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Re-description of *Rosacea cymbiformis*, a prayine siphonophore (from the Mediterranean Sea), with comments on nectophore designation and bract orientation

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This updated re-description of the prayine siphonophore *Rosacea cymbiformis* includes figures of all zooids (except larval nectophores) and is based on material held in the collections of the Natural History Museum (NHM), London. *Rosacea cymbiformis* was originally described in 1830 under the name *Physalia cymbiformis*, and subsequently reported many times during the 19th Century. However, during the 20th Century it was confused with the closely related species *R. plicata*, and the two species are still not clearly differentiated. Previous descriptions are reviewed herein, including conflicting interpretations of nectophore designation in *R. plicata*, and bract orientation in *R. cymbiformis* and *R. plicata*. To identify these siphonophores to species level and separate them from other closely related prayines, it is essential to distinguish the first definitive nectophore from the second, and the right paired bracteal canals from the left canals. This becomes critical when only detached siphonophore zooids are available, as for example, in plankton samples collected with nets. A summary of the differences between *R. cymbiformis* and the five other currently recognized *Rosacea* species, *R. plicata*, *R. repanda*, *R. limbata*, *R. flaccida* and *R. arabiana*, is presented. The full synonymy of *R. cymbiformis* is too long for inclusion here and is deferred to a later paper.

INTRODUCTION

The genus name *Rosacea* was introduced by Quoy & Gaimard (1827, p. 176) for two prayine siphonophore species collected from the Strait of Gibraltar in 1826. One species has never been found again, and the second, originally named *R. plicata*, is now referred to *Desmophyes annectens* Haeckel, 1888. Later, Bigelow used the name *R. plicata* for material collected in the Bay of Biscay (1911a, p. 341) and tropical East Pacific (1911b, p. 201), though his species differed from that of Quoy & Gaimard. *Rosacea plicata* is now known to be common (Kirkpatrick & Pugh, 1984, p. 54), but the name is a homonym of Quoy & Gaimard's name, so the earlier name has priority. However, a case has been made to the International Commission of Zoological Nomenclature to conserve the name *R. plicata* for Bigelow's species (Mapstone & Pugh, 2004) which hopefully will be accepted, invalidate Quoy & Gaimard's name, and make Bigelow's species the type species of the genus.

Rosacea cymbiformis was first described (as *Physalia cymbiformis*) by Chiaje (1830) and referred to *Rosacea* by Schneider (1898). Since Bigelow's work on *R. plicata* in 1911, four more species have been added: *R. flaccida* Biggs et al., 1978, *R. repanda* and *R. limbata* Pugh & Youngbluth, 1988, and *R. arabiana* Pugh, 2002. A fifth species, *Rosacea villafrancae* Carré 1969, is now referred to *Desmophyes* (Pugh & Harbison, 1987, p. 90). *Rosacea plicata* and *R. cymbiformis* have not been fully redescribed since the publications of Bigelow (1911b) and Totton (1965) so the first aim of this paper is to update the description of *R. cymbiformis* using specimens held at the Natural History Museum, London.

A prayine siphonophore consists of two nectophores attached to the stem at the apex, with stem groups, or cormidia (comprising bract, gastrozooid and gonophore) arranged serially below. Nectophores develop sequentially, and are not identical when mature. Bracts vary in the arrangement of the canals that arise from the stem canal, and unpaired bracteal canals originate from either a right or a left paired canal (Pugh & Harbison, 1987, table 1). The two nectophores of *R. plicata* have been variously designated in the past, and confused with either nectophore of *R. cymbiformis*. Isolated prayine bracts are difficult to identify to species level, but in

R. cymbiformis and *R. plicata* have been further muddled in the literature by different applications of 'right and left' to the paired canals. A second aim of this paper, therefore, is an overdue re-assessment of nectophore designation in *R. plicata*, and orientation of canals in the bracts of both *R. cymbiformis* and *R. plicata*. Siphonophores are extremely delicate colonial organisms, and almost invariably break-up into their constituent zooids when collected. It is vital, therefore, that future researchers avoid past mistakes and are able to identify detached nectophores and bracts of *R. cymbiformis* and *R. plicata* in isolation.

MATERIALS AND METHODS

Rosacea cymbiformis

Unless otherwise stated, the following material was collected at the surface by A.K. Totton from the Mediterranean Sea, off Villefranche-sur-Mer, Nice, between 1949 and 1962, relaxed in $MgCl_2$ for several hours and preserved in 4% formaldehyde. Sample material typically consists of N_1 and N_2 nectophores, a stem with numerous attached stem groups and some loose zooids. British Museum of Natural History Registration nos: 1902.7.29.7, 1903.3.2.1, 1903.10.1.1 (Naples, alcohol, each with detached broken N_1 and N_2, stem); 1932.7.20.1-6 (Naples, 2 detached N_1, 3 detached N_2, N_2 with stem, immature, 3 stems); 1952.9.23.175, 1952.9.23.177, 1952.9.23.179-181, 1952.9.23.191, 1952.9.23.193, 1952.9.23.200, 1952.9.23.202, 1952.9.23.204, 1952.9.23.642 (each with detached N_1 and N_2, stem); 1952.9.23.195 (detached N_2, stem); 1952.9.23.196, 1952.9.23.199 (detached N_1, N_2 with stem); 1952.9.23.182-187 (3 N_2 with stems, from Villefranche; detached N_1 and N_2, N_2 with stem, from Cap Ferrat); 1952.9.23.192 (detached N_1, broken N_1, 2 detached N_2, 3 stems); 1952.9.23.194 (2 N_2 with stems); 1952.9.23.197 (N_2 and immature both attached to stem, 2 detached N_2, N_2 with stem, immature); 1952.9.23.198 (detached N_1, 2 detached N_2, N_2 with stem, immature, 1 stem); 1952.9.23.201 (4 detached N_1, N_1 with stem, 4 detached N_2, N_2 with stem, immature, 2 immatures with stems); 1952.9.23.203 (5 detached N_1 and N_2, 5 stems); 1952.9.23.605 (8 stems); 1952.9.23.189 (8 large and 2 small detached bracts); 1973.5.15.53 (detached N_1 and N_2); 1973.5.15.54 (N_1 and N_2 both attached to stem); 1973.5.15.63 (42 loose bracts); 1985.12.16.1 (3 detached N_1 and N_2, 1 stem).

Rosacea plicata

Registration nos: 1939.6.10.1 (detached N_1 and N_2, collected and identified by H.B. Bigelow, Bay of Biscay, selected as lectotype by P.R. Pugh from original sample); 1957.9.14.71 (detached N_1 and N_2, Discovery Station 3374); 1959.6.25.1 (detached N_1 and N_2, 31 bracts, Discovery Station 1729); 1985.12.9.10-16 (joined N_1 and N_2, Discovery Station 3239). Discovery Station material identified by A.K. Totton.

Rosacea arabiana

Registration no. 2001.6920 holotype (joined N_1 and N_2, detached N_1 and N_2, 3 bracts, 2 gonophores; 24º13.2'N 58º36.3'E; 201–152 m).

Specimens were transferred to a deep-sided Petri dish, examined under a Zeiss binocular microscope, and illustrated using an attached camera lucida.

Abbreviations

In the following figures: alk, apico-lateral keel (of gonophore); bl, bracteal lamella; br, bract; dbs, descending branch of somatocyst; dc, dorsal canal; drc, dorsal radial canal; fl, flap; ga, gastrozooid; gf, gonophore furrow; go, gonophore; grc, gonophore radial canal; hc, hydroecial cavity; hp, hydroecial pocket; hw, hydroecial wing; hwb, hydroecial wing base; ior, in-rolled ostial region; lbh, limit of bracteal hydroecium; lc, lamellar canal; lcr, lamellar canal rudiment; lhc, left hydroecial canal; lhl, left hydroecial lobe; llc, left longitudinal canal; lmh, limit of hydroecium (of nectophore); lml, lower muscular lamella; lrc, lateral radial canal; lrc-$lp_{1–3}$, loops of lateral radial canal; mb, manubrium; mc, mantle canal; mlN_2, muscular lamella of detached N_2 nectophore; N_1, first definitive nectophore; N_2, second definitive nectophore; $nb_{1,2}$, nectophore bud(s); ns, nectosac; orc, ostial ring canal; os, ostium; ov, ovum; pac, pallial canal; pc, pedicular canal; rhc, right hydroecial canal; rhl, right hydroecial lobe; rhl_{1-2}, parts of right hydroecial lobe; rlc, right longitudinal canal; sb, siphosomal buds; sg, stem group; sp, surface papillae; st, stem (siphosomal) of colony; tm, mass of tentilla arising from basigaster; uml, upper muscular lamella; upc, upper pallial canal; vc, ventral canal; vl, ventral lobe; vrc, ventral radial canal.

SYSTEMATICS

Order CALYCOPHORAE Leuckart, 1854
Family PRAYIDAE Kölliker, 1853
Subfamily PRAYINAE Chun, 1897
Genus *Rosacea* Quoy & Gaimard, 1827
Rosacea cymbiformis (Chiaje, 1830)
(Figures 1–5)

Diagnosis

Definitive nectophores with: ostium opening dorso-basal; no apico-lateral swellings; mesoglea flaccid; hydroecial cavity elongate with opening extending length of nectophore in N_1 and N_2, without basal 'sill'; radial canals of nectosac arise together from pedicular canal, lateral canals follow complex S-shaped course, comprising three loops, but no cross branch.

Bracts with: dorsal canal originating from right longitudinal canal proximal to point of origin of right hydroecial canal.

Description

Definitive nectophore: many identified as listed under Materials and Methods; mature N_1 average length 25 mm, range 17–53 mm, mature N_2 average size 22×11 mm length by width, length range 16–48 mm (largest not measurable); cylindrical, without ridges or frills, with slightly flattened apico-dorsal area (Figures 1 & 2C); hydroecium with prominent wings; latter extend from nectophore apex or sub-apex almost to base and terminate at indentation; indentation inconspicuous in N_1, more easily discerned in N_2 (Figure 2B,C); left hydroecial wing larger than right in N_1 (Figure 2A) or vice versa, folded inwards towards mid-line with one wing open when nectophore dorsal side down in dish; both wings folded inwards with edges touching or overlapping in N_2 (Figure 2B); dorsal hydroecial wall forms pocket on each side of somatocyst in N_2 (Figure 2C); somatocyst comprises pallial canal between lamellar canal and pedicular canal, elongate upper pallial canal from lamellar canal to sub-apex, and descending branch from pedicular canal to 1–3 mm above nectophore base; pedicular canal inserts onto somatocyst at approximately 2/5 nectophore height, and lamellar canal from stem apex to upper pallial canal inserts at 3/5 nectophore height; muscular lamella extends between upper pallial canal/pallial canal and lamellar canal, with upper portion only in N_1, upper and lower portions in N_2 (Figure 1); nectosac with velum and lower margin typically rolled inwards in most nectophores, obscuring bases of radial canals (Figure 2C), atypically less in-rolled so radial canal course discernible (Figure 2D); dorsal and ventral radial canals either straight throughout or with irregular courses at distal ends only (Figure 2A,B); lateral radial canal with three loops (Figure 2C,D), with loop 2 smaller than loop 1, and loop 3 largest; long descending limb of loop 3 passes over dorsal nectosac

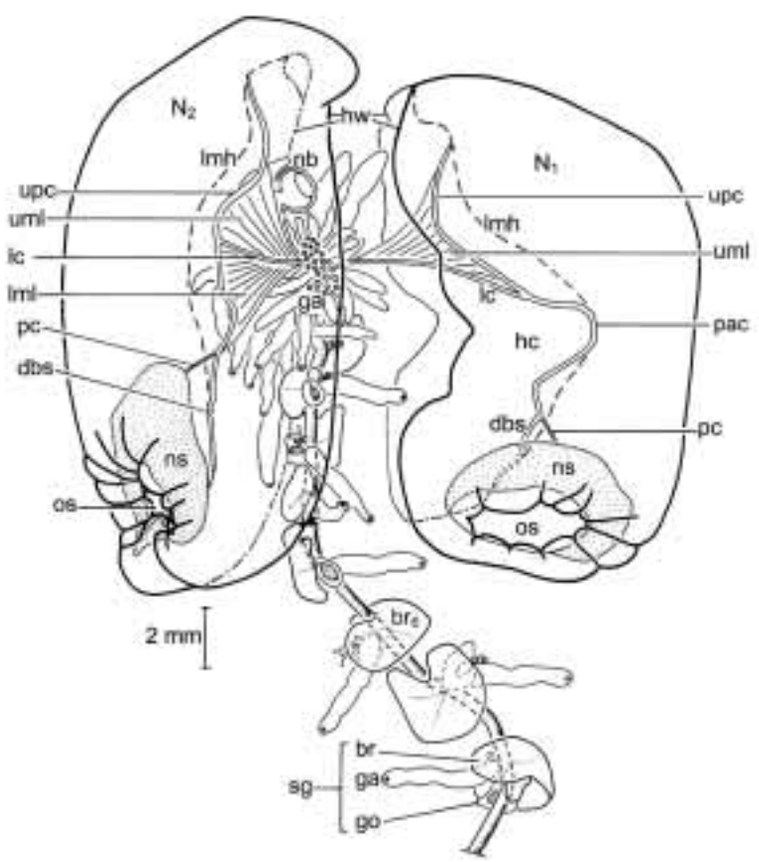

Figure 1. *Rosacea cymbiformis* pair of joined definitive nectophores with stem, including attached bract br_6 (BMNH Reg. no. 1973. 5.15.54). Abbreviations listed under Materials and Methods.

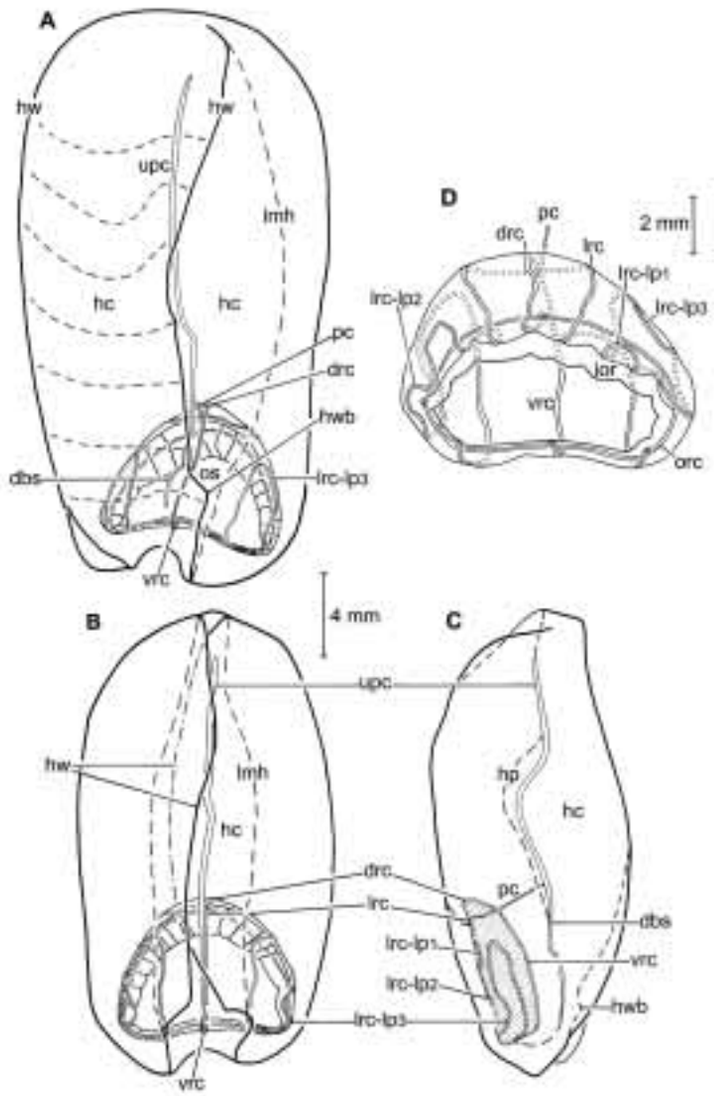

Figure 2. *Rosacea cymbiformis* definitive nectophores: (A) N_1 definitive nectophore, ventro-lateral view; (B) N_2 definitive nectophore ventral view, and (C) lateral view (BMNH Reg. no. 1952.9.23.177); (D) N_2 nectosac, dorsal view (BMNH Reg. no. 1973.5.15.53). Abbreviations listed under Materials and Methods.

wall to ostial ring canal, discernible in dorsal view (Figure 2A,B).

Immature nectophore: seven identified, size range 5×3 mm to 15×6.5 mm length by width; mesoglea turgid and apico-dorsal area flattened; hydroecium deep and hydroecial wings rigid, not touching along mid-line and with obvious indentations at bases; right wing smaller than left (Figure 3A,B), or vice versa; somatocyst thick and hydroecial cavity without dorsal pockets (Figure 3B); pedicular canal and nectosac radial canals thick (Figure 3A,B).

Reserve nectophore bud: buds identified on 46 of 55 stem apices studied, 0.5–4 mm long, with average length 1 mm, 3 mm long bud in one sample (Figure 1); atypically two buds identified (Figure 3D); buds with thick radial canals and lateral radials with three loops where discernible (Figure 3C); nectophore bud(s) and siphosomal budding zone adjacent, marking stem apex; N_2 nectophoral muscular lamella attached immediately below nectophore bud (Figure 3D), with N_1 nectophoral lamella discerned further below bud in some apices; large gastrozooids on side of siphosomal budding zone furthest from nectophore bud, representing older stem groups.

Stem groups: best preserved groups young, comprising bract typically wrapped cloak-like around stem and partially covering gastrozooid and gonophore (br_6 in Figure 1, Figure 4A–E). Bract rounded, with convex upper 'proximal' surface (closest to stem apex) and

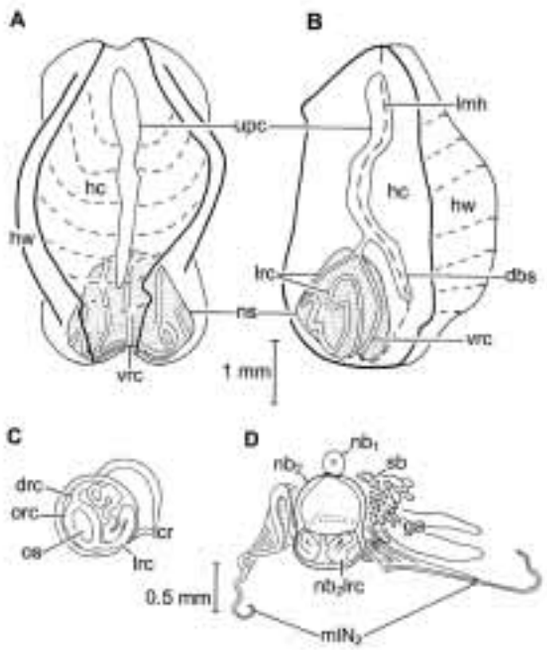

Figure 3. *Rosacea cymbiformis* immature nectophores and buds: (A) immature nectophore ventral view, and (B) latero-ventral view (BMNH Reg. no. 1952.9.23.198); (C) nectophore bud lateral view (BMNH Reg. no. 1952.9.23.198); (D) nectophore bud ostial view (BMNH Reg. no. 1952.9.23.200). Abbreviations listed under Materials and Methods.

concave lower 'distal' surface (furthest from stem apex) (Figure 4A–E), typically flatter when detached (Figure 5A–C); bracts 2–9 mm in length; detached bracts extend outwards at right angles to groove for stem, narrow in axial plane, with hydroecial axis longer than axial axis; upper surface with many small papillae (Figures 4A–E & 5A); bract with ventral and hydroecial lobes; latter subdivided into large proximal 'left' hydroecial lobe and smaller distal 'right' lobe (Figure 5C); right lobe subdivided into larger sub-lobe with small flap on inner (hydroecial) surface (rhl_1), and smaller sub-lobe partially enclosing stem (rhl_2) (Figure 4C–E), except in smallest bracts; bracteal canals six, comprise unpaired dorsal and ventral canals, paired longitudinal and hydroecial canals; longitudinals short, parallel to stem axis, terminate as small spurs (Figures 4C & 5A) and connect bracteal canals to stem canal; ventral canal longer and passes into ventral lobe close to bracteal hydroecium (Figures 4A,B & 5A–C); dorsal canal long and thin, with swollen base in young bracts, arises from right longitudinal canal proximal to right spur, passes out through mesoglea at right angles to stem axis (Figure 4A–D) and terminates in small dilation just below slight depression in bract surface; hydroecial canals extend along each side of bracteal hydroecium with left longer, originating from left longitudinal canal proximal to spur, passing into left hydroecial lobe (Figures 4B–D & 5A–C), and right shorter, originating from right longitudinal canal distal to dorsal canal but proximal of right spur, passing down into right hydroecial lobe (Figures 4B–E & 5A–C); bracteal lamellae arise from longitudinal, hydroecial and ventral canals and attach bract to stem (Figure 4C–E). Gastrozooid elongate, except near stem apex, average length 3.5 mm, with tentacle attached to proximal basigaster bearing many tentilla at different developmental stages; latter typically contracted and appear as tentillar mass under bract in most stem groups (Figures 1 & 4A,B & D,E). Gonophore height range 1.9 mm to 6 mm, flattened in plane of asymmetric apico-lateral keel and with two sub-equal surface mantle canals; in many small gonophores, longitudinal furrow extends from tip of longer mantle canal (on outer surface) to ostium (Figure 5E), but furrow not discerned in large gonophores; similar furrow on inner surface in some gonophores (not illustrated); nectosac with four straight radial canals, and ostium with diameter related to degree of contraction at preservation, small and outwardly directed in most small gonophores, larger and opening basally in large gonophores (Figure 5D); some gonophores with sperm on manubrium, others with one or more ova (Figure 5D,E); pedicular canal extends from nectosac apex to origin of two mantle canals on inner surface;

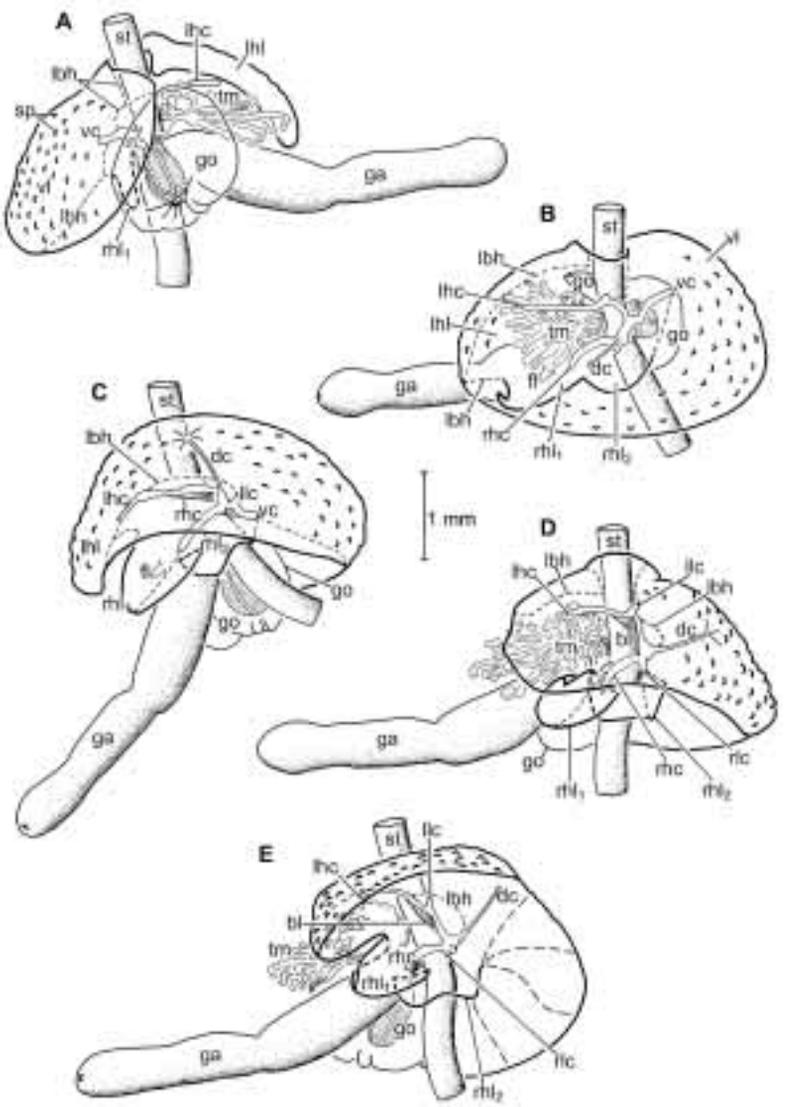

Figure 4. (A–E) Five views of *Rosacea cymbiformis* bract br_6 attached to stem, with tentillar mass omitted from (C) (BMNH Reg. no. 1973.5.15.54). Abbreviations listed under Materials and Methods.

longer mantle canal extends up over gonophore apex and onto outer surface, shorter passes down inner surface; gonophoral lamellae connect gonophore to stem from mantle canals (not illustrated).

DISCUSSION

Historical review

The original plate of *Rosacea cymbiformis* (as *Physalia cymbiformis*) is dated 1830 by Sherborn (1922, p. xxxvii), not 1822 as quoted by other authors, and the specimen was collected by Chiaje off Naples. Further Mediterranean specimens were described by Gegenbaur (1853) and Chun (1885) as *Praya maxima*, and by Leuckart (1853, 1854) as *Praya cymbiformis*. A colony from the Canary Islands was described by Haeckel as *Praya galea* (1888, plate 3), but his nectophore illustrations are poor and his bract illustrations (as *Eudoxella galea*, plate 32) include certain structures which do not exist, and others which have misleading labels because he incorrectly assumed that the bract was medusoid, whereas it is now known to be polypoid (Totton, 1965, p. 25, 120). However, Haeckel was the first to orientate the bract of *R. cymbiformis* along the axis of the hydroecial cavity, and designate the hydroecial canals as left and right, albeit as radial canals. This bract orientation was later applied by Bigelow & Sears (1937, p. 7) to the paired bracteal canals of a mature *Nectopyramis thetis* eudoxid from the Mediterranean, and it is this orientation which has been followed in all modern works on prayids, as stated by Pugh (1992a, p. 282) in the introduction to a paper revising the prayid sub-family Nectopyramidinae.

In a report on siphonophores from the Albatross Expedition, also published in 1911, Bigelow gave clear and mostly accurate figures of specimens of *R. cymbiformis*

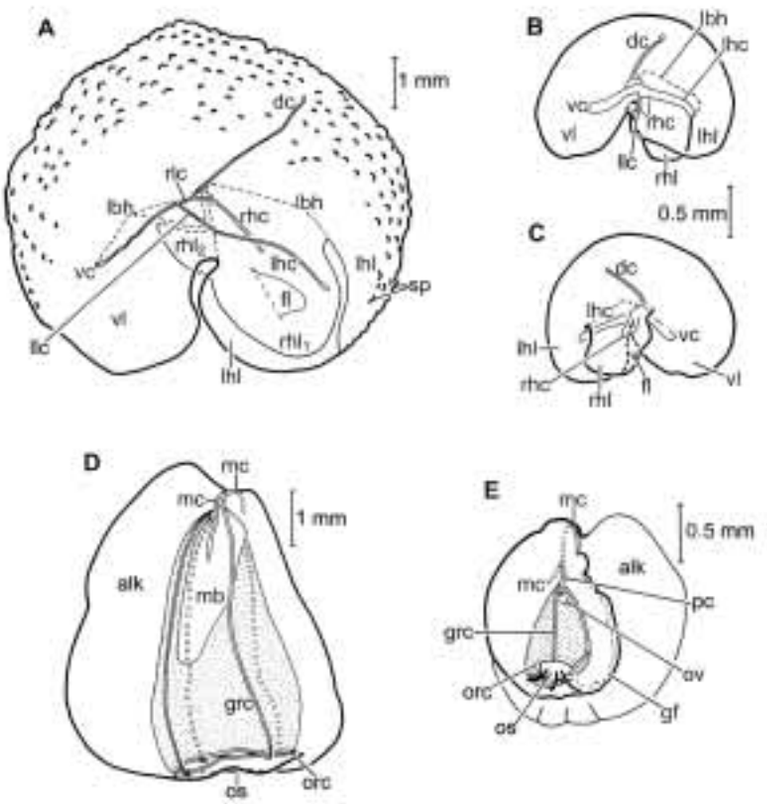

Figure 5. *Rosacea cymbiformis* detached bracts and gonophores: (A) mature bract, proximal view (BMNH Reg. no. 1973.5.15.63); (B) immature bract, proximal view, and (C) distal view (BMNH Reg. no. 1952.9.23.189); (D) male gonophore, lateral view of inner surface (BMNH Reg. no. 1902.7.29.7); (E) female gonophore, lateral view of outer surface (BMNH Reg. no. 1973.5.15. 54). Abbreviations listed under Materials and Methods.

from the tropical East Pacific (Bigelow, 1911b, plate 2, as *Praya cymbiformis*), including an attached pair of definitive (mature) nectophores, a stem apex, and two views of a bract (figures 4, 6, not oriented). Kawamura illustrated another colony from Sagami Bay, Japan, but did not orientate the bract (Kawamura, 1915, p. 318, plate 7, figures 4, 5, as *P. cymbiformis*), and later Bigelow & Sears (1937, figures 6–8), illustrated more nectophores from the Mediterranean. Totton (1965a, figure 68) included a good camera lucida drawing of a living definitive nectophore from Villefranche, with excellent figures of the course of the lateral radial canals over the nectosac and a good description of the bracteal lobes (p. 119) and lamellae. However, in his sketches of a living stem group (figure 69D, p. 120), he labelled the left hydroecial canal of Bigelow & Sears (1937) the right canal, and vice versa. Totton (1965) used the same orientation for the bracteal canals of *R. plicata*, except in his figure 66B. Carré (1969a,b) followed Bigelow & Sears orientation in bracts of two other new prayine species but used Totton's interpretation of left and right hydroecial canals in his figure of the bract of *Lilyopsis rosea* Chun, 1885 (Carré, 1969c, figure 2), although he reverted to Bigelow & Sears usage in the text on p. 76. Pugh also followed Bigelow & Sears in descriptions of bracts of a number of new prayine species (Biggs et al., 1978; Pugh & Harbison, 1987; Pugh & Youngbluth, 1988; Pugh, 1992c, 2002), and in re-descriptions of *Praya* species bracts (Pugh, 1992b). The bract characters of all prayine species described up to 1987 are summarized by Pugh & Harbison (1987, table 1), who provide a good baseline for all prayine bract descriptions, although unfortunately these were not followed for the bracts of *R. cymbiformis* and *R. plicata* in two commonly used siphonophore identification books (Kirkpatrick & Pugh, 1984, p. 54, 56; Pugh, 1999, p. 486).

Colonies of prayine siphonophores typically comprise a pair of apposed definitive nectophores and a long stem. A *Rosacea cymbiformis* colony was used by Pugh (1992a, figure 1) to illustrate basic prayine structure in a review of the subfamily Nectopyramidinae. The first nectophore to be formed in prayines is a spherical larval nectophore, and it has a small slit-like hydroecium inside which the first definitive nectophore develops. The larval nectophore is soon shed and inside the hydroecium of the first definitive nectophore a second nectophore is formed (Totton, 1965,

p. 110). Both nectophores may subsequently be lost and replaced by reserve buds, as discussed below. In a mature colony of *Rosacea cymbiformis*, Totton (1965, p. 118) described the first definitive nectophore as 'partially embracing the second in its hydroecium', but gave no details about the hydroecium of the second nectophore, although for the younger nectophore of *Praya dubia* (Quoy & Gaimard, in de Blainville, 1830) he described it as deep and 'running the entire length of the nectophore' (p. 122); this also applies to the younger *R. cymbiformis* nectophore. Unfortunately, in his description of *R. plicata*, Totton (1965, p. 118) stated that 'definitive nectophore number 1' had 'a deeper shorter, circumscribed hydroecium' and that the 'second (later) definitive nectophore' was 'comparatively larger, more closely resembling that of *R. cymbiformis*'. However, this is incorrect, and Bigelow had already shown in 1911 that in *R. plicata* the younger nectophore is the one with a deep short hydroecium (1911a, p. 343; 1911b, p. 202, plate 2, figures 7, 8), and this is confirmed here in a joined pair of *R. plicata* nectophores from the NHM collections (Reg. no. 1985.12.9.9). The older and younger definitive nectophores of prayine colonies (excluding reserve bells) were first designated as N_1 and N_2 by Carré (1969b, figure 1) and these acronyms have been used for nectophores of all new prayine species since, including the four *Rosacea* species listed above. A joined N_1 and N_2 pair of *R. cymbiformis*, with one small reserve bud, is shown in Figure 1.

Nectophores

Hydroecium and lamellae. The two definitive nectophores of *Rosacea cymbiformis* are more similar morphologically than those of *R. plicata*, though there are differences between them. The average length of a Mediterranean N_1 is slightly greater than the corresponding N_2, although the largest nectophores in the collection may indeed have reached, or even exceeded, the 6 cm quoted by Totton (1965, p. 118) for a specimen held in the Musée de Villefranche. Although the hydroecium is elongate in both nectophores, in the *R. cymbiformis* N_1 it is wide and open (Figures 1 & 2A) and partially encloses the N_2 in life (not evident in Figure 1 because the specimen was relaxed first in $MgCl_2$), whereas in the N_2 it is closed-up and resembles an elongate gutter (Figure 2B).

Totton's term pedicular canal (1965, p. 35) for the canal arising from the point of origin in the stem to the nectophore, has been split into two parts in this paper, and is restricted to the canal from the pallial canal (on the nectophore surface) to the nectosac. A new term lamellar canal is introduced for the canal from the stem to the pallial canal ('somatocyst', see below). A muscular lamella extends between the pallial canal and the lamellar canal, and consists of an upper portion only in the N_1, whereas in the N_2 a lower portion is also present (Figure 1). N_1 lamellae of this type, together with associated N_2 lamellae, were found in 19 apices, but others were either too densely pigmented or too small for accurate assessment. Bigelow & Sears (1937, figure 7) illustrate a similar N_1 lamella in a joined pair of *R. cymbiformis* nectophores from Naples. However, in another smaller joined pair from the tropical East Pacific, Bigelow (1911b, plate 2, figure 1) shows the N_1 (labelled 'N.P.') with both upper and lower portions to the lamella. The Naples N_1 was 31 mm long, whereas the Pacific specimen is only 14 mm long (Bigelow's figure 1 is probably magnified five times, not 2.5 as given in the legend) indicating that the lower portion of the lamella may only occur in the N_1 when young, and be resorbed with age. In the joined pair in Figure 1, the N_1 lamella lacks a lower portion, suggesting greater maturity than Bigelow's specimen, though it may initially have had an N_2 type lamella and lost the lower section when the hydroecium broadened to accommodate the growing N_2. The lamella of the nectophore shown by Totton (1965, figure 68C), which has a stem protruding from between closely aligned hydroecial wings, still has a lower portion, indicating that it is an N_2.

The hydroecial wings of the present *R. cymbiformis* nectophores are well developed and each terminates basally at an indentation in the ventral edge of the hydroecial cavity a short distance from the base of the nectophore (Figure 2C). This notch may be difficult to discern in preserved material since the wing edges are thin and may be folded inwards. It is more pronounced in the living nectophore shown in Totton's lateral view (1965, figure 68C), and also in the turgid preserved NHM immature nectophores (Figure 3A,B). There is asymmetry in *R. cymbiformis* nectophores, with one hydroecial wing slightly larger in the N_1 and one hydroecial pocket slightly larger in the N_2. Pockets are absent in immature nectophores and develop with age. They are also illustrated, though not labelled, by Bigelow & Sears (1937, figure 7) and Totton (1965, figure 68C). A slightly flattened apicodorsal area in the present N_2 nectophores (Figure 2C), is more prominent in immature nectophores (Figure 3B), and can also be identified in Totton's figure drawn from a living specimen (1965, figure 68C).

Somatocyst. In prayine siphonophores the somatocyst is an important diagnostic structure, occurring either as a simple tube (in *Rosacea*, *Craseoa*, *Mistoprayina* and

Prayola), or with an ascending branch from the apex which penetrates deeply into the mesoglea (*Praya*, *Desmophyes*, *Lilyopsis* and *Stephanophyes*) (Pugh & Harbison, 1987, table 1). The short apical somatocyst extension found in *Rosacea* nectophores does not qualify as an ascending branch because it does not penetrate deeply into the mesoglea. A descending branch is also present in the somatocysts of several prayine species (Pugh & Harbison, 1987, table 1), but differs from the ascending branch in never penetrating into the mesoglea, instead remaining close to the hydroecium throughout. It is simply a basal extension of the main somatocyst from the pedicular canal down the dorsal wall of the hydroecium towards the ostium, albeit of variable length. A descending branch is present in all *Rosacea* nectophores, and therefore is diagnostic of the genus. No term has yet been applied to the main region of the somatocyst, between the pedicular canal and the apex, and it is here termed the 'pallial canal', with a subdivision the 'upper pallial canal' from the insertion of the lamellar canal to the apex. Totton (1965, p. 35) defined the pallial canal as the upper and lower diverticula of the (surface) canal of the nectophore. The term mantle canal, which Totton gave as an alternative to pallial canal, is now restricted to the equivalent surface canal(s) in the gonophore (see Figure 5D,E; also Pugh & Harbison, 1987, p. 74, 78, 83; Pugh & Youngbluth, 1988, p. 645, 653). The term pallial canal used by Kirkpatrick & Pugh (1984, figure 3A, p. 147) is misleading because, as noted above, this canal is now known as the pedicular canal.

The somatocyst in *Rosacea cymbiformis* is a simple tubular structure lying along the mid-line of the dorsal surface of the hydroecium. Nectophores do not exhibit a short apical extension from the somatocyst into a pad of mesoglea, as reported in some *R. plicata* nectophores (Pugh & Harbison, 1987, p. 88), in the N_1 of *R. flaccida* (Biggs et al., 1978, p. 212), and in both nectophores of *R. repanda* and *R. limbata* (Pugh & Youngbluth, 1988, p. 638, 647).

Confusion has arisen in the past between the two definitive nectophores of *R. cymbiformis* and the N_1 nectophore of *R. plicata* (Bigelow, 1911b, p. 202), because the hydroecial opening is elongate in the former species, and variable in the latter nectophore, with a relatively long descending branch of the somatocyst in both. In *R. cymbiformis* the dorsal wall of the hydroecium continues basally from the lower end of the descending branch of the somatocyst (approximately level with the indentation at the bases of the hydroecial wings) without any changes of angle, until it joins the ostium (in the mid-line). However, in *R. plicata* the dorsal wall of the hydroecium passes through a distinct angle beyond the end of the descending branch before it continues to the ostium. This is most obvious in the N_2, but is also seen in the N_1, as shown in Totton's lateral view of an N_1 (1965, figure 65C, incorrectly given as an N_2). This angle marks the base of the hydroecium in *R. plicata* and is here termed the basal 'sill'. It tends to be more basal in the N_1 than the N_2, but in the *R. plicata* lectotype it is at a similar height in both nectophores; this lectotype appears distorted around the nectosac region, probably because it is preserved in alcohol. In two *R. plicata* specimens (Reg. nos. 1957.9.14.71, 1959.6.25.1, preserved in formaldehyde) the sill of the N_1 is at a similar height to that shown by Totton, and lower than the sill of the N_2. A sill is also shown in the N_1 of a joined pair of *R. plicata* nectophores figured by Bigelow & Sears (1937, figure 9), but this character is not found in *R. cymbiformis*.

Lamellar canal and nectosac. The lamellar canal of *Rosacea cymbiformis* inserts onto the pallial canal at 3/5 nectophore height (averaged from 15 specimens), which is slightly higher than the 2/5 shown by Totton (1965, figure 68C). However, it is less than the 7/10 measured in a figure of *R. flaccida* drawn by Biggs et al. (1978, figure 1) from a photograph of a live colony. In the latter species the lamellae of both nectophores consist only of an upper portion whereas in *R. cymbiformis* the N_2 has two portions, as discussed above. In a joined pair of *R. plicata* nectophores (Reg. no. 1985.12.9.10-16) both upper and lower lamellae portions are present in both nectophores. The N_1 lamella of a joined *R. plicata* pair shown by Bigelow & Sears (1937, figure 10) also exhibits this feature. Thus, in *R. plicata* the N_1 may have a persistent lower portion to its lamella, unlike *R. cymbiformis*. In contrast, the N_1 of the joined pair from the holotype of *R. arabiana* lacks a lamella, measures only 5 mm so may be immature, and is connected to the N_2 via a lamellar canal ('stem' of Pugh) which inserts 'roughly in the middle of the somatocyst' of the latter (Pugh, 2002, p. 171). There is a lamella in the N_2, though the lamellar canal does not pass through it in the detached nectophore of the holotype. The colony stem is fused to its free edge, except basally where it leaves the lamella and passes into the hydroecium; here it bears the largest (and possibly oldest) of several gastrozooids (personal observation).

The nectosac of *R. cymbiformis* nectophores extends to 1/4–1/3 nectophore height in the present specimens. The nectosac of *R. flaccida* was compressed into a shorter and narrower cavity when preserved, due to contraction of the ostial muscles (Biggs et al., 1978, p. 212), but this was not seen in the present *R. cymbiformis* specimens. The best preserved nectosacs are similar in shape to the live specimen illustrated by Totton (1965, figure 68C), probably because they were first relaxed in $MgCl_2$. In these nectosacs the lateral radial

canals have three loops (Figure 2C,D), even in young nectophore buds only 1 mm long (Figure 5C), although the second loop is always smaller than the first and third loops (Figure 2C,D), possibly explaining its absence from other published figures (Bigelow, 1911b, plate 2, figure 1; Pugh, 1999, figure 3.38). However, it can be discerned between the two larger loops in Totton's ventral view of a living *R. cymbiformis* nectosac (1965, figure 68A), and in a large NHM nectosac fragment (Reg. no. 1902.7.29.7).

In the present specimens, the angle of the ostium relative to the long axis of the nectophore is dorso-basal, and indeed lies almost parallel to the long axis in some nectophores (Figure 2C). It is also dorso-basal in Totton's 1965 figure 68C of a live nectophore. An earlier figure by Bigelow (1911b, plate 2, figure 1) shows the ostia more basally directed, but Totton (1965, p. 118) indicates these were not accurately represented. The ostial angle in *R. cymbiformis* thus resembles that shown for the nectophores of a live colony of *R. flaccida*, but the lateral radial canals of the latter only have two loops (Biggs et al., 1978, figure 1). In other *Rosacea* species, the ostia are more basally directed, and the lateral radial canal of *R. repanda* has a unique cross-branch, while in *R. limbata* it only has a single loop (Pugh & Youngbluth, 1988, figure 3A–D). In *R. arabiana* the origin of the lateral radial canal is from the dorsal radial canal (Pugh, 2002, p. 171) whereas in all other *Rosacea* species it is from the pedicular canal. The angle of the ostium in *R. plicata*, although basal in well preserved nectophores, sometimes appears dorso-basal if a thick wedge of mesoglea is present between the sill and the nectosac, as illustrated by Bigelow & Sears (1937, figure 9). The presence of a sill and greater turgidity of the mesoglea still serves to distinguish the nectophores of *R. plicata* from those of *R. cymbiformis*.

Buds. A small bud for a reserve nectophore was identified on most *Rosacea cymbiformis* stem apices studied, but only rarely were two buds found. Chun (1885, p. 523) studied the formation of buds in this species (as *Praya maxima*) and noted that a bud could develop 'overnight', from a stage in his plate 2, figure 9 to that shown in plate 2, figure 10. He did not give sizes in his text, nor magnifications for his figures, but comparison with the present material indicates that the bud shown in figure 9 is 2 mm long, while that shown in figure 10 might be 5 mm. Chun's observations suggest, therefore, that in favourable conditions, the mesoglea, hydroecial wings, muscular lamellae and a somatocyst rudiment of a reserve bud are formed within 24 hours, and that buds increase in length by up to 3 mm per day. From this Chun concluded that two new reserve buds can replace a pair of definitive nectophores in as little as a week—a truly rapid succession. In the apices of NHM *R. cymbiformis* specimens, new stem groups occur next to a nectophore bud, and are considered the siphosomal budding zone. Lamellae for the two definitive nectophores arise from the stem immediately below a nectophore bud and on the opposite side from the siphosomal budding zone; larger gastrozooids (representing slightly older stem groups) lie on the side of the siphosomal budding zone furthest from the nectophore bud (Figure 3D). This confirms that in *R. cymbiformis*, as noted by Totton for other prayids and calycophorans, the nectosomal and siphosomal budding zones arise together from the stem apex, and that 'the increase in length of nectosome and siphosome takes place in opposite directions' (1954, p. 24). The larger reserve nectophore buds in the present *R. cymbiformis* specimens resemble definitive nectophores in all characters except the thicker somatocyst and lack of hydroecial pockets. The reserve nectophore described by Pugh & Youngbluth (1987, p. 651) for *R. limbata* also has a thicker somatocyst, but in *R. cymbiformis* this nectophore is smooth with a relatively tall nectosac, whereas in *R. limbata* it has external mesogleal swellings, longitudinal frills and a smaller nectosac.

Bracts

The present *Rosacea cymbiformis* bracts are longest along their hydroecial axis, and reach a maximum length of 9 mm, similar to those reported by Totton (1965, p. 119). Bracts of *R. plicata* (Totton, 1965, p. 118) are twice the size of *R. cymbiformis*, and the largest *R. plicata* bract in one NHM specimen (Reg. no. 1959.6.25.1) reached 20 mm. Bracts of *R. limbata* are also twice as large as *R. cymbiformis*, and *R. repanda* bracts three times the size (Pugh & Youngbluth, 1988, p. 642, 652). Bracts of *R. flaccida* (Biggs et al., 1978, p. 213) are the same length as *R. cymbiformis*, whilst those of *R. arabiana* are smaller (Pugh, 2002, p. 171).

The best preserved bracts of *R. cymbiformis* exhibit a surface covered with small papillae (Figures 4 & 5A), which are also found on bracts of *R. repanda* and *R. limbata* (Pugh & Youngbluth, 1988, p. 645, 653).

One *R. cymbiformis* bract still attached to its stem shows the upper convex 'proximal' surface composed of the ventral and left hydroecial lobes, while the right hydroecial lobe hangs down from the lower concave 'distal surface beneath the left lobe (Figure 4A–E). Similar lobes were observed on the bract of *R. plicata* (Totton, 1954, text figures 41–42, where right and left hydroecial canals were transposed), *R. repanda* (Pugh & Youngbluth, 1987, p. 638, 642, figures 4, 5), and *R. limbata* (Pugh & Youngbluth, 1987, figure 11). In bracts of *R. cymbiformis* the inner

surface of the right hydroecial lobe bears a small flap, and a similar flap is present in the four above mentioned species. However, the bracts of *R. flaccida* and *R. arabiana* differ from this basic plan, suggesting they may be less closely related to *R. cymbiformis* than the four other *Rosacea* species.

Bracts attach to the stem via muscular bracteal lamellae from the longitudinal, ventral and hydroecial canals (Figure 4C–E), and these are well illustrated and described in Totton's account of *R. cymbiformis* (1965, figure 69B,D, p. 120, where left and right hydroecial canals are again transposed), but have not been described in any other *Rosacea* species. Young bracts of *Rosacea cymbiformis* have thick canals, except for the dorsal canal (Figures 4 & 5B,C), and in mature bracts the canal tips are slightly swollen (Figure 5A). The ventral and left hydroecial canals are not inflected into the mesoglea distally as they are in *R. repanda* and *R. limbata* (Pugh & Youngbluth, 1988, p. 645, 653). Bracts of *R. cymbiformis* have short longitudinal canals, aligned parallel to the stem and adjacent to a short groove through which the stem passes. In attached bracts this groove is extended by the small sub-lobe of the right hydroecial lobe (Figure 4, rhl_2), which partially encloses the stem distally. In mature detached bracts the groove is less easily discerned, but occurs below the right and left spurs of the longitudinal canals, at right angles to the hydroecial axis of the bract (Figure 5A). In detached bracts of *R. plicata* the groove is similarly marked by spurs (Totton, 1965, figure 66B; Pugh & Harbison, 1987, figure 13F) and in *R. repanda* and *R. limbata* by a short left longitudinal spur and the dorsal canal/right longitudinal canal junction (Pugh & Harbison, 1987, p. 643). In *R. arabiana* the bract is nearly spherical, with a deep hydroecium and shallow lateral incisions for the stem (Pugh, 2002, p. 171). The bract in *R. flaccida* is markedly asymmetric with longitudinal canals the longest of all *Rosacea* species (Biggs et al., 1978, figure 2), though it is atypical of the genus. In all *Rosacea* bracts (except *R. arabiana*) the left hydroecial canal is longer than the right: only slightly longer in *R. plicata* (Totton, 1965, figure 66) and *R. flaccida* (Biggs et al., 1978, figure 2), but considerably so in *R. repanda* and *R. limbata*, and may have side branches in *R. limbata* (Pugh & Youngbluth, 1988, figures 5, 11). The unpaired ventral canal of *R. cymbiformis* resembles that of *R. plicata* and *R. arabiana* in length, is shorter than that of *R. repanda* and *R. limbata* and much shorter than *R. flaccida*. The dorsal canal is thinner in *R. cymbiformis* than other canals, and passes out from the right longitudinal canal towards the proximal, or 'upper' surface of the bract, where it dilates slightly and terminates below a small surface depression (Figure 4C). In young bracts the origin of the right longitudinal canal is thickened (Figure 4C,D), but this is lost in older bracts (Figure 5A). Mature bracts of *R. plicata* show the dorsal canal terminating below a surface depression (Pugh & Harbison, 1987, figure 13F), but in *R. repanda* and *R. limbata* it (or a side branch from it) ends beneath a superficial transverse furrow (Pugh & Youngbluth, 1988, figures 5, 11).

Gonophores

Gonophores of NHM *Rosacea cymbiformis* specimens are up to 6 mm in height (Figure 5D), though most are only 2–4.5 mm. The gonophore illustrated as Figure 5E is of similar size to that shown by Bigelow & Sears (1937, figure 8). Gonophores are attached to the stem between the gastrozooid and the ventral lobe of the bract, with a prominent apico-lateral keel projecting away from the stem, and the ostial opening of the nectosac facing outwards (Figure 4A). In many gonophores the ostium is small (Figures 4A & 5E), but in others it is larger (Figure 5D), resembling the gonophore figured by Pugh & Harbison (1987, figure 13D), with ostial diameter presumably dependent upon degree of contraction at preservation. In NHM gonophores the apico-lateral keel is not as tall as that shown by Pugh & Harbison for *R. cymbiformis* (1987, figure 13D). Two main surfaces are identifiable: an 'inner' surface lying adjacent to the gastrozooid, and an 'outer' surface onto which the ostium opens. In detached gonophores, the pedicular canal opens onto the inner surface at or near the apex, and gives rise to two mantle canals of different lengths. The shorter extends down the inner surface of the gonophore (Figure 5D), and the longer passes over the apex onto the outer surface where it typically terminates at the top of a vertical groove (Figure 5E). This groove passes down to the ostium, though is not apparent in all gonophores, including the large example shown in Figure 5D. Another vertical groove may pass down the inner surface (Pugh & Harbison, 1987, figure D), but is not illustrated here. The nectosac of *R. cymbiformis* reaches up to 9/10 gonophore height, with straight radial canals.

Gonophores are also asymmetric in other *Rosacea* species (except *R. flaccida*), and again all have straight radial canals on the nectosac. However, the nectosac is slightly shorter in *R. plicata* (Pugh & Harbison, 1987, figure 13D), shorter still in *R. repanda* and *R. limbata* (Pugh & Youngbluth, 1988, figures 6, 12), and considerably shorter in *R. arabiana* (Pugh, 2002, figure 2D), reaching only 1/2 gonophore height. In contrast, it fills the entire gonophore in *R. flaccida* (Biggs et al., 1978, plate 3, figures 3, 4). A prominent but slightly differently shaped apico-lateral keel is illustrated in

the most recently published figure of an *R. plicata* gonophore (Pugh & Harbison, 1987, see above), while in *R. repanda* and *R. limbata* the keel is less developed, and in *R. arabiana* it is small and relatively insignificant (references quoted above). In *R. plicata* and *R. arabiana* the apex of the nectosac is rounded, as in *R. cymbiformis*, but in *R. repanda* and *R. limbata* it is constricted apically, and in the latter species forms a unique narrow elongate diverticulum (Pugh & Youngbluth, 1988, figure 12). Totton (1965, p. 121) made several observations on living colonies of *R. cymbiformis* and noted that active pulsations of the gonophores help spread the stem for feeding.

CONCLUSIONS

A re-description of *Rosacea cymbiformis* is presented and characters distinguishing its nectophores and bracts from those of the five other *Rosacea* species discussed. Throughout this discussion the designation of N_1 and N_2 definitive nectophores for *Rosacea* species is reinforced, with emphasis on *R. plicata*. This paper also addresses the varied (and muddled) use in the literature of 'right and left' to bract orientation, and adopts a consistent approach throughout.

The nectophores of *R. cymbiformis* are flaccid with a smooth surface, have a lower muscular lamella portion in the N_2, a dorso-basal ostium, an elongate hydroecial opening that is broad in the N_1, narrow in the N_2, a somatocyst without an apical extension into the mesoglea or any side branches from the upper pallial canal, no sill at the base of the hydroecial cavity, and a nectosac with a three looped lateral radial canal which originates from the pedicular canal. The bracts are of moderate size when mature, flattened at right angles to the stem, have ventral and left hydroecial canals that are not ?-shaped distally and lack side branches, and a dorsal canal which originates from the right longitudinal canal proximal to the right hydroecial canal.

In *R. plicata* the nectophores are turgid, the ostium typically basal, the hydroecial opening elongate in the N_1 only, the somatocyst with or without an apical extension, a sill marking the base of the hydroecial cavity, and lateral radial canals with only two loops. Bracts are larger when mature, and have a dorsal canal which originates from the right longitudinal canal distal to the right hydroecial canal.

Rosacea repanda nectophores have a frill where the hydroecial wings join the nectophore body, and a somatocyst with an apical extension, a pallial/upper pallial canal with short branches in the N_2, and lateral radial canals with a unique cross branch. Bracts are much larger when mature, have longer ventral and left hydroecial canals which are ?-shaped distally, and a dorsal canal that originates from the tip of the right longitudinal canal.

In *R. limbata* the nectophores also have a frill, and two prominent apico-lateral swellings, the somatocyst has a small apical extension in both nectophores, branches from the pallial/upper pallial canal in the N_2, and the lateral radial canals have only one loop. Bracts are also larger when mature, have longer ventral and left hydroecial canals which are ?-shaped distally, with side branches from the left hydroecial, and a dorsal canal which originates from the tip of the right longitudinal canal and exhibits a side branch.

Rosacea arabiana nectophores have an elongate hydroecial opening in the N_1 only, the somatocyst has a shorter descending branch, and the lateral radial canals uniquely originate from the dorsal radial canal. Bracts are sub-spherical and the dorsal canal originates from the tip of the right longitudinal canal.

Finally, *R. flaccida* nectophores are slightly more flaccid, have only upper portions to the muscular lamellae in both nectophores, an apical extension to the somatocyst in the N_1, and lateral radial canals that have only two loops. Bracts have an enlarged ventral lobe flattened parallel to the axis of the stem, reduced hydroecial lobes, a particularly elongate ventral canal, and a dorsal canal which originates from the right longitudinal canal.

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Note. This paper was accepted before the paper by Haddock, Dunn & Pugh (2005)* (introducing a new terminology) was submitted to this issue.

* Haddock, S.H.D, Dunn, C.W. & Pugh, P.R., (2005). A re-examination of siphonophore terminology and morphology, applied to the description of two new prayine species with remarkable bio-optical properties. *Journal of the Marine Biological Association*, **85**, 695–707.