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Redescription of *Marrus orthocanna* (Kramp, 1942) (Cnidaria, Siphonophora)

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Abstract. A monoecious colony of *Marrus orthocanna* (Kramp) from the FRAM I Ice Drift Expedition (84°36'N, 9°W) is described, and the development of nectophores, bracts, gastrozooids, and gonophores figured.

INTRODUCTION

Marrus orthocanna was previously known from incomplete specimens without gonophores, taken in deep water (1000-2000 m) at temperatures from -0.4°C to 0.0°C off West Greenland between 67°42'N and 74°50'N (Kramp 1942), and had been found as far south as west of the Faroes (Totton 1965). On the basis of his finds in West Greenland, Kramp (1942) considered it a high-arctic species, probably identical to a species observed in the surface water of Robeson Channel and in Lady Franklin Bay (Moss 1879, Fewkes 1888), which with some hesitation they referred to *Stephanomia (Nanomia) cara*. The finds by the FRAM I establish it as a species at least of high-arctic occurrence, and the capture of a single, almost complete, colony made it possible to enumerate and to describe the development of the secondary components adhering to the stem, including the previously undescribed gonophores.

Acknowledgements

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MATERIAL

The FRAM I, 12. iv. 1979; 84°36'N, 9°W; depth 50 m. A colony 11.3 cm long, missing part of the siphosome, preserved in 2% formaldehyde (sea water + 20% formaldehyde in distilled water) with borax (pH = 8.2), is described. Additional observations from the FRAM I include a c. 45 cm long colony (alive) brought up by a current meter (not preserved), and fragments in three samples pumped from 40, 50, and 60 m, respectively. A total of 155.75 m^3 water from 0 to 100 m were filtrated (80 μm), giving one colony per 38.9 m^3. From 40 to 60 m, 54.3 m^3 were filtrated, giving one colony per 13.5 m^3, or c. 1.5 colonies per m^2. Ambient temperatures were from -1.77°C to -1.75°C, and the salinity ranged from 32.5‰ to 32.7‰. Sampling was done through 2 to 2.5 m thick ice which covered at least 80% of the surface, allowing no more than about 1‰ of the surface irradiance to reach the water. Kramp's specimens from the Godthaab Expedition to West Greenland, including his holotype (in 4% formaldehyde in sea water with pH = c. 5), have been examined, along with Totton's holotype (nectophore) of *Marrus antarcticus* (1954).

DESCRIPTION

Marrus orthocanna (Kramp)

Stephanomia orthocanna Kramp, 1942: 17-20. Holotype including stem with pneumatophore, nectophore, bract, and gastrozooid with tentilla (Zoological Museum, University of Copenhagen) [examined].

Marrus orthocanna; Totton 1965.

The FRAM I specimen is considered identical to Kramp's *Stephanomia (Marrus) orthocanna* due to its morphological similarity. Only the vertical ridges on the nectophores and auxiliary teeth on the bracts of the FRAM I specimen make it differ. These characters are lacking in Kramp's specimens, perhaps due to difference in age and/or state of preservation, involving discrepancies in proportions and colour. The characters, therefore, do not justify the erection of a new species comparable to the *Halistemma striata* which Totton (1965) distinguished from *H. rubrum* (Vogt) by the vertical ridges on the nectophores, although Totton (1954, p. 59) mentions "... the absence of any oblique ridge dividing the lateral facets" as a generic character.

Pneumatophore (Fig. 1). Banana-shaped, 4.5 mm long, greatest diameter 1.4 mm (Kramp's specimens up to 2 mm), constricted to c. 0.8 mm just above the dilated base. The inner structures indistinct. The distal half more transparent than the sharply defined proximal half. The nectophore is placed askew at the summit of the nectosome, and turned c. 60° to the side opposite the nectophorous groove, as if forced to one side by the small nectophores clumped together in the budding zone at its base.

Nectosome (Fig. 1). In life the nectosome of the FRAM I specimen was

orange-brown, not bright scarlet as mentioned by Totton (1965). Preserved, it has turned a pale yellow, whereas Kramp's specimens remain scarlet-brown. Presumably, it is considerably contracted, to a length of c. 13.5 mm and a thickness of from 2 to 2.5 mm, whereas Kramp's specimens are thicker, up to 3.5 mm, and possibly more contracted to a length of 4 mm. Externally, about 140 longitudinal muscle fibres project, extending throughout the length of the

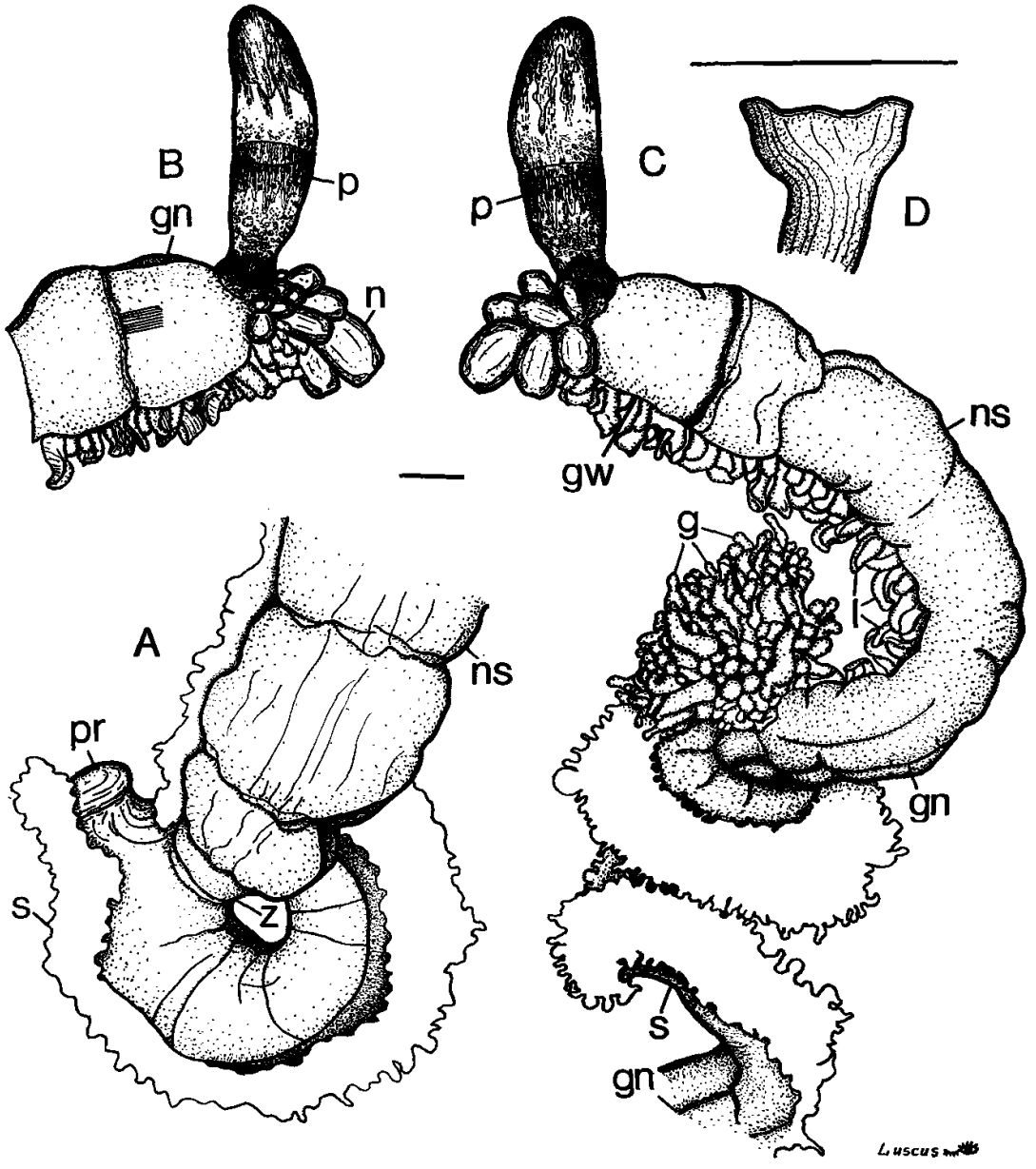

Fig. 1. *Marrus orthocanna*. A: Part of stem of a specimen from West Greenland. B–D: The FRAM I specimen. B–C: Stem. Muscle fibres shown in B. D: Pedicular lamella from nectosome. g = gastrozooid; gn = narrow groove; gw = wide groove; l = lamellae; n = nectophore; ns = nectosome; p = pneumatophore; pr = projection; s = siphosome; z = zone of limited growth. Scale 1 mm.

nectosome, to some degree anastomosing (Fig. 1 B). In cross-section the nectosome is roughly circular, with two grooves, a narrow and a wider and more prominent, running in straight lines on opposite sides from the pneumatophore to the siphosome. When intact, the nectophores are situated on lamellae (Fig. 1 D) which when preserved are cramped together in the larger of the two furrows. Since there must be room for eight nectophores in various stages of development and at least 23 fully developed ones, each c. 6 mm thick, in addition to the 15 small nectophores still adhering to the stem, the nectosome most probably has contracted to less than one-fifth of the original length. Placed in two rows the full-grown nectophores alone cover at least 72 mm.

Siphosome (Fig. 1). In life the FRAM I specimen was coloured as the nectosome, and preserved it is slightly paler, whereas Kramp's specimens have retained their scarlet-brown colour. The siphosome is unbranched, c. 1.6 mm thick (Kramp's specimens up to 2 mm). No specimens have been found complete with protozooids. The siphosome measures 9.5 cm to the broken end (Kramp's specimens measure up to 15 cm, and a live specimen, at least 40 cm long, was observed by the FRAM I). No muscle fibres are visible. The siphosome continues in varying spirals from the distal end of the nectosome. It starts with an about 1.6 mm projection extending to one side, below the nectophorous groove of the nectosome (Fig. 1 A). It is contracted, especially proximally, and the projection as well as a bulge running down the entire length of the siphosome as a continuation of the nectophorous groove of the nectosome are densely packed with gastrozooids and gonophores in different stages of development, flanked by bracts also in different stages of development. Single cormidia,

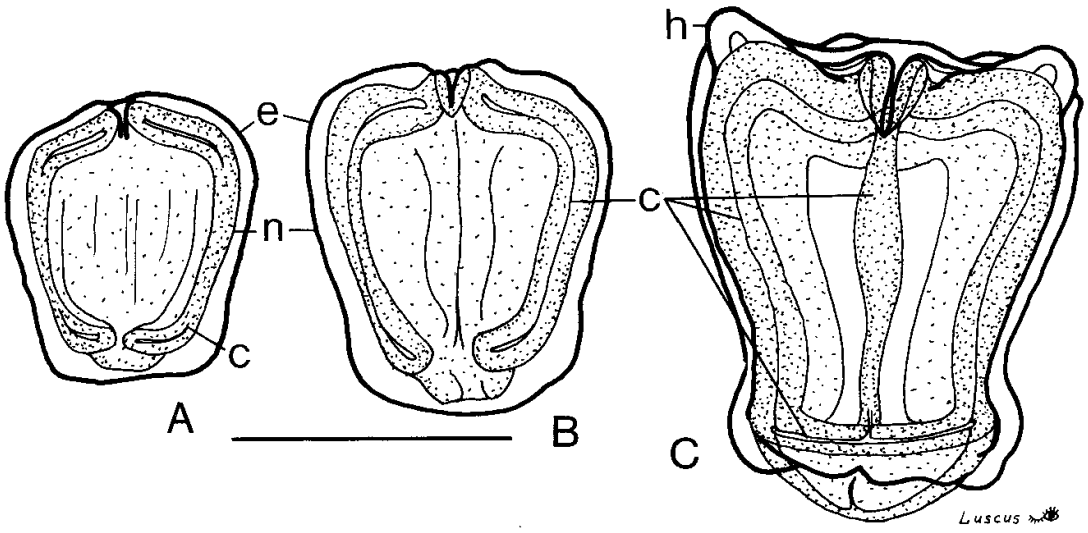

Fig. 2. *Marrus orthocanna* from FRAM I. The three youngest detached nectophores, showing the ectoderm (e) and the nectosac (n) with developing canals (c). The largest specimen, viewed from below, shows the first traces of developing horns (h) with ridges. Scale 1 mm.

nodes and internodes are not discernible. Besides the large number of primarily immature bracts, gastrozooids and gonophores still adhering to the siphosome, the sample contains c. 1100 bracts, 1 to 8 mm long, and numerous smaller ones, 1300 gastrozooids of which 30 measure more than 1 mm, and numerous

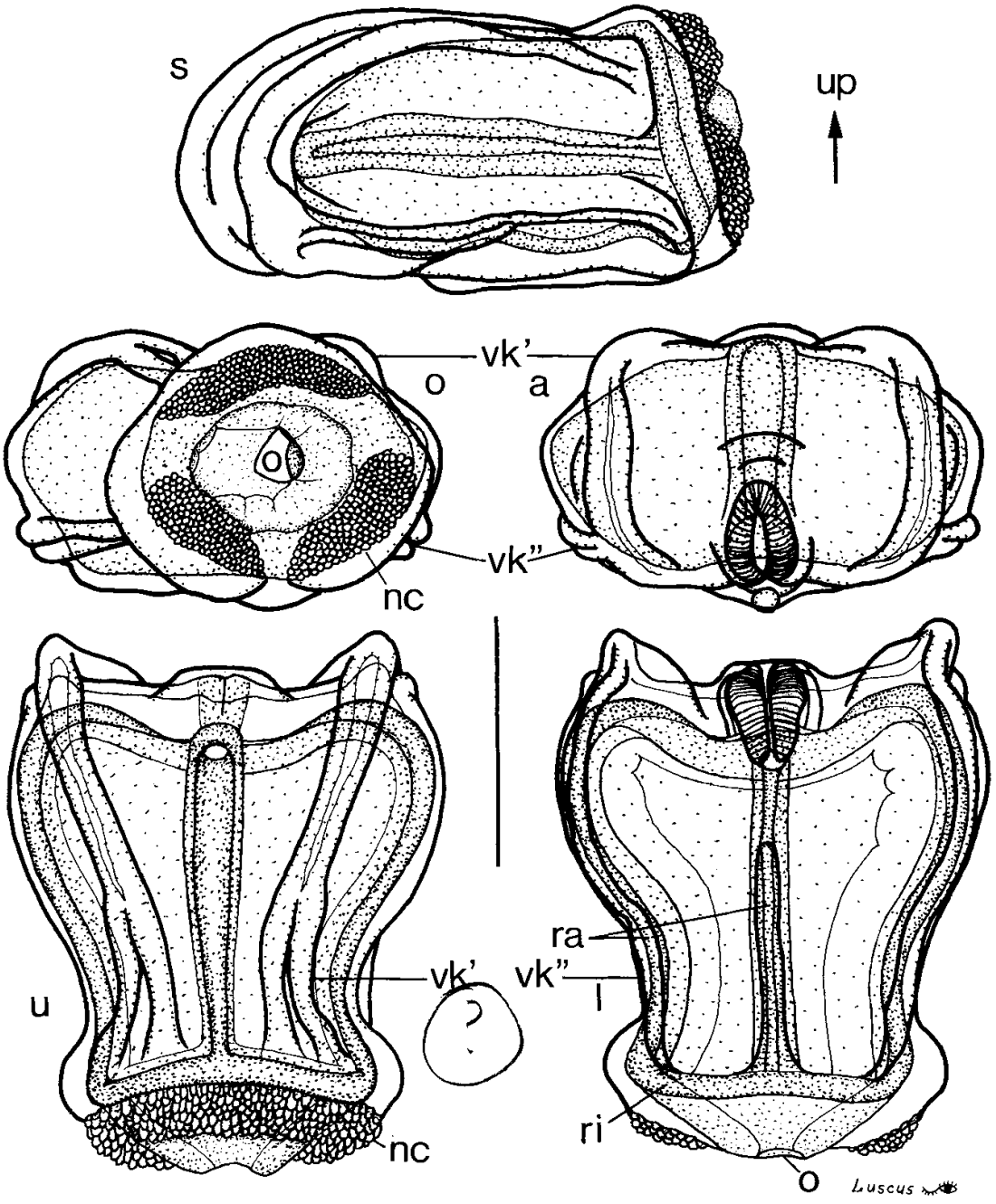

Fig. 3. *Marrus orthocanna* from FRAM I. The nectophore succeeding the largest one in Fig. 2, showing the fully developed ring (ri) and radial (ra) canals, the upper (vk') and the lower (vk") lateral ridges, the patches of nematocysts (nc) on the velum, and the ostium (o). Shown in adaxial (a), lower (l), ostial (o), side (s), and upper (u) view. Scale 1 mm.

smaller ones, and equal numbers of distinctly male (275) and distinctly female (270) gonophores, and numerous smaller ones.

Nectophores (Figs 1-7). In life the nectophores are transparent, with two orange-yellow ostial chromatophores (as in *Halistemma striata* Totton), one on each side of the velum. These chromatophores disappear during preservation. The nectophores are 14 to 15 mm long, 6 to 7 mm thick, and 12 to 13 mm wide proximally to c. 6.8 mm, tapering to c. 5.2 mm distally, where they are broadly cone-shaped to cylindrical. The horns are bluntly rounded, and the median "upper" lappet has a slight, central indentation seen from above or below. In lateral view (Fig. 7) the outline is roughly trapezoid, except the upper lappet. In this view, the prominent features are the acutely pointed horns, the "lower" indentation of the ectoderm, also seen in the quite similar *M. antarcticus* Totton (1954), and the protruding "upper" and "lower" rims of the velar area. The ectoderm adjoins the lateral dilations of the nectosac in an area from which ectodermal lines radiate (Figs 5, 6).

During early development (Figs 2-4), the "Y"-shaped upper as well as lower lateral ridges (VK' and VK" of Claus 1879) are prominent features. When horns develop, they first turn upwards making the "Y"-shaped ridges meet medially (Figs 4B, 5A, 6A). Ultimately, when the final size is attained (apparently by

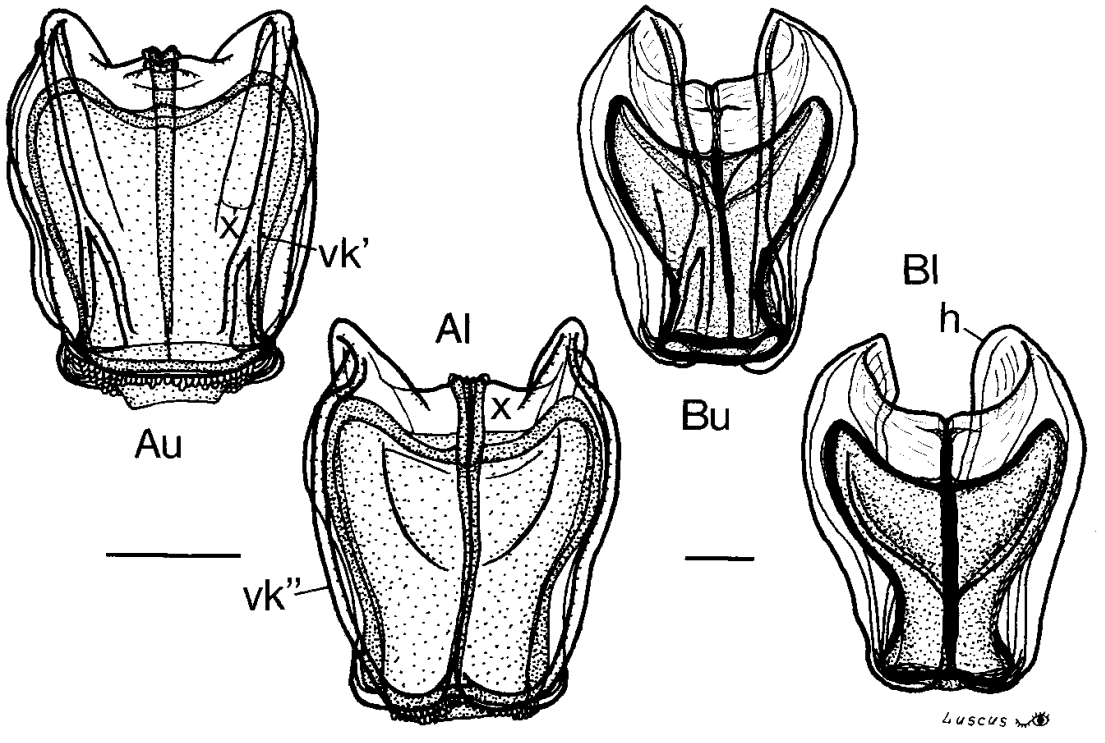

Fig. 4. *Marrus orthocanna* from FRAM I. A-B: The two nectophores succeeding the one in Fig. 3 in size, in upper (u) and lower (l) view. h = horn; vk' = upper lateral ridge; vk" = lower lateral ridge; x = smooth part of ectoderm. Scale 1 mm.

"inflation" of the mesogloea which makes the horns swing out and the width increase by 30-50%) the "Y"-shaped ridges shift to a lateral position.

The course of the four radial canals is straight, from the ring canal to the summit. The somatocyst is deeply sunk into a narrow furrow which is a continuation of the indentation on the median lappet. As in *M. antarcticus* and in *Pyrostephos vanhoeffeni* Moser, no cells occur on the adaxial surface of the nectosac. The deep longitudinal depression on the underside, described by Kramp, involving the nectosac and making it horseshoe-shaped in cross-section, does not exist. A transverse depression is present and discernible from the early stages (Fig. 4B), but the depression and the distinctly protruding cleft lower border to the velar area, shown by Kramp in his fig. 4a,b, is an artifact due to collapse (cf. Fig. 7A).

The surface structure is either smooth (smooth areas occur already in young nectophores (x in Fig. 4A) or it consists of numerous tiny (20 μm) globular mounds, each placed in the centre of a penta- or hexagonal cell c. 60 μm across (Fig. 7B). The young nectophores have an "upper" and two "lower" patches of nematocysts on the velum, as in *Forskalia edwardsi* Kölliker. These patches disappear when the nectophores mature. The fully developed nectophores have two pairs of (semi-)vertical lateral ridges (r in Fig. 5B), similar to those in *Halistemma striata* but not equally conspicuous. Such ridges have not previously been observed in this species, probably because the nectophores were not fully developed, or due to age or poor preservation.

Bracts (Fig. 8). The bracts are almost invisible when full-grown, and up to 8 mm long. The young stages have a compact apical band of nematocysts, as in *Halistemma rubrum* (Vogt), while in the older stages this band is dilated and diffuse. The cellular surface structure of the young stages is divided into irregular patches (Fig. 8D), except in the apical facies which makes the latero-terminal teeth curve inwards. Proximal to each of these teeth a small auxiliary tooth occurs (at in Fig. 8), a prominent feature of the developing bracts. These teeth are less distinct in the largest specimens. The bract shown by Kramp in his fig. 4e is collapsed, but it demonstrates the same characteristic pointed apex, clearly distinguishing it from the triangular bracts of *M. antarcticus* (Totton 1965, fig. 27) and not unlike the bracts of *Halistemma rubrum*. Both lack auxiliary teeth.

Gastrozooids (Fig. 9). Up to 9.5 mm long. When full-grown, the basigaster is dark brown to nearly black and the remaining part light brown to yellow. The gastrozooids develop on gastrodendra (Fig. 9A) which, together with numerous gonodendra, form a band, flanked by bracts, running down one side of the siphosome. In the youngest specimens, the basigaster forms a prominent sheath around the proximal half, while in the larger specimens it is thinner and stretched, as in Kramp's specimens, or it has a globular base making the ten-

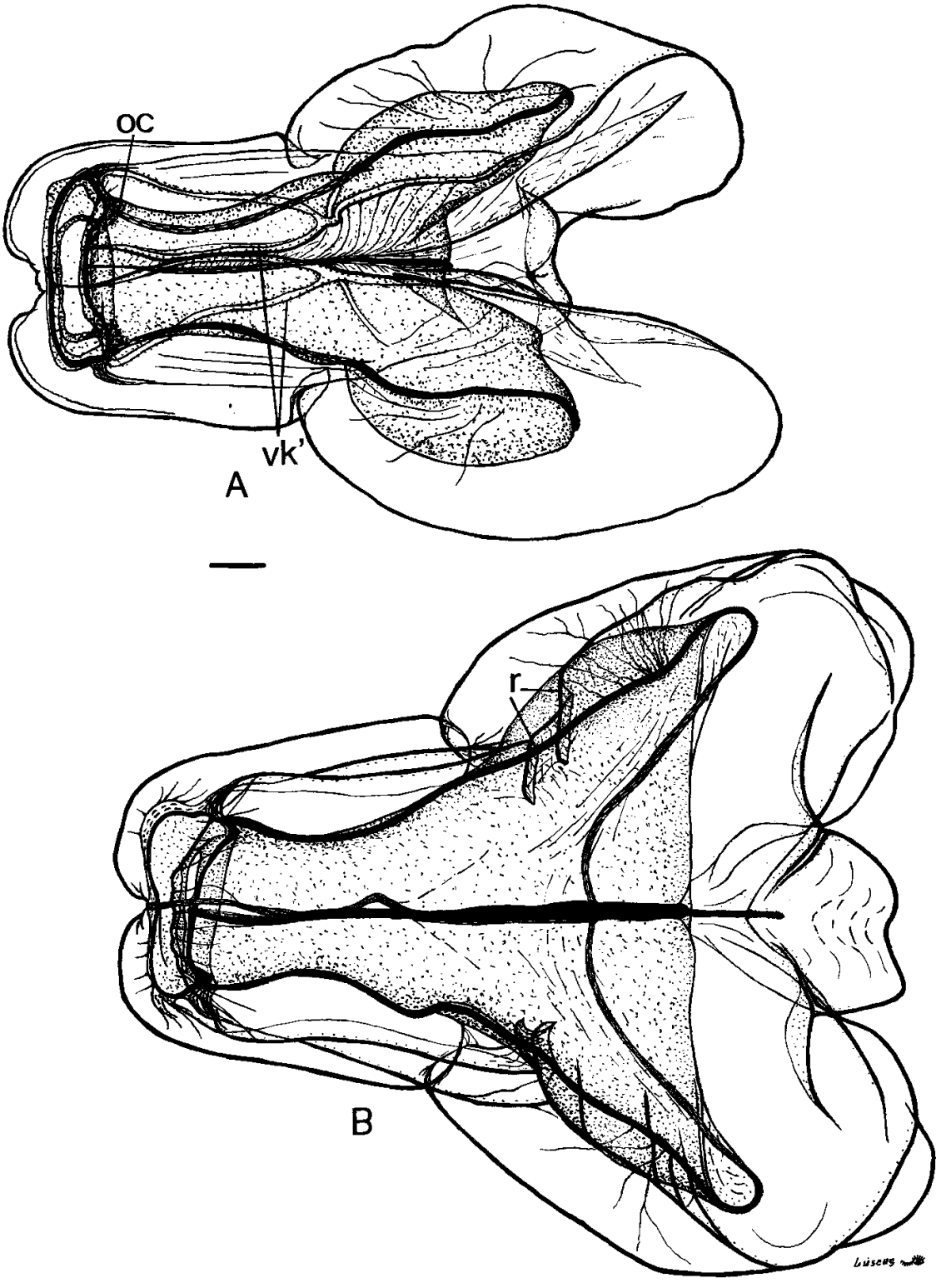

Fig. 5. *Marrus orthocanna* from FRAM I. Upper view of the last developmental stage of a nectophore (second stage following that shown in Fig. 4B) before full size is reached (A) and a full-grown nectophore (B). oc = ostial chromatophore; r = vertical ridges; vk' = upper lateral ridge. In A the hidden structures of the lower side, including parts of the radial canals, are not shown. Scale 1 mm.

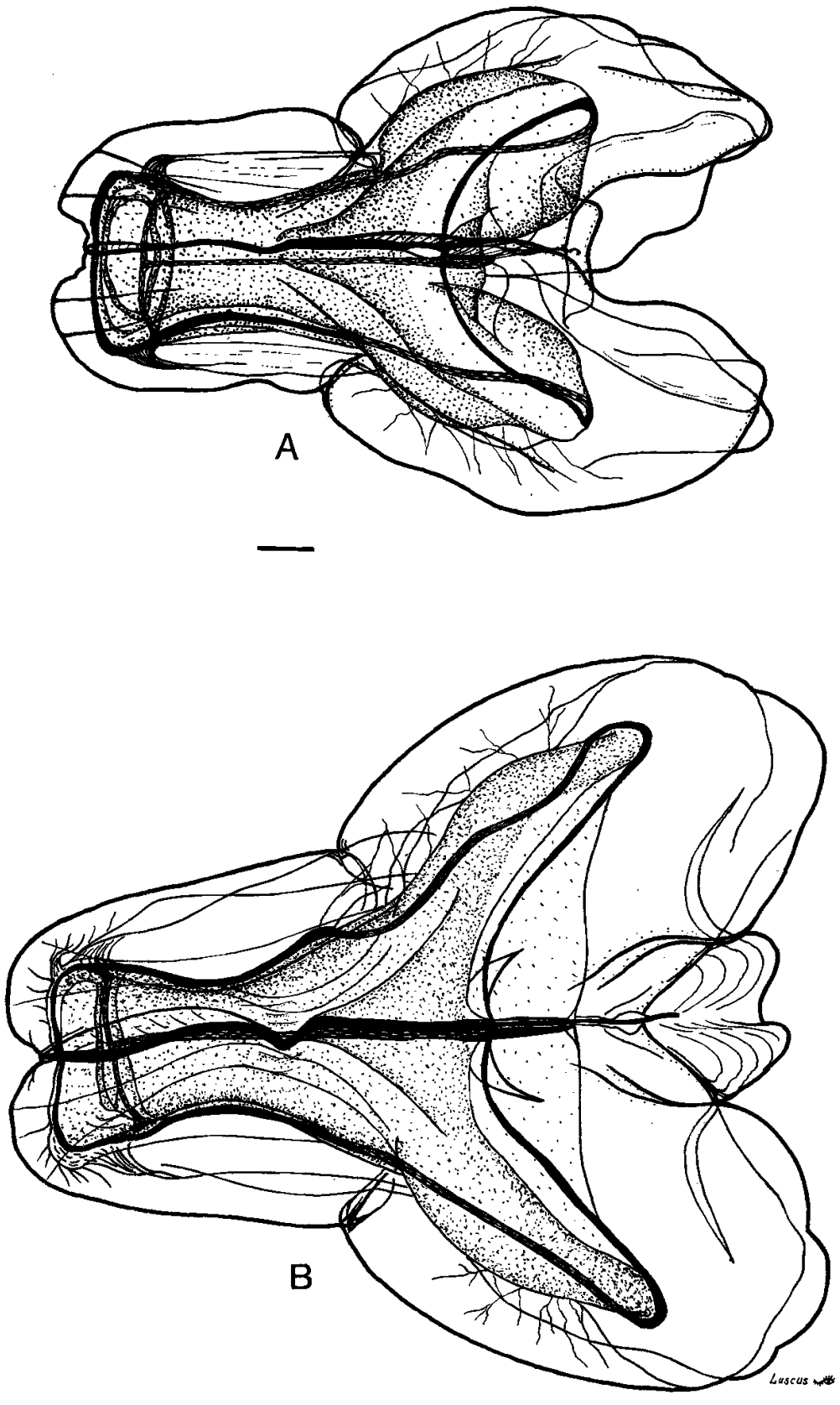

Fig. 6. *Marrus orthocanna* from FRAM I. A-B: Lower view of A and B in Fig. 5. Scale 1 mm.

tacle extrude from the underside rather than laterally. The proximal 1/2 to 3/5 of the gastrozooids, including the basigaster, has a more or less vacuolized endoderm, and in the largest specimens a glandularlike integument with longitudinally arranged glands. The vacuoles and/or glands of the endoderm taper into five points or lines (folds) towards the mouth (cf. Fig. 9). The stomach may be trumpet-shaped or swollen, with a yellow content of lipids and stacked with exosceletons of copepods.

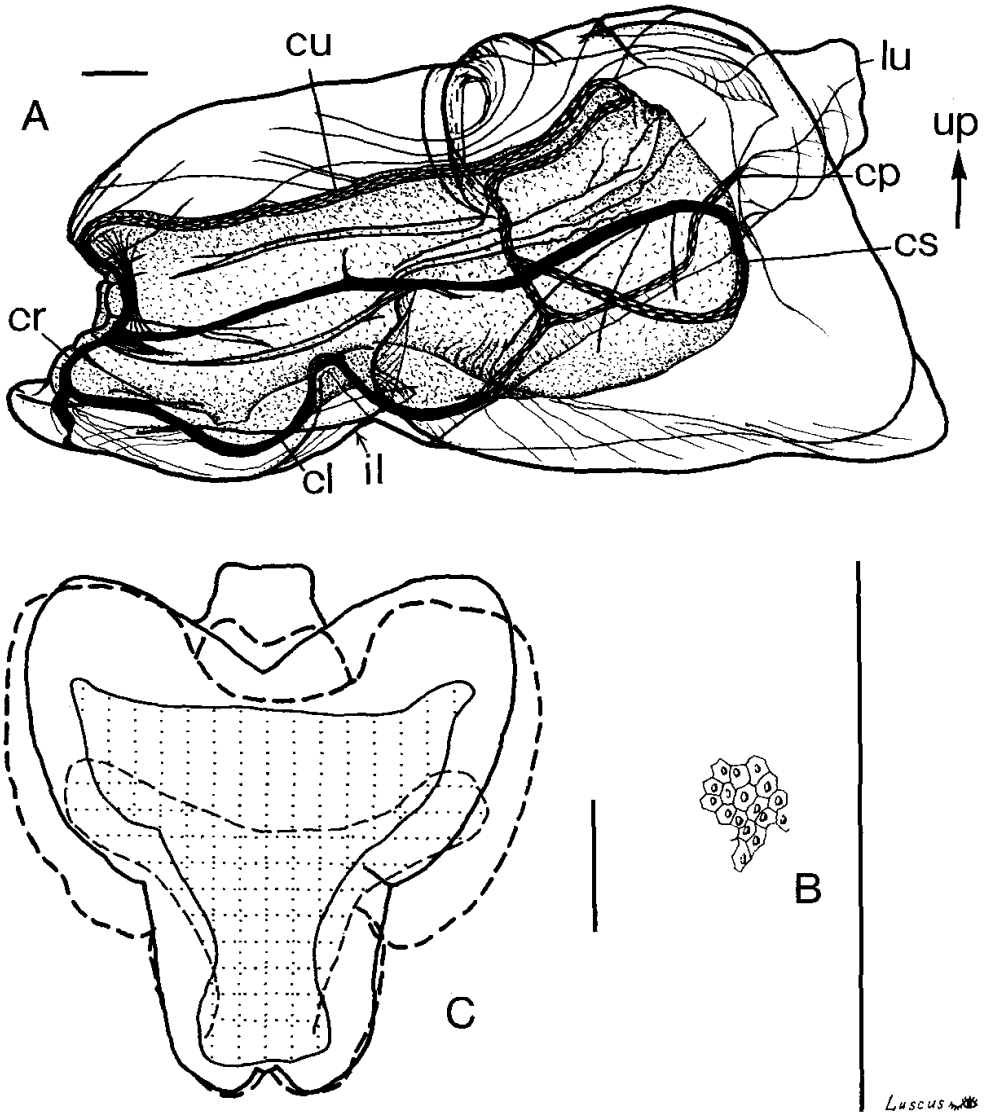

Fig. 7. A-B: *Marrus orthocanna* from FRAM I. A: Lateral view of nectophore B in Figs 5 and 6, showing the pedicular canal (cp), ring canal (cr), lower, upper, and lateral radial canals (cl, cu, cs), lower indentation (il), and upper lappet (lu). B: Surface structure of part of A. C: Outlines of nectophores and nectosacs (dotted) of Totton's (1954) holotype of *M. antarcticus* (- - -), and of a specimen of *M. orthocanna* from FRAM I (——). Scale 1 mm.

The basal tentacle starts as digitiform, and maintains a thickness of c. 200 μm near the base. Then it lengthens and becomes irregularly spiralled and develops a weak segmentation. In young stages each segment carries a transverse

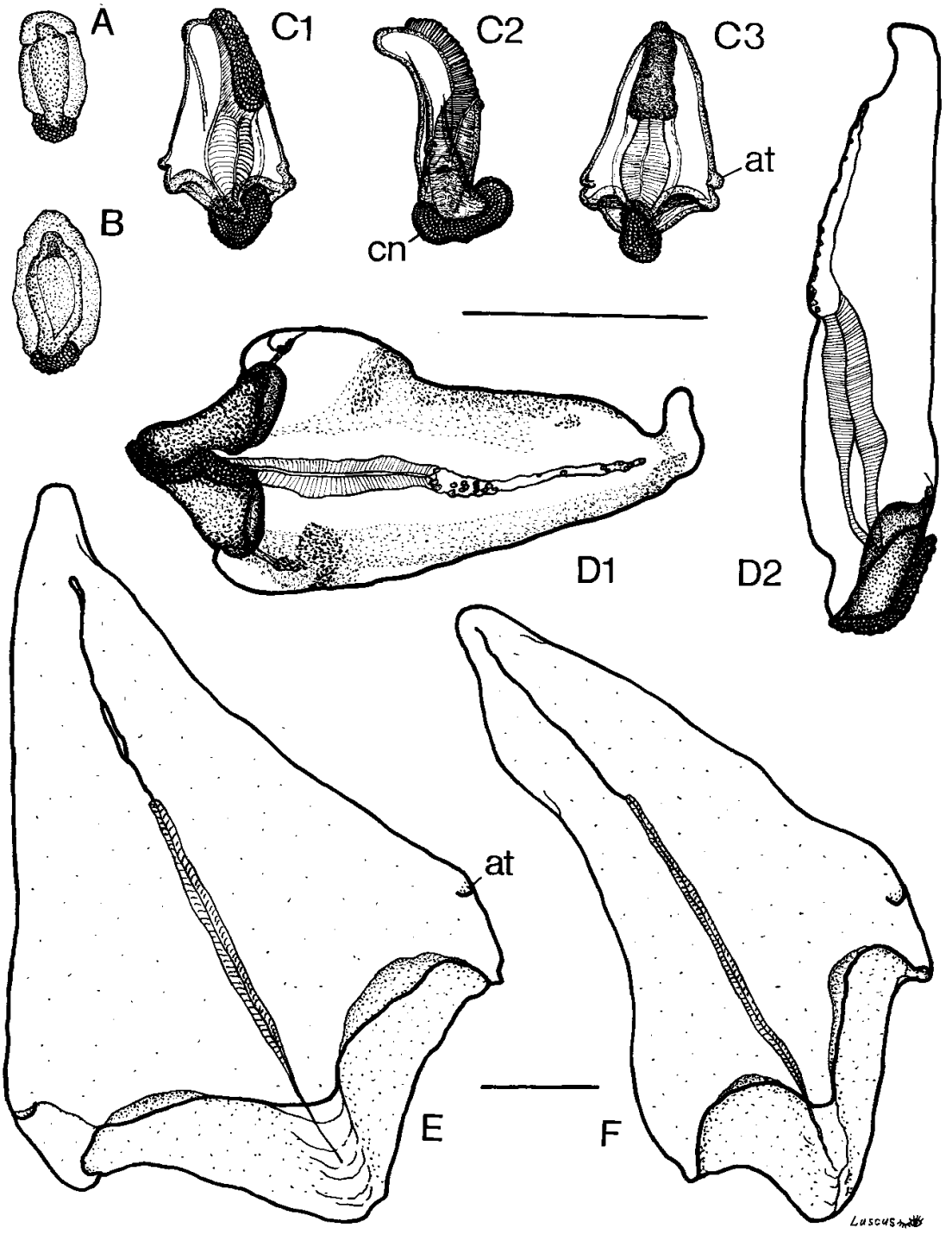

Fig. 8. *Marrus orthocanna* from FRAM I. A-D: Series of young to half grown bracts. N O. Full-grown bracts. at = auxiliary bracteal tooth; cn = cnidoband. C2 and D2 in lateral view. Two scales (both 1 mm) apply to A-D and E-F, respectively.

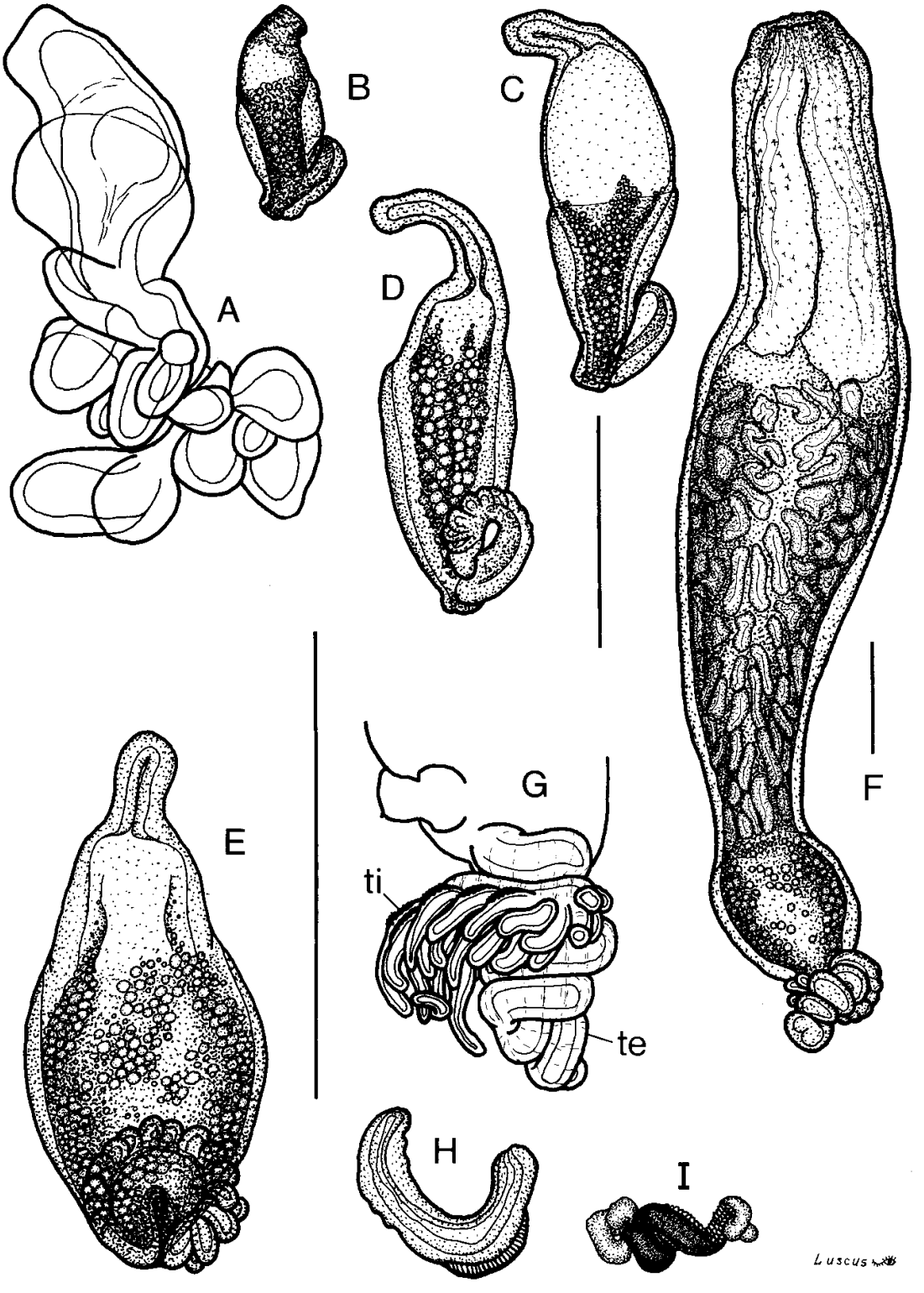

Fig. 9. *Marrus orthocanna* from FRAM I. A: Contour drawing of a young gastrodendron. B-F: Series of young to full-grown gastrozooids. G: Basigaster with tentacle and young tentilla from large gastrozooid. H: Young tentillum. I: Fully developed tentillum. te = tentacle; ti = tentillum. Three scales (all 1 mm) apply to A and H, to F, and to the remainder, respectively.

row of tentilla which are shortest near the base of the tentacle. In older stages only the proximal part bears tentilla, while the 150 µm thick distal part is naked. Many tentilla are detached. They are 1.6 to 2 mm long and 100 µm thick from the base to the flagellum which is c. 75 µm thick. They are unicornuate, without involucrum, irregularly spiralled with an about 1 mm long cnidoband. In contrast to those in Kramp's specimens, the tentacles are contracted in irregular spirals.

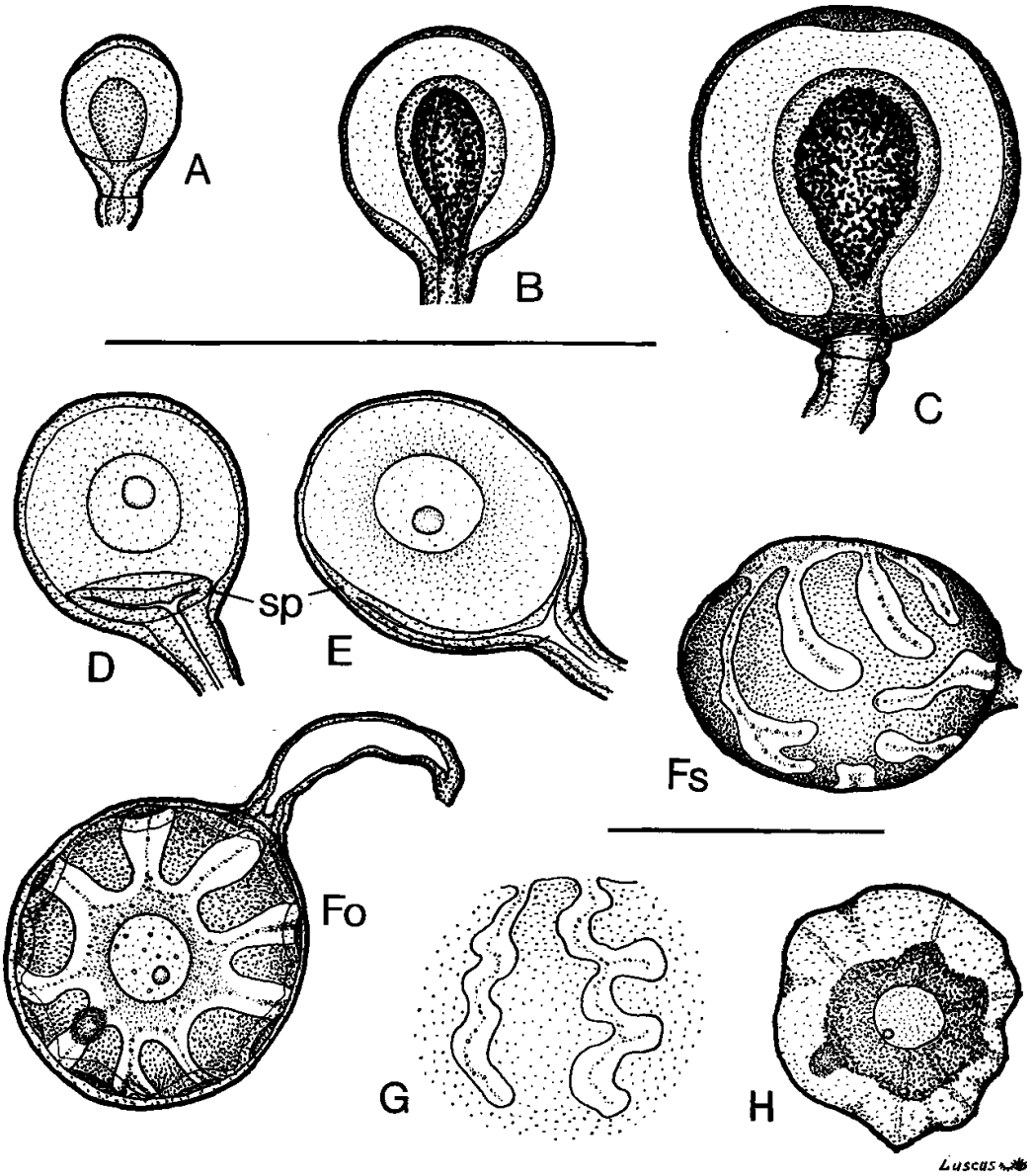

Fig. 10. *Marrus orthocanna* from FRAM I: A-C: Young to oldest ♂♂ gonophores. D-F: Young to oldest ♀♀ gonophores, the latter in ostial view (o) and lateral view (s). G: Detail of spadix of F. H: Medusoid dissected out. sp = spadix. Two scales (both 1 mm) apply to A-E and F-H, respectively.

Gonophores (Fig. 10). *M. orthocanna* is monoecious. The gonophores occur on gonodendra quite similar to those of the dioecious *M. antarcticus* but without palpons. There are c. 10 gonophores of one sex on each gonodendron. The males are ovoid and reach a length of c. 0.63 mm. The females are slightly compressed, reaching a size of c. 1.2 x 1.1 x 0.95 mm. The spadix is at first disc-shaped, then becomes irregularly lobed, almost enclosing the monovon medusoid which is clearly distinguishable in the most advanced stages (Fig. 10H).

DISCUSSION

Generic taxonomy in Siphonophora is mainly based on the nectophores. The genus *Marrus*, with three species, was erected by Totton (1954), partly on the feature that the nectophores have unlooped lateral radial canals, in contrast to the condition in *Halistemma* Huxley, 1859; this trait had by Kramp (1942) been considered a specific character. If nectophores are missing, or if only nectophores are present, identification to species and even to genus and family may be difficult. The list below enumerates the species with which *Marrus orthocanna* might be confused.

Marrus antarcticus Totton, 1954. Nectophore holotype examined. The nectophores of this antarctic "counterpart" (so termed by Totton 1954, p. 60) of *M. orthocanna* are hardly distinguishable from those of *M. orthocanna*, except for the vertical ridges and the shape and proportions which in *M. antarcticus* are shorter and wider, with a shorter distal part, and a shorter nectosac. These differences might be due to preservation (cf. Fig. 7C). *M. orthocanna* lacks palpons on the gonodendra, it is monoecious, and has "diamond-shaped" bracts with auxiliary teeth. *M. antarcticus*, however, like the third species of *Marrus, M. orthocannoides* (the nectophores of which cannot be confused with those of *M. orthocanna*), has palpons, is dioecious, and possesses triangular bracts without auxiliary teeth.

Halistemma rubrum (Vogt, 1852). The gonodendra and the bracts with conspicuous cnidoband are quite similar, except that the gonodendra have palpons and the bracts lack auxiliary teeth.

H. striata Totton, 1965. The nectophores, the only fragments known, are similar by having ostial chromatophores and vertical ridges, though not in equal number, but they differ by having looped lateral radial canals.

Erenna richardi Bedot, 1904. The bracts have auxiliary teeth, are somewhat "diamond-shaped" but are longer, and the teeth differ in shape and location.

Pyrostephos vanhoeffeni Moser, 1925. Moser's figure (1925) is strikingly similar as to the morphology of the stem, the one-sided attachment of the zooids, and the proportions. Also the gastrozooids are much alike. The nectophores, however, are different, only the absence of cells in the adaxial part of the nectosac is a common feature.

Forskalia edwardsi Kölliker, 1853. Only the presence and location of the nematocysts on the velum of the highly differing nectophores, with straight lateral radial canals and auxiliary teeth on the somewhat differing bracts, are common features.

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