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Redescriptions of two physonect siphonophores, *Apolemia uvaria* (Lesueur, 1815) and *Tottonia contorta* Margulis, 1976, with comments on a third species *Ramosia vitiazi* Stepanjants, 1967 (Cnidaria: Hydrozoa: Apolemiidae)

Abstract Two species referable to the physonect siphonophore family Apolemiidae are re-described: *Apolemia uvaria* (Lesueur, 1815), the type species, and *Tottonia contorta* Margulis, 1976. Descriptions, based mainly on three colonies from the Mediterranean (*A. uvaria*) and three taken off California (*T. contorta*) contain new information on some zooids and update previous information on others. Figures show the arrangement of nectophores on the nectosomal stem, budding zones, possible degenerative zones and all zooid types (except gonophores in *A. uvaria*). The morphology of these two species is discussed in relation to a third species *Ramosia vitiazi* Stepanjants, 1967. These descriptions provide a benchmark for up to 10 putative new species of apolemiids believed to exist but not yet described.

Key words *Apolemia uvaria*, Apolemiidae, Cnidaria, Hydrozoa, morphology, Physonectae, *Ramosia vitiazi*, Siphonophora, *Tottonia contorta*

Introduction

The aims of this paper are threefold. First, to provide more complete morphological descriptions than currently exist of the type species *Apolemia uvaria*, and of a second apolemiid species *Tottonia contorta*. Full descriptions of the structure and arrangement of nectophores and nectosomal tentacles on the nectosome in *A. uvaria*, as well as descriptions of the gonophore on the siphosome of *T. contorta*, are currently lacking from the literature. Second, to relate these findings to a third known apolemiid species *Ramosia vitiazi*. Finally, to update previous descriptions of siphosomal zooids in *A. uvaria*, some over 150 years old, and bring them into the wider public domain.

Apolemiids are widely distributed in the world's oceans but are more difficult to identify to species level than those in other physonect families, because apolemiids lack tentilla. This increases the significance of nectophore morphology, in particular the structure of any diverticula that may arise from the lateral radial canals of the nectosac. This paper provides more accurate descriptions of the course of this canal than is shown in recently published figures of *Apolemia uvaria* (Kirkpatrick & Pugh, 1984 fig. 6; Pagès & Gili, 1992, fig. 4; Pugh, 1999*a*, fig. 3.5). Figure 1 summarizes the terminology used in this paper.

Apolemiids were first distinguished from other physonect siphonophores by Huxley (1859), who erected a new family based on the single species *Apolemia uvaria* with tentacles between the nectophores. These nectosomal tentacles are unique and were considered by Totton (1965: 47) to represent aboral larval tentacles of ancestors of the siphonophores. They are quite different to siphosomal tentacles which are probably oral in origin (Leloup, 1954).

Totton described the species *Apolemia uvaria* as 'one of the most interesting, most difficult to study and least understood' of all the physonects (Totton, 1965: 45). In his monograph he includes a reproduction of the original plate by Lesueur from a specimen collected in the Mediterranean and published in 1815 (reproduced here as Fig. 14), but his own description is relatively brief and his original figures are few. Totton's illustrations of the nectophore (1965, fig. 14a–b) do not include an axial view, and in his abaxial view the ventral furrow is inaccurately shown. Several lengthy descriptions followed Lesueur's publication, chiefly in German (Eschscholtz, 1829; Gegenbaur, 1853*b*; Kölliker, 1853; Leuckart, 1853, 1854; Claus, 1863). Some are based on immature specimens (Gegenbaur, 1853b, fig. 1) and none describe and illustrate a mature nectophore showing both the complete canal system and surface furrows. More recent figures of the species, although of better quality, are of questionable

identification as noted above. The present description of *A. uvaria* is based on several specimens held in the collections of The Natural History Museum, London (NHM), formerly the British Museum (Natural History) (BMNH), and includes more detailed figures than previously published.

Since the publication of Totton's monograph, two new apolemiid species *Ramosia vitiazi* (Stepanjants, 1967) and *Tottonia contorta* (Margulis, 1976) have been described, and several giant species are known to exist (Mackie *et al.*, 1987). The original description of *R. vitiazi* is brief, and, although the original description of *T. contorta* was later expanded, based on further material in 1980, it also remains inadequate. This paper gives a fuller description of three larger and more mature *T. contorta* colonies collected off California, with comments on the paratype of *R. vitiazi*. It concludes with a discussion of affinities between the three apolemiid species so far described.

Materials and methods

APOLEMIA UVARIA. BMNH 1952.9.23.85; 1952.9.23.86–92, 1952.9.23.94, 1952.9.23.95; 1952.9.23.96 comprise parts of five colonies collected by Totton at Villefranche in the Mediterranean, relaxed in $MgCl_2$ and preserved in formalin, with a single nectophore collected on 21.3.49 in 1952.9.23.85, six nectophores collected from a specimen 5 m long (when alive) on 21.3.49 in 1952.9.23.86–92, 29 bracts collected on 21.3.49 in 1952.9.23.94, a single nectophore collected on 23.3.49 in 1952.9.23.95, and seven loose nectophores, as well as the nectosomal stem and the upper part of the siphosomal stem from a specimen 10 m long (when alive) collected 0.5 km off Villefranche on 23.4.49 in 1952.9.23.96. The stem of the latter specimen is relatively supple and easy to manipulate, but also transparent due to loss of epidermis and associated pigment during storage. These specimens are referred to collectively as the 'Villefranche specimens'. BMNH 1898.5.7.21 is an almost intact colony taken from off the Zoological Station at Naples in the Mediterranean, preserved in alcohol, and purchased by the NHM as part of the 'Norman Collection' in 1898. BMNH 1902.7.29.8 is another almost intact colony from Naples, originally mounted on a glass rod in a thin glass cylinder (probably for display purposes) and purchased by the NHM in 1902. Both specimens are firm with a noticeably contracted stem, but do not appear to have been relaxed prior to preservation. Their nectophores are somewhat distorted, but their epidermis is well preserved, has an opaque yellowish colour, and the nectosomal stems show considerable lengths of siphosomal stem attached. These two are referred to below as the 'Naples specimens'.

Apolemiid specimens examined from the NHM collections and elsewhere not specifically referable to *Apolemia uvaria* include BMNH 1957.3.22.53 and 1957.3.22.54 (15 nectophores from 53°22.6′S 56°02′W and 12°08.0′N 20°53.5′W respectively), 1960.12.2.1–5 (Scotia Collection, Shetlands, quoted in Fraser, 1955), Discovery Station No. 9791-12 held at Southampton Oceanography Centre (illustrated in Kirkpatrick & Pugh, 1984, fig. 6), and Dublin Museum Reg. No. 141.1985 from Gearies Pier, Bantry Bay, Ireland held at the Dublin Museum (quoted in Minchin, 1987). Other apolemiid material examined at an early stage in this study came from Discovery Stations 9790-2, 9756-1, 9791-6, 9794-2, and is probably also not *A. uvaria*. A specimen of *Apolemia* sp. from the Benguela Current Collection No. SNEC II: E-73 P-2 (1) (illustrated in Pagès & Gili, 1992 as *Apolemia uvaria*) was kindly loaned by F. Pagès.

TOTTONIA CONTORTA. Three specimens taken off Point Conception, California during a Childress Expedition in March 1993 and kindly donated to the author by S. Haddock of the University of California, Santa Barbara have been deposited in the NHM collections. They comprise BMNH 2002.787 which includes 12 loose nectophores, untwisted nectosomal stem, and six sections of siphosomal stem all collected from 1400 m at approx 34°50.68′N 122°45.00′W on 8.3.95, BMNH 2002.788 which includes five loose nectophores, nectosome with one twist and a short portion of attached siphosome from 400–100 m at 34°59.39′N 123°02.10′W and collected on 8.3.95, and BMNH 2002.789 which consists of eight loose nectophores, nectosome with two twists and a similar short portion of attached siphosome collected from 1500 m at 34°50.71′N 122°55.40′W on 9.3.95. Two nectophores from the holotype figured by Margulis (1976, figs 7–11) taken by RS "Pyotr Lebedev VII" from 600–583 m at Station 11 (07°35′N 87°54′E) and kindly loaned by S. Stepanjants were also examined.

RAMOSIA VITIAZI. A paratype specimen comprising four nectophores and two stem fragments, held at the Zoological Academy of Sciences, St Petersburg No. 3/9902 collected from 1765 m at 53°04′N 146°10.5′E by the "Vitiaz" on 21.7.51 was kindly loaned by S. Stepanjants.

Specimens were transferred to a Petri dish of distilled water using a perforated teaspoon and examined with a Zeiss binocular microscope and attached camera lucida. Where possible specimens were drawn lying freely on the bottom of the dish, but were supported occasionally in a deep-sided Petri dish using various combinations of small perspex bridges and blocks held together with 'Blu-Tack'. Substage lighting was used for transparent material, supplemented with lateral lighting for opaque material using two Schott flexitube lights. This precluded the necessity for staining, which, in gelatinous material, can sometimes make certain structures more difficult to discern.

Terminology and orientation

Descriptions in this paper are based primarily on the terminology used by Pugh (1999*a*) for physonect siphonophores, with some terms taken from Totton (1965). Apolemiids are long-stemmed physonects and, for the purposes of the present descriptions, the colony is viewed and orientated in a vertical position in the water with the gas-filled float, the pneumatophore, uppermost (Fig. 1). In life, however, physonects typically adopt other positions when swimming (Lesueur, 1815, un-numbered plate, reproduced here as Fig. 14). Below the terminal pneumatophore is the nectosome with nectophores

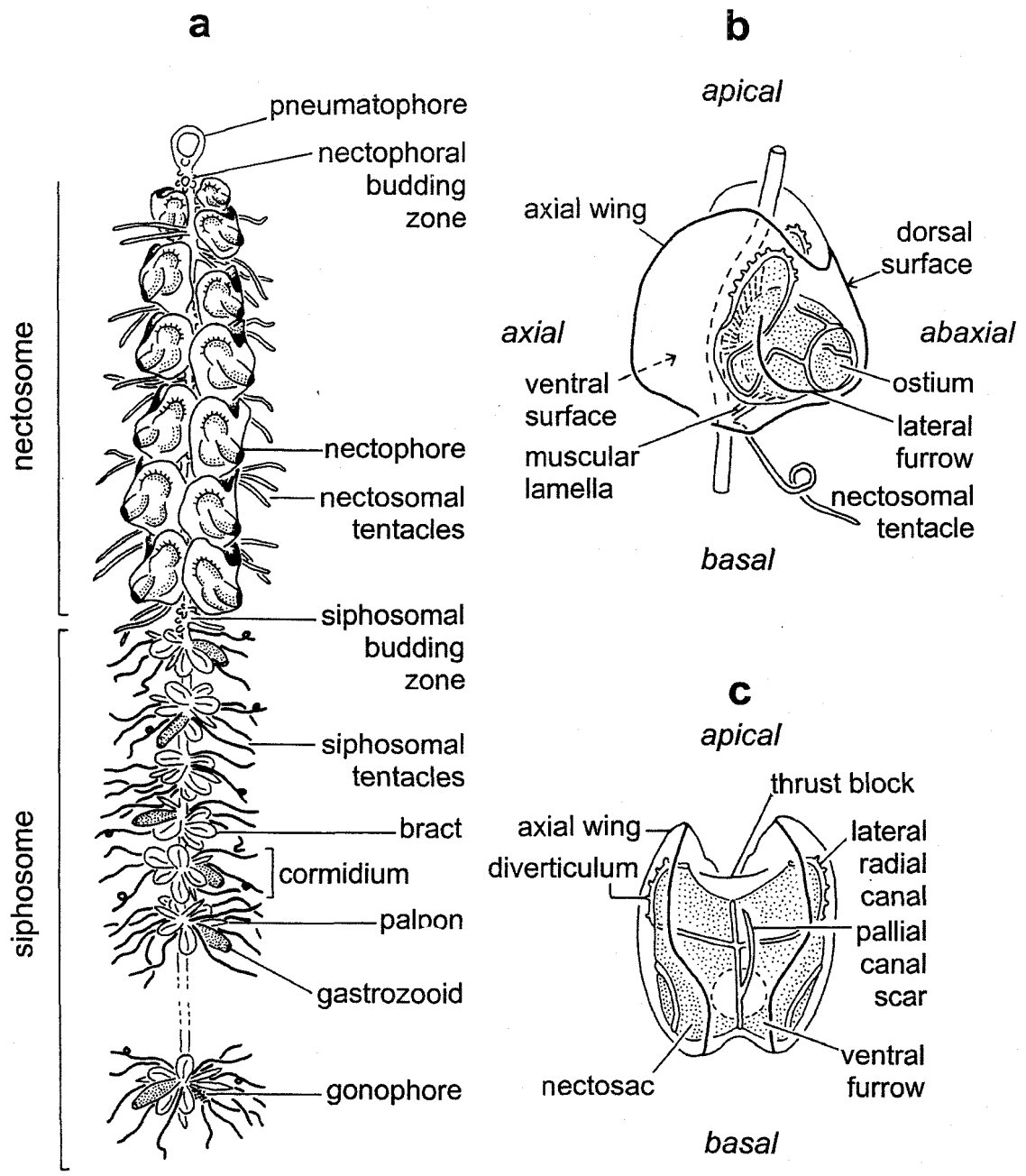

Figure 1 Schematic representation of *Apolemia uvaria*, **a**: whole colony; **b** and **c**: two views of nectophore illustrating orientation on the stem and main morphological features.

for propulsion, followed by the siphosome with zooids for feeding, defence and reproduction; the latter are typically clustered together into groups known as cormidia.

The pneumatophore, which is considered a neoformation (Mackie, 1999), is formed by an invagination of ectoderm at the planula stage (Carré, 1967, 1969). It is thickened apically, with an outer wall, the pneumatocodon, and an inner chitin-lined sac containing gas, the pneumatosaccus; the latter has a gas gland, the pneumadenia, in its basal region. The pneumatophore is typically borne on a thin stalk or pedicel, which can be considerably contracted in preserved material.

At the top of the elongate nectosome is the nectophoral budding zone, which lies on the ventral side of the stem. Below are a number of mature nectophores, also attached to the ventral surface by a series of muscular lamellae opposite a dorsal groove. Nectophores are medusoid in origin (Pugh, 1999*a*), and each contains a muscular nectosac for propulsion, which opens via an ostium on the abaxial (dorsal) surface furthest from the stem. The lamellae insert onto the opposite axial (ventral) surface of the nectophore, with the upper part of this surface deeply hollowed out and bordered by two large axial wings which extend around the stem. When an apolemiid colony is disturbed, mature nectophores frequently detach (Totton, 1965), probably as a result of sudden contractions of the longitudinal stem muscles and associated lamellae. When a lamella shortens the nectophore is ripped off, and sometimes

this causes the mesoglea to split in the axial mid-line. Since the latter is typically thick and turgid, this split does not significantly affect the shape of the nectophore. If a detached nectophore is placed in a flat-bottomed dish, it is most easily viewed axially (viewing the ventral surface) whilst lying on its relatively flat abaxial surface. To obtain a good abaxial view (view of the dorsal surface), it may be necessary to support the lower part of the nectophore with one or more perspex blocks, as noted above. Support may also be required for a good lateral view, particularly if the tips of the axial wings are widely flared. Between the axial wings is the thrust block, a thickened area of mesoglea, which may cushion the nectophore during swimming. A ventral furrow extends downwards from the base of the thrust block in the mid-line, under the basal region of the nectophore and terminates just short of the ostium. Two lateral furrows extend from the ostium under the basal region of the nectophore and up over the lateral surfaces.

The radial canals of the nectosac originate from the endodermal stem canal, and are connected to it by a short pedicular canal. At the point where the latter passes through the muscular lamella, it gives off a blind-ending upper pallial canal, which extends apically to near the top of the thrust block. In stems from which the nectophores have become detached, this canal is visible at high magnification as a gutter-like scar extending along the torn edge of the muscular lamella, from the pedicular canal to the lamella apex. Its complement on the nectophore, here termed the pallial canal scar, is also apparent as a gutter passing up the surface of the thrust block. The pedicular canal inserts onto the dorsal and ventral radial canals at the surface of the nectosac, just below the junction with the pallial canal. Two lateral radial canals originate from the dorsal canal a short distance above the insertion point of the pedicular canal, and all four radial canals pass over the surface of the nectosac to insert separately onto the abaxial ostial ring canal. In life, the lower half of the muscular lamella is attached to the ventral radial canal, but in detached nectophores this canal is present only as an elongate gutter-like ventral canal scar on the axial nectophore surface. The muscular lamella itself remains attached to the nectosomal stem, and the complement of the ventral canal scar passes along its torn edge from the pedicular canal to the lamella base.

Siphosomal zooids are produced in a budding zone on the stem immediately below the last nectophoral lamella, in the ventral mid-line. Each cormidium comprises four types of zooids: bracts, palpons, gastrozooids (which are of polypoid origin) and in a reproductively mature colony, gonophores (which are medusoid). Bracts are numerous, rounded, gelatinous and important for providing buoyancy to the siphosome. Each has a single bracteal canal and is attached to the stem via a bracteal lamella. Palpons (or dactylozooids) are slender, elongate and play an important role in digestion (Mackie & Boag, 1963). Gastrozooids are typically larger, with a distal mouth for ingestion of prey, muscular walls with internal ridges, and a basal cnidogenic band where all the nematocysts of the colony are manufactured (Mackie *et al.*, 1987). The ridges, also known as hepatic stripes, are thought to consist of secretory cells (Carré and Carré, 1995). Palpons and gastrozooids each have a single highly extensible tentacle arising from the base which bears stinging nematocysts along its length for prey capture; tentacles arising from palpons are often termed palpacles. Gonophores lack a tentacle because they are medusoid (Totton, 1965) and are either distributed throughout the length of the siphosome or restricted to the distal end. Male gonophores consist of an umbrella enclosing a manubrium, or spadix, which bears many sperm. In female gonophores the subumbrellar cavity is filled with (typically) a single large yolky, or centrolecithal, ovum; the manubrium, which originally bears the ovum, is displaced to one side and forms a number of manubrial, or spadicine, canals which grow over the ovum surface. Sex cells originate in the ectoderm.

Abbreviations used in figures

aml	apex of nectophoral muscular lamella (subscript denotes relationship to numbered muscular lamella)
axp	axial process (of nectosac)
axw	axial wing
bad	basal disc (of gastrozooid)
bc	bracteal canal
bcs	bracteal canal scar
bd	developing bract
bf	buccal fold
bk	bracteal keel
bml	base of nectophoral muscular lamella (subscript denotes relationship to numbered muscular lamella)
br	bract (subscript denotes relationship to numbered cormidium)
cb	cnidogenic band
ch	chitin
coa	circum-ostial opaque area
com	cormidium (com_1 – first cormidium on siphosome, etc.)
dg	dorsal groove
dgo	developing gonophore
div	diverticulum
dnt	distal end of nectosomal tentacle
drc	dorsal radial canal
$drcn_2$, $drcn_4$	dorsal radial canals of n_2 and n_4 respectively
gc	gas cavity
gmo	gastrozooid mouth
grc	gonophore radial canal
gte	gastrozooid tentacle
gvc	gastrovascular canal
hs	hepatic stripe
ir	inner ridge of palpon
lf	lateral furrow
lrc	lateral radial canal
mbc	manubrial canal (spadicine canal)
ml	nectophoral muscular lamella
n_1, n_2	nectophores still attached to nectosome
nb	nectophoral bud
nbz	nectosomal budding zone
$n_2$ml	muscular lamella of n_2

nem	nematocysts
ns	nectosac, enclosing subumbrellar cavity
nst	nectosomal stem
nt	nectosomal tentacle (subscript denotes relationship to numbered muscular lamella)
nt_1–nt_z	nectosomal tentacles from lamellae 1-z
ntb	nectosomal tentacle base (subscript denotes relationship to numbered muscular lamella)
ot	ostium
opa	opaque palpon (*A. uvaria*)
opp	opaque patch
opr	ostial process
ops	opaque spot
orc	ostial ring canal
pac	pallial canal
pe	pedicel (of gonophore)
pec	pedicular canal
pal	palpons (*T. contorta*)
pas	pallial canal scar
pcl	palpacle
pcb	palpacle base
pcc	pericystic cavity
pn	pneumatophore
pnc	pneumatocodon
pnd	pneumadenia (gas gland)
pns	pneumatosaccus
pnt	proximal end of nectosomal tentacle
ppa	pigmented palpon (*A. uvaria*)
ppb	bud of pigmented palpon
rs	refractile sphere
sbz	siphosomal budding zone
sst	siphosomal stem
tb	thrust block
te	tentacle of gastrozooid or palpon
teb	tentacle base(s)
umb	umbrella of gonophore
ve	velum
vf	ventral furrow
vrc	ventral radial canal
vrs	ventral radial canal scar
yo	yolk

Systematic descriptions

Apolemia uvaria (Lesueur, 1815) (Figs 2–8)

Stephanomia uvaria Lesueur, 1815: un-numbered plate; Risso, 1826: 306.

Apolemia uvaria Eschscholtz, 1829: 143 (*in partim*), pl. 13 fig. 2a–e; Gegenbaur, 1853*a*: 109; Gegenbaur, 1853*b*: 319 (*in partim*), pl. 18 figs 1–4; Kölliker, 1853: 18 (*in partim*), pl. 6 figs 6–9; Leuckart, 1853: 3, pl. 1 figs 2–3, 17; pl. 2 fig. 22; Leuckart, 1854: 313 (*in partim*), pl. 12 figs 6–8, 10–11; Huxley, 1859: 127 (*in partim*), pl. 12 fig. 8; Keferstein & Ehlers, 1861: 25, pl. 1 figs 11–13, 22–23 (*in partim*); Claus, 1863: 537 (*in partim*), pl. 46 figs 1–12, 14–15; Korotneff, 1884: 231, pl. 14 figs 8–9, pl. 17 fig. 67, pl. 19 figs 93, 95–96; Haeckel, 1888*a*: 39 (*in partim*); Haeckel, 1888b: 213 (*in partim*); Willem, 1894: 354 (*in partim*), pl.1 figs 1–5; Iwanzoff, 1896: 338, pl. 5 figs 24–33; Schneider, 1898: 117 (*in partim*); Lo Bianco, 1904: 57 (*in partim*), pl. 36 fig. 152; Bigelow, 1911: 348 (*in partim*); Weill, 1934: 511, figs 83–84; Totton & Fraser, 1955: 2, figs 3, 8*a–c*; Trégouboff & Rose, 1957: 352, pl. 79 fig. 6; Totton, 1965: 45 (*in partim*), pl. 8, txt figs 13–17; Carré & Carré, 1973: 237, txt figs 1–4, figs 1–32; Carré, 1974*a*: 208, pl. 3 figs 1–3, pl. 4 figs 1–4; Carré & Carré, 1980: 110, figs 6, 12; Margulis, 1980: 347; Bonnemains & Carré, 1991: 51, fig. 10; Carré & Carré, 1995: 541, figs 174, 186–187, 202.

Apolemia urania Blainville, 1834: 119 (*in partim*), pl. 3 fig. 1, 1a, 1b.

?*Apolemiopsis dubia* Brandt, 1834: 36.

Physophora ulophylla Costa, 1835: 12, pl. 4.

Apolemia lesueuria Lesson, 1843: 518 (*in partim*).

Agalma punctata Vogt, 1854: 83, pl. 12, figs 1–8 (*in partim*).

Apolemia uviformis Haeckel, 1888*a*: 39; Römer, 1902: 177 (*in partim*).

Apolemopsis uviformis Haeckel, 1888*b*: 213.

?*Apolemia dubia* Haeckel, 1888*a*: 39.

?*Apolemopsis dubia* Haeckel, 1888*b*: 213.

?*Dicymba diphyopsis* Haeckel, 1888*a*: 39 (*in partim*); H[illegible]kel, 1888*b*: 210, pl. 18 figs 1–7.

?*Apolemia uvaria* Kirkpatrick & Pugh, 1984: 28, fig. 6a–b; Minchin, 1987: 255; Alvariño *et al.*, 1990: 5, fig.1a–b; Pagès & Gili, 1992: 70, fig. 4; Båmstedt *et al.*, 1998: 79, fig. 3; Wrobel & Mills, 1998: 45 fig. 61; Pugh, 1999*a*: 481, figs 3.5, 3.21.

?*Apolemia* sp. Östman, 2000: 32, fig. 1b–e, fig. 3a–d.

HOLOTYPE. Since there is no extant holotype of *Apolemia uvaria* in existence, and BMNH 1902.7.29.8 is the most complete preserved specimen of this species in the NHM collection, it is here designated as a neotype.

DIAGNOSIS. Nectosomal tentacles in groups of 4–6 at base of each nectophore; lateral radial canals of nectophore S-shaped, with distinct diverticula penetrating into mesoglea from proximal part (on nectosac axial process) and distal part forming deep loop over latero-basal nectosac surface; dorsal radial canal straight. Bract with swollen tip to bracteal canal and canal penetrating into mesoglea distally, dividing into upper branch in mesoglea, and lower branch fusing with lower surface of bract; upper surface of bract with nematocysts clustered into small opaque spots.

DESCRIPTION

PNEUMATOPHORE. Pale yellow or translucent in present material and up to 5 mm long and 3 mm in diameter in Villefranche specimen, tapering gradually into nectosome without distinct stalk (Fig. 2a–b); obscured by attached nectophores in Naples specimens (Fig. 3a); in Villefranche specimen greater extension indicating pneumatophore likely

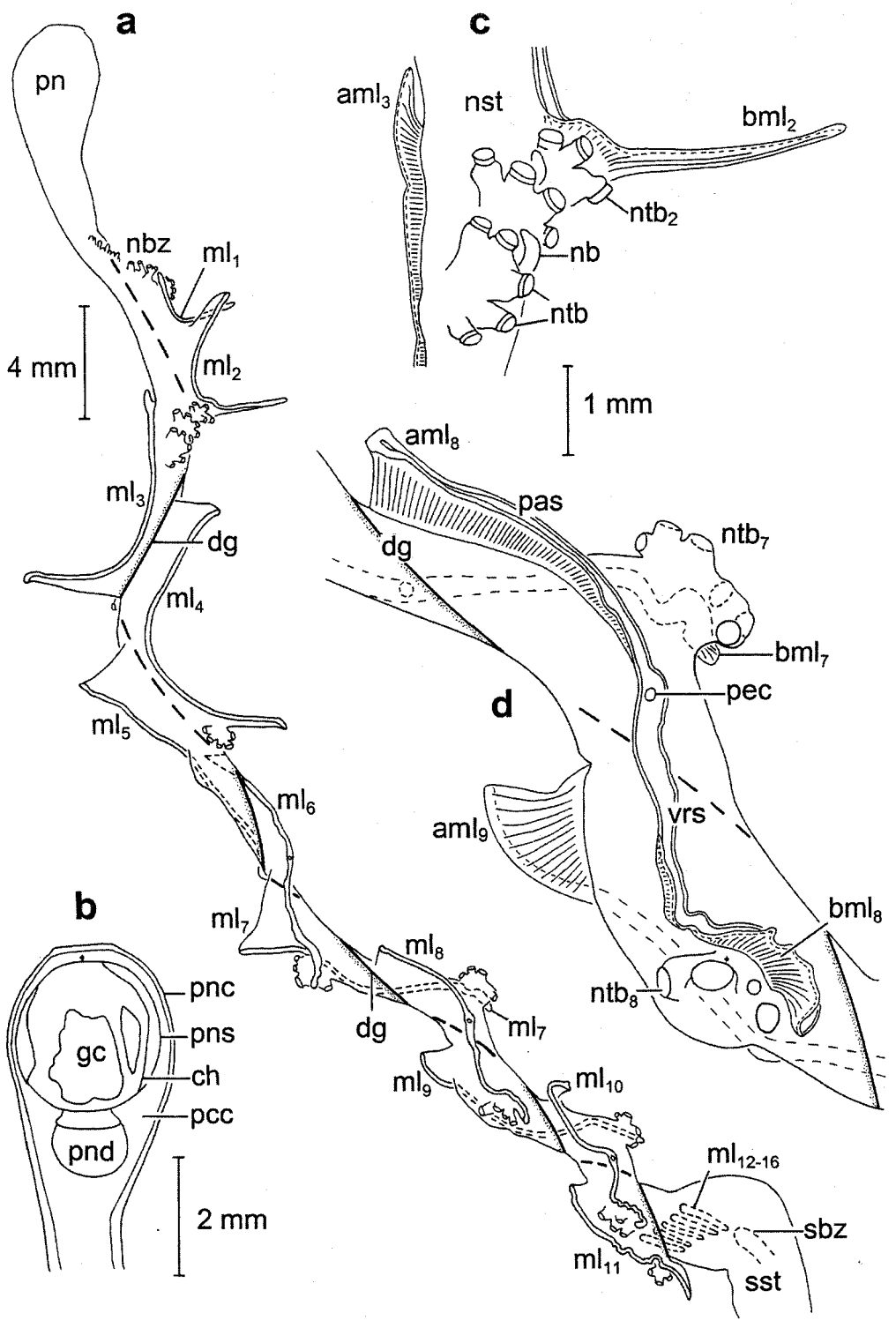

Figure 2 *Apolemia uvaria*, Villefranche specimen 1952.9.23.96; **a**: nectosome showing spiral stem; **b**: detail of pneumatophore; **c**: detail of parts of two muscular lamellae and intervening tentacle groups from upper region of nectosome showing two nectophore buds (nb), each with associated nectosomal tentacle bases (ntb), base of muscular lamella bml_2 (with associated nectosomal tentacle bases ntb_2) and apex of muscular lamella aml_3; **d**: detail of muscular lamella ml_8 from apex aml_8 to base bml_8 from lower region of nectosome, also showing position of pedicular canal and tentacle bases ntb_8. For abbreviations see list in text. Prefixes 'a' in aml_8 and 'b' in bml_2 and bml_8 only included in figs **c** and **d**.

to protrude above level of nectophores in life; apex with raised circular area bearing traces of pigment, but no apical pore discernible; chitin lining of pneumatosaccus preserved in latter specimen, occupying upper 2/3 of pneumatophore and forming collar around lower spherical pneumadenia (Fig. 2b).

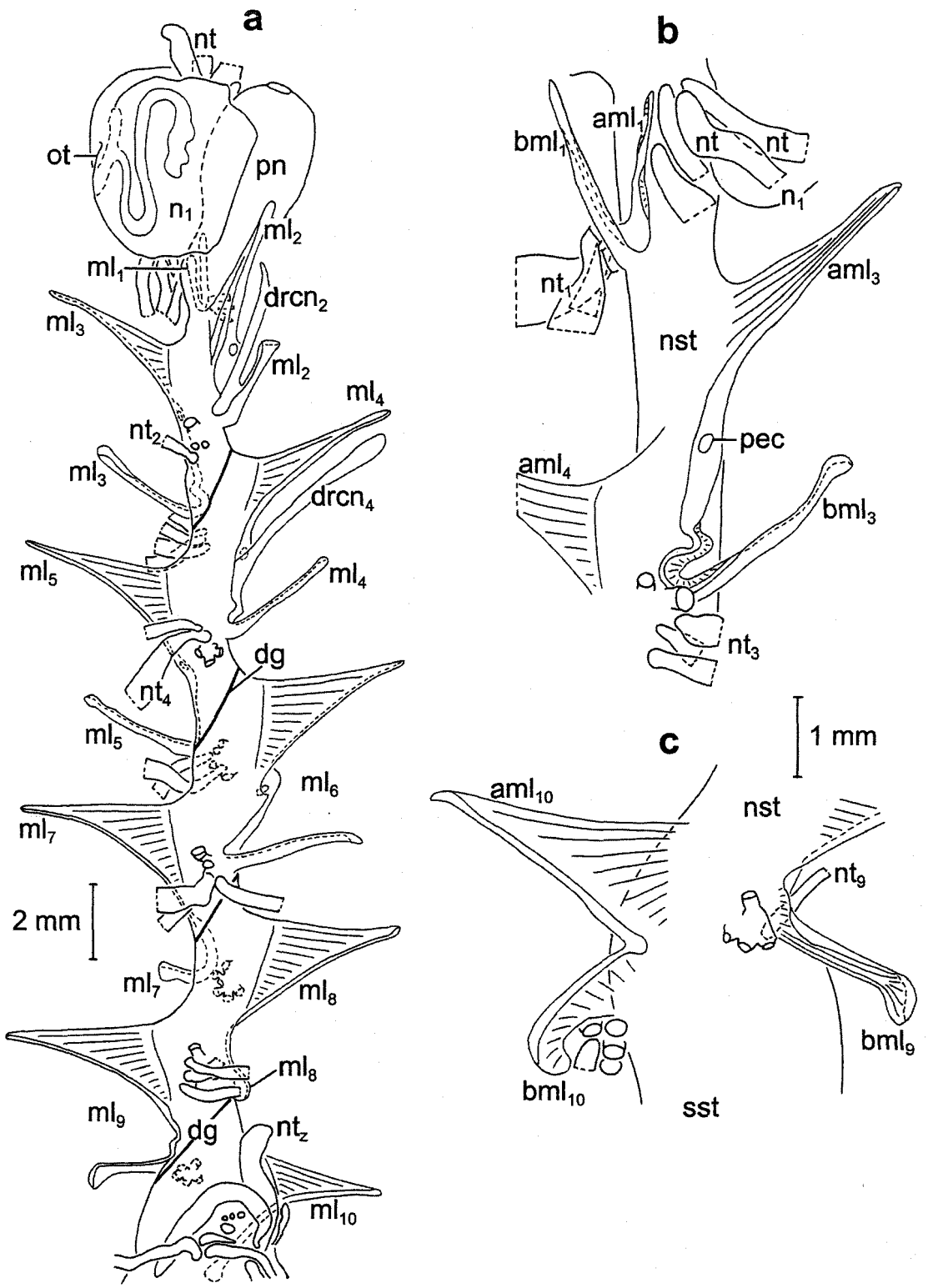

Figure 3 *Apolemia uvaria*, Naples specimen 1898.5.7.21; **a**: nectosome showing spiral stem; **b**: detail of muscular lamella ml_3 from apex aml_3 to base bml_3, viewed from reverse side on upper part of nectosome just below pneumatophore; **c**: detail of two muscular lamellae ml_9 and ml_{10}, viewed from near base of reverse side of nectosome. For abbreviations see list in text. Prefixes 'a' in aml_3, aml_4 and aml_{10} and 'b' in bml_3, bml_9 and bml_{10} only included in figs **b** and **c**.

NECTOSOMAL TENTACLES. Translucent or whitish, sometimes with slightly brownish distal tip; tentacle bases in Villefranche specimen and attached tentacles in Naples specimens arising in bunches from nectosomal stem near right side of base of each muscular lamella (Figs 2a, 2d, 3a–c), with portion of stem supporting tentacles typically

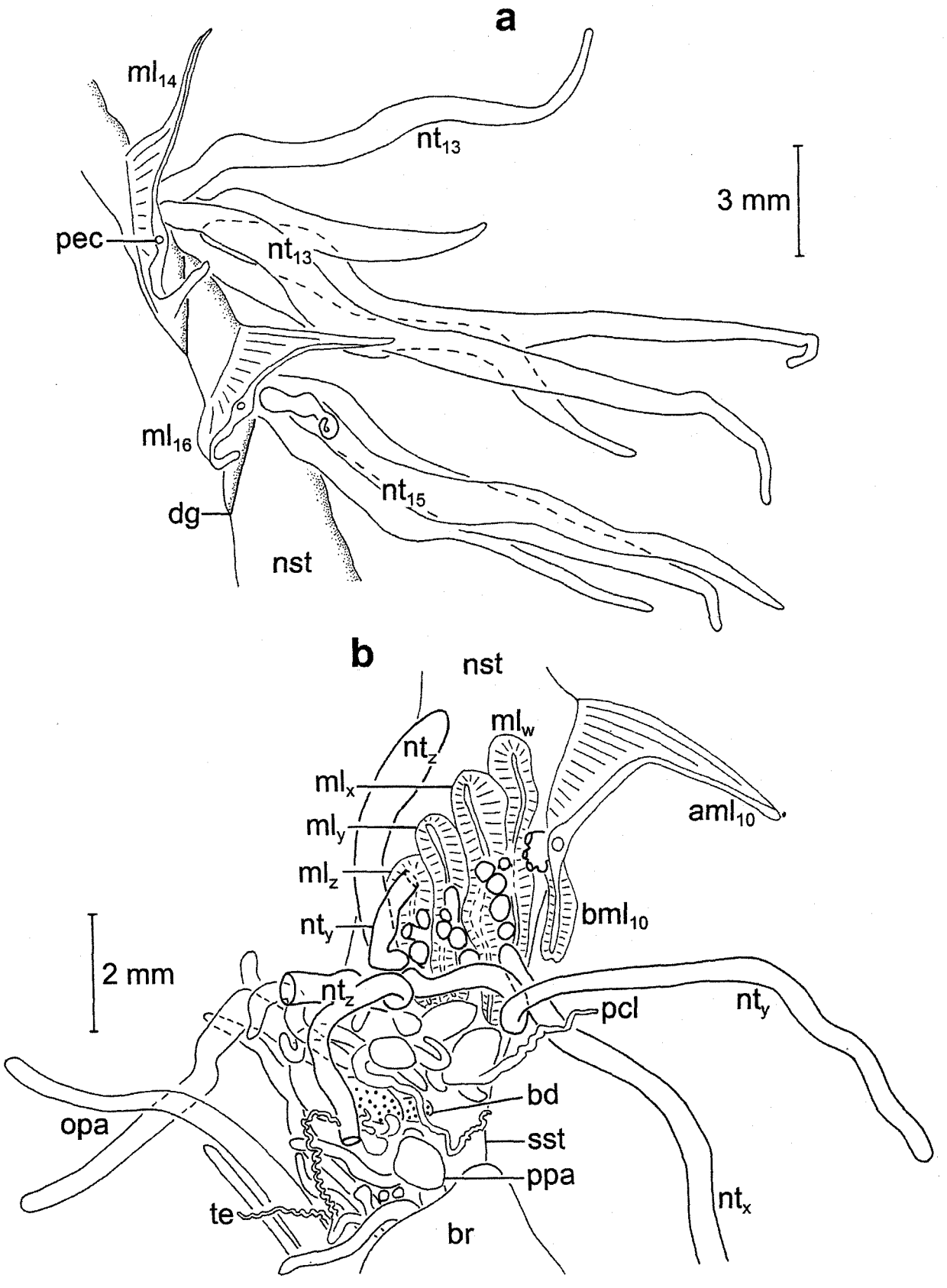

Figure 4 *Apolemia uvaria*, **a–b**: Naples specimen 1902.7.29.8, two muscular lamellae ml_{14} and ml_{16} from lower region of nectosome with nectosomal tentacles nt_{13} and nt_{15} protruding from reverse side of nectosome and associated with obscured muscular lamellae ml_{13} and ml_{15}; **b**: Naples specimen 1898.5.7.21 at junction of nectosome (nst) and siphosome (sst) showing detail of old muscular lamellae ml_w – ml_z (possibly degenerating) and siphosomal budding zone with developing pigmented palpons (ppa) and bracts (br). For abbreviations see list in text.

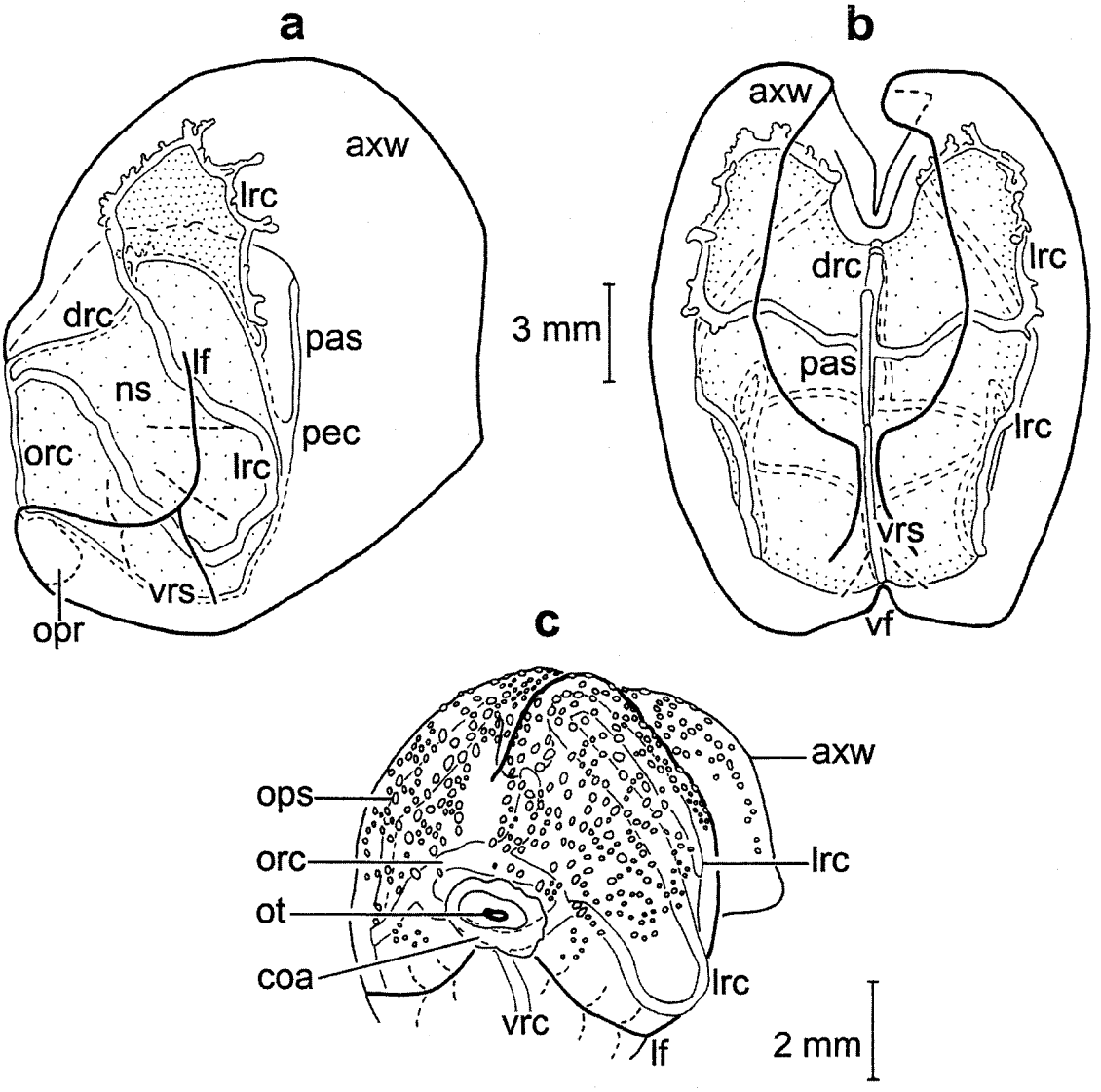

Figure 5 *Apolemia uvaria*, **a–b**: Villefranche specimen 1952.9.23.96, young detached nectophore (originally attached near top of nectosome shown in Fig. 2a) **a**: lateral view, **b**: axial view; **c**: Naples specimen 1902.7.29.8, abaxial view of newly formed nectophore still attached near top of nectosome to show distribution of opaque spots. For abbreviations see list in text.

swollen in relaxed Villefranche specimen (Fig. 2d); attached tentacles in Naples specimens up to 23 mm in length, 1 mm in width, becoming narrower distally with rounded tip (Fig. 4a). Small dense cells visible at high magnification in epidermis, particularly around tentacle tip, which may be nematocysts.

NECTOSOMAL STEM. Opaque grey-yellow, contracted in all samples, but less in Villefranche specimen (Fig. 2a) than in Naples specimens (Fig. 3a), measuring 32–50 mm long; stem twisted to varying degree with lamellae attached on ventral surface and dorsal groove opposite; latter following spiral course around stem from just below pneumatophore to siphosome (Figs 2a, 3a, 4a); 11 fully formed lamellae identifiable in Villefranche specimen, with another five presumed non-functional lamellae below (Fig. 2a); Naples specimens each with 10 fully formed lamellae, and additional four presumed non-functional lamellae below in BMNH 1902.7.29.8 (Fig. 4b) and three in BMNH 1898.5.7.21; fully formed lamellae with torn edges bearing pallial canal scar and ventral canal scar clearly discernible, and with pedicular canal also typically evident (Figs 2d, 3b, 4a).

NECTOPHORES. Grey-brown in Naples specimens with firm mesoglea, while transparent in Villefranche specimens (due to loss of epidermis) with softer mesoglea; colony with up to 17 nectophores in life, most large and mature. Immature nectophores up to 17 mm in height, with tips of axial wings either touching (Fig. 5c) or close together (Fig. 5b); epidermis with opaque spots on all abaxially directed surfaces; radial canals of nectosac thicker than in mature nectophores and diverticula smaller; several small young nectophores present in Naples specimens, including one still attached to nectosome (Fig. 5c) and larger detached immature nectophore in Villefranche specimen. Mature nectophores up to 21 mm in height and 16 mm in width, deep in axial/abaxial plane with well developed axial wings; latter broadest apically with tips coming to rounded points (Fig. 6a–b); Naples nectophores

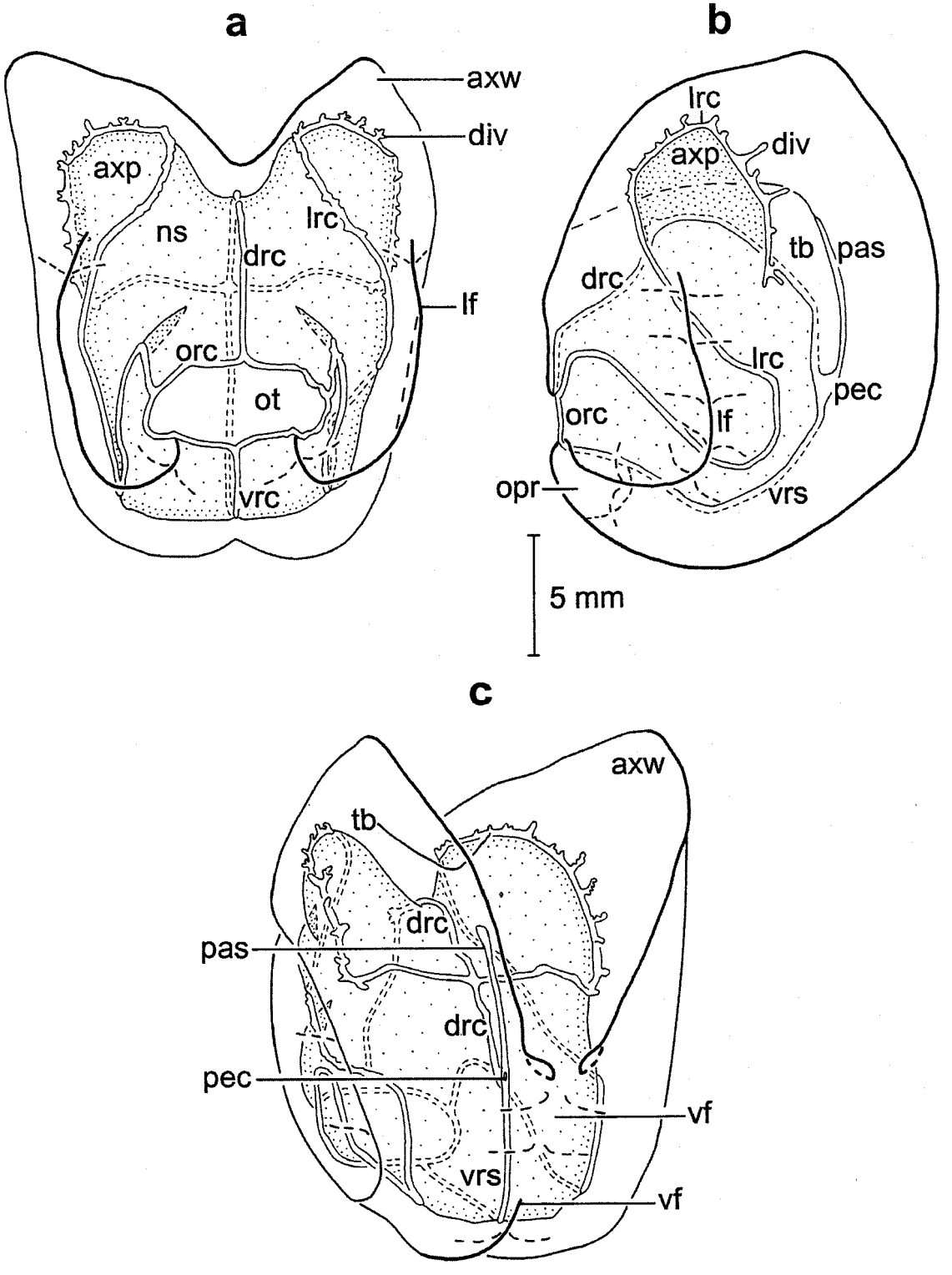

Figure 6 *Apolemia uvaria*, Villefranche specimen 1952.9.23.96, mature detached nectophore (originally attached in mid-lower region of nectosome shown in Fig. 2a) **a**: abaxial view; **b**: lateral view; **c**: axio-lateral view. For abbreviations see list in text.

with small opaque spots in epidermis on upper and lateral surfaces, spots typically thicker than surrounding epidermal layer and each consisting of tightly packed cells similar to those on upper surface of bract; indentations in external mesogleal surface indicating presence of spots in mature Villefranche nectophores; ostium typically elliptical in Naples specimens, delimited by broad velum and outer dense opaque area of many small brown pigment spots (this area shown in young nectophore in Fig. 5c); axial surface with distinctive borders of axial wings extending from tips down towards

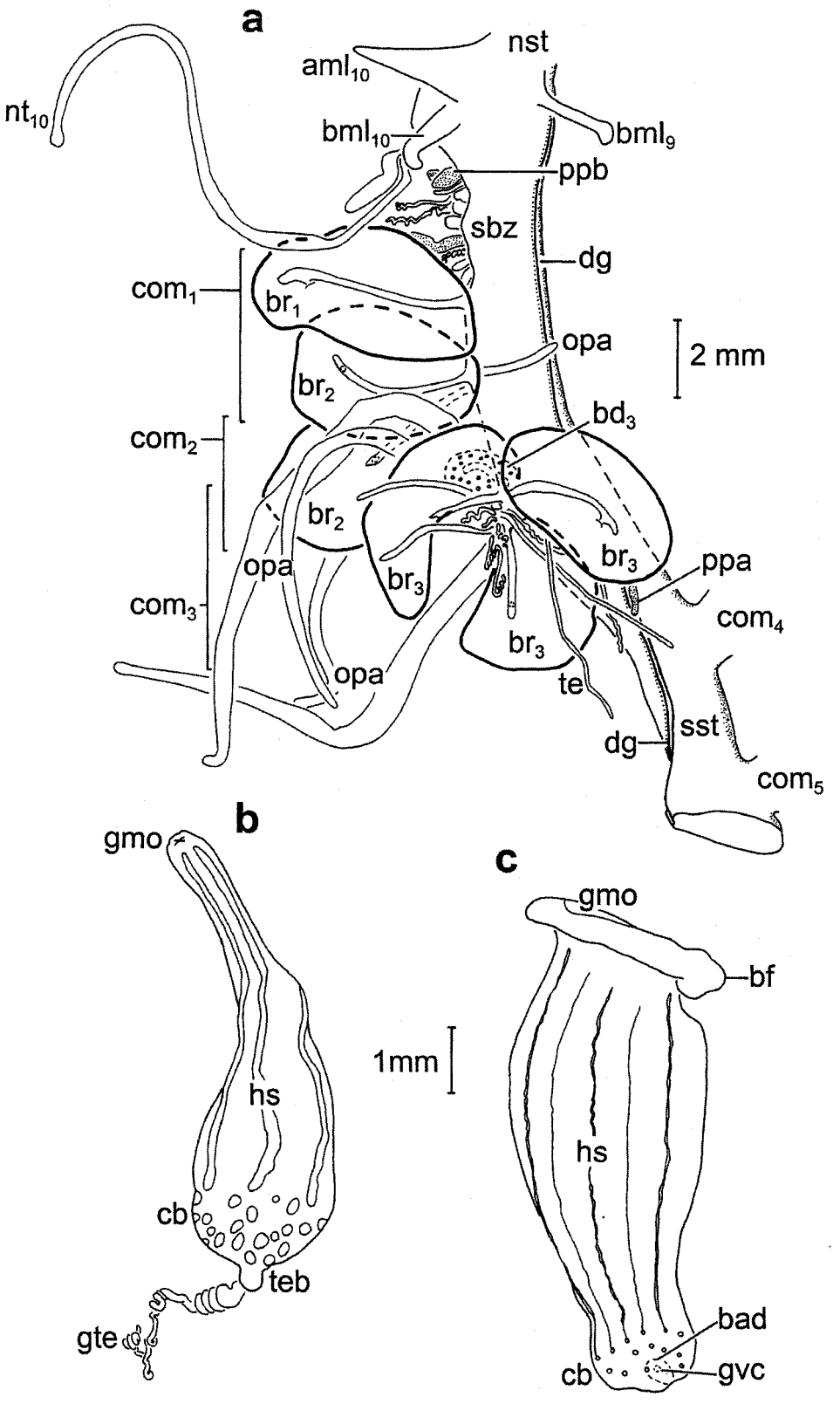

Figure 7 *Apolemia uvaria*, **a–b**: Naples specimen 1902.7.29.8, **a**: cormidia at upper end of siphosome, **b**: gastrozooid with closed mouth; **c**: Villefranche specimen 1952.9.23.96, gastrozooid with open mouth. For abbreviations see list in text.

mid-ventral (axial) line, terminating close to latter (Fig. 6c) with wing margins thinnest basally; mesoglea thickened between axial wings as thrust block; lateral furrows each arising from latero-basal portion of ostium, passing under abaxio-basal region of nectophore, then vertically up lateral nectophore surface and terminating just above 1/2 nectophore height (Fig. 6a–b); ventral furrow extending from bases of axial wings down to base of nectophorein mid-ventral line

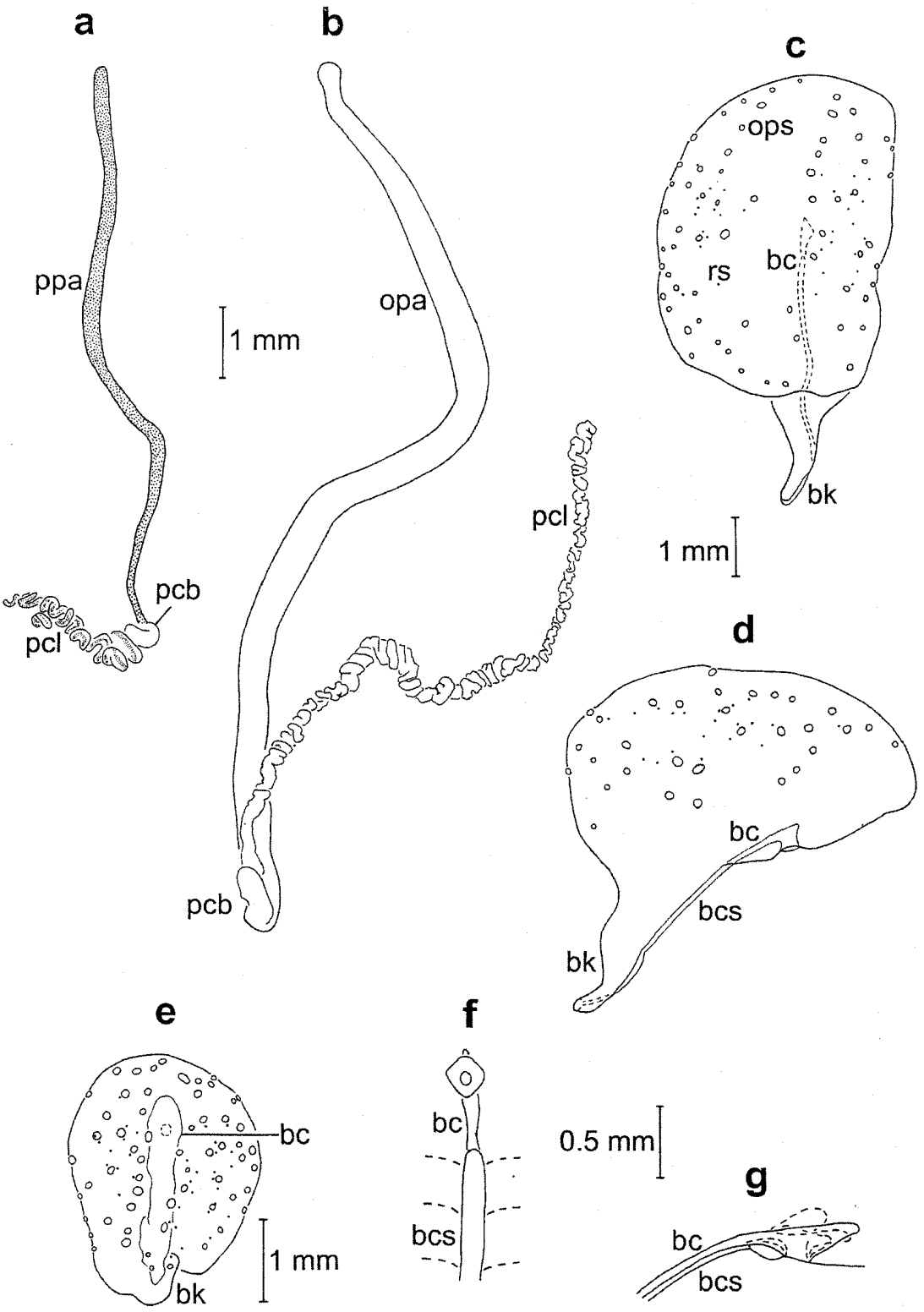

Figure 8 *Apolemia uvaria*, Naples specimen 1902.7.29.8: **a**: pigmented palpon with palpacle; **b**: opaque palpon with palpacle; **c**: bract, upper view; **d**: bract, lateral view; **e**: young bract, upper view; **f**: detail of distal end of bracteal canal, lower view; **g**: variation in shape of distal end of bracteal canal with tips of bracteal canals from several different bracts superimposed and shown in lateral view. For abbreviations see list in text.

(Fig. 6c), under basal region and terminating on axial side of ostial process.

Nectosacs yellowish and opaque in Naples specimens but somewhat distorted due to preservation in alcohol; nectosacs transparent and detached from nectophores in Villefranche specimens, but outlines conform to inner contours of mesoglea (Fig. 6a–c); nectosac contours mirror those of nectophore with two broad rounded axial processes extending into axial

wings; radial canals pale brown-yellow in Naples nectophores, and discernible as distinct grooves on both inner nectosac walls and inner mesogleal surface in Villefranche nectophores (Fig. 6a–c); dorsal radial canal straight and smooth-walled, except for 1–2 small diverticula at junction with abaxial surface (Fig. 6b–c); lateral radial canals smooth-walled, except over extensions into axial wings,with diverticula developed of varied length, with or without branches, arising at approximately regular intervals from main canal and always penetrating deeply into mesoglea (Fig. 6a–c); ventral radial canal forming gutter-like scar on floor of ventral furrow from pedicular canal to axial side of ostial process, becoming true canal for short distance from ostial process to ostial ring canal (Fig. 6b); pallial canal scar also gutter-like, arising from short pedicular canal and extending apically over thrust block in mid-line almost to apex, slightly enlarged apically (Fig. 6b–c); ventral radial and pallial canals complete and still attached to nectosome in mature nectophores of Naples specimen BMNH 1902.7.29.8.

SIPHOSOMAL STEM. Pale grey in colour and up to 725 mm long in Naples specimens, and 200 mm in relaxed Villefranche specimen; three small discrete cormidia attached to ventral side of siphosomal stem immediately below nectosome (Fig. 7a) with seven more identified distally; many cormidia on remainder of siphosome, but exact number difficult to determine; dorsal groove identifiable opposite cormidia throughout, with some twisting apparent, twists looser than in nectosome; siphosomal budding zones identified in all specimens (Fig. 2a, 7a).

GASTROZOOIDS. Pale grey-brown in Naples specimens, measuring up to 9mm by 3 mm with 1–3 per cormidium; size related to age and degree of contraction; six pale hepatic stripes visible through column wall of most gastrozooids (Fig. 7b), occasionally five, sometimes alternating with six (or five) thinner stripes (Fig. 7c); stripes representing vertical ridges of endoderm extending from just below mouth to basal region, above cnidogenic band; latter visible through column as series of opaque patches; stripes and patches only slightly opaque in translucent gastrozooids of Villefranche specimen; some gastrozooids with reflexed buccal fringe (Fig. 7c); in Naples specimens basal region with slightly enlarged white base to tentacle arising from one side (Fig. 7b) but basal disc not visible; in illustrated Villefranche gastrozooid (Fig. 7c) tentacle detached, and basal disc and aperture for gastrovascular canal shown with broken lines (Fig. 7c); in other gastrozooids tentacle seen arising from side of basal disc; gastrozooid tentacle with similar structure to palpacles of palpons (Fig. 8a–b), having row of nematocysts along one side of tentacle with latter typically tightly contracted into spiral and tangled with other tentacles in present specimens; longest portion of tentacle dissected out in present study 3.5 mm in length.

PALPONS. Two forms identified: first opaque and off-white with distinct brownish tip in Naples specimens, transparent in Villefranche specimen; measuring up to 26 mm long and 1 mm wide, slightly thinner distally (Fig. 8b) and many per cormidium; second golden-brown, up to 12 mm long and 0.5 mm wide, tapering slightly towards apex (Fig. 8a), some with pointed tips and few per cormidium. Single palpacle from base of each palpon, similar in both types, with swollen white base and thin opaque tightly coiled distal tentacle; finer distal section successfully dissected out in some palpons revealing row of slightly darker coloured nematocysts on one side, extending from base to tip (Fig. 8a).

BRACTS. Translucent, bluish in colour, measuring up to 9 mm long and 4 mm wide, typically still attached in Naples specimens with many per cormidium; transparent and mostly detached in Villefranche specimen; mature bracts somewhat scaphoid (shaped like upturned boat) with rounded upper surface and bilaterally flattened keel at proximal end (abutting stem) (Fig. 8c–d); bracts with many small opaque spots of nematocysts (see discussion), except in mid-line, interspersed with smaller refractile spheres (Fig. 8c); bracteal canal arising from stem canal at end of keel, and extending along lower surface in mid-line; present as gutter-like bracteal canal scar in detached bracts for most of length due to separation from bracteal lamella at preservation; distal bracteal canal with short, narrow upper branch of variable shape (Fig. 8g), and lower branch with diamond-shaped area fused to lower bracteal surface (Fig. 8f); young bracts more rounded with denser distribution of opaque spots and refractile spheres on upper surface (Fig. 8e).

GONOPHORES. No gonodendra or loose gonophores identified in any samples.

REMARKS

In the synonymy, earlier descriptions and records are deemed correctly identified as *Apolemia uvaria* if the nectophores have lateral radial canals with diverticula penetrating into the mesoglea and a branch from the tip of the bracteal canal penetrating into the mesoglea distal to the point of fusion with the lower bracteal surface. If these criteria are not met, and the specimen was collected from the Mediterranean, where so far no other apolemiid species have been collected (see below), then it is also deemed correctly identified. However, if the above correct identifications are accompanied by an incorrect synonymy, they are considered *in partim*; in most cases the inaccuracy is due to the inclusion of Eschscholtz (1829) who, despite drawing an accurate bract, showed no internal structure in his nectophore figure (pl. 13 fig. 2e), and his specimen came from the North Atlantic.

A neotype is designated because no other author has ever mentioned a holotype, including Totton (1965) whose extensive treatment of the history of *Apolemia uvaria* covers three pages of his monograph without reference to a holotype.

GEOGRAPHIC DISTRIBUTION

Apolemia uvaria has been found off Nice, including Villefranche and Monaco (Lesueur, 1815; Risso, 1826; Leuckart, 1854; Vogt, 1854; Iwanzoff, 1896; Moser, 1917; Leloup, 1935, 1936*a*, *b*; Totton, 1965; Carré & Carré, 1973; Carré, 1974*a*; present work), off Naples and environs (Gegenbaur, 1853*a*, *b*; Keferstein & Ehlers, 1861; Korotneff, 1884; Chun, 1888; Willem, 1894; Schneider, 1898; Lo Bianco, 1904), and off Messina (Costa, 1835; Kolliker, 1853; Gegenbaur, 1853*a*;

Keferstein & Ehlers, 1861; Claus, 1863). These records include only colonies where a nectosome was collected, or if it was not, then only colony fragments from areas coincidental with whole colony records. Reliable records for *A. uvaria* are all from the Mediterranean Sea. Siphosomal fragments collected in the North Atlantic with bracts which fit the diagnosis for *A. uvaria* (Eschscholtz, 1829, between the Azores and English coast; Minchin, 1987, off the southern Irish coast) indicate that this species may also occur in that part of the Atlantic influenced by Mediterranean outflow, as noted by Totton & Fraser (1955). However, additional samples with both nectosomes and bracts are needed to substantiate these records. The identity of other *A. uvaria* records from the North Atlantic (Leloup, 1955; Fraser, 1955, 1961, 1967; Pugh, 1974; Kirkpatrick & Pugh, 1984) and elsewhere (Alvariño *et al.*, 1990; Pagès & Gili, 1992; Båmstedt *et al.*, 1998; Pugh, 1999*a*; Östman, 2000) remain doubtful pending collection of fragments which include nectosomal tentacles in groups of 4–5, nectophores with diverticula from the lateral radial canals penetrating into the mesoglea, or bracts with a branch of the canal tip penetrating into the mesoglea. Although some of these doubtful records contain nectophore illustrations, they do not show these diagnostic features. Similarly, if nectophores are only described in the text, then the diagnostic features are not mentioned.

Tottonia contorta Margulis, 1976 (Figs 9–13)

Tottonia contorta Margulis, 1976: 1246, figs 7–11; Margulis, 1980: 342, fig. 1a–m, fig. 2a–m; Mackie *et al.*, 1987: 116.

DIAGNOSIS. 1–2 nectosomal tentacles at base of each nectophore; lateral radial canals of nectophore without diverticula penetrating into mesoglea from proximal part (on nectosac axial process) and distal part not forming deep loop on latero-basal nectosac surface, instead with angular turn at ostial level and slightly undulating in large nectophores; dorsal radial canal zigzagging on abaxial surface. Bract with swollen tip of bracteal canal fusing with lower bracteal surface, but canal not penetrating into mesoglea distally; upper surface of bract with nematocysts clustered into large irregular opaque patches.

DESCRIPTION

PNEUMATOPHORE. Opaque white colour, up to 5 mm long, 2.5 mm wide, with basal region distinctly demarcated from nectosome and flattened apex lacking apical pore (Fig. 9a); pneumatosaccus with large air bubble of silvery appearance, wall extending as collar around the upper section of pneumadenia.

NECTOSOMAL TENTACLES. White to translucent, arising from left-hand side of nectosomal stem in present contracted specimens, on right side of base of each muscular lamella (Fig. 9b–c); in BMNH 2002.787 two tentacles attached near nectosome apex associated with nectophores n_1 and n_2 (obscured in Fig. 9a); 21 tentacle bases identifiable on remainder of nectosome, dispersed between 17 muscular lamellae (Fig. 9c); five large detached tentacles found in sample jar, measuring up to 23 mm in length, 3 mm in width, most with enlarged proximal region and narrow distal region, and each with flattened basal disc and central gastrovascular canal connecting tentacle to stem (Fig. 10a); two attached tentacles identified in BMNH 2002.788, and one attached and five loose tentacles identified in BMNH 2002.789.

NECTOSOMAL STEM. Orange to yellow, extremely contracted and preserved intact in all three specimens; measuring 12–14 mm in length, with stem more contracted on dorsal than ventral surface; in BMNH 2002.787 nectosome untwisted with C-shaped appearance in lateral view (Fig. 9a–b); in BMNH 2002.788 and 2002.789 nectosome with one and two twists respectively; 17 muscular lamellae identifiable on ventral nectosomal surface in each specimen, lying almost at right angles to long axis of nectosome; each lamella translucent, with upper (apical) end protruding from right side of stem and lower (basal) end protruding from left side (Fig. 9c); last two lamellae shorter and possibly being resorbed; central region of lamella with opening of pedicular canal discernible in some lamellae, pallial canal scar and ventral radial canal scar discernible in all (Fig. 9c).

NECTOPHORES. Pale cream to white with firm mesoglea; colony with up to 19 nectophores in life (based on attached nectophores and number of muscular lamellae), most large and mature, and with two smallest nectophores still attached to nectosome in BMNH 2002.787 (Fig. 9a–b: n_1 and n_2); immature nectophores up to 18 mm in height with tips of axial wings either lying close together (Fig. 10b), or touching; epidermis with opaque patches and small refractile spots; radial canals thicker than in mature nectophores and dorsal radial canal following slightly zigzag course on abaxial nectosac surface (Fig. 10b); mature nectophores measuring up to 28 mm in height and 21 mm in width, widest at tips of rounded axial wings and with characteristically thick opaque nectosacs; epidermis with opaque patches and refractile spots discernible, and, where patches abraded, nectophore surface retaining characteristic depressions marking their positions; patch distribution most dense on dorsal and lateral surfaces of nectophore body, and on borders of axial wings; ostium surrounded by particularly opaque area extending onto lateral surfaces of nectophore (Fig. 11a), also present in immature nectophores (Fig. 10a); axial nectophore surface with borders of wings widely spaced apically, coming somewhat closer together basally (Fig. 11c), wing margins thick; mesoglea also thickened between axial wings forming triangular thrust block with upper margin a flattened 'V' shape (in axial view); lateral nectophore surfaces each bisected by deep elongate lateral furrow originating from latero-basal region of ostium, extending under abaxio-basal corners of nectophore, passing up lateral surface and terminating in upper lateral region (Fig. 11b); shallow ventral furrow in mid-ventral line extending from just below pedicular canal down to base of nectophore and terminating on axial side of ostial process (Fig. 11c).

Nectosac pale yellow-white, translucent, filling most of nectophore body and with two large axial processes extending into axial wings (Fig. 11a–b); radial canals white, opaque; dorsal radial canal following approximately straight course up

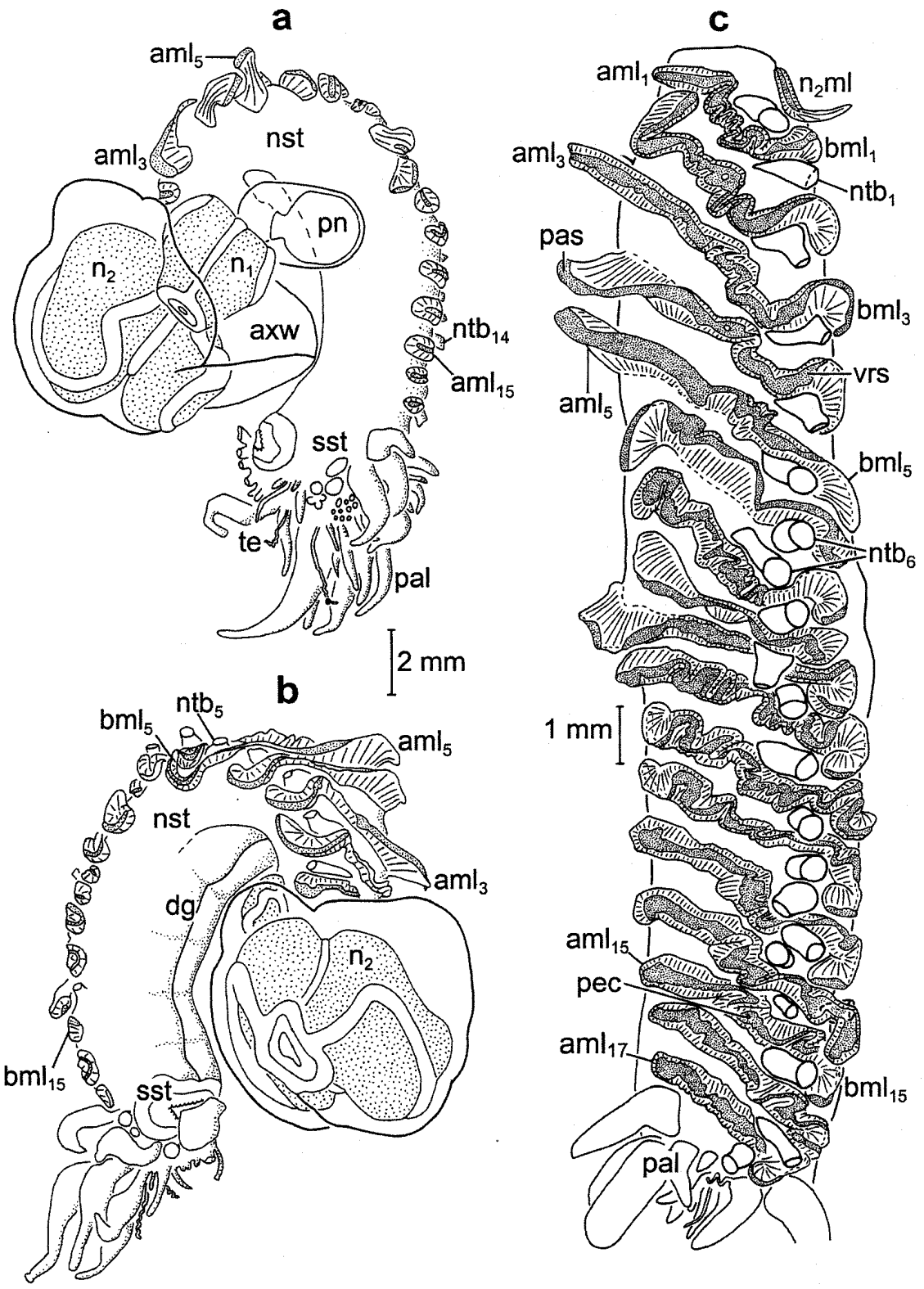

Figure 9 *Tottonia contorta*, Pt. Conception specimen 2002.787, **a**: nectosome with pneumatophore, left lateral view; **b**: nectosome right lateral view; **c**: plan of nectosome illustrating distribution of muscular lamellae on ventral surface from ml_1 (including apex aml_1 and base bml_1) through ml_3, ml_5, ml_{15} (including apex aml_{15} and base bml_{15}) down to ml_{17}. For abbreviations see list in text.

axial surface, becoming wider where emerging onto abaxial surface (Fig. 11a) and sometimes with small lateral outgrowths in this region, then narrowing and following regular and characteristic zigzag course on abaxial surface down to ostial ring canal (Fig. 11a); lateral radial canals approximately straight with slight irregularities in walls, particularly over upper lateral regions of nectosac, and with small diverticula (not penetrating into mesoglea) at regular intervals in some nectophores

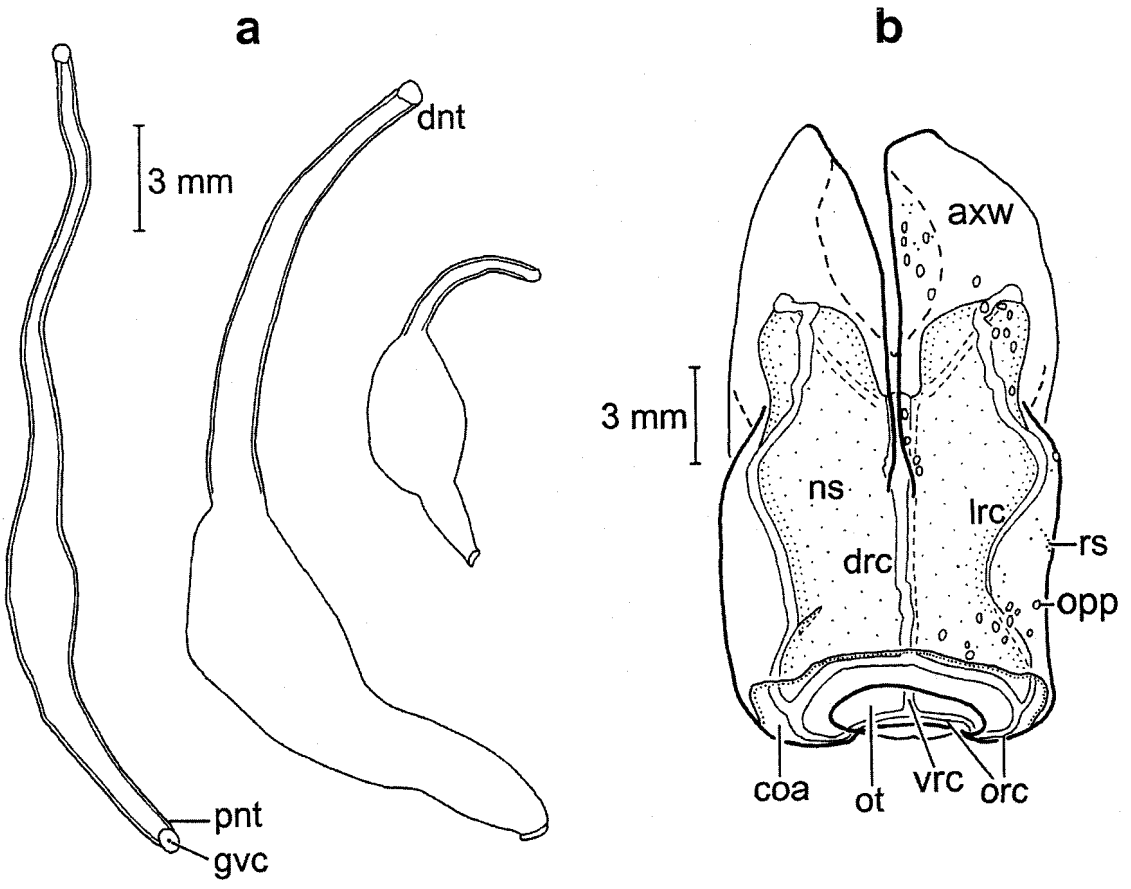

Figure 10 *Tottonia contorta*, Pt. Conception specimen 2002.787, **a**: three unattached nectosomal tentacles, **b**: young detached nectophore (originally attached near top of nectosome shown in Fig. 9a–c) abaxial view. For abbreviations see list in text.

(Fig. 11b); ventral radial canal present as scar in ventral furrow in most nectophores, forming complete canal only where passing through ostial process (Fig. 11b), with short swollen section on axial side of ostial process in one nectophore; pallial canal scar prominent and elongate, extending from short pedicular canal up axial surface of thrust block almost to apex, becoming slightly broader distally (Fig. 11c); ventral radial and pallial canals complete in attached nectophores n_1 and n_2.

SIPHOSOMAL STEM. Pale orange in colour and with six separate portions found in BMNH 2002.787 collectively measuring 96 mm and all bearing gonophores; approximately 6 mm of siphosomal stem identified in BMNH 2002.788 and 2002.789, continuous with nectosomal stem in both specimens; all stem portions greatly contracted, preventing detailed study of discrete cormidia, but dorsal groove discernible in all, contiguous with that of nectosomal stem; siphosomal budding zones short due to contraction of stem.

GASTROZOOIDS. Deep red in colour, large, measuring up to 16 mm by 4 mm, with red pigment in epidermis over most of column but whitish around mouth and in basal region (Fig. 12a); pigment obscuring cnidogenic band in large gastrozooids (Fig. 12a), but band visible through column as more opaque patches in basal region of smaller gastrozooids (Fig. 12d); band more extensive and occupying half column height in immature examples (Fig. 12b); tentacle attached to basal region short and thick in detached mature gastrozooids, though longer distal portion identified in attached gastrozooids, but tentacle only successfully dissected out intact in immature detached gastrozooids (Fig. 12b); all tentacles with row of nematocysts similar to those illustrated for palpacle (Fig. 12e–f); hepatic ridges discernible through column only in immature gastrozooids (Fig. 12b), and on inside of gastrozooids with open mouth and reflexed buccal fringe (Fig. 12d); apices of ridges with red pigment; average number of ridges six, sometimes with minor ridges between.

PALPONS. Only one type identified: opaque or partly translucent, whitish in colour with pale yellow tip, measuring up to 11 mm in length and 2 mm in width; main portion either slightly inflated in mid-region (Fig. 12c) or of similar diameter throughout, and with three opaque stripes alternating with three translucent stripes (representing inner ridges); internally narrower distal portion separated from main column by three endodermal swellings containing refractile cells (Fig. 12c); palpon tip with enlarged 'cap' of yellowish epidermal cells; palpon base with basal disc having central gastrovascular canal aperture and whitish palpacle arising from one side; palpacle typically short, thick, spirally coiled and bearing strip of refractile nematocysts along one side (Fig. 12f); in some palpacles longer thinner distal region identified (but attempts to dissect this out unsuccessful); many small

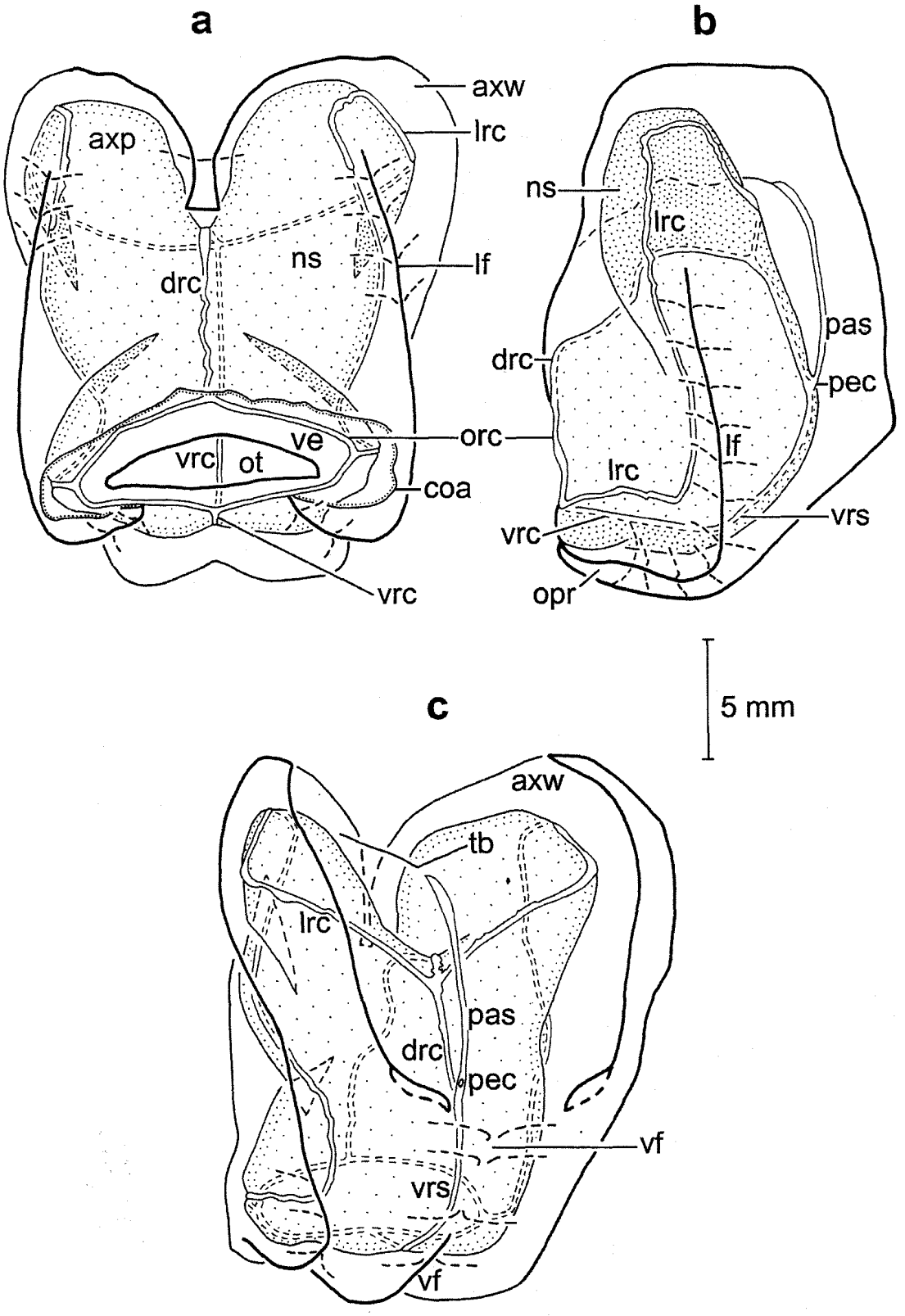

Figure 11 *Tottonia contorta*, Pt. Conception specimen 2002.787, mature detached nectophore (originally attached in mid-lower region of nectosome shown in Fig. 9a–c) **a**: abaxial view; **b**: lateral view; **c**: axio-lateral view. For abbreviations see list in text.

translucent palpons distributed between larger ones, typically 1.75 mm in length with blunt pale yellow tip of thickened epidermal cells, thickened opaque collar near the base and palpacle 2.5 mm long (Fig. 12e); latter of similar structure to palpacle of mature palpon.

BRACTS. Translucent, whitish and measuring up to 11 mm long and 4 mm wide; all detached in present specimens, except two immature bracts; bracteal lamellae identified on siphosome indicating few bracts per cormidium; mature bracts elongate, rounded distally and flattened from upper to lower

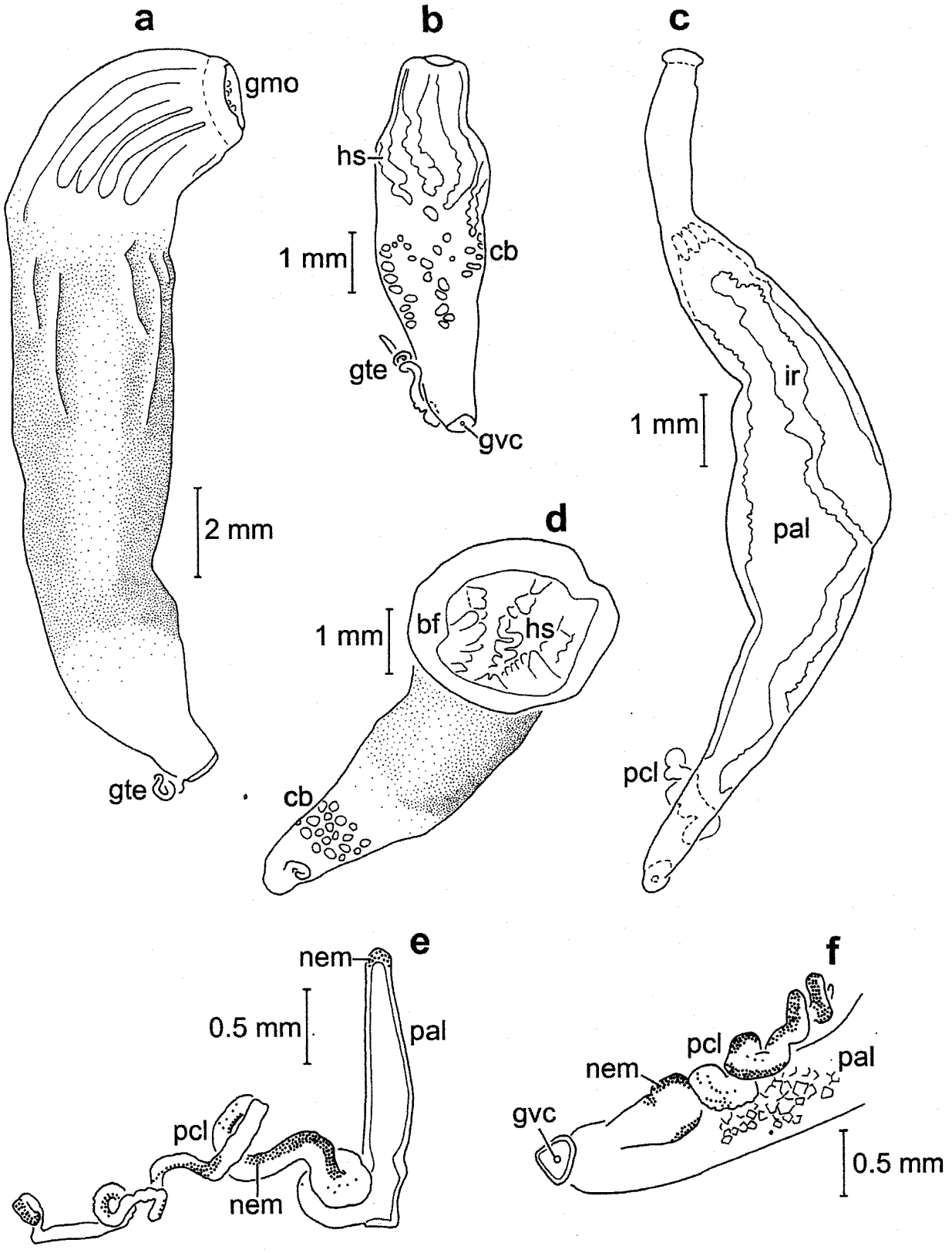

Figure 12 *Tottonia contorta* Pt. Conception specimen 2002.787, siphosomal elements: **a**: mature red pigmented gastrozooid with tentacle; **b**: immature unpigmented gastrozooid; **c**: palpon; **d**: view into mouth of mature gastrozooid with lips rolled backwards and hepatic stripes exposed; **e**: newly formed palpon with enlarged palpacle bearing broad strip of nematocysts; **f**: detail of base of palpacle and palpon. For abbreviations see list in text.

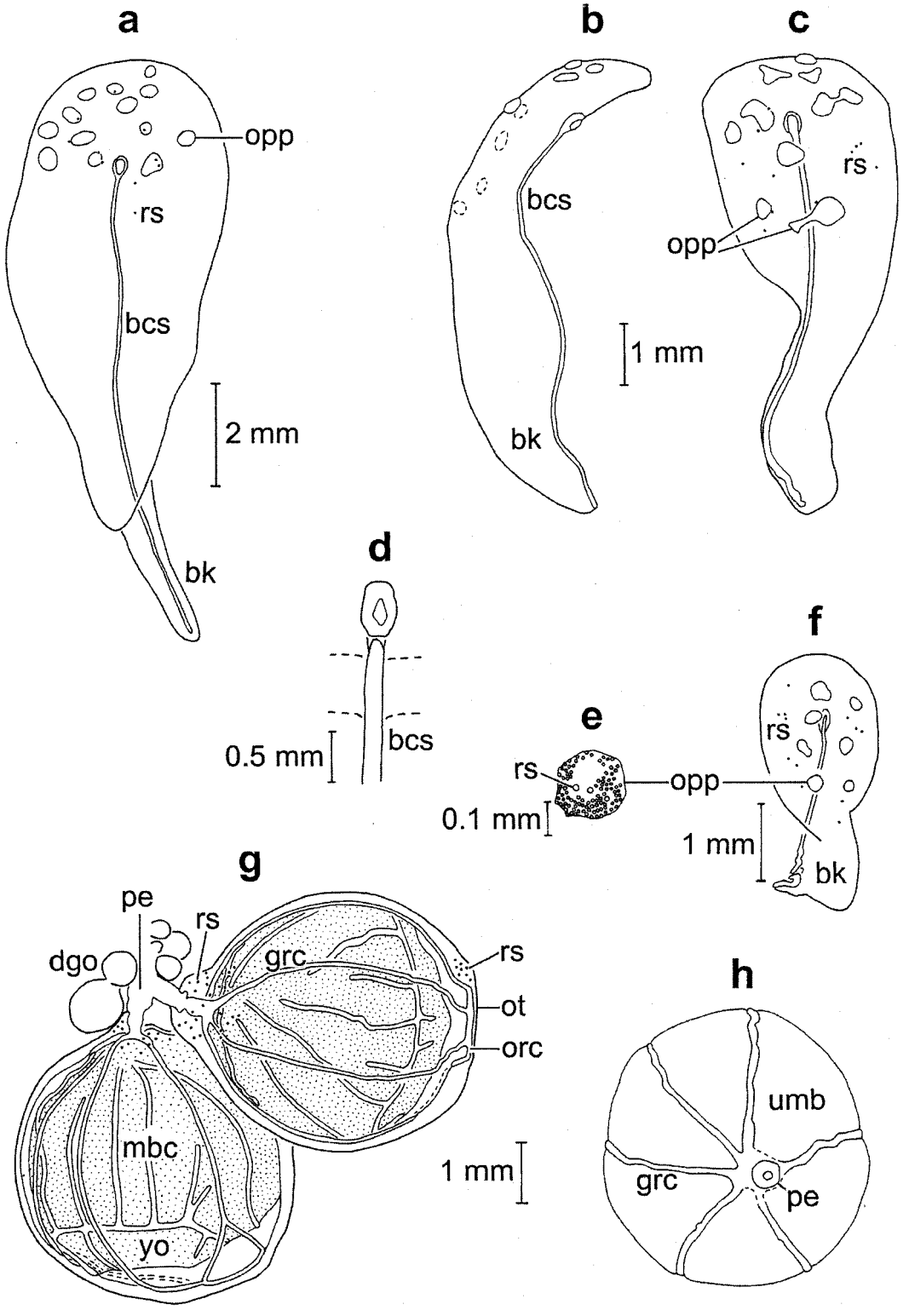

Figure 13 *Tottonia contorta* Pt. Conception specimen 2002.787, more siphosomal elements: **a**: large bract, upper view; **b–c**: lateral and upper views of smaller bract; **d**: detail of upper end of bracteal canal, lower view; **e–f**: detail of opaque patch on upper surface of young bract; **g**: two mature gonophores attached to siphosome; **h**: basal view of detached gonophore showing six radial canals. For abbreviations see list in text.

surfaces except for bilateral flattening of keel at proximal end (Fig. 13a–c); upper surface with opaque patches of varied shape containing hexagonal nematocysts, and with some small refractile spheres irregularly scattered between them (Figs 13a–c, 13e); spheres also found within (or above) opaque patches (Figs 13a, 13c); bracteal canal present as scar on lower surface, originating from stem canal at proximal end of keel and terminating just short of bracteal canal tip; tip

forming somewhat swollen bulb, fused to lower surface of bract (Figs 13b, 13d), without upper branch (Fig. 13b); young bracts of similar shape, all with keels contracted and with more regularly shaped opaque patches (Fig. 13f).

GONOPHORES. Only identified in colony BMNH 2002.787, all female, yellow-orange in colour, up to 5 mm in height, and arising in small clusters on short branches from lateral regions of ventral surface of siphosome at approximately regular intervals; each gonophore comprising large centrolecithal ovum surrounded by branching manubrium, or spadix, and enclosed within outer tunic, or umbrella, opening via small ostium (Fig. 13g); gonophores each connected to common stalk by thin pedicel with discoidal thickening at level of gonophore base; pedicular canal passing through pedicel from stem canal to gonophore, and dividing into six radial canals in endoderm of umbrella (Fig. 13h); each radial canal following meridional course to ostial ring canal (Fig. 13g); manubrium forming network of manubrial (or spadicine) canals encompassing ovum and comprising single circumferential canal (just above equator of ovum) and several approximately meridional canals (Fig. 13g); ovum comprising numerous small dense yolky spheres; mesoglea around ostium and base with refractile spheres.

GEOGRAPHIC DISTRIBUTION

Tottonia contorta was previously recorded only from the NW Indian Ocean (Margulis, 1976) and equatorial Pacific (Margulis, 1980). This paper extends the range to include the NE Pacific region. So far there are no published records from the Atlantic Ocean, though the author has briefly examined specimens from this region which are no longer available.

Discussion

Apolemia uvaria

LESUEUR'S WORK. *Apolemia uvaria* was first taken off Nice in the Mediterranean by Péron and Lesueur on 6.4.1809, and again on 9 May of the same year. There is a brief description of these specimens in an unpublished document written by Lesueur, which now forms part of Manuscript 1734 held at the Museum of Paris entitled 'Note sur les Stephanomies' (Document 882). It was probably deposited there by Lesueur after Péron's death in 1810 (Goy, 1992). In 1815 Lesueur published a detailed plate based on his annotated sketches (now designated as Documents 916, 917 and 918 by the Paris Museum) which remains to this day the best figure yet produced of a mature colony (see Fig. 14, F.1). The common name given to the species by Lesueur at that time was 'Stephanomia au grains de raisins' reflecting the similarity of the female gonophores to a miniature bunch of grapes (Fig. 14, F.14). In Document 882, Lesueur described the colony as resembling a garland, or ribbon, with a series of organs suspended from it. These 'organs' are the cormidia with a cylindrical sucker (the gastrozooid), tentacles (palpons and palpacles) and ovaries with protection (referring to the bracts which extend down the length of the siphosome covering and partially obscuring the other zooids). In Lesueur's figure, the colony is shown swimming, and the siphosomal stem is contracted between the cormidia, presumably to reduce drag. Illustrations by Gegenbaur (1853*b*, pl. 18 fig. 1, reproduced in Totton, 1965 as text fig. 14) and Trégouboff & Rose (1957, pl. 79 fig. 6) show the cormidia separated by long internodes, indicating colonies which have probably adopted a relaxed fishing posture. Thus the stem of apolemiids varies greatly in length depending on the degree of contraction which makes the morphology difficult to interpret. In the present study, the arrangement of nectophores was first investigated in the relatively extended *A. uvaria* colony from Villefranche, followed by observations on two contracted specimens from Naples and finally three contracted specimens of *Tottonia contorta* taken off California.

Lesueur's hand-written notes (in Document 882) on live *Apolemia uvaria* were checked for comments on colour, since any red pigment in the present specimens may have leached out during preservation. Lesueur only recorded colour in the gastrozooids, which have a red-brown tint, and at the base of the palpons, which are 'russet-white'. The nectophores are described as a transparent milky-white, sometimes bluish, and covered with small white spots. No mention is made of any colour in the radial canals, whereas Kölliker (1853) describes a red colour in the text and shows it in good quality figures (pl. 6 figs 6–9). Claus's observations (1863), however, agree better with Lesueur, since he noted red pigment only in the hepatic cells (stripes) of the gastrozooids, and in the red-brown 'tentacles' (brown palpons), neither of which 'was prominent through the yellow ground colour of the stem and zooids'. Gegenbaur (1853*a*) also notes 'yellow-brown' pigmented stripes in the gastrozooids of his specimen (quotes from translation). On balance, it seems that Kölliker may have been mistaken, and that in *A. uvaria* the radial canals are not red in life (pale yellow brown in the present Naples specimens), whereas the gastrozooids may have a reddish hue (pale grey-brown in the present material).

Since a full description of *Apolemia uvaria* was not published with Lesueur's plate, the different zooids which make up the colony were described at various dates throughout the 19th century, when later workers collected further specimens. Such material was rarely complete, however, since *Apolemia uvaria* is prone to autotomy (Schaeppi, 1906; Totton, 1965; Mackie *et al.*, 1987). Colonies described varied in length from 35 cm (as 1 ft; Leuckart, 1854) to 2.4–2.8 m (as 7–8 ft; Claus, 1863), but *A. uvaria* can grow much longer, to 20 m (Trégouboff & Rose, 1957), 30 m (quoted in Mackie *et al.*, 1987), and perhaps to 50 m or more (Totton & Fraser, 1955; Totton, 1965). In the water, it resembles a floating length of wool ('lana' of Italian fishermen, and 'woolly rope' of SCUBA divers) and is likely to be cumbersome and unwieldy. Since each colony has relatively few nectophores for locomotion, autotomy of sections of siphosome could possibly benefit the species by aiding distribution through the water mass. Autotomy may also explain why the gonophores of *A. uvaria* have only infrequently been collected; they are known to develop only at the distal end of the siphosome of mature individuals (Totton, 1965), and it is just this section which most frequently breaks off.

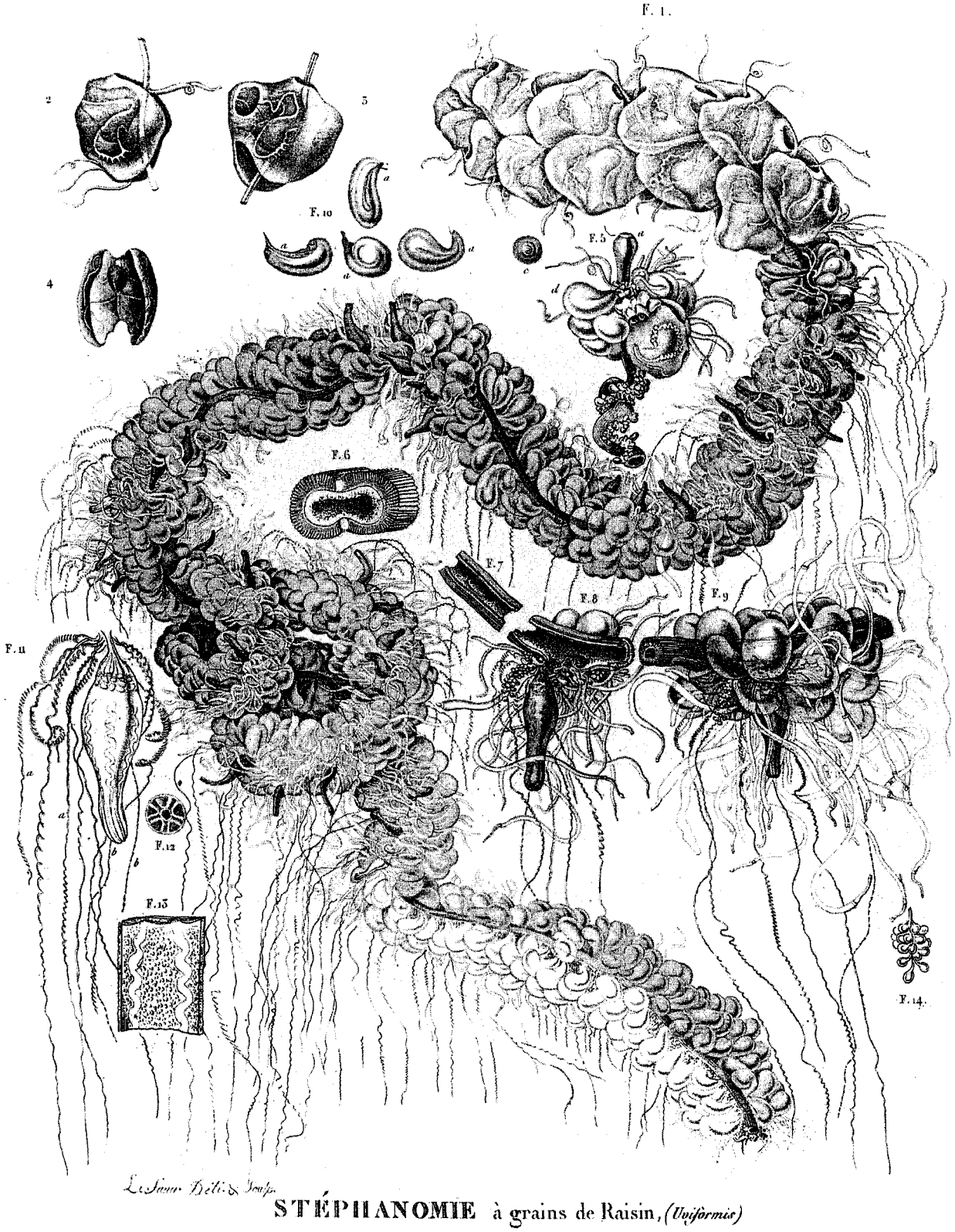

Figure 14 *Apolemia uvaria* whole colony, reproduced from Lesueur's 1815 plate. **F.1**: whole colony; **F.2–4**: 3 views of nectophore (upside down); **F.5**: pneumatophore; **F.6–8**: stem sections; **F.9**: discrete cormidium attached to stem; **F.11–13**: gastrozooid; **F.14**: gonophore.

PNEUMATOPHORE. The relative position of the pneumatophore with respect to the uppermost muscular lamella illustrates well that when the colony is relaxed (i.e. the present Villefranche specimen) the pneumatophore projects above the uppermost nectophores (Fig. 2a), whereas when it is contracted (i.e. the Naples specimens) the pneumatophore is obscured by them (Fig. 3a). Totton (1965, fig. 15) illustrates an intermediate condition in his specimen though his figure shows little detail of the internal structure of the pneumatophore. In the Villefranche specimen, the pneumatosaccus can be clearly discerned, with much of its lining of chitin still intact (Fig. 2b). Pneumatophore formation and differentiation of the chitin layer, which prevents escape of gas from the gas cavity, probably occurs in a similar way in *Apolemia uvaria* to that described and illustrated by Carré for *Forskalia edwardsi* (1967, fig. 4). A distinct collar of chitin develops around the top of the pneumadenia (gas gland) in both species, which was first illustrated for *A. uvaria* by Leuckart (1854, pl. 12 fig. 6). Korotneff (1884, pl. 19 fig. 93) showed one stage in the formation of the chitin layer which he termed the 'cuticle'. Carré (1969) also studied this process in detail in *Nanomia bijuga*. In the present specimens the pneumatophore measures up to 5 mm in length, whereas in Leuckart's and Gegenbaur's colonies it was 7 mm long. There is no evidence of an apical pore in any apolemiids so far studied. Huxley (1859) summarised earlier findings, noting that in *A. uvaria* the pneumatophore is wholly devoid of pigment.

NECTOPHORES. The number of nectophoral muscular lamellae found in the present *Apolemia uvaria* specimens indicates that in life there could be up to 17 nectophores in a colony. Fewer nectophores were recorded by earlier workers, from six (Gegenbaur, 1853*b*; Kölliker, 1853; Vogt, 1854) to 11–12 or more (Lesueur, MS 1734; Leuckart, 1854; Totton & Fraser, 1955), and it is probable that the last few lamellae are non-functional because nectophores are thought to be shed spontaneously from the base of the nectosome as more are budded from the top (Mackie *et al.*, 1987).

The unusual and distinctive shape of the present *Apolemia uvaria* nectophores (Fig. 6a–c) matches that of Totton (1965, fig. 14a–c) and earlier authors (Kölliker, 1853, pl. 6 figs 7–9; Vogt, 1854, pl. 12 figs 3–4). They are characterized by rounded contours and surface furrows instead of ridges (as in other physonects), with the borders of the axial wings the only discernible edges. The latter are wide apart apically and gradually approach each other on the axial surface (Fig. 6c). Totton described them as 'coming together to form a keel', but their bases do not actually join. Instead they enclose a narrow and sometimes deep ventral furrow, noted as early as 1854 by Leuckart. This ventral furrow continues down the axial surface, under the base of the nectophore, and terminates on the axial side of the ostial process. It is also shown, though not labelled, in Totton's lateral views of two *A. uvaria* nectophores (1965, figs 14b, 15), but is not featured in the figure of Pagès & Gili (1992, fig. 4), though the apparent immaturity of the latter nectophore implies that its referral to *A. uvaria* is uncertain. The present nectophores measure up to 21 mm height, slightly taller than those found by Totton (1965), but shorter than the tallest recorded by Leuckart (1853, 1854) at 24 mm. In the youngest Naples nectophores (Fig. 5c), the abaxial and lateral surfaces of the nectophore are covered with distinctive opaque spots, and similar spots are described in the nectophores of freshly collected colonies (Lesueur, MS 1734; Gegenbaur, 1853*b*, pl. 18, fig. 1; Vogt, 1854, pl. 12, figs 2–4). Although many of these spots are abraded in the present nectophores, their positions are apparent as clear patches in the epidermis. Early authors found that the spots consisted of a hexagonal arrangement of tightly packed nematocysts.

The nectosac in *Apolemia uvaria* is larger than in other long-stemmed physonects and its contours closely follow those of the nectophore. This feature is characteristic of the Family Apolemiidae and was first noted and illustrated in *A. uvaria* by Kölliker (1853). The radial canals in *A. uvaria* are described as large, visible to the naked eye in freshly caught material, lined with ciliated epithelium and with a maximum diameter of 0.9 mm (Leuckart, 1853, 1854). They are connected to the stem via a short and broad pedicular canal from which a blind-ending pallial canal extends upwards to the top of the thrust block (Fig. 6b–c). The diverticulum is clearly shown, though not labelled, in Totton's lateral views of two *A. uvaria* nectophores (1965, figs 14b, 15). It becomes split lengthways in apolemiids if the nectophore is detached from the stem, leaving a shallow open fissure or scar on both the surface of the nectophore (Fig. 6b) and the edge of the muscular lamella (Fig. 2d). The ventral radial canal is similarly split as far as the axial side of the ostial process. In nectophores still attached to the stem, these canals are clearly visible as intact structures, and their relationship to the muscle fibres of the nectophoral lamella resembles that shown by Totton (1965, fig. 15). The function of the pallial canal may be to supply nutrients to the upper section of the lamella during active swimming, since this lamella is separated from the dorsal radial canal of the nectosac by a cushion of mesoglea known as the thrust block.

The point of insertion of the pedicular canal onto the radial canals marks the points of origin of the dorsal and ventral radial canals, and in *Apolemia uvaria* the dorsal radial canal extends apically for a short distance before giving rise to the lateral radial canals (Figs 5b, 6b). A similar arrangement appears in Totton's lateral view of a mature *Apolemia uvaria* nectophore (1965, fig. 14b), but is incorrectly drawn in the older publication by Leuckart (1854, pl. 12 fig. 7). In mature *A. uvaria* nectophores the lateral radial canals leave the dorsal canal at right angles (also shown by Kölliker, 1853 pl. 6 fig. 7 and Leuckart, 1854, pl. 12 fig. 6), and on reaching the outer borders of the nectosac give off a series of distinctive blind-ending diverticula which penetrate directly into the mesoglea. These blind-ending diverticula should not be confused with diverticula close to the nectosac surface which never penetrate into the mesoglea, such as in the nectophore illustrated by Kirkpatrick & Pugh (1984, fig. 6) and Pugh (1999*a*, fig. 3.5), though this is probably from a different apolemiid species. In the present *A. uvaria* specimens, the length of the diverticula agrees well with those shown by Kölliker, Leuckart and Totton, and these diverticula arise only in that part of the lateral radial canal which passes over the axial processes of the nectosac. Small swellings in the walls of the lateral radial canals outside

this region and in the dorsal radial canal where it passes onto the abaxial surface of the nectosac (Fig. 6c) do not constitute true diverticula.

The present investigation shows that in *Apolemia uvaria* the nectophores are attached to the nectosomal stem in a single row, not two rows as stated by other authors (Gegenbaur, 1853*a*, *b*; Leuckart, 1854; Vogt, 1854; Trégouboff & Rose, 1957; Totton, 1965; Pagès & Gili, 1992). The stem in the present specimens is spirally twisted throughout its length, making it difficult to distinguish the linear alignment of the ventral surface, to which all zooids are attached (Figs 2a, 3a). Kölliker (1853) was the first to note this feature, describing the nectosome as 'lightly tortuous', and Leuckart (1854) mentioned 'mild convolutions' in the siphosomal stem. Similarly, Claus (1863) studied the stem of *A. uvaria* in great detail and described it as forming a right-winding spiral, with all zooids arising from the ventral surface. A dorsal groove lies opposite the line of muscular lamellae on the ventral surface and is traceable for much of the stem length in the present specimens. It is clearest in the extended Villefranche stem (Fig. 2a) though even here relaxation is not complete and most lamellae still partially overlap their neighbours. The degree of overlap is greater in lamellae further down the nectosomal stem indicating greater stem contraction in this region. It is assumed that in life the nectosomal stem is extended sufficiently to allow nectophores to take up positions around the stem in a loose spiral, and spaced sufficiently far apart to enable effective nectosac contraction during swimming.

Nectosomal tentacles arise as bunches in *Apolemia uvaria* and are attached at the base of each muscular lamella on its right side. Again, this is clearest in the Villefranche specimen where the portion of stem to which each bunch is attached is typically swollen (Fig. 2d). In the more contracted Naples specimens, the bunches are attached in the same position relative to each muscular lamella, but arise closer together and any swollen regions have been lost (Fig. 3a). As already noted, nectosomal tentacles are unique to the Apolemiidae, and were considered by Totton (1965, p. 47) to represent the aboral larval tentacles of the progenitors of siphonophores. Many tentacles are still attached in the Naples specimens (Figs 3a, 4a), and all have rounded and sometimes slightly club-shaped tips, as shown by Totton (1965, fig. 15). In life nectosomal tentacles extend well beyond the nectophores, and were described as 'groping around' by Gegenbaur (1853*b*), though their function is unclear. Since nematocysts may be present at their tips, these tentacles may be defensive. There are 3–6 tentacles per bunch in the present NHM material, which accords with Leuckart's 3–4 (1854) and Totton's 5–6 (1965).

SIPHOSOMAL ZOOIDS. There are typically two gastrozooids per cormidium in the discrete cormidia studied in the present *Apolemia uvaria* specimens, similar to the 3–4 of Trégouboff & Rose (1957), 1–3 of Gegenbaur (1853*a*) and 2–4 of Claus (1863). Claus also noticed smaller developing gastrozooids in many cormidia. Immature apolemiid colonies typically only contain one gastrozooid per cormidium (Haeckel, 1888*b* in *Dicymba diphyopsis*, Pagès & Gili, 1992). The present gastrozooids are probably tinted red-brown in life (see above) with a whitish area around the mouth due to the presence of numerous nematocysts (Claus, 1863) which probably aid transfer of prey from the tentacles, as in *Nanomia bijuga* (Mackie & Boag, 1963). The shape of individual gastrozooids may depend on the stage of digestion at preservation. If digestion is underway the mouth is likely to be closed (Fig. 7b), whereas if food is either being ingested or large indigestible fragments are being voided at the end of the digestive cycle, then the mouth is likely to be wide open with the buccal fringe rolled back (Fig. 7c). The digestive sequence in *A. uvaria* was studied by Willem (1894), whose description of the process is similar to that determined for *Nanomia bijuga* (Mackie & Boag, 1963). Morphologically, a gastrozooid can be divided into a column comprising proboscis (with mouth) and stomach, and a cnidogenic band (basigaster). In *A. uvaria* 5–6 opaque hepatic stripes are visible through the column wall and, depending on the degree of contraction of the gastrozooid, these may also form ridges on the outside. Internally these stripes alternate with 5–6 translucent raised longitudinal hepatic swellings which probably represent longitudinal endoderm fibres containing enlarged secretory cells for extracellular digestion (Carré & Carré, 1995). Six stripes and multiples of six are also recorded by other authors for *A. uvaria* (Gegenbaur, 1853*b*; Leuckart, 1854; Claus, 1863) and five are shown in Lesueur's section through the proboscis region of one gastrozooid (Fig. 14, F. 12). Ciliated movement has been observed in *A. uvaria* gastrozooids (Willem, 1894) which in *N. bijuga* is known to aid food engulfment, distribution and flushing of wastes (Mackie & Boag, 1963). Some authors have also noted cilia on the external surface of gastrozooids in *A. uvaria* (Gegenbaur, 1853*b*; Claus, 1863).

In most siphonophores, the cnidogenic band, or cuff, at the base of the gastrozooid is where all nematocysts for the colony are manufactured (Skaer, 1973, 1988; Carré, 1974*a*). However, according to earlier studies (Carré & Carré, 1973; Carré, 1974*a*) a cnidogenic band is also present in *Apolemia uvaria* at the base of the palpon, or dactylozooid, though it could not be identified at macroscopic level in the NHM specimens. Given that palpons are considered to be reduced gastrozooids (Totton, 1965), it is perhaps not surprising to find nematocyst production in these zooids. The cnidogenic band consists of discrete groups of nematocysts, known as cnidogenous clumps (Carré, 1974*a*), which appear in the NHM gastrozooids as translucent patches in the gastrozooid wall (Fig. 7b–c). Similar patches are present in *Tottonia contorta* (Fig. 12b, 12d), and have also been illustrated in gastrozooids of *Nanomia bijuga* (Mackie & Boag, 1963, fig. 4a), *Agalma okeni* (as *Crystallodes vitrea*, Haeckel, 1888*b*, pl. 17, fig. 4) and other physonects. Nematocyst production in the cnidogenous clumps has been studied in a number of species, and they are formed by nematoblasts grouped into clones (Carré, 1974*a*). Four categories of nematocysts are identified in *A. uvaria*, three of which are represented by two size categories (Carré & Carré, 1973), giving a complete cnidome for this species of: microbirhopaloides and macrobirhopaloides, microstenoteles and macrostenoteles, microisorhizas and macroisorhizas, and mastigophores. Good light and scanning electron microscope images have also been published of birhopaloides, isorhizas

and mastigophores from an undetermined apolemiid taken off California (Östman, 2000).

Carré (1974*a*) estimated the numerical composition of nematoblasts in each clone of *Apolemia uvaria*, while for other physonects she followed the migration of nematocysts from the clump to their definitive positions in the colony (Carré, 1974*c*). Most migrate by amoeboid movement through the ectoderm, typically into the gastrozooid tentacle and the palpacle, but in *A. uvaria* some go to other sites (see below). It must be emphasized that in apolemiids, unlike all other siphonophores, the nematocysts do not migrate into cnidosacs on side branches (tentilla) of the tentacles, as shown by Carré's generalized diagram (1974*a*, fig. 1), but simply pass along the tentacle to their definitive positions. This point has not perhaps been emphasized in Carré's work, though their study of the differentiation and maturation of nematocysts in *A. uvaria* and several other siphonophore species (Carré & Carré, 1973; Carré, 1974*a–c*) is second to none.

Two categories of palpons occur in *Apolemia uvaria*, and both have been identified in the NHM material. Translucent palpons are very long and slender, with a slightly thickened knob at the tip but no apparent apical pore, though a pore was observed by Willem (1894) in a live specimen. The morphology of the present brown palpons agrees well with the earlier descriptions of Leuckart (1853, 1854) and Claus (1863). Totton (1965) described their nematocysts as large and banana-shaped, measuring 0.77 mm long with a long barbed hampe, and capable of inflicting a sharp burning pain on the hands. Carré & Carré (1973) followed the migration of macrobirhopaloides, stenoteles and mastigophores into the apical region of a number of palpons (without distinguishing which type), and also saw isorhizas migrating to the general palpon surface. In life the palpons are very active and maintain constant worm-like movements (Gegenbaur, 1853*a*, *b*; Haeckel, 1888*b*; Totton, 1965). They play an important role in digestion and this has been described in detail for *A. uvaria* (Willem, 1894).

Siphosomal tentacles arise singly from the base of each gastrozooid and palpon as described above, and typically form a tangled mass which is almost impossible to unravel. Even the tentacles of the present Villefranche specimens, which were first anaesthetized in $MgCl_2$, mostly remain contracted in a spiral (see Fig. 8b, labelled as palpacles). Indeed, Totton (1965) found a gastrozooid tentacle measuring 4 cm in one specimen (when straightened out) and commented that it would reach 3–4 times this length when completely extended in life. Such an expanded state is shown in Lesueur's 1815 plate (reproduced in Fig. 14 F.1, F.9, F.11), and Gegenbaur (1853*b*) also mentions palpacles typically measuring 3–4 times the length of palpons. Because the tentacles in the present material are still partially contracted, they all resemble Lesueur's type 'a' (Fig. 14 F.11), with a band of closely spaced paired nematocysts one side, as illustrated by Claus (1863, pl. 46 fig. 10). Expanded tentacles, shown as 'type b' by Lesueur (1815, Fig. 14 F.11) and also by Claus (1863, pl. 46 fig. 9), have a nodular appearance with each nodule consisting of a pair of birhopaloides nematocysts. These are unique to the Apolemiidae, and each nodal pair has a diameter of 1/8 mm, separated by internodes of 1/8 mm diameter (Totton, 1965). It is concluded, therefore, that the dark spots forming a band down the length of the tentacles in the present material are all birhopaloides. At the base of each tentacle is a small glistening whitish swelling described as russet-white in life (see above), and which shows up well in the present *Apolemia uvaria* palpons (Fig. 8a–b). It was first described in this species by Leuckart (1853), but its function is unclear.

The bracts of *Apolemia uvaria* are soft, rounded and club-shaped with a slightly concave lower surface. Like the nectophores they have no ridges, and differ considerably from the leaf-like or prismatic bracts of most other physonects. Due to the contracted nature of the present material, it is not possible to estimate the number of bracts in a fully developed cormidium, but other authors have recorded 20–40 bracts per cormidium (Haeckel, 1888*b*; Trégouboff & Rose, 1957), with fewer in immature colonies (Gegenbaur, 1853*a*, *b*). Bracts appear bluish in the present Naples specimens, and the largest is 9 mm long, shorter than those measured by Gegenbaur and Haeckel (11 mm and 15–25 mm respectively), but longer than the loose bracts illustrated by Totton (1965, fig. 14c) which were only 6 mm. The upper surface of each bract bears a number of opaque spots which are more densely packed on small bracts (Fig. 8e) than on larger bracts (Fig. 8c–d). In NHM bracts spots do not extend onto the bracteal keel as shown by Pugh (1999*a*, fig. 3.21). They are similar to the opaque spots found on the nectophores (see discussion above) and to the white spots (or 'warts') mentioned by many other authors (Gegenbaur, 1853*a*, *b*; Leuckart, 1853; Vogt, 1854; Huxley, 1859; Haeckel, 1888*b*; Totton, 1965; Kirkpatrick & Pugh, 1984; Pagès & Gili, 1992; Pugh, 1999*a*). Each consists of a number of closely packed cells, or nematocysts, known in *A. uvaria* to be isorhizas (Carré & Carré, 1973). Small refractile spheres scattered between the spots or patches in Figs 8c–e could represent another type of nematocyst, since their dimensions are different, but further investigation is needed to verify this hypothesis. In life young *A. uvaria* bracts may have a ciliated surface (Leuckart, 1853).

The bracteal canal in *Apolemia uvaria* passes along the lower surface of the bract for most of its length, then penetrates into the mesoglea, where after a short distance, it forks into a short upper extension and a broad lower section which fuses with the lower surface. The canal shown in Fig. 8d was split open lengthwise when the bract became detached from its muscular lamella (in the same way as that described for the pallial canal of the nectophore), so is present as a gutter-like scar from its origin to the point where it penetrates into the mesoglea to become a true canal again. The upper extension of the bracteal canal can be blunt or elongate (Fig. 8g) and is similar to that shown by other authors (Totton, 1965, fig. 14c; Eschscholtz, 1829, pl. 13 fig. 2), though as noted above, the specimens of Eschscholtz cannot be referred with certainty to *A. uvaria*. The latter author describes an opening from the lower section of the bracteal canal onto the lower surface of the bract, which he says connects the canal system directly to the seawater. In the present bracts, however, all the canals are closed and resemble those described by Gegenbaur (1853*b*) and Leuckart (1853). In some early figures of *A. uvaria* bracts, the bracteal canal is shown as being uncharacteristically large (Vogt, 1854, pl. 12 fig. 6; Keferstein & Ehlers, 1861, pl. 1

fig. 13), but this probably represents the scar of the bracteal lamella, which attaches the bract to the stem, and is similar to the scar left by the pallial canal and ventral radial canals in detached nectophores. This lamella terminates where the bracteal canal penetrates into the mesoglea (Fig. 8d) so in detached bracts of *A. uvaria*, the bracteal canal exists for much of its length as a gutter-like scar. The bracteal lamella is muscular and enables independent movements of bracts in live colonies, a phenomenon which was observed by several early workers (Gegenbaur, 1853*b*; Leuckart, 1853; Haeckel, 1888*b*).

Bracts are numerous in *Apolemia uvaria* and probably provide most of the buoyancy for the colony, offsetting the heavier weight of other siphosomal zooids. Although some lift may be gained from the pneumatophore, in *A. uvaria* it is small compared with length of the stem, and lacks a pore so cannot contribute to buoyancy control. Similarly, the pneumatophores of species of *Agalma* and *Forskalia* also lack pores and compensate with a large number of bracts (Mackie *et al.*, 1987). Båmstedt *et al.* (1998) has commented that in *A. uvaria* buoyancy is gained both from the tentacles and the bracts, and although the tentacles may reduce the sinking rate by increasing the surface area of the colony when extended for feeding, the main lift is likely to come from the bracts. Bracts contain more mesoglea, the density of which is reduced in siphonophores as in other gelatinous zooplankton species, by the exclusion of heavy sulphate ions (Bidigaire & Biggs, 1980). This mechanism enables the extremely long stems of apolemiid colonies, as shown in photographs of complete colonies (Båmstedt *et al.*, 1998, fig. 3a) to remain floating horizontally in the water, similar to those of the calycophorans *Sulculeolaria*, *Rosacea* and *Praya* (Bidigaire & Biggs, 1980).

Tottonia contorta

MARGULIS'S WORK. *Tottonia contorta* was originally described as a new species of Agalmatidae from a sample taken in the Indian Ocean (Margulis, 1976) which included separate nectophores and a portion of stem comprising the nectosome and top part of the siphosome. A nectophore from this holotype loaned to the present author is of similar shape to one of the nectophores illustrated by Margulis (1976, figs 7–8), but the axial wing tips are touching and it measures only 5.5 mm in length, indicating it might be immature. Indeed, it closely resembles the immature Californian *T. contorta* nectophore (Fig. 10b), except that the latter is 18 mm tall. The other Indian Ocean nectophore illustrated by Margulis (1976, figs 9–10) has diverging axial wings, measures 8.5 mm in length and appears more mature. It is similar to two further *T. contorta* nectophores collected from the equatorial Pacific which were described by Margulis in 1980, and to *T. contorta* nectophores of similar size collected off the Bahamas and made available to the present author early in this project, though later withdrawn. Although the Indian Ocean and equatorial Pacific nectophores are both smaller and narrower than the mature Californian nectophores, other features are similar, including straight lateral radial canals, tall broad axial processes to the nectosac and long lateral furrows (Fig. 11a–b). It is therefore concluded that the present specimens are giant examples of *T. contorta*, possibly similar to other giant 10 m long apolemiids collected elsewhere with submersibles (Mackie *et al.*, 1987). Another important character of *T. contorta* mentioned by Margulis (1980) and also displayed by the Californian specimens is the presence of nectosomal tentacles between the nectophores, which prompted Margulis to correctly reassign *T. contorta* to the family Apolemiidae.

PNEUMATOPHORE AND NECTOSOME. Pneumatophores of the present Californian *Tottonia contorta* specimens are also of similar appearance and proportions to those illustrated by Margulis (1976, fig. 11; 1980, pl. 1 figs a–b) except that they are almost twice the size, measuring up to 5 mm by 2.5 mm. The largest described by Margulis (1980), in a specimen from the equatorial Pacific, measures only 3.5 mm by 1.5 mm. Similarly, the nectosome in the present specimens is 12–14 mm long, whereas in the equatorial Pacific specimen it measures only 6 mm. The nectosomal and siphosomal stems are distinctly orange-yellow in the present specimens, contrasting with the whitish nectosomal tentacles and muscular lamellae, and the nectosomal stems are not continuously twisted as in *Apolemia uvaria*. The present detailed study of the nectophoral muscular lamellae in the three Californian *T. contorta* nectosomes shows that, in this species, the nectophores are attached to the nectosome in a single row, as in *A. uvaria*, not two rows as stated by Margulis (1980). She assumes, wrongly, that the triangular protuberances at each end of a single lamella attach to separate nectophores, not a single nectophore as noted above. Perhaps she was misled by the fact that the nectosome in her specimen is extremely contracted, as it is in the Californian specimens, with the result that the muscular lamellae lie almost at right angles to the long axis of the nectosome. In the present specimens (with the pneumatophore taken as occupying an apical position at the top of the stem) the apices of the lamellae protrude from the right side of the nectosome and the bases from the left side, with much shorter fibres in the central region where the pedicular canal opens (Fig. 9c). Margulis states correctly that the nectosomal tentacles are attached in a single row, but, because she illustrates a ventral view of the stem (1980, fig. 1b), she concludes that this row lies on the right side, whereas in fact it lies on the left. In the Californian *T. contorta* specimens there are only 1–2 nectosomal tentacles per nectophore, in contrast to the 4–6 in *A. uvaria*. These tentacles are typically more swollen basally than apically in *T. contorta*, and seem better preserved in the Californian material (Fig. 10a) than in Margulis's specimen which has a very thin and long distal portion (1980, fig. 1a–b). This could be attributable either to shrinkage during storage or to differential contraction of the tentacle muscles at preservation.

In the three Californian *Tottonia contorta* specimens, the number of nectophoral lamellae observed suggests that there could be up to 15 nectophores per colony in life, but as the last two lamellae are smaller in all the specimens, they may already have shed their nectophores and be undergoing resorption, as suggested for *Apolemia uvaria*. A nectophoral budding zone is identifiable in *T. contorta*, as in *A. uvaria*, but is not apparent in Fig. 9a–b because the buds are masked by the two small

attached nectophores. The siphosomal budding zone is more difficult to discern in the present *T. contorta* specimens than in *A. uvaria* due to greater contraction of the siphosomal stem.

NECTOPHORES. Attached nectophores of *Tottonia contorta* have a pedicular canal, which divides into an upper pallial canal and a lower ventral radial canal, as in *Apolemia uvaria*, and in detached nectophores these canals are split length-wise in the same way. The canal scars on the muscular lamellae are shown as a stippled strip in *T. contorta* (Fig. 9c), and are relatively broader and more folded than in *A. uvaria*, due to greater contraction of the *T. contorta* lamellae. The nectophores of *T. contorta* are of similar construction to those of *A. uvaria*, except that they have slightly less depth in lateral view, a more prominent nectosac, and there are no true diverticula on the lateral radial canals where they pass over the axial processes of the nectosac (Fig. 11a–c). Instead these canals follow a slightly undulating course for most of their length (Fig. 11b), as does the dorsal canal where it passes down the abaxial nectosac surface to the ostium (Fig. 11a). Undulations are also mentioned in Margulis's description of nectophores from the Pacific Ocean (1980, p. 342), but are less pronounced in her illustrations of Indian Ocean nectophores (Margulis, 1976, figs 8, 10) than in the present specimens. The dorsal radial canal of the latter typically has small lateral expansions in its walls close to its point of origin from the ventral radial canal on the abaxial surface (Fig. 11c), but these are not true diverticula and could be caused by shrinkage during preservation.

SIPHOSOMAL ZOOIDS. Colour in the present Californian specimens of *Tottonia contorta* is limited to orange-yellow pigment in the stem (as noted above) and deep red pigment on the column of the largest gastrozooids, with variable amounts of red pigment on the internal crests of the hepatic ridges and on the column of smaller gastrozooids. There is no red pigment on the surface of the nectophore, whereas in the holotype nectophores examined, the nectosac is pale pink to tan, and there is a faint blackish pigment in the circum-ostial opaque area and at the bases of the axial wings, with a blackish band of mesoglea just abaxial of the lateral furrows in one nectophore. The black pigment may have darkened during preservation and in life could be a deep red, since this colour is characteristic of deep-water cnidarians. Some of the pigmented epidermis may have abraded during collection and handling, though one would expect pigment in the mesoglea to remain intact. Perhaps colour distribution is patchy and variable in *T. contorta*. In material from the Indian Ocean and equatorial Pacific, colour is mentioned only in relation to gastrozooids and some small palpon-like zooids (Margulis, 1980) not identifiable in the Californian specimens. In the large Californian gastrozooids only the column is red, with the mouth, proboscis and basal regions lacking pigment (Fig. 12a), and small gastrozooids typically only have red flecks, a colour range similar to that reported by Margulis (1980). Nematocysts may occur around the mouth of *T. contorta* gastrozooids, as in *Apolemia uvaria*, but were not specifically mentioned by Margulis. The diameter of the mouth opening varies in the present specimens, as in *A. uvaria*, being typically tightly closed or partly open, but in a few the buccal fringe is rolled back to reveal the hepatic ridges (Fig. 12d), as also shown by Margulis (1980, fig. 1zh). These gastrozooids might be ingesting food or voiding wastes, as suggested above for *A. uvaria*. Margulis concludes, erroneously, that one of her gastrozooids lacks a mouth, though it is apparent from fig. 1g that this zooid is distorted. Californian gastrozooids have an average of six hepatic ridges (Figs 12b, 12d), similar to that typically found in *A. uvaria*, and similar structures may be indicated by longitudinal lines in two of Margulis's gastrozooid illustrations (figs 2z, 2ee). All gastrozooids in the present *T. contorta* specimens are detached, with part of a tentacle arising from the base adjacent to the basal disc (Fig. 12a–c), but these tentacles are shorter and thicker in the present *T. contorta* specimens than the tentacles of the best preserved *A. uvaria* gastrozooids; probably the thinner distal portion broke off during capture. At high magnification a strip of nematocysts is evident on one side of the tentacle similar to that shown on the palpacles of the palpons (Fig. 12e–f), and although Margulis shows similar tentacles for two of her gastrozooids (1980, figs 2z, 2ee), she missed them in most, probably because they remained with the stem when the gastrozooid detached, thus leading her to erroneously conclude an absence of gastrozooid tentacles is the normal condition for *T. contorta*.

In the present *Tottonia contorta* colonies only one type of palpon is identifiable, typically translucent with a yellowish opaque tip, measuring up to 11 mm in length, a large inflated mid-region and a basal disc for attachment to the stem. Long irregular ridges of endodermal cells are discernible through the walls of the palpon, similar to those described for *Apolemia uvaria* (Willem, 1894), and where these ridges converge apically three refringent swellings occur (Fig. 12c) which in life are thought to absorb food particles (Willem, 1894). The present *T. contorta* palpons are longer and more inflated than those described by Margulis (only 2 mm in length), who also recognizes different types based on the shape of the tips. In most Californian palpons the tips are similar to Margulis's fig. 2b (1980), but some resemble her fig. 2a. As already noted Margulis also identified a smaller dark yellow or light brown coloured palpon (figs 1l, 2d, 2k) which, apart from being pigmented, appears similar to the young Californian palpon (Fig. 12e); its paler colour suggests it is probably not equivalent to the smaller pigmented palpon of *A. uvaria*. A short palpacle is attached just above the base of the palpon in Californian *T. contorta* specimens, which like the gastrozooid tentacle, is typically tightly coiled and shorter than the palpacles of *A. uvaria* (Fig. 8a–b); it has probably lost a thin distal portion (Fig. 12e). There is a strip of nematocysts along one side, as in *A. uvaria*, and this appears thicker basally due to greater contraction of the palpacle in this region (Fig. 12f). Margulis found both oval and round nematocysts in the palpon tips of *T. contorta* (1980, figs 2a–b, 2v, 2g, 2e, 2zh), which she identifies as 'round atrichs and microbasic euryteles', but are more accurately classified as isorhizas and birhopaloides, the latter a nematocyst type unique to the Apolemiidae.

Bracts of *Tottonia contorta* are soft and rounded like those of *Apolemia uvaria*, but slightly longer at up to 11 mm in length, and narrower proximally in upper view (Fig. 13a), with less depth between upper and lower surfaces in lateral view

(Fig. 13b); the keel is also deeper in lateral view (Fig. 13b). In mature bracts the upper surface is covered with opaque patches, of regular or irregular shape; these are fewer in number than the opaque spots of *A. uvaria*, and in the present specimens distributed only at the distal end (Fig. 13a–c). Each opaque patch protrudes further from the surface than the opaque spots of *A. uvaria*, and probably also comprises closely packed nematocysts (Figs 13c, 13e), possibly isorhizas as in *A. uvaria* (Carré & Carré, 1973). In young bracts opaque patches are distributed over most of the upper surface. Small refractile spheres scattered between opaque patches in *T. contorta* (Figs 13a, 13c, 13e–f) appear similar to those of *A. uvaria*, and could represent another type of nematocyst, since their dimensions differ from those in the patches. Opaque patches are also found in the epidermis of the nectophores, being most prominent (but smaller and more regular) in immature nectophores (Fig. 10b); in the present mature nectophores these patches have mostly been abraded leaving clear areas in the epidermis, as in *A. uvaria*. The bracteal canal does not penetrate into the mesoglea in *T. contorta* but remains close to the lower surface throughout. In detached bracts it is present as a gutter-like bracteal lamella scar, as in *A. uvaria*, but in *T. contorta* the scar is longer and only becomes a true canal at the canal apex where it is swollen and fused to the lower surface (Fig. 13d). Bracts found by Margulis (1980) are extremely folded, probably due to poor preservation, and some are actually said to have palpons attached (fig. 1k), though in the Californian material such adherent palpons can always be carefully teased away using fine forceps.

Well developed female gonophores are described for the first time in *Tottonia contorta*, but no male gonophores were found. Margulis (1980) identifies both male and female gonophores in her Indian Ocean material and suggests that this species might be monoecius, but both are small and lacking in detail (figs 2k, 2l) and since the female gonophores she illustrates are on a different portion of siphosome to male gonophores, it is unclear how many colonies the fragments actually represent. The single mature Californian colony contains only female gonophores which suggests that *T. contorta* might be dioecius, and although gonophores were not identified in the present *Apolemia uvaria* material, this species is known to be dioecius (Claus, 1863), as, typically, are other colonial hydrozoans (Mergner, 1971), including most siphonophores for which developmental details are known (Mackie *et al.*, 1987). The present gonophores are large, yellowish in colour, and arranged in groups on the stem, but the stalk is short (unlike that shown by Margulis) and does not appear to be associated with a palpon, so is probably not a gonodendron. Refractile spheres in the mesoglea of the ostium and basal region are similar to those present in the bracts, and may be nematocysts (Fig. 13g). Each ovum is enclosed in an outer umbrella (Carré, 1969), or tunic (Totton, 1965), which has a small apical ostium and six radial canals (Fig. 13g–h). Thus the female gonophores of *T. contorta* differ from those of *A. uvaria* which Totton (1965, fig. 17) stated have suppressed radial canals and no endoderm in the tunic of the exumbrella, though some short canals are shown in the basal half of the tunic by earlier authors (Leuckart, 1853, pl. 2 fig. 22; 1854, pl. 12 fig. 11; Claus, 1863, pl. 46 fig. 14). In other physonects where the gonophores have a retained umbrella, only four radial canals are present (Kölliker, 1853, *Forskalia edwardsi*; Haeckel, 1888*b* *Agalma okeni*; Totton, 1965, *Marrus antarcticus* and *Moseria convoluta*; Carré, 1969, *A. elegans* and *Cordagalma cordiformis*). In *T. contorta* the ovum is also covered with a network of branching endodermal manubrial canals (Fig. 13g), similar to canals described in *A. uvaria* (Claus, 1863; Totton, 1965) and other physonects (Metschnikoff, 1870; Weismann, 1883; Totton, 1954). Their function appears to be nourishment of the growing egg (Mergner, 1971).

Ramosia vitiazi

The third previously described apolemiid is *Ramosia vitiazi* Stepanjants, 1967, and in this species the colonies are small, like the *Tottonia contorta* specimens described by Margulis (1976, 1980), and the paratype studied here, which is part of a series of *R. vitiazi* specimens collected between 1949 and 1959 in the North Pacific (Stepanjants, 1970). It includes four loose nectophores, one fragment comprising pneumatophore, nectosome and the top part of the siphosome, and a second fragment comprising siphosome only. The nectosome shown in Fig. 15a is much contracted, particularly on the dorsal side, measures 6.5 mm in length and is a deep-red colour. The muscular lamellae are white, typically with dark red pigment edging their basal borders, and their arrangement resembles that in *T. contorta* (Fig. 9c). As in *Apolemia uvaria* and *T. contorta*, the apices of the lamellae protrude from the right side of the stem (left in the ventral view shown in Fig. 15a), and the bases from the left side, but in the *R. vitiazi* paratype the bases tend to protrude relatively further than in the other two genera. Although Stepanjants (1967) shows the apices of the lamellae protruding from the right side of the stem in her fig. 75 (they appear on the left in her ventral view), she unfortunately concludes, like Margulis (1980) for *T. contorta*, that they represent attachment points for whole nectophores and missed the opening of the pedicular canal in the centre of the lamella. In the paratype of *R. vitiazi* this is typically pigmented red, and thus easier to discern than in *A. uvaria* or *T. contorta* (see Fig. 15a). The nectosomal tentacle bases are large, often with red pigment in the epidermis, and are similar to those shown by Stepanjants (1967, fig. 75).

In the holotype of *Ramosia vitiazi* Stepanjants shows a mature nectophore attached to the nectosome (1967, fig. 74), but in the present paratype only a small immature nectophore (with the ostium not yet open) remains attached, just below the pneumatophore in the nectophoral budding zone (Fig. 15a: n_1). The mature nectophores probably detached at preservation during a strong contraction of the stem, as typically occurs in apolemiids. In the *R. vitiazi* paratype, the nectophoral lamellae on the stem indicate that in life up to nine nectophores are attached, though only four were collected with the stem fragments. Since the last two lamellae lie closer together than the others, their nectophores may have been lost prior to capture, and the lamellae be degenerating, as suggested for *Apolemia uvaria* and *Tottonia contorta*. It seems probable, therefore, that in *R. vitiazi* there is a total of 7–9 nectophores per colony, which agrees with the findings of Stepanjants (1967), and is

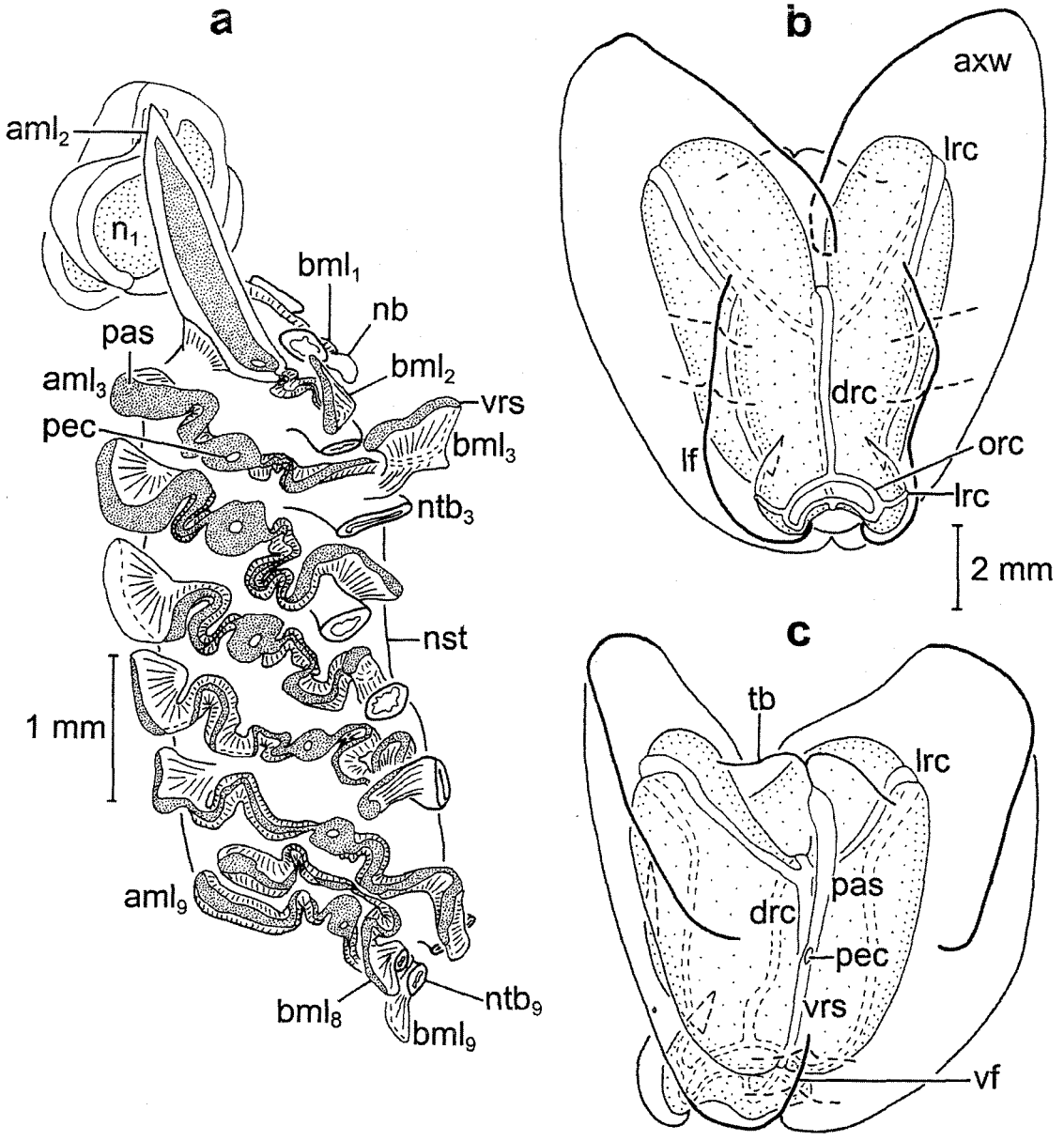

Figure 15 *Ramosia vitiazi* Paratype, Zoological Academy of Sciences, St Petersburg Specimen No. 3/9902, **a**: plan of distribution of muscular lamellae ml_1 to ml_9 on ventral surface of nectosome (excluding pneumatophore); **b**: mature nectophore, abaxial view; **c**: mature nectophore axio-lateral view. For abbreviations see list in text.

fewer than in *A. uvaria* and *T. contorta*. This is not surprising given the smaller size of the *R. vitiazi* colonies so far collected.

The nectophores of *Ramosia vitiazi* are a typical apolemiid shape (Fig. 15b–c) but are broader apically than the nectophores of *Apolemia uvaria* and *Tottonia contorta*, and the mesoglea of their axial wings thicker and more turgid. However, in the first *R. vitiazi* specimens described (Stepanjants, 1967) which includes the paratype, the ostium appears relatively small, and the mesoglea surrounding it soft, with the lower part of the nectophore narrow in abaxial view (Fig. 15b; Stepanjants, 1967, fig. 76a); in specimens collected later the ostial region is broader (Stepanjants, 1970, fig. 2b). Lateral furrows occur on the lateral surface (visible in abaxial view, Fig. 15b) with a ventral furrow on the lower axial surface (Fig. 15c) as in nectophores of *A. uvaria* and *T. contorta*. The nectophores of the paratype bear traces of red pigment on the axial surface, near the pallial canal and ventral radial canal scars, in the ventral furrow, at the bases of the axial wings, and between the inner wing bases (above the dorsal radial canal). It seems likely that in life the whole epidermis is pigmented since the nectophores are described by Stepanjants as brown-red, but in the paratype much of this layer has been abraded. The thrust block in *R. vitiazi* has a bilobed profile in axial view (Fig. 15b–c), and differs from the thrust blocks of *A. uvaria* and *T. contorta*, which have flattened U and V-shaped profiles respectively in this view (Figs 6c, 11c). The nectosac is translucent in the *R. vitiazi* paratype and the walls of the lateral

radial canals have only small irregularities, similar to those found in *T. contorta*, though slightly larger ones are illustrated in the lateral radial canals of the holotype (Stepanjants, 1967, fig. 77). However, these irregularities still do not constitute true diverticula because they do not penetrate into the mesoglea. The pallial canal is thicker and broader apically in the *R. vitiazi* paratype (Fig. 15c) than in *A. uvaria* and *T. contorta*, though was not shown in the axial view drawn by Stepanjants (1967, fig. 76b). It has a pointed apex which terminates in the median groove of the thrust block on the axial surface of the nectophore. This broad pallial canal scar on the nectophore is mirrored by a similarly shaped scar on the apical part of the muscular lamella (Fig. 15a).

The zooids in the cormidia of *Ramosia vitiazi* are borne on much longer and more prominent branches than those in the present *Apolemia uvaria* and *Tottonia contorta* specimens, and the cormidia of the paratype appear similar to those illustrated by Stepanjants (1967, fig. 78). Palpons are the most numerous zooids found, and are white, 1.5–2 mm in length with a slightly swollen column and narrower apex. Groups of pale pink buds are attached at the bases of many palpons, and appear similar to the small gonophores illustrated by Stepanjants. However, although a few of the larger gonophores contain an ovum, further work is needed to confirm whether all these buds are gonophores. No intact gastrozooids are identifiable in the paratype cormidia, but they may have broken off during preservation. Some white cup-like bases, approximately one per cormidium, are present which may be the bases of gastrozooids, but further material needs to be examined to verify this. Although two gastrozooids are illustrated by Stepanjants (1967, fig. 78), no mouth or hepatic stripes are shown. All bracts in the paratype cormidia, together with a few bracteal lamellae (from which the bracts have detached), are still attached to the siphosome, and are situated between the secondary cormidial branches, as shown by Stepanjants. They are much smaller (2 mm) than those of *A. uvaria* and *T. contorta* and their upper surfaces are covered with red pigment and the epidermis packed with refractile spheres (probably nematocysts) which together obscure the bracteal canal.

Conclusions

It is concluded from the present study that the diagnostic features of the Family Apolemiidae include the following: long-stemmed physonect siphonophores with large nectophores which arise from the stem in a single row with one or more unique nectosomal tentacles attached at the nectophore bases on the right side; nectophores with rounded contours, surface furrows (but no ridges) and two large axial wings bordering a deeply hollowed axial surface; muscular nectosac filling the nectophore; bracts also rounded with groups of nematocysts on the upper surface and tip of the bracteal canal fused to the lower surface; gastrozooids and palpons each with a single filiform tentacle which lacks tentilla. Other characters such as pneumatophore size and presence or absence of an apical pore, spacing of the cormidia, presence of pigmented palpons, and gastrozooids without tentacles included in the diagnoses of other authors (Stepanjants, 1967; Margulis, 1980) are either not relevant or incorrect. Pneumatophore characters are not of taxonomic value in physonects (Pugh & Harbison, 1986), cormidial spacing is related to degree of contraction, pigmented palpons may be a specific character, and it is well known that all siphonophore gastrozooids possess tentacles (Totton, 1965; Mackie, 1986).

Specific differences between *Apolemia uvaria, Tottonia contorta* and *Ramosia vitiazi* include the number of nectosomal tentacles per nectophore, the presence in the nectophore of true diverticula from the lateral radial canals where they pass over the axial processes of the nectosac, the profile of the nectophore thrust block in axial view, the course of the distal part of the bracteal canal in the bract, and, possibly, the distribution of red pigment throughout the colony. Most of these characters are included in the diagnoses given above for *A. uvaria* and *T. contorta*, and a comparable diagnosis for *R. vitiazi* might read as follows: one nectosomal tentacle at base of each nectophore; nectophore pigmented red; lateral radial canals without diverticula penetrating into mesoglea from proximal part (on nectosac axial processes) and distal part not forming deep loop, but canal walls with irregularities; dorsal radial canal straight; bract with red upper surface and densely packed nematocysts; course of distal end of bracteal canal unknown. Characters such as branching of the cormidium, and relative thickness of the nectosomal tentacles mentioned by other authors (Stepanjants, 1967; Margulis, 1980) are more likely to be related to the degree of contraction at preservation or to subsequent shrinkage during storage than to differences between species. Similarly, the smaller size and more elongate shape of the *T. contorta* nectophores from the Indian Ocean and equatorial Pacific (Margulis, 1980) are probably attributable to growth. In hydroid colonies generally "the size at which sexual maturity is reached depends on local conditions . . . and the dimensions of the colony and its various component parts may vary in the same way" (Cornelius, 1995, p. 6), and the same phenomenon may also occur in iterative siphonophore colonies.

The final question which arises from this present work is: 'do the differences between the three species discussed really reflect generic characters, or are they only of specific importance?' Characters which distinguish genera in other physonect families show much greater variation in nectophore shape than is observed between *Apolemia uvaria*, *Tottonia contorta* and *Ramosia vitiazi*. For example, in the Family Pyrostephidae the shape of the mature nectophore differs considerably between the genera *Pyrostephos* and *Bargmannia*. In *Pyrostephos* the nectophore is broader than it is long, the thrust block does not project beyond the nectophore wings, and the lateral radial canals follow a looped course over the nectosac. *Bargmannia*, in contrast, has a nectophore which is longer than it is broad, a thrust block which projects well beyond the nectophore wings, and lateral radial canals which are straight for most of their length (Pugh, 1999*b*). The differences between nectophores in the apolemiid genera seem insignificant indicating that they are probably only specific character differences. However, given that there are at least 10 more apolemiid species still to be described (Pugh, 1999*a*), it seems best to defer consideration of

the specific status of *Tottonia* and *Ramosia* until such further descriptions are published.

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