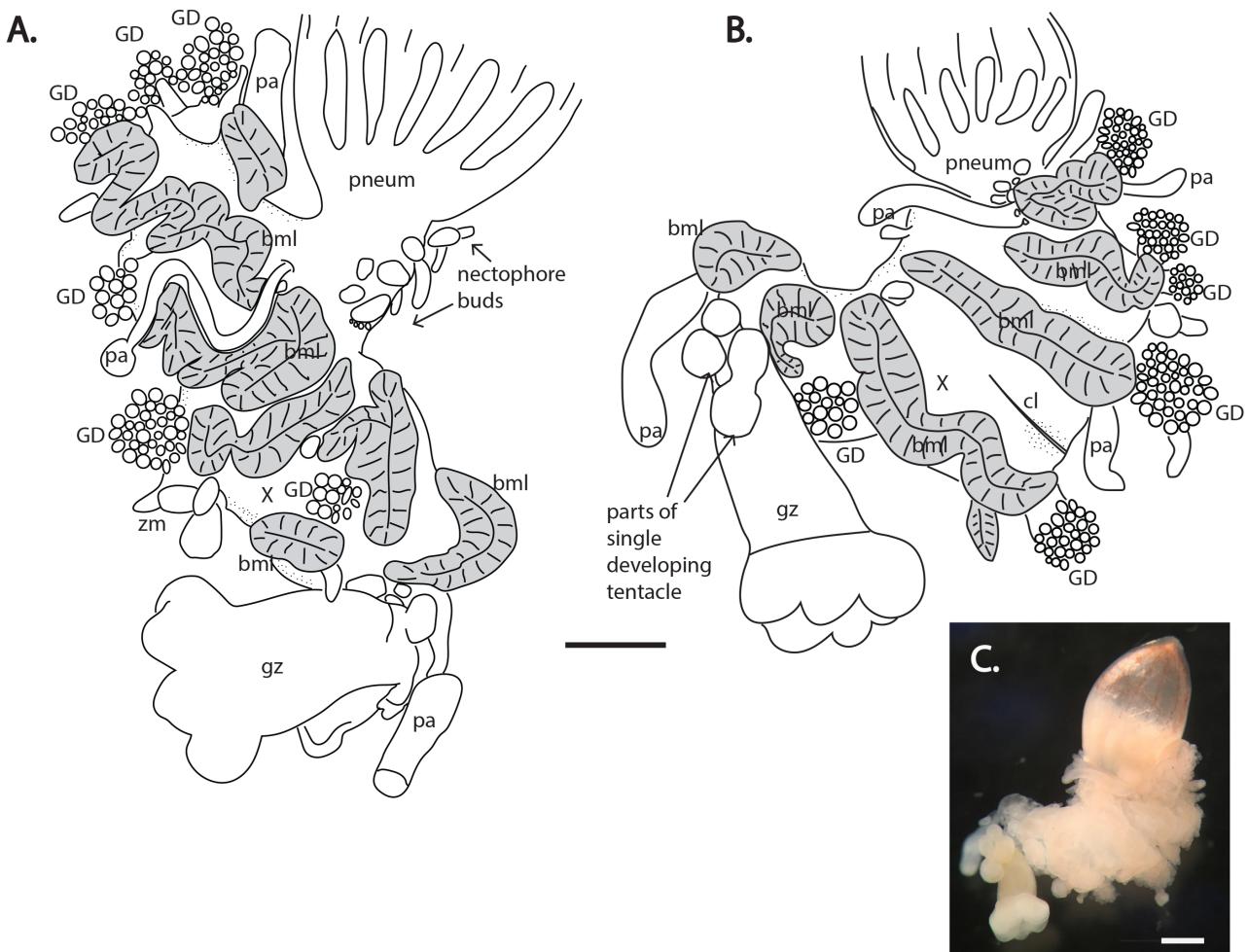


FIGURE 8. Gulf of Mexico *Melophysa melo* immature corm (Sample 7, Table 1). A. ‘Left’ lateral view; B: ‘Right’ lateral view; C: ‘Right’ lateral view image; scale bars—1 mm. Abbreviations: bml—bracteal lamella; cl—cormidial line; GD—gonodendron; gz—gastrozooid; pa—palpon; pneum—base of pneumatophore; X—bare regions of siphosome; zm—zooid meridian..

The first author to identify nectophores of *Melophysa melo* was Chun (1897, Taf. IV, Figs. 1, 3) from a large specimen collected at the surface in the Sargasso Sea during the Humboldt-Stiftung Plankton Expedition of 1887–1888. This colony measured at least 4 cm in diameter with the pneumatophore projecting above the corona of bracts, although the corm was mostly denuded. Selected figures from Chun’s plate (Fig. 11), illustrate two small nectophores attached just below the pneumatophore, and the muscular lamella for a third (in his Fig. 1). This corm bore several bracteal muscular lamellae, male and female gonodendra, and two zooids identified as palpons. However, although Chun found no gastrozooids or tentacles in this particular specimen, he did identify two gastrozooids amongst some young specimens collected earlier from the Canary Islands (Chun 1888). In this paper he noted that the brownish pigmentation of the tentilla occurred in the involucrum, although, apparently, these particular tentilla lacked a distal ampulla. In the text of his 1897 paper, on page 51, Chun notes that in the larger tentilla from his Sargasso *Athorybia melo* (= *Melophysa melo*) specimen, the cnidoband had as many as seven spirals, and was completely covered by the involucrum. The Sargasso Sea bracts were 24 mm long, 9 mm wide with 8 ridges on the outer surface, and a bracteal canal on the inner surface, for connection to the gastrovascular system of the corm (see his Fig. 2 in Fig. 11).

The next author to describe *Melophysa melo* (as *Athorybia rosea*, confusingly), was Bigelow (1931) from seven ‘fragmentary’ corms and 30 loose bracts collected at five stations during the Pacific leg of the Arcturus Expedition Feb–July 1925. Only two of the corms had attached appendages, as illustrated by Bigelow (Figs. 217 and 218), and these appendages had some typical tentilla (see Fig. 12). Bigelow (1931) muddled the synonymy with older synonyms of the modern species *Athorybia rosacea*. His specimens were *Melophysa melo* since both the corms had a very short nectosome as well as a more swollen siphosome. Distinctive, large ribbed bracts were also collected.

One corm had an attached definitive nectophore, but, as Totton (1954, p. 37) indicated, this nectophore must have been twisted through 180° at capture, as so often happens in physonect nectophores, since the pedicular canal should ascend rather than descend the mid-line of the proximal surface of the nectophore. Bigelow (1931 Figs. 219, 220) illustrated two tentilla, with five and seven coiled cnidobands respectively (plus ampulla and two terminal filaments), but their involucra are incomplete and in the larger tentillum had shrunk back to the base, suggesting that perhaps they were not mature.

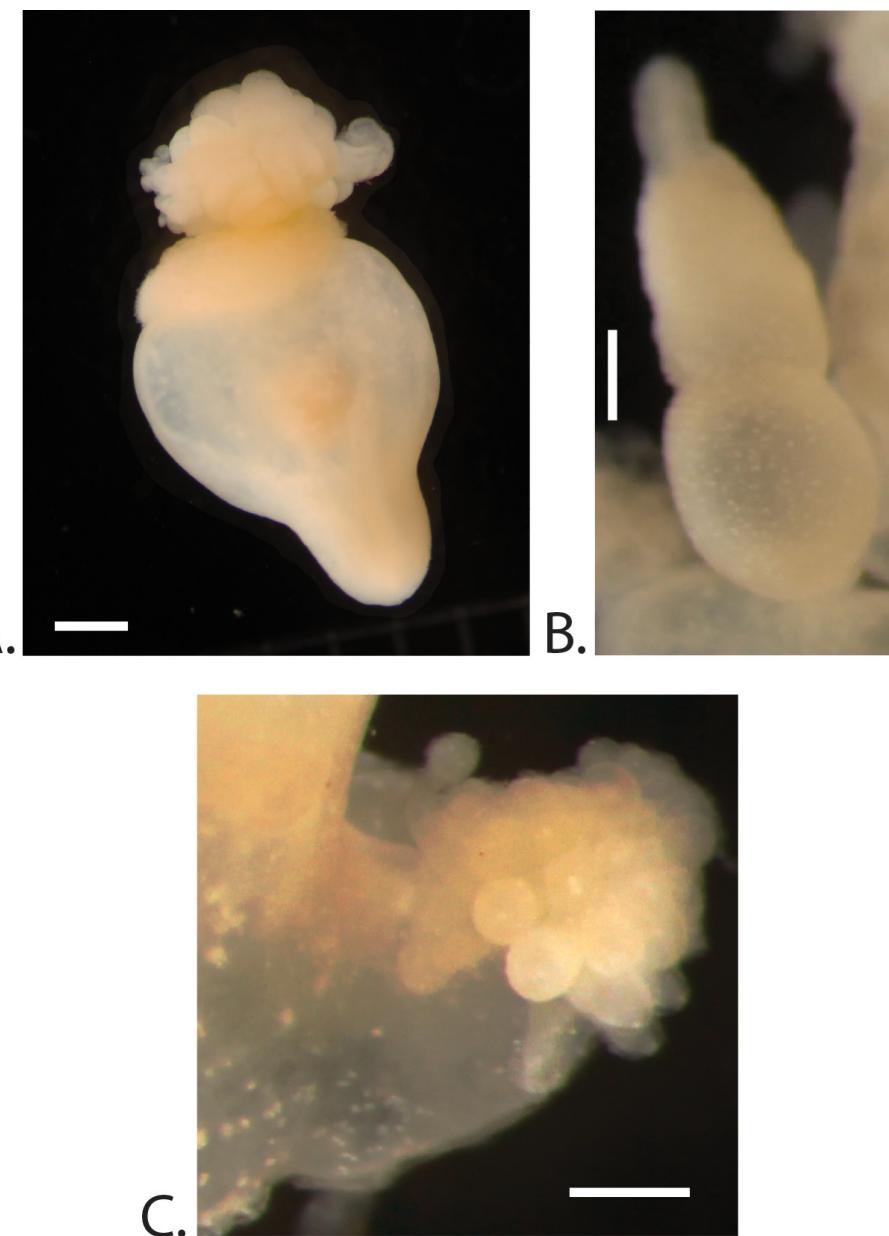


FIGURE 9. *Melophysa melo* siphosomal zooids from corm 6. A: detached gastrozooid, scale bar 1 mm; B: palpon, still on corm, scale bar 0.5 mm; gonodendron, still on corm, scale bar 0.5 mm. Images adjusted for brightness and contrast.

Melophysa melo specimens were collected by Totton (1954) from the Indian Ocean and the tropical Atlantic. Nine specimens were obtained from around Bermuda by Beebe (1929–1934). However, the nectophores illustrated in Totton's text-fig. 7 were drawn from distorted specimens (Pugh 1999, present observations). Totton (1954) illustrated a post-larva from Bermuda in text-figs. 8–9 (not reproduced here) and noted that in this specimen the single smooth larval bract was attached near the tip of the siphosomal horn (as 'nectostyle'), with scars of more bracts further down the horn. He particularly mentioned that the axis of the horn lies orthogonal to that of the pneumatophore in *Melophysa*, whereas in *Athorybia rosacea* the horn overlaps the pneumatophore. Unfortunately, Totton was unable to identify any nectophore buds in this larva, but these buds might be apparent when more *Melophysa* larvae are collected in the future.

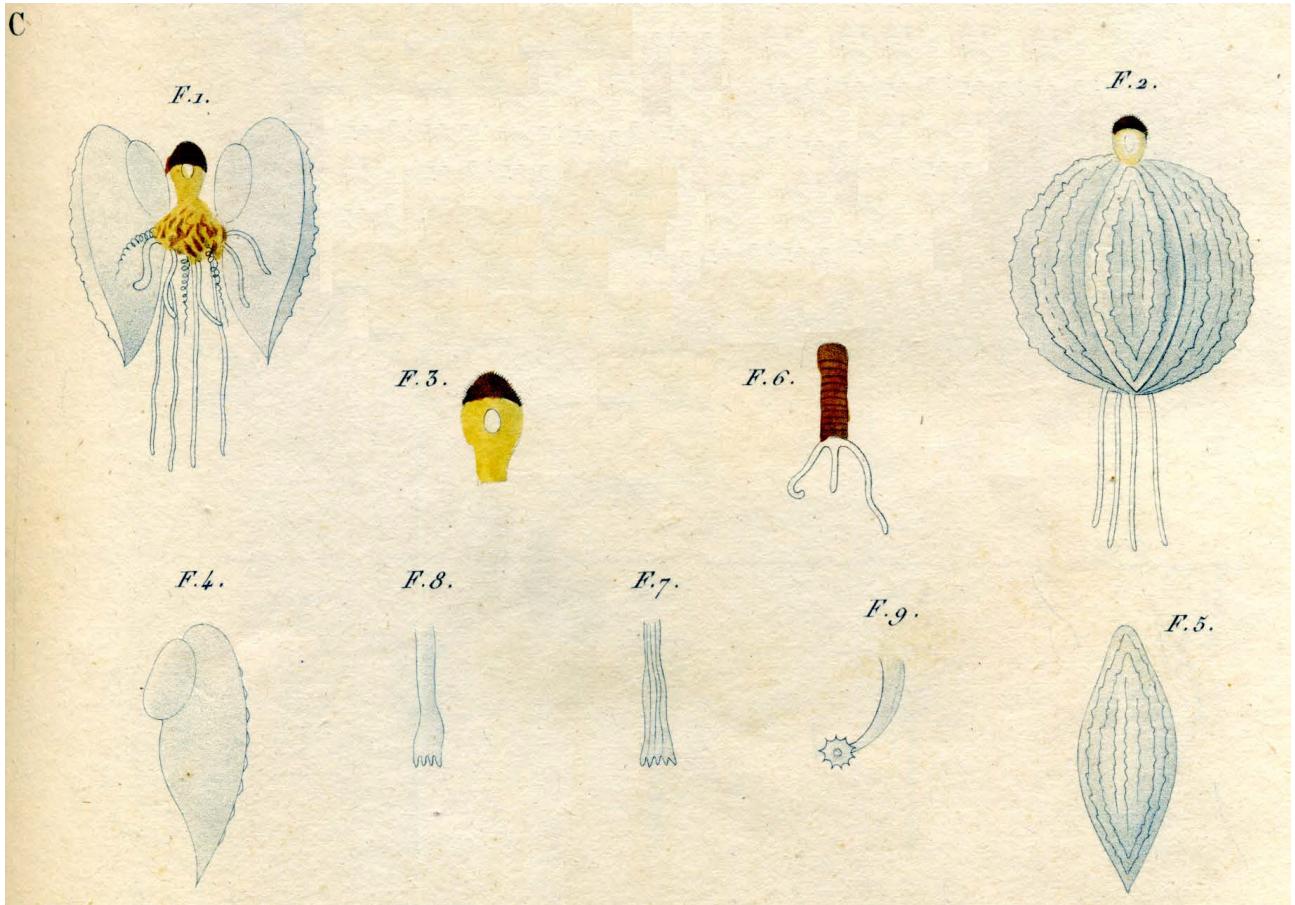


FIGURE 10. Original figures of *Melophysa melo* (as *Rhizophysa melo*) from Quoy & Gaimard (1827, Pl.5C; 5B removed). F.1: Specimen as collected, natural size, with two bracts still attached, exposing pneumatophore, corm (with red pigmented gonodendra) and attached palpons and gastrozoooids with extended tentacles; F.2: reconstructed specimen as it would appear in life (max width c. 3.2cm); F.3: pneumatophore; F.4: bract, lower ('inside') view; F.5: bract, upper ('outside') view; F.6: tentillum with red-coloured cnidoband (of c.11 coils), two lateral terminal filaments and a non-swollen central ampulla; Figs 7–9: three views of different gastrozoooids.

Synonymy:

Rhizophysa melo Quoy & Gaimard, 1827, p.180 text, pl. 5C atlas.

Athorybia melo Eschscholtz, 1829, p.154; Chun, 1888, p.245; Chun, 1897, p. 49–60, pl.4.

Stephanomia melo Quoy & Gaimard, 1833, p.65 text, pl. 2 figs 7–12 atlas.

Melophysa melo Haeckel, 1888a p.42; Haeckel, 1888b, p.274; Totton, 1954, p.40, txt-figs 7–9; 1965 p.89, txt figs 49–50; Daniel, 1974, p.68–70, txt-fig. 5 I–O; Pugh, 1983, p.171; Daniel, 1985, p.107–109, fig. 25a–f; Pugh, 1999, p.484, fig. 3.18; 2006, p.41; Grossmann *et al.* 2015, p.55; Morita *et al.* 2017, p.267.

Anthophysa rosea Bigelow 1931, p.577–584 (excluding parts of p.577, 579, 581 and 582 which describe *Athorybia rosacea*), figs 217–220.

The above list includes all accurate accounts of *Melophysa melo* from 1827 to the present, which include, or summarize, any new information given. *M. melo* was confused so many times with *Athorybia rosacea* in the past (until Totton 1954); these incorrect references are excluded from the above list for clarity, rather than being included as 'non'. Although *M. melo* was distinguished from the short-stemmed species *Athorybia rosacea* when first described by Quoy & Gaimard (1827), these authors placed both species in the genus *Rhizophysa*, later restricted to long-stemmed species in the sub-order Cystonectae only (Haeckel 1887). Huxley (1859) introduced a separate family, the Athorybiidae, for *A. rosacea* and *M. melo*, still retaining them in the same genus *Athorybia*. Later, Haeckel (1888a) introduced a separate genus *Melophysa*, for *melo*, though this was based solely on differences he observed in the tentilla; a more fundamental difference was identified by Chun (1897) who described nectophores in *M. melo* for the first time, as noted above.

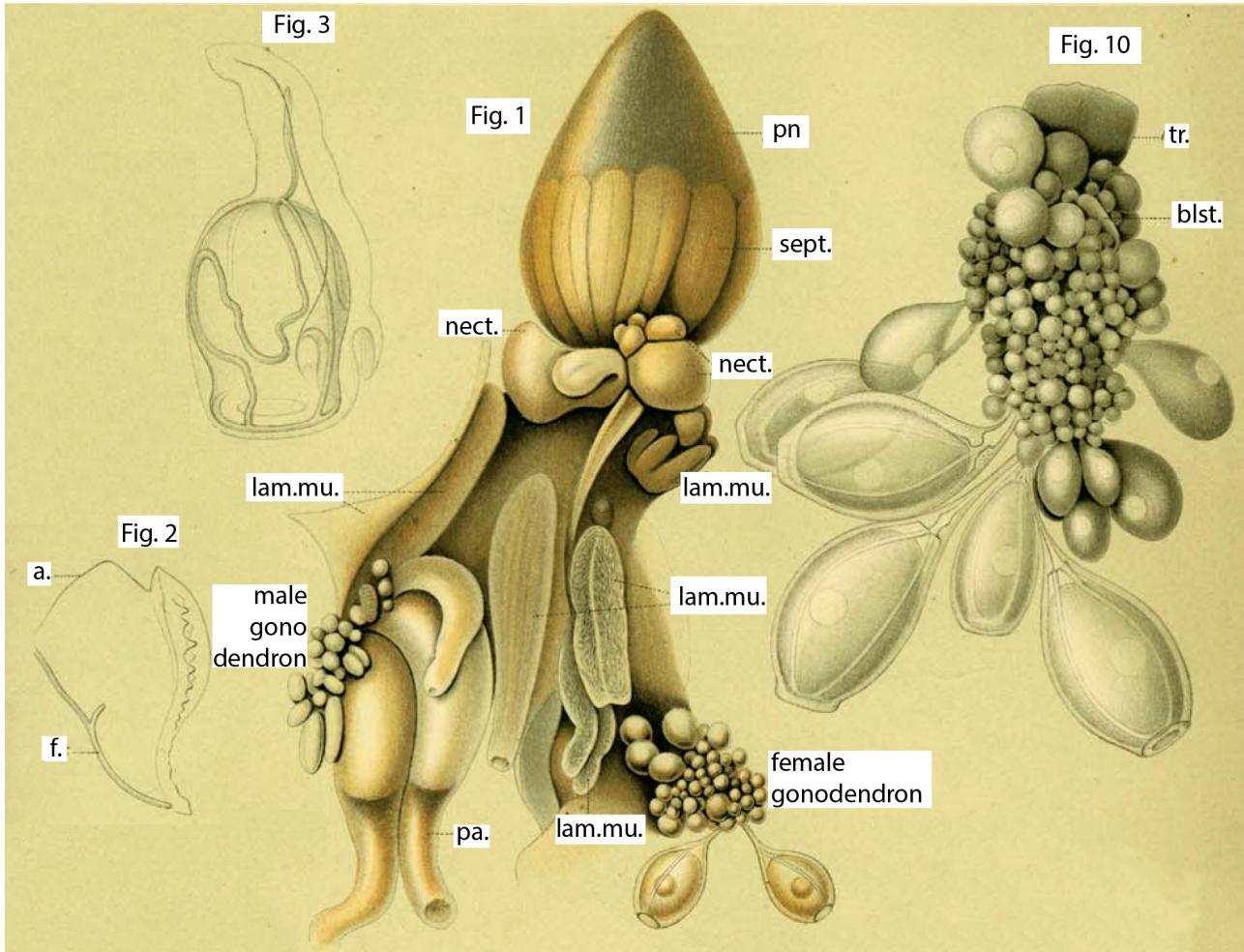


FIGURE 11. Selected figures of *Melophysa melo* (as *Athorybia melo*) from Chun (1897, Taf. 4). Fig. 1: Corm after removal of bracts; Fig. 2: young bract (detached); Fig. 3: oldest nectophore (detached); Fig. 10: female gonodendron with female gonophores. Abbreviations: a.—wing-shaped proximal part of bract; blst.—blastostyle; F.—bracteal canal; go—gonodendron; lam. mu.—bracteal muscular lamellae plus single nectophoral lamella (below nectophore); nect.—nectophore; pa—palpon; pn—pneumatophore; sept.—septum of pneumatophore; tr—stem.

Only since the first molecular phylogeny of the Siphonophora, including 45 species, was *Athorybia rosacea* shown to be closely related to the long-stemmed physonect *Agalma elegans* (Dunn *et al.* 2005), despite the fact that in *A. rosacea* the nectosome has been lost. The next year, Pugh (2006) confirmed that the short nectosome in *Melophysa melo* is dorsal, which led him to disband the family Athorybiidae and assign both these ‘short-stemmed’ species to the family Agalmatidae *sensu stricto*.

Discussion and conclusions

Few colonies of *Melophysa melo* have been collected over the years. The original specimen, described from the Strait of Gibraltar, measured 7–10 cm in length (ca. 5 cm diameter), but others were smaller (2 to 4 cm diameter; Pugh 1999, Daniel 1985, Chun 1897). The larger colony from the Gulf of Mexico, based on the corm diameter plus thickness of two bracts, had a maximum diameter of ca. 3.2 cm, which is intermediate between Quoy and Gaimard’s large specimen and smaller ones described from the Indian Ocean and north central Pacific. The largest collection of *M. melo* zooids was made from the Indian Ocean over a six-year period by Daniel (1985) [including the International Indian Ocean Expedition and material from Zoological Survey of India, Z.S.I., Madras]. Daniel (1985) listed 27 colonies, 12 nectophores, 80 bracts and a few loose palpons and gastrozooids, and estimated colonies to be 2–2.5 cm in diameter.

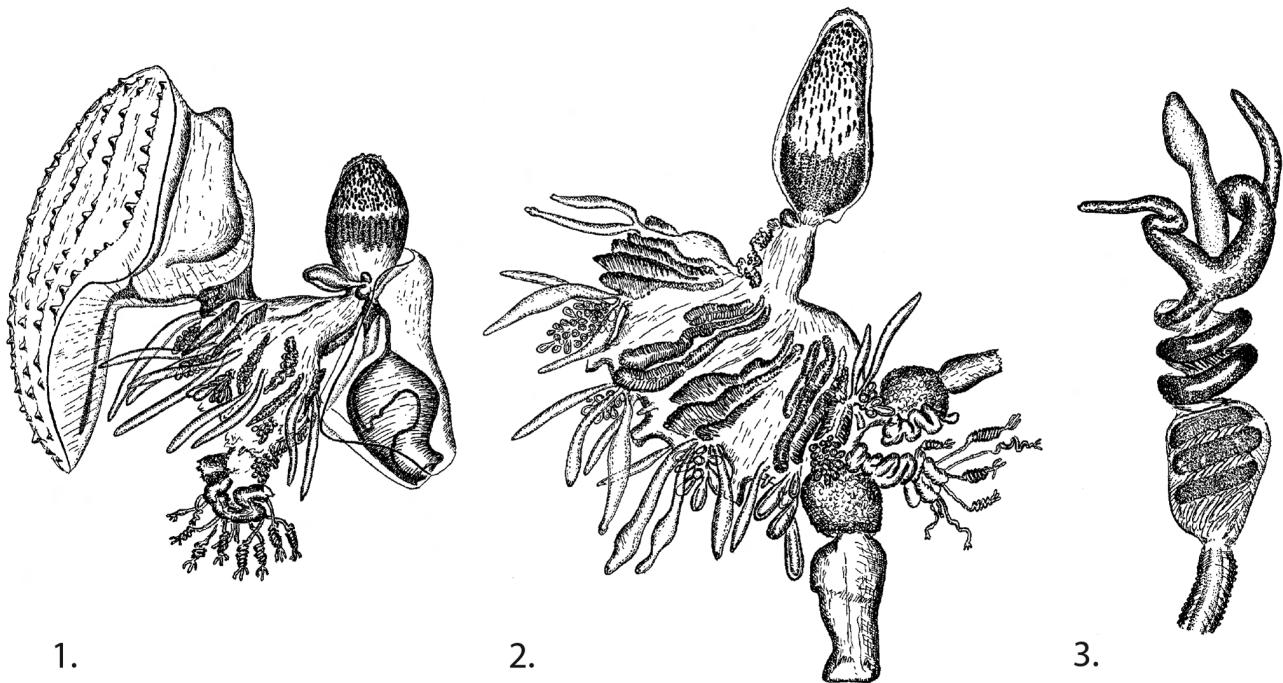


FIGURE 12. Two mostly denuded corms of *Melophysa melo* (as *Athorybia rosacea*) from the tropical eastern Pacific and a preserved tentillum, by Bigelow (1931, Figs 217, 218, 219). 1. Colony with one attached bract, and one attached but twisted nectophore; also a nectophore bud, several bracteal lamellae, attached palpons and gonodendra, and a contracted tentacle bearing several tricornuate tentilla. 2. Colony with shortened nectosome with four nectophoral lamellae, swollen siphosomal corm with four groups of c. three bracteal muscular lamellae, interspersed with groups of palpons and gonodendra; two attached gastrozooids with contracted tentacles. 3. Tentillum magnified.

The two mature nectophore types from the northern Gulf of Mexico have a basal process either orthogonal or parallel to the nectophore body (Figs 1 E, F), and are similar to those described by Daniel (1985) from the Indian Ocean, although her figures are less detailed and her mature nectophores 4–8 mm shorter. She concluded that the longer, oblique nectophore (14 mm in length) is younger, and the shorter, orthogonal nectophore (10 mm in length) is older, which coincides with the mature nectophores collected in the Gulf of Mexico. These nectophores were found mainly in Samples 3, 4, 6 and 7. Other smaller nectophores were distorted, and unreliable for a morphological overview. Some nectophores (Samples 1, 2, 4, 7; not illustrated) were folded over, with the basal process lying flat against the nectophore body, or projecting from the body at a non-life-like angle. Totton (1954) examined a number of nectophores from the Indian Ocean, and described three small ridges above the ostium along the distal surface (his Fig. 7B). These ridges were conspicuous in the mature nectophores from the Gulf of Mexico (Figs 1G, H), and noted by Daniel (1985). However, Totton's nectophores were distorted (Pugh 1999), with a very small 'basal process' (see Totton 1954 Fig. 7E) unlike the more prominent process observed in almost all nectophores collected in the Gulf of Mexico, irrespective of size (except those in Sample 9).

Attachment of nectophores to the stem is via an obvious nectophoral muscular lamella in most physonect and prayid siphonophores (see Mapstone 2009 Figs 5A–E), although the lamella could not be identified on the GoM corm 6 without dissection, which was not performed. Nectophore attachment is via an ascending and descending mantle canal in agalmatid nectophores (in Mapstone 2009, Fig. 6, as 'asd' and 'dsd'), and mantle canals are identified here in *Melophysa melo* for the first time, on the proximal surface of the basal process in the mid-line (Figs 1 E, F). An external pedicular canal links the stem canal to junction of the mantle canals in agalmatids, and typically a short internal pedicular canal passes from this junction to the nectosac (see Mapstone 2009, Figs 5B, C). In the nectophores from the Gulf of Mexico, the internal pedicular canal is longer than that shown by Chun (1897 pl. 4 Fig. 3) and longer than that shown, though not labelled, by Totton (1954 Fig. 7E).

The courses of the radial canals, which originate at the 5-way junction on the proximal end of the nectosac, were first accurately shown by Totton (1954, Fig. 7C), but other aspects of the nectophore drawings are poor, as noted above. This paper provides the first accurate lateral views of mature nectophores (Figs. 1E, F) and a more

accurate view of the nectosac canals from above (Fig. 1H, upper view). The lower radial canal is straight, as first noted by Totton (1954), whilst the other three canals are sinuous; all pass over the nectosac surface to the distal end where they insert onto the ostial ring canal. As noted above, the ostium is narrow and distorted in most Gulf of Mexico nectophores, somewhat similar to that shown by Totton (1954, Fig. 7D), but broader in a few (Fig. 1D). A prominent feature of *Melophysa melo* nectophores is the girdle, not previously described (although perhaps shown in Chun's nectophore figure and possibly some of Totton's figures), which circumscribes the widest part of mature nectophores (Figs 1A, B, E–H). From the girdle, two weak ridges pass down the length of the basal process on the proximal side in some mature Gulf of Mexico nectophores ('a' and 'b' in Figs 1 E), and delimit a proximal nectophore surface.

The bracts of *Melophysa melo*, the main diagnostic character of the species, are very thick with tuberculate ridges, and easily distinguished from the thin and relatively smooth bracts of *Athorybia rosacea* (Totton 1965). Despite this obvious difference, some publications have muddled the two species, including parts of the text in Bigelow (1931; questionable paragraphs noted in the synonymy given above). Quoy and Gaimard (1827) were the first to show the prominent ridges on *M. melo* bracts in their Plate 5C Figs 2 and 5. In the GoM bracts (Fig. 2), the ridges vary in number from 6 rows in immature bracts to 8–9 rows in mature bracts. Daniel (1985) noted that each row comprises 25–30 tubercles, or conical papillae. New tubercles were observed forming between some of the tubercle rows in some large bracts from the Gulf of Mexico (Fig. 2E). At least one outer row of tubercles continues around the proximal end of the bract (upper surface) and becomes contiguous with an equivalent outer row on the opposite side (Fig. 2F). All bracts had a keel, as first shown in Quoy and Gaimard's Fig. 4 and in Bigelow's Fig. 217 (see Figs 9 and 11 in this paper); the keel varied in size depending on maturity, was typically demarcated from the upper bract body by a groove (Fig. 2F), and bore a narrow gutter along its lower edge representing the bracteal canal scar, where the bract was attached to the corm in life via a bracteal muscular lamella. In several bracts, the keel edge at the proximal end bulged beyond the proximal tip of the upper surface, as shown in the bract by Chun (1897, Pl. 4, Fig. 2); in others, this bulge was absent and the proximal profile of the bract more closely resembled that illustrated by Bigelow (1931 Fig. 217). In mature bracts, most of which are relatively large, a bracteal canal, which is thinner than shown by Bigelow (1931), extends from the distal end of the bracteal lamella scar along the lower surface of the bract to the distal end (Fig. 2F). The bracteal canal illustrated by Bigelow, has a blind-ending diverticulum at the junction of the keel with the bract body in some bracts (Fig. 2C). Immature bracts have not been described previously, and are characterized by a very thick bracteal canal (Fig. 2A), as in many other young physonects (Mapstone 2003).

The larger corm from the GoM collection was well preserved and presents some features not apparent in the corm figures published by Bigelow (1931, Figs 217–218). Specifically, there are two rows of bracteal lamellae on the corm, as shown in Fig. 4; one pair of lamellae occurred on all but two of the 8 cormidia identified in this corm. There is a single lamella on the upper surface and a second lamella on the lower surface linked by two gonodendra on the lateral surface which are connected by a line of zooids. Bigelow (1931) did not describe individual cormidia in detail, nor observe any white lines delimiting each cormidium. However, he did conclude that there might be 8 gastrozooids, one per cormidium, and many more palpons. The arrangement of cormidia on our larger corm is similar to that described by Chun (1897) in young specimens of *M. melo* collected in Tenerife in February 1888; Chun notes in his paper that the cormidia were arranged in two spirals on a 'bubble-shaped' corm, though he did not detect this arrangement in his larger colony from the Sargasso Sea. Buds for new bracts might have formed below the gonodendra in our larger corm. Similarly, in the post-larva described and figured by Totton (1954 text-Figs 8–9), buds for younger bracts were attached much lower down on the 'body' of the specimen than older bracts. Bigelow (1931), in contrast, concluded that new bracts are likely to be budded off between mature bracts. Evidence that the larger GoM corm is younger than those figured by Bigelow comes from the immature state of the gonodendra, which did not bear any gonophores of recognizable sex, unlike those shown by Chun (1897) in his mature Sargasso Sea specimen. Only a single gastrozooid develops per cormidium in *Melophysa melo*, suggesting that the larger GoM corm is at a later stage of development than Chun's young colonies from the Canaries, which bore only 5 gastrozooids.

Totton (1954, p.41) found a single larval bract in a post-larval specimen from Bermuda, and two gastrozooids with the bract surface being smooth. This single larval bract may have originally been attached to the upper side of cormidium 1 (the oldest cormidium) and later lost, together with the bracteal lamella. Totton (1954) noted that buds for younger bracts developed further down the 'nectostyle' (horn) in the post-larva, which agrees with the disposi-

tion of cormidia on our two corms. Here, in our larger corm, cormidium 8 is the youngest and situated closest to the pneumatophore, while the oldest cormidium 1 lies at the far (free) end of the short thick, spiral corm, with a lower bract and associated muscular lamella not yet developed.

Sadly, no attached gastrozooids were found in the larger and more mature corm from the Gulf of Mexico (corm 6), only a single detached one (Fig. 8A), although the tentacle had already been lost. Only a tentacle rudiment was present on the small attached gastrozooid of corm 7, in which individual tentilla could not be discerned. Fortunately, the tentilla of *Melophysa* have been described in previous studies, and shown to have up to 8 spiral coils to the cnidoband, covered in life by a brown-tinged complete involucrum (Chun 1897). In young tentilla from the Canaries specimens, the cnidobands bear only the two terminal filaments distally (Chun 1897), as noted above, suggesting that the ampulla must develop later. Interestingly, this type of tentillum development is similar to that found in the closely related species *Agalma clausi* (Mańko and Pugh 2018). More specimens need to be collected to confirm that this tentillum type is the only one formed in *Melophysa melo*. If so, the tentillum will demonstrate another morphological difference between *Melophysa* and the two *Athorybia* species, with two tentillum types occurring in the abundant short-stemmed species *Athorybia rosacea* (Bigelow 1911), and a third different type in the rare species *Athorybia lucida* (Biggs 1978).

Fresh specimens of *Melophysa melo* collected in the future should be preserved for genetic analyses to bolster the above descriptions and conclusions (Bucklin *et al.* 2010).

Geographical distribution

Melophysa melo has been recorded throughout the tropical and sub-tropical regions of all three oceans, mostly in the upper 200 m of the water column, but infrequently. The GoM specimens from 27.0–28.5°N, 87–90°W fall within the latitudinal range for *M. melo* elsewhere, which is restricted to circa 27°26'N to 46°5'S worldwide. Most records come from tropical locations (Table 3), although evidence shows that *M. melo* breeds in the semi-tropics, around Bermuda and the Canaries (Totton 1954, Chun 1888). However, the most northerly record from the Strait of Gibraltar (at ca. 36.0° N, 5.7°) in the Atlantic suggests that the original specimen described by Quoy and Gaimard (1827) was probably transported there in oceanic water, and was not breeding, since no records exist at all for *M. melo* inside the Mediterranean Basin (Table 3). Records are sparse from the Pacific Ocean, with most coming from the tropical eastern sector, a few from offshore Japan (38°00'N, 147°15'E) except for the highest abundance of *M. melo* ever recorded from the Sulu Sea in the west, during February 2000 (Grossmann *et al.* 2015, but *M. melo* data in Table 4 are incorrect, since in their discussion on p. 62, these authors note that *M. melo* was only collected once in the Celebes Sea, between 25 and 50 m during the day. Yet in Table 4 it is shown to occur in three night-time depth ranges but no day time range. From this we conclude that the Night list for *M. melo* in the Celebes Sea was inadvertently pasted in from the Day list for the Sulu Sea during drafting of this paper). Here, perhaps competition from surface-living diphymorph calyphorans was effectively lacking, due to much reduced water inflow from surrounding Pacific waters, and this relationship apparently enabled *M. melo* to flourish throughout the thermocline layer during the day, as noted in their Table 3. Records are sparse in the Indian Ocean, where most specimens were collected in the east during both monsoon periods (Daniel, 1985, Maps 19–20), together with a few from the Indian sector of the Southern Ocean around the Prince Edward Island archipelago during the austral autumn (Hunt *et al.* 2001; Pakhomov and Froneman 2000, Froneman *et al.* 2002). The present new records and morphological information from the Gulf of Mexico make this update an important contribution to our understanding and distribution of the short-stemmed agalmatid *M. melo*.

Acknowledgments

The collection of gelata and water column data presented in this paper was supported by Contract AB133C-11-CQ-0050 Agreement No. 5700-NOVA and GoMRI RFP-IV Grant Agreement SA15-2, awarded to Tracey Sutton, Nova Southeastern University. Assistance from research associates April Cook, Lacey Malarkey, Nina Pruzinsky, Michael Novotny, Katie Bowen, Alexandria Pickard, Wendy Mooring and Sarah Peake is appreciated. Collection of the specimens was made possible by a grant from The Gulf of Mexico Research Initiative. Data are publicly avail-

able through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at <https://data.gulfresearchinitiative.org> (doi: 10.7266/N7VX0DK2, 10.7266/N70P0X3T, 10.7266/N7XP7385, 10.7266/N7902234).] The pertinent comments and constructive suggestions of the reviewers improved the manuscript.

TABLE 3. Summary of previous records for *Melophysa melo* worldwide.

Author	Location	Depth	Material
Alvariño 1974	Both sides of Panama canal, Red Sea	140/150–0m	No details
Araujo 2012	Equatorial Atlantic.	200–0 m	No details
Bigelow 1931	Tropical Eastern Pacific, at 5 stations between Cocos and Galapagos Islands (4°50'N–1°51'S; 80°41'W –89°39'W)	Probably from near surface, but overall depth range sampled, ca. 3100–0m	Several fragmentary corms, two with attached zooids; 30 loose bracts
Chun 1888 (See Chun 1889 for translation)	Atlantic, Canary Islands	Surface waters	Young specimens with only two tentacles from two gastrozooids
Chun 1897	N Atlantic in Sargasso Sea just north and west of Canary Islands	Surface	1 specimen
Daniel 1974	Eastern Indian Ocean, 3 stations	200–0 m	2 nectophores, 14 bracts, other zooid fragments
Daniel 1985	Indian Ocean, scattered stations	200–0 m	24 colonies, 12 nectophores, 80 bracts, & other zooid fragments
Froneman <i>et al.</i> 2002	Prince Edward Islands, Southern Ocean	300–0 m	At one 36 hour station in 1998; no zooid details
Gasca 2002	Mexican Pacific, Gulf of California	No details	No details
Grossmann <i>et al.</i> 2015	Indo-Pacific, Celebes and Sulu Seas	25–50 m in Celebes Sea, 100–200 m in Sulu Sea	Dominated in Sulu Sea in Feb 2000 (highest abundance ever recorded: < 0.24 colonies/m ³)
Hunt <i>et al.</i> 2001	Prince Edward Islands, south of South Africa, Southern Ocean	300–0 m	Recorded in 1996, 1997, 1998, 1999, but no details
Morita <i>et al.</i> 2018	Offshore Japan 38°00'N, 147°15'E	100–150 m	3 nectophores, 12 bracts, 3 gastrozooids, 4 palpons
Pakhomov & Froneman 2000	Prince Edward Islands, south of South Africa, Southern Ocean	300–0 m	Collected 1989, 1997; zooid details not given
Pakhomov <i>et al.</i> 1999	S Atlantic, along transect 0–18°E from Antarctica to S Africa	0 and 300 m	Collected 1993. No zooid details
Quoy & Gaimard 1827	Strait of Gibraltar, NE Atlantic	Probably near surface	Single specimen
Schiariti <i>et al.</i> 2018	South-western Atlantic	Unknown	No details
Totton 1936	Bermuda, from 2 stations	183 m, 1828 m	2 specimens
Totton 1954	Indian Ocean, from 7 stations	Varied depths	No details
Totton 1954	Tropical Atlantic, from 9 stations	All to 0m except one	No details
Totton 1954	Bermuda, from 9 stations	Varied depths	Post-larva and other specimens
Totton 1965	SE Pacific, 2 William Scoresby Stations (4–5°S)	Varied depths to 315 m	No details

Absent from the Mediterranean Sea. Other records, without details, by Pugh 1999, Haeckel 1888b

References

- Angel, M.V. (2012) Towards a full inventory of planktonic Ostracoda (Crustacea) for the subtropical Northwestern Atlantic Ocean. *Deep-Sea Research Part II*, 57, 2173–2188.
<https://doi.org/10.1016/j.dsr2.2010.09.020>
- Araujo, E.M. (2012) *Sistemática y distribución de los Sifonóforos (Cnidaria, Hydrozoa) del Océano Atlántico Sudoccidental*.

- PhD Thesis, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata, 228 pp. [in Spanish]
- Beebe, W. (1926) The Arcturus Oceanographic Expedition. *Zoologica, New York*, 8, 1–45.
- Beebe, W. (1929–1934) The Bermudan Oceanographic Expedition and Bermuda Station Data. *Zoologica, New York*, 13, 2–45.
- Bigelow, H.B. (1911) Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer “Albatross”, from October, 1904, to March, 1905, Lieut.—Commander L. M. Garrett, U. S. N., commanding. XXIII. The Siphonophorae. *Memoirs of the Museum of Comparative Zoölogy at Harvard College*, 38, 173–401, 32 pls.
- Bigelow, H.B. (1931) Siphonophorae from the Arcturus Oceanographic Expedition. *Zoologica, New York*, 8, 525–592.
- Biggs, D.C. (1978) *Athorybia lucida*, a new species of siphonophore (Physonectae, Athorybiidae) from the North Atlantic Ocean. *Bulletin of Marine Science*, 28, 537–542.
- Bucklin, A., Nishida, S., Schnack-Schiel, S., Wiebe, P.H., Lindsay, D., Machida, R.J. & Copley, N.J. (2010) A census of zooplankton of the global ocean. In: McIntyre, A.D. (Ed.), *Life in the World's Oceans: Diversity, Distribution, and Abundance*. Wiley-Blackwell, Oxford, pp. 247–265.
<https://doi.org/10.1002/9781444325508.ch13>
- Chun, C. (1888) Berichte über eine nach den Canarischen Inseln im Winter 1887/88 ausgeführte Reise. *Sitzungsberichte der Preussischen Akademie der Wissenschaften zu Berlin für 1888*, 1141–1173. [English translation in *Annals and Magazine of Natural History*, Series 6, 3 (23), 214–246 (1889)]
- Chun, C. (1897) *Die Siphonophoren der Plankton-Expedition. Band II. Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*. Lipsius and Tischer, Kiel and Leipzig, 126 pp., 8 pls. [in German]
- Daniel, R. (1974) Siphonophora from the Indian Ocean. *Memoirs of the Zoological Survey of India*, 15, 1–242.
- Daniel, R. (1985) *The fauna of India and the adjacent countries. Coelenterata: Hydrozoa, Siphonophora*. Zoological Survey of India Publication, Calcutta, 440 pp.
- Eschscholtz, F. (1829) *System der Acalephen. Eine ausführliche Beschreibung aller Medusenartigen Strahlthiere*. Berlin, Ferdinand Dümmler, Berlin, 190 pp., 16 pls. [in German]
<https://doi.org/10.5962/bhl.title.10139>
- Froneman, P.W., Pakhomov, E.A., Gurney, L.J. & Hunt, B.V.P. (2002) Predation impact of carnivorous macrozooplankton in the vicinity of the Prince Edward Island archipelago (Southern Ocean) in austral autumn 1998. *Deep-Sea Research Part II*, 49, 3243–3254.
[https://doi.org/10.1016/S0967-0645\(02\)00081-4](https://doi.org/10.1016/S0967-0645(02)00081-4)
- Gasca, R. (2002) Lista faunística y bibliografía comentados de los sifonóforos (Cnidaria: Hydrozoa) de México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México Serie Zoología*, 73, 123–143. [in Spanish]
- Grossmann, M.M., Nishikawa, J. & Lindsay, D.J. (2015) Diversity and community structure of pelagic cnidarians in the Celebes and Sulu Seas, southeast Asian tropical marginal seas. *Deep-Sea Research Part I*, 100, 54–63.
<https://doi.org/10.1016/j.dsr.2015.02.005>
- Haeckel, E. (1887) *System der Siphonophoren auf phylogenetischer Grundlage entworfen*. Gustav Fischer, Jena, 46 pp. [in German]
- Haeckel, E. (1888a) System der Siphonophoren auf phylogenetischer Grundlage entworfen. *Jenaische Zeitschrift für Naturwissenschaft*, 22, 1–46. [in German]
- Haeckel, E. (1888b) Report on the Siphonophorae collected by H. M. S. Challenger during the years 1873–1876. Report on the scientific results of the voyage of H. M. S. Challenger during the years 1873–76. *Zoology Report*, 28, 1–380, 50 pls.
<https://doi.org/10.5962/bhl.title.3968>
- Hunt, R.P.V., Pakhomov, E.A. & McQuaid, C.D. (2001) Short-term variation and long-term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biology*, 138, 369–381.
<https://doi.org/10.1007/s002270000467>
- Huxley, T.H. (1859) *The Oceanic Hydrozoa: a description of the Calycophoridae and Physophoridae observed during the voyage of HMS Rattlesnake 1846–1850*. Ray Society, London, 143 pp.
<https://doi.org/10.5962/bhl.title.10033>
- Mańko, M.K. & Pugh P.R. (2018) *Agalma clausi* (Bedot, 1888) (Siphonophora: Physonectae)—complimentary description with notes on species distribution. *Zootaxa*, 4441 (2), 311–331.
<https://doi.org/10.11646/zootaxa.4441.2.7>
- Mapstone, G.M. & Ljubenkov, J.C. (2013) New observations on *Dromalia alexandri* Bigelow, 1911, a rhodaliid physonect siphonophore from Southern Californian waters. *Marine Ecology*, 34 (Supplement 1), 96–112.
<https://doi.org/10.1111/maec.12029>
- Morita, H., Toyokawa, M., Hidaka, K., Nishimoto, A., Sugasaki, H. & Kikuchi, T. (2017) Spatio-temporal structure of the jellyfish community in the transition zone of cold and warm currents in the northwest Pacific. *Plankton Benthos Research*, 12, 266–284.
<https://doi.org/10.3800/pbr.12.266>
- Pakhomov, E.A., Perissinotto, C.D. & McQuaid, C.D. (1994) Comparative structure of the macro-zooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. *Marine Ecology Progress Series*, 111, 155–169.
<https://doi.org/10.3354/meps111155>

- Pakhomov, E.A., Perissinotto, C.D. & Froneman, P.W. (1999) Predation impact of carnivorous macrozooplankton and micronekton in the Atlantic sector of the Southern Ocean. *Journal of Marine Systems*, 19, 47–64.
[https://doi.org/10.1016/S0924-7963\(98\)00023-2](https://doi.org/10.1016/S0924-7963(98)00023-2)
- Pakhomov, E.A. & Froneman, P.W. (2000) Composition and spatial variability of macroplankton and micronekton within the Antarctic Polar Frontal Zone of the Indian Ocean during austral autumn 1997. *Polar Biology*, 23, 410–419.
<https://doi.org/10.1007/s003000050462>
- Pugh, P.R. (1999) Siphonophorae. In: Boltovskoy, D. (Ed.), *South Atlantic Zooplankton I*. Backhuys Publishers, Leiden, pp. 467–511.
- Pugh, P.R. (2001) A review of the genus *Erenna* Bedot, 1904 (Siphonophora, Physonectae). *Bulletin of the Natural History Museum Zoology*, Series 67, 169–182.
- Pugh, P.R. (2005) A new species of *Physophora* (Siphonophora: Physonectae: Physophoridae) from the North Atlantic, with comments on related species. *Systematics and Biodiversity*, 2, 251–270.
<https://doi.org/10.1017/S1477200004001483>
- Pugh, P.R. (2006) The taxonomic status of the genus *Moseria* (Siphonophora, Physonectae). *Zootaxa*, 1343 (1), 1–42.
<https://doi.org/10.11646/zootaxa.1343.1.1>
- Quoy, J.R.C. & Gaimard, J.P. (1827) Observations zoologiques faites à bord de l'Astrolabe, en mai 1826, dans le Détroit de Gibraltar. *Annales des sciences naturelles*, Series 1, 10, 1–21 + 172–193., Atlas 10, pls. 1–2 + 4–9. [in French]
- Quoy, J.R.C. & Gaimard, J.P. (1833) Zoologie. IV. In: Tastu, J. (Ed.), *Voyage de découvertes de l'Astrolabe exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont D'Urville*. J. Tastu, Paris, pp. 1–390 (texte), pls. 26 (atlas). [in French]
- Schiariti, A., Dutto, M.S., Morandini, A.C., Nagata, R.M., Pereyra, D.Y., Tapia, F.A.P., Briz, L.D. & Genzano, G. (2018) An overview of the Medusozoa from the Southwestern Atlantic. In: Hoffmeyer, M.S., Sabatini, M.E., Brandini, F.P., Calliari, D.L. & Santinelli, N.H. (Eds.), *Plankton Ecology of the Southwestern Atlantic*. Springer-Verlag, Cham, pp. 413–449.
https://doi.org/10.1007/978-3-319-77869-3_19
- Totton, A.K. (1954) Siphonophora of the Indian Ocean together with systematic and biological notes on related specimens from other oceans. *Discovery Reports*, 27, 1–162.
- Totton, A.K. (1965) *A Synopsis of the Siphonophora*. British Museum (Natural History), London, 230 pp.
- WoRMS Siphonophora List. (2019) World Register of Marine Species website. Available from: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=1371> (accessed 2019 July 19)