

***Gattya wimleni* spec. nov. (Cnidaria: Hydrozoa), a new hydroid from Madagascar, and an identification key to the *Gattya* species**

N. Gravier-Bonnet

Gravier-Bonnet, N. *Gattya wimleni* spec. nov. (Cnidaria: Hydrozoa), a new hydroid from Madagascar, and an identification key to the *Gattya* species.

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Nicole Gravier-Bonnet, Laboratoire d'Ecologie Marine, Université de La Réunion, 15 Avenue R. Cassin, BP 7151, 97715 St DENIS, Messag, Cédex 9, France, e-mail: Nicole.Gravier-Bonnet@univ-reunion.fr.

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Gattya wimleni spec. nov. is referred to the family Halopterididae (Hydroida, Thecatae). Colonies were collected at Tuléar (SW Madagascar, Indian Ocean) on the deeper part of the lower sloping platform, at 35 to 45 metres depth on the outer slope of the great barrier reef. The specimens were studied in transmitted light and by SEM. They differed from the eight species of *Gattya* already known in having a hydrothecal margin provided with four large rounded teeth of equal size - one abcauline, one adcauline and two lateral, curving inwards over the aperture, the laterals being hidden behind the lateral nematothecae in profile view. Its closest affinities are with the species *G. multithecata* (Jarvis, 1922) and *G. aglaopheniaformis* (Mulder & Trebilcock, 1909). A key is given for the identification of the species. Some of the descriptive characters are discussed: nodes and joints, bithalamy, and mobility of the nematothecae.

Introduction

The genus *Gattya* Allman, 1886, was abandoned for a long time in favour of *Plumularia* Lamarck, 1816, *Halopteris* Allman, 1877, and *Paragattya* Warren, 1908, before Millard (1962: 270, 281) used it to separate a few species with toothed hydrothecae from untoothed ones (which she referred to *Halopteris*). It is placed in the family Halopterididae (superfamily Plumularoidea Agassiz, 1862), following Bouillon (1985: 166), who attributed family rank to the subfamily Halopteridinae Millard, 1962 (who used the incorrect spelling Halopteriinae) of the family Plumulariidae Agassiz, 1862. Cornelius (1995/part 1: 82; 1995/part 2: 114-116, 120) maintained the subfamily Halopteridinae (as Halopteriinae) of the Plumulariidae.

The taxonomic history of the superfamily (including the Plumulariidae, Halopterididae, Kirchenpaueriidae and Aglaopheniidae) was discussed by Bogle (1975: 17). The family Halopterididae has been recently reviewed by Schuchert (1997).

Only eight species of *Gattya* have been described before: *G. aglaopheniaformis* (Mulder & Trebilcock, 1909), *G. balei* (Bartlett, 1907), *G. conspecta* (Billard, 1907a), *G. heurteli* (Billard, 1907b), *G. humilis* Allman, 1886, *G. multithecata* (Jarvis, 1922), *G. trebilcocki* Watson, 1973, and *G. tropicalis* Millard & Bouillon, 1973. Following Millard (1975), *Paragattya intermedia* Warren, 1908, is considered conspecific with *G. humilis*; and *Plumularia quadridentata* Jarvis, 1922, with *G. heurteli*. Descriptions of the species are found in Schuchert (1997).

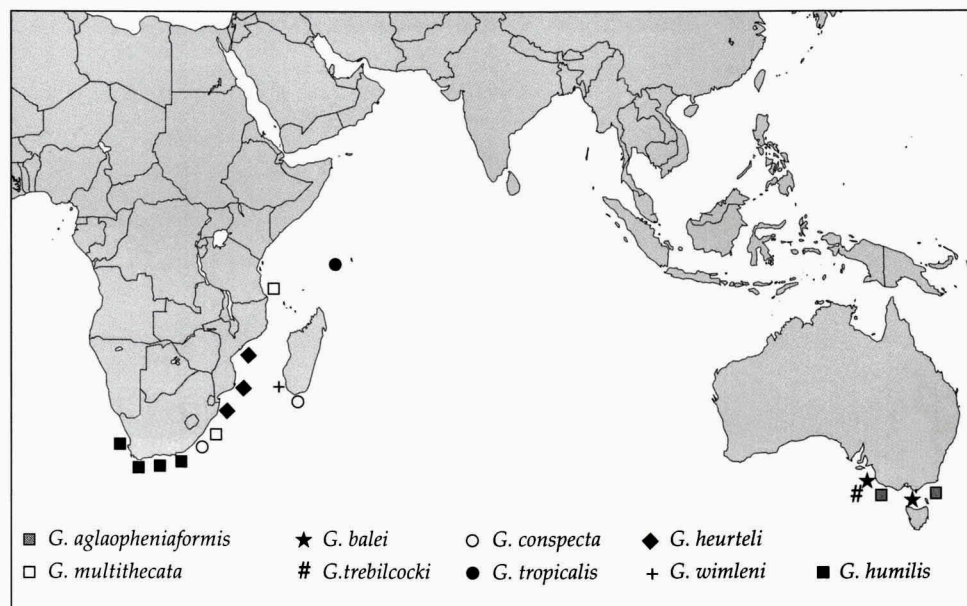


Fig. 1. World-wide distribution of the species of the genus *Gattya*.

Though the related genus *Halopteris* is widely distributed around the world, all the *Gattya* species have been collected from two restricted areas of the southern hemisphere (fig. 1), in water less than 70 m deep. Five are known from the SW Indian Ocean, between the equator and the south of Africa (*G. conspecta*, *G. heurteli*, *G. humilis*, *G. multithecata*, and *G. tropicalis*); and three from the province of Victoria in SE Australia (*G. aglaopheniaformis*, *G. balei* and *G. trebilcocki*). An undescribed species, *G. wimleni* spec. nov., was collected from Madagascar, in the first area, a supplementary finding which seems to confirm Schuchert's hypothesis concerning the monophyletic origin of the genus and its recent evolutionary radiation (1997: 143). The Australian species are more different from each other than are those from the SW Indian Ocean, among which, however, the two having short lateral nematothecae (*G. heurteli* and *G. humilis*) can be set apart from the others which have long ones (*G. conspecta*, *G. multithecata*, *G. tropicalis* and *G. wimleni* spec. nov.). Schuchert (1997: 143) noted that the *Gattya* species are mostly quite distinct and easily separable. However, several species are very similar, which is so of *G. wimleni* with *G. multithecata* and *G. aglaopheniaformis*. The latter is the only Australian species to have strong affinity with the last group, *G. trebilcocki* having short lateral nematothecae and *G. balei* an intrahydrothecal septum. Except *G. heurteli*, all species are small in size, the colony being less than two cm high. Typically they have been found settled on algae or on invertebrates (sponges and hydroids).

The specimens here described from Madagascar, though few in number and sterile, have stable and peculiar characters in comparison with previously known species. Descriptive characters of the genus *Gattya* are discussed based on a comparative study of the specimens of *G. wimleni* by light and scanning electron microscopy (SEM), and a key to the species is given.

The discovery of *G. wimleni* in the coastal waters of Madagascar was made long ago, during a period of investigation of the hydroid fauna of the Tuléar region in the south-west (1964-1973). The shallow water of the littoral and of the barrier reef were investigated by snorkelling, scuba-diving and dredging. Since this discovery, the author has collected hydroids from surrounding islands in the SW Indian Ocean, especially La Réunion, but the species has not been found again and can hence be considered as possibly endemic to Madagascar. Data on the hydroid fauna of Tuléar can be found in Gravier (1970a; 1970b) and Gravier-Bonnet & Fontaine (1981), and supplementary data from Madagascar in Gravier-Bonnet (1979).

Methods

The description of the new species has been made from observation of specimens by transmitted light and by scanning electron microscopy (SEM), the two methods giving complementary data on structures not easy to define.

The treatment of specimens for SEM, which involved dehydration, is responsible for some deformation of the skeleton of the material of *G. wimleni* spec. nov., as for example the formation of longitudinal folds on the surface of the thickest parts (fig. 7a-b, f), or the everting of the top of a superior nematotheca (fig. 7d). It also accentuated other characters of the thinnest parts, the curving of the adcauline tooth of the hydrotheca (fig. 6b), for example, or the folding of the adcauline (fig. 5e).

The holotype will be deposited in the Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie, RMNH), Leiden, The Netherlands, under no RMNH Coel. 20258. Paratype material will be deposited in the Muséum national d'Histoire naturelle, Paris (MNHN).

Descriptive part

Gattya wimleni spec. nov. (figs 2-7)

Material.— Samples from three stations located on the outer slope of the Barrier Reef of Tuléar (SW Madagascar) in the part of the reef locally called the lower sloping platform. All the material collected was sterile.

1/ T64V-93: P. Vasseur collection, dredging, 24.iii.1964, depth unknown, on the hydrorhiza of a colony of *Halicornaria ferlusi* Bolland, 1901 (usually present at 25-50m depth).

2/ T69N-204: Gravier-Bonnet collection, scuba-diving, 10.x.1969, 45m, "radiale n°C" (cf. Gravier-Bonnet & Fontaine, 1981: 104), attached to base of large colony of an undescribed aglaopheniid.

3/ T71P-268: M. Pichon collection, dredging, 27.ix.1971, "coupe intermédiaire no. 1" (cf. Gravier-Bonnet & Fontaine, 1981: 104), 36-41m deep, small well preserved specimen (the holotype, RMNH Coel. 20258) settled on rhodophyte with other hydroid species.

Material in the National Museum of Natural History, Paris examined for comparison:

Plumularia conspecta Billard, 1907: slide no. 1208; annotated "type", and listed as type by Van Praët (1979: 919).

Plumularia heurteli Billard, 1907: slides no. 1274-1275; annotated "types", and listed as syntypes by Van Praët (1979: 924).

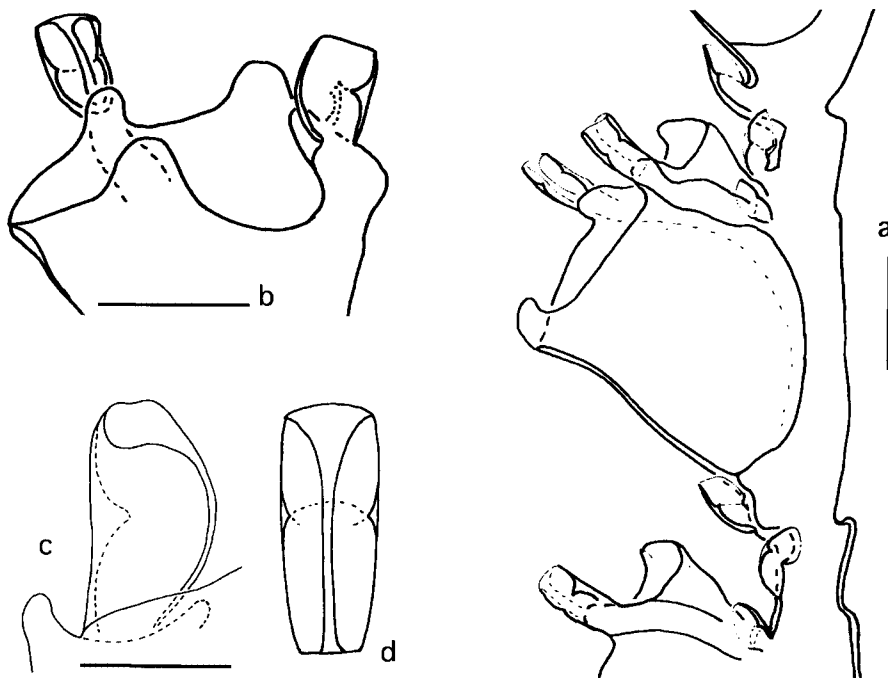
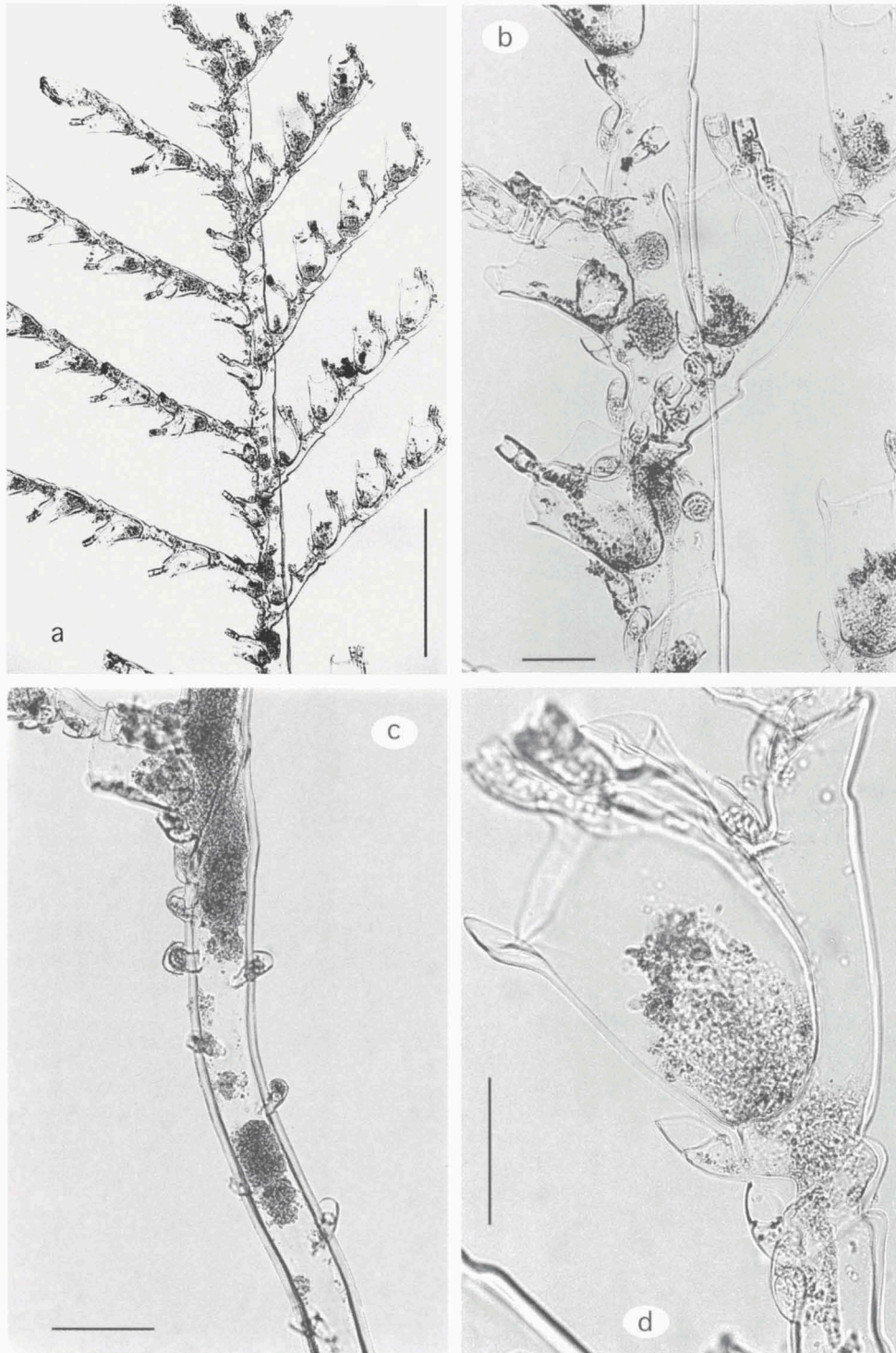


Fig. 2. *Gattya wimleni* spec. nov. a, profile view of an internode from a hydrocladium, with hydrotheca and one median inferior, one median superior, one pair of laterals (on peduncle) and one pair of superior nematothecae; b, frontal view of the aperture of the hydrotheca. Note the four equal sized teeth and the position of the lateral nematotheca; c-d, lateral nematotheca in frontal (c) and inner (d) view. It is set on a small platform at the top of the peduncle, next to the lateral tooth (c, dotted points on the right). Note the emargination from base to top. Scale: a-b = 0.1 mm, c-d = 0.05 mm.

Hydrorhiza simple, provided with tubular two-chambered nematothecae. Stem unfascicled, unbranched (fig. 3a), reaching 12 mm in height, with an anterior face which bears, and towards which are directed all hydrothecae, nematothecae and hydrocladia; comprising a short basal part and a long distal hydrocladia-bearing part, the two separated by an oblique hinge-joint (fig. 3c). Basal part with a few irregular transverse nodes and scattered pedunculate nematothecae which open versus the hydrocaulus and backwards. Distal part with hydrocladia divided by oblique nodes

Fig. 3. *Gattya wimleni* spec. nov. Transmitted light photomicrographs of preserved material. a, general view of the top of a plume with a general homonomous arrangement. Hydrocladia on the right are viewed laterally, having been squashed by the coverslip. b, enlarged view of the stem. Note the small difference in the shape of the hydrothecae on stem and on hydrocladium, the first athecate internode at the base of the hydrocladium, and the oblique nodes. c, base of the stem with long athecate part having nematothecae and ending in a conspicuous hinge-joint below the first cauline hydrotheca. d, hydrocladial hydrotheca. Note the ad- and abcauline teeth largely over-reaching the hydrothecal margin (the laterals are not seen since they are hidden behind the lateral nematothecae), the median inferior nematotheca over-reaching the base of the hydrotheca, the single median superior and the pair of superiors just below the end of the segment. A supplementary athecate internode provided with a single nematotheca occurs below the hydrothecate internode. Scale: a = 1 mm, b-d = 0.1 mm.



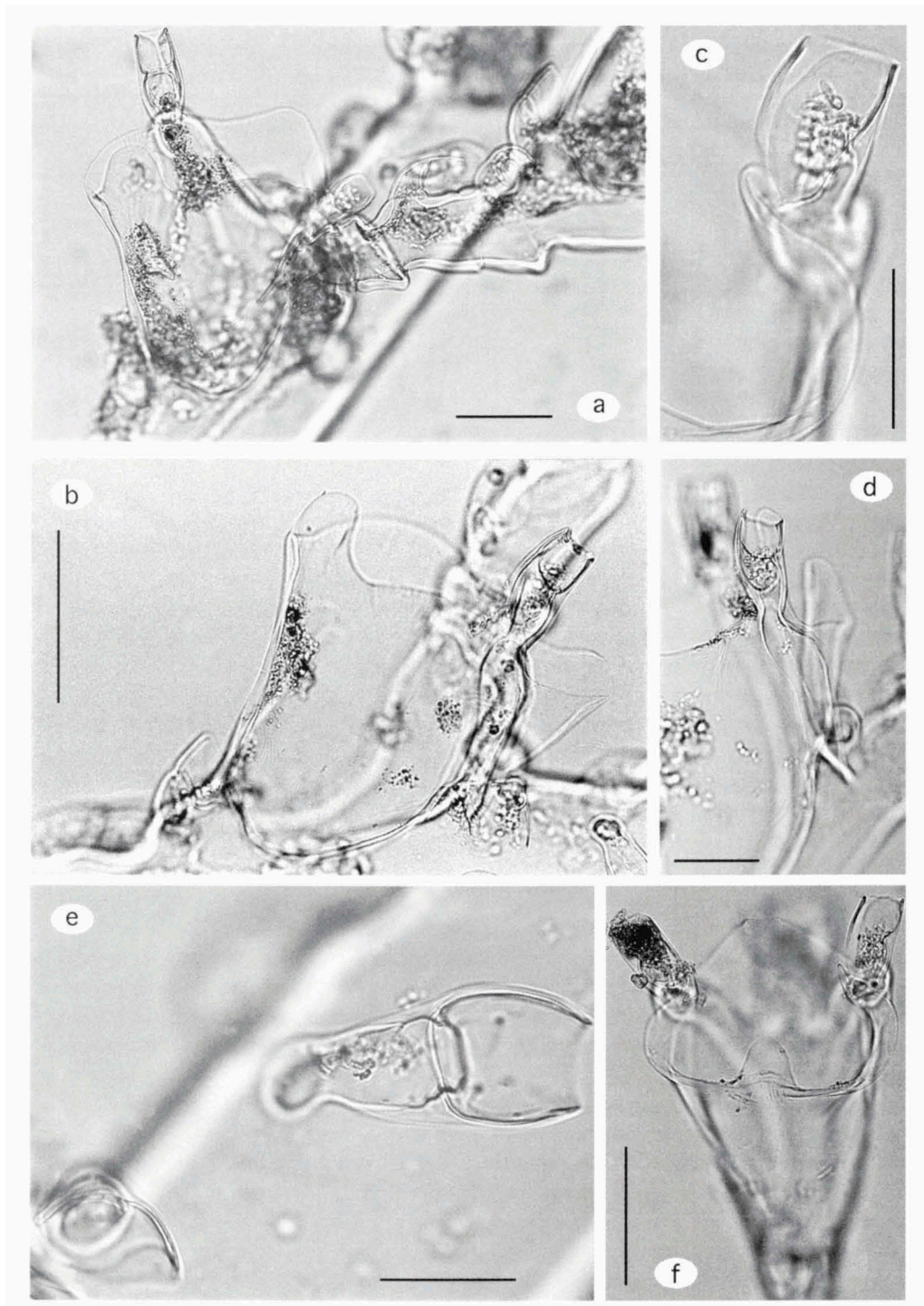
into hydrothecate internodes, the nodes being often difficult to distinguish except by a small depression in the perisarc wall just under the median inferior nematotheca. The first internode may bear opposite hydrocladia (fig. 5c), but remaining hydrothecate internodes bear alternate hydrocladia (fig. 3a). Internodes each comprising a hydrotheca, a hydrocladial apophysis and typically seven nematothecae: one median inferior, one pair of laterals with the one at the basis of the hydrocladia being smaller than the "normal" one opposite, one pair of median superior (a term introduced by Millard, 1975, but named supracalcine by several authors or suprahydrothecals by Billard, 1907) which is set at the base of the free adcauline wall of the hydrotheca, perpendicular to the axis with openings oriented versus the base, and one pair of superiors obliquely set on each side of the middle of the axis and dorso-apically oriented (figs 3b, 4a, 5a-b). Hydrocladial apophysis short, large, arising from process supporting the small lateral nematotheca, with ventral opening (figs 4a, 5b, d). The two rows of hydrocladia not in one plane, but curved, set and directed towards the anterior surface of the stem.

Hydrocladium typically comprising a short basal athecate internode without nematothecae, delimited by two straight nodes, a second longer one bearing a single median nematotheca and ending in an oblique node, and up to eight hydrothecate internodes bearing ventral hydrothecae (figs 3a-b, 4a, 5a-d). No intermediate athecate internodes between the hydrothecate ones (fig. 3a). Five to seven nematothecae on each hydrothecate internode: one median inferior, one pair of laterals, typically one or two median superiors, and one or two superiors. Hydrocladium ending just above a median superior nematotheca (figs 5e-f, 6b), except where a new internode is formed.

Hydrotheca cup-shaped and deep, two-thirds adnate, without intrathecal septum; adcauline wall straight, abcauline convex, in a few hydrothecae thickened and curved below the aperture (figs 2a, 3d). Margin forming an angle of 30° to 35° with internode, with four large and equal rounded teeth, one adcauline, one abcauline and two lateral. A few of these teeth are externally concave and slightly curved over the aperture (figs 2a-b, 3d, 4a-b, f, 5e-f, 6a-b). In profile under transmitted light, the ad- and abcauline teeth appear sharp and thick, but the lateral ones are not visible because they are hidden by the lateral nematothecae (figs 2a, 3d). Typically the cauline hydrothecae are shorter than the hydrocladial, and since they have a similar aperture diameter they appear more dumpy and larger (fig. 3b).

Median inferior nematotheca borne below the hydrotheca and over-reaching hydrothecal base except on stem; two-chambered (bithalamic), the distal opening

Fig. 4. *Gattya wimleni* spec. nov. Transmitted light photomicrographs of preserved material. a-b, cauline hydrothecae viewed from the two lateral sides. Note the single lateral nematotheca entirely over-reaching the hydrothecal margin on the left and the small second on the right, set on the apophysis at the base of the hydrocladium (a), and the nematothecae (b): the median inferior, the lateral on its peduncle fused with the hydrothecal wall, the median superior and superior (both paired). c-d, lateral nematotheca. Note the bivalve shape in profile due to strong emargination from base to top and the position on the side of the hydrothecal margin (hydrotheca in frontal view) and the small oval nematocysts (c), the sharp shape of the adcauline tooth compared with other views more ventral (a, b, f). e, enlarged view of one of the two nematothecae, median superior (left) and superior (right). f, frontal view of a hydrotheca. Note the spine shape of the lateral tooth (right) just at the base of the lateral nematotheca, the inward curve of the abcauline tooth and the rounded shape of the adcauline. Scale: a-b, f = 0.1 mm, c-e = 0.05 mm.



towards the hydrotheca; with strong asymmetry in profile due to shortness of adcauline wall (figs 2a, 3d, 4b, 7f).

Lateral nematotheca arising from a long peduncle attached to the hydrothecal wall and reaching above the hydrothecal margin from the base of the lateral tooth (figs 2a, 3b, 4a-d, f, 6a-f); deeply emarginate from base to top on inner side facing hydrotheca (figs 2c-d, 4c, 6a, d, f). On opposite side, a thickening well visible in transmitted light between basal and distal chambers (figs 2c, 4a-d, f) does not form any internal limit but corresponds to an external constriction (figs 6a-d, f) at the level of which inside nematotheca small folds function to attach nematophore (figs 4c, 6e). The nematotheca is an open gutter, the rims of which are drawn closer and composed of two parts which by SEM appear separated by a weak constriction, the basal part thick and the distal part thin (fig. 6c).

Median superior nematothecae, typically in one or two pairs behind free part of adcauline hydrothecal wall on stem, lying and opening near the hydrocladium and spreading out at 180° from one another; two-chambered, the basal more or less pedunculate and the distal very enlarged and curved at the aperture to overly the curvature of the substrate (figs 2a, 4c, 5a-d). On the hydrocladium there is in many specimens a single median superior which is larger and dumpy, not pedunculate and erect, parallel with the hydrotheca and with its aperture towards it (figs 3d, 5e-f).

Paired superior nematothecae pointing latero-dorsally and forming an acute angle with one another, two-chambered, the basal chamber pedunculate and the distal strongly enlarged, scalloped, and overlapping the hydrocladium or the hydrocaulus (figs 2a, 3d, 5a-b, 7a-d).

Nematocysts, easily visible in the lateral nematothecae (fig. 4c) and in the hydrocladia and oval in outline, were not seen everted. They were probably microbasic mastigophores.

Hydranth having 12-14 tentacles.

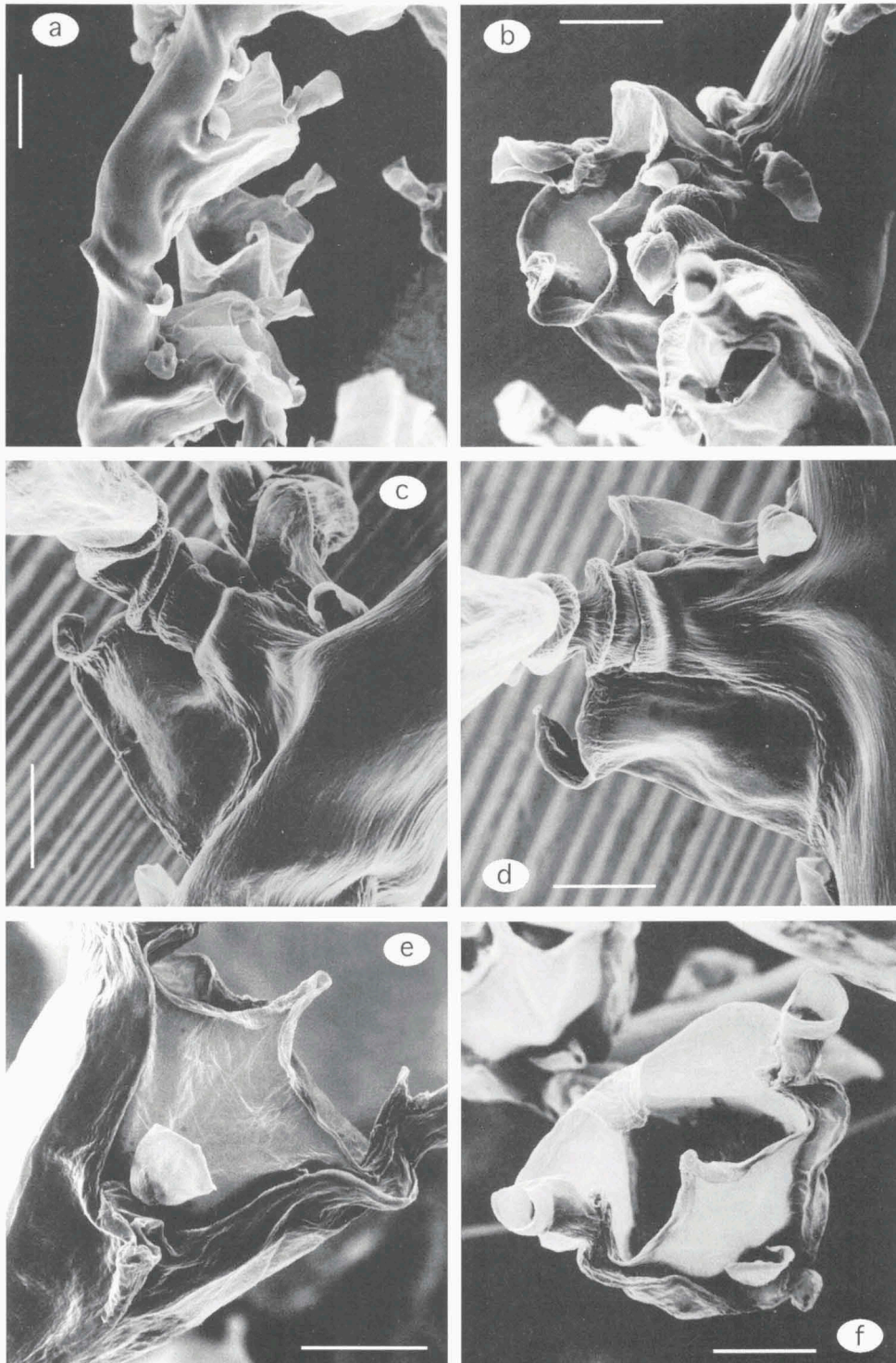
Gonosome unknown.

Dimensions (in profile view).— Internodes (mm): on stem, length 0.30-0.40, diameter 0.10-0.15; on hydrocladia, length 0.22-0.37, diameter 0.06-0.07.

Hydrothecae (mm): cauline, abcauline length, 0.16-0.19, aperture diameter 0.17-0.20; hydrocladial, abcauline length 0.19-0.22, aperture diameter 0.16-0.19.

Nematothecae (mm): lateral, length (without peduncle) 0.06-0.08, aperture diameter 0.02-0.03; median inferior, length 0.05-0.07; aperture diameter 0.04-0.05; median superior, length 0.03-0.05; aperture diameter 0.03-0.04; superior, length 0.04-0.06; aperture diameter 0.02-0.03; cauline (base of stem), length 0.17-0.20; aperture diameter 0.20-0.25.

Fig. 5. *Gattya wimleni* spec. nov. Scanning electron micrographs. a, dorso-lateral view of a stem, with oblique nodes delimiting cauline internodes. b-d, cauline hydrotheca (compare b with fig. 2a). Note the two different lateral nematothecae, the smaller being at the base of the hydrocladium in front, the four prominent marginal teeth (the abcauline being curved inwards the aperture of the hydrotheca) and the pair of median superior nematothecae (in the right corner are the superiors). c, rear view of the proximal hydrotheca with the set of two opposite hydrocladia. d, lateral view of the base of the hydrocladium: note the obvious discontinuity with the apophysis (straight joint) under the strong node (compare with fig. 2a). e-f, distal hydrocladial hydrotheca in dorsal and apical views, with a single large median superior nematotheca. Note the spine shape of the lateral tooth and the folding of the adcauline. Scale: a-e = 0.1 mm.



Nematocysts (microns): length 10; width 3-4 (undischarged).

Variation.— Hydrothecal internodes of stem typically bearing seven nematothecae as described above, but in some specimens one large single median superior occurs instead of a pair, and one single superior or three instead of one pair. A straight node may appear between the median superior and the superior. At the base of the hydrocladia, there may be, between the second athecate and the first hydrothecate internode, a supplementary one bearing a single median nematotheca. Mainly on the hydrocladia, variation in the number of median superior and of superior nematothecae were also noted, with the following frequencies (45 counted): 2+1(3), 1+2(3), 1+1(27), 2+2(12). A straight node was present in many specimens between the median superior and the superior nematothecae, delimiting an intermediate internode (restricted heteromorous segmentation). Finally, the proximal hydrothecate internode may be followed by a short supplementary internode bearing a single nematotheca (fig. 3d).

Etymology.— The species is dedicated to my friends Wim and Len Vervoort (*wimleni*).

Discussion

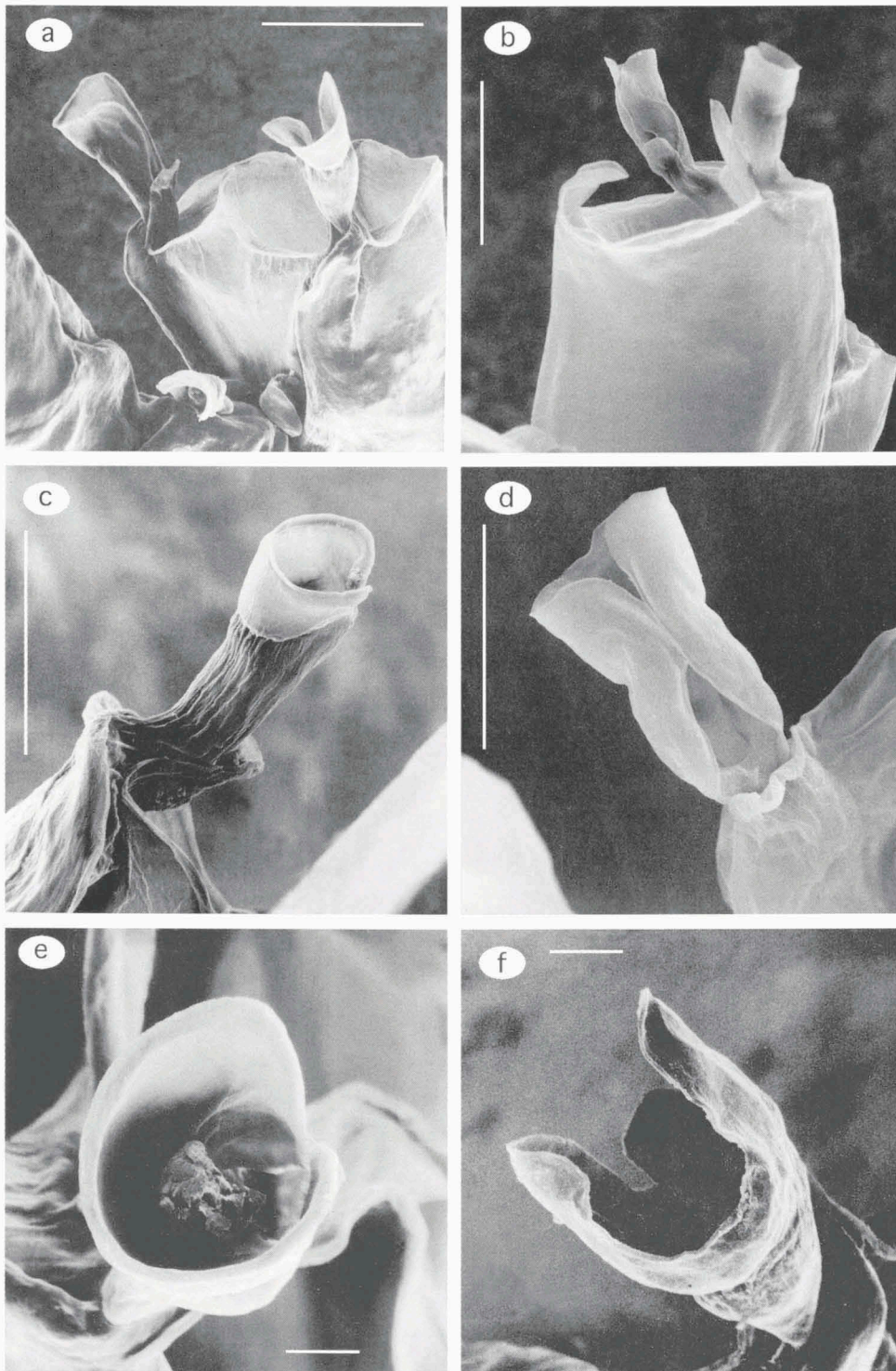
Descriptive characters

For the whole family Halopteridae, Schuchert (1997) gave useful drawings and descriptions of seven different shapes of the lateral nematotheca seen from the inner side. That of *G. wimleni* spec. nov. does not fit into that series and can be regarded additional to it, and described as tubular with emargination from base to top on the inner side.

SEM observations give evidence of some descriptive characters not easy to see clearly by transmitted light:

1) Structures occurring between two successive segments: nodes and joints. Nodes, or annulations according to some authors, which are set between each internode, are numerous on the colony. It is obvious with SEM that they are the result of successive folds and constrictions of the perisarc (fig. 5a, c-d), more or less oblique with respect to the main direction of the tube (oblique nodes in light microscopy, figs 2a, 3b, d, 4a). Hughes (1992: 271) reiterated, using the sertulariid *Dynamena pumila* (Linnaeus, 1758), that the inner layer of the perisarc is composed of flexible protein lamellae and that annulations allow the hydrocaulus to bend. These nodes, with both

Fig. 6. *Gattya wimleni* spec. nov. Scanning electron micrographs. a-b, hydrocladial hydrothecae, in dorso-lateral and latero-ventral views. Note the adcauline tooth (a), inward curve of the abcauline tooth (b), lateral teeth (b), lateral nematotheca with peduncle and bivalve shape (a), median superior and superior nematothecae (a). c-f, enlarged views of the lateral nematotheca and lateral marginal tooth, lateral (c), front (d) and apical views. The two sides of the nematotheca are well separated in f (normal posture, as in a, above, and fig. 2b), but they are joined together in d and e, probably following preparation for SEM. Well visible are the small folds in the perisarc onto which is set the nematophore inside the nematothecae (e) and the rounded shape of the lateral tooth in the background (f). Note that the skeleton is thinner and smoother on young (b, d) structures than on old (a, c), the former being just formed at the top of the hydrocladium (b, right). Scale: a-b = 0.1 mm, c-d = 0.05 mm, e-f = 0.01 mm.

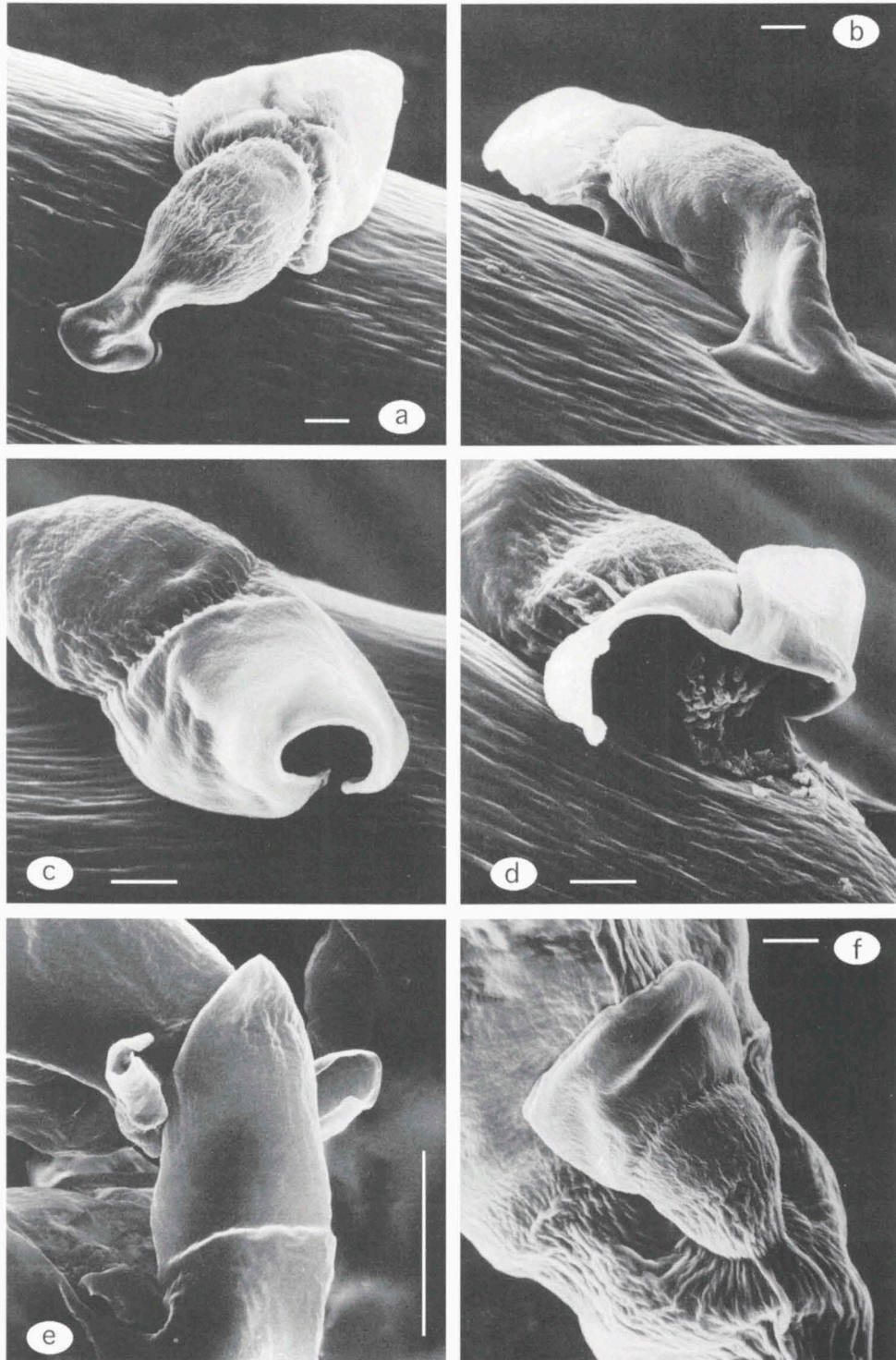


their structure and morphology, are thinned to give flexibility to the skeleton. In contrast, joints, or articulations, are few. A single strong one (fig. 3c), named hinge-joint by Millard, occurs on the stem at the base of the plume. It is an oblique articulation which, as discussed by Hughes & Henderson (1989) and Hughes (1992: 272), allows the upper part of the hydrocaulus to rotate in either direction. Straight joints also occur, a single one at the base of the hydrocladium between the apophysis and the first athecate internode (straight nodes in light microscopy). It appears as a true discontinuity under SEM, as a narrow groove at the surface of the skeleton (fig. 5d). They are preferential points of rupture for the hydrocladia which, after a breakage, may regenerate from these points.

2) Nematothecae. In light microscopy, although accurate observation detected emargination from the base to the top on one side of the lateral nematotheca, which is evident with SEM, it was impossible to elucidate the internal structure. In contrast, SEM provided apical and enlarged views showing the inside which enable one to conclude that no transverse septum exists where a line is visible in transmitted light at the level between the two 'chambers' (fig. 6). 'Chambers' is a misleading term. Nutting (1900: 14) discriminated bithalamic from monothalamic nematophores by the presence of an "internal circular ridge or shelf partially dividing the interior into two chambers". The only internal skeletal structures at this point on the nematothecal wall are small folds which support the nematophore (fig. 6e). It should be noted that this line between the two levels of the nematotheca is seen under SEM as a small linear depression around the nematotheca, a depression which not only is not seen at all with transmitted light but moreover appears as a thickening (fig. 4)! This might be an optical artefact. The depression appears late in the development of a nematotheca, as is shown by its weakness on the terminal internode; whereas its presence is obvious on the subterminal and older ones (fig. 6a-d) where, moreover, the perisarc is thinner distally than basally (fig. 6c). In other nematothecae, no internal observation has been possible under SEM because they lie too close to the hydrocladia and hydrocaulus to be studied internally.

It can be hypothesized that all of them differ in their morphogenesis. Some have a basal chamber in the form of a pedicel, with the perisarc apparently emerging from holes in the surface, as if only linked to the deep skeletal levels of the tubes (figs 5b, 7a-b) in the same manner as the operculum of *Dynamena pumila* (cf. Hughes, 1992: 271, fig. 2). This is so in the pairs of median superiors, in the superior and in the cauline at the base of the stem. Some others have a stouter basal chamber, with the perisarc in total continuity with that of the tubes. This is so of the median inferior (fig. 7f) and the laterals (fig. 6c). It should be noted that the median superiors, typically paired, lack the form of pedicel of the basal chamber when they occur alone (fig. 5e). It would be interesting to research the relation in life between the morphological dif-

Fig. 7. *Gattya wimleni* spec. nov. Scanning electron micrographs of nematothecae, superior (a-e) and inferior (f). a-c, a single superior nematotheca in dorsal, dorso-lateral and frontal views. Note the linkage of the perisarc with the lowest levels of the one of the hydrocladia (at base), the form of peduncle of the basal chamber, and the constriction below the upper and everted chamber. d, retracted nematophore inside a superior nematotheca, the opening of which has been accidentally folded. e, backward opening revealed by dorsal view of a hydrocladium. Note the strong oblique node and the low straight one. f, inferior nematotheca set at the base of a hydrotheca, in frontal view. Scale: a-d, f = 0.01 mm, e = 0.1 mm.



ferences observed and the nature of the mobility of these nematothecae. The mobility seems not to be strictly related to the mono- or bithalamic structure as, for example, according to Millard (1975: 348) the median inferior two-chambered nematothecae of *G. multithcata* are immovable though the lateral two-chambered are movable. In *G. wimleni*, it is not certain that the lateral nematotheca is mobile because the surface of the perisarc is strictly in continuity with that of its substratum (fig. 6). Pedunculate ones (fig. 7a-b) would probably be more mobile than the others because, as in the operculum of *Dynamena pumila*, which opens when the hydranth extends, they might be pushed away by the extension of the nematophore and shut when it contracts. As with the operculum, the peduncle might be put under tension during the extension, causing closure when the nematophore withdraws.

The character of mobility was used by Nutting (1900: 14) to separate the Eleutheroplea from the Statoplea but this has seldom been followed. Nutting himself stated that "intergradations between free and fixed nematophores" occur, and it seems that it is not a useful character. However, it would be interesting to look at it in life in representative specimens of the whole super-family, to obtain additional comparative data between the families and for an evolutionary perspective.

Taxonomy

Gattya wimleni spec. nov. is the ninth species to be referred to the genus *Gattya* (cf. Introduction). All the species have been rarely reported except *G. balei*, *G. heurteli* and *G. humilis*. The gonothecae are known only of *G. balei*, *G. conspecta* and *G. humilis*. Shepherd & Watson (1970: 140, tab. 1) reported a fertile colony of *G. aglaopheniaformis* but did not describe the gonosome. In such a situation, the only comparison that can be made between the species is, inevitably, of their trophosomes, as recently done by Schuchert (1997, tab. 39). The species have several characters in common: hydrocladia not in one plane but borne on the anterior face of the stem; the two basalmost hydrocladia typically opposite but all the others alternate; the hydrothecae always opening on the anterior face of the colony; the number of nematothecae per hydrothecate internode varying between 4 and 7; the forming of intermediary internodes on hydrocauli and hydrocladia, which may induce a heteromerous character, but without regularity. The stem is simple, not higher than 1,5 cm, except in *G. heurteli* which has a fascicled stem up to 18 cm. The distinctive species *G. balei* (recognised by its intrathecal septum), *G. heurteli* and *G. humilis* (which have short lateral nematothecae) are left out of the comparison with *G. wimleni*.

The main affinities of *G. wimleni* are with both *G. multithcata* and *G. aglaopheniaformis*, based on a tendency to heterometry, the general shape of the hydrothecae, the abcauline tooth curved towards the centre of the aperture, and the shape and position of the lateral nematothecae. Moreover, *G. wimleni* is very similar to *G. multithcata*. The same variation in the shape and number of superior and median superior nematothecae occurs in the two species; and Jarvis noted in the species she described the small size of the lateral nematotheca set on the hydrocladial apophysis (Jarvis, 1922: 347, fig. 19A-D), as observed in *G. wimleni*. The dimensions are similar in the two species (Jarvis, 1922: 347; Millard, 1975: 348), as is the angle between the hydrothecal margin and the hydrocladium (40°). In spite of these strong similarities, *G. wimleni*

differs from *G. multithcata* by having two well-marked lateral teeth rather than a sinuate margin, and by the adcauline tooth being the same size as the abcauline. The first species has four equal teeth and the second has a single distinct one, the abcauline. However, it should be noted that, in *G. multithcata*, the descriptions of Jarvis and Millard differed concerning the adcauline margin of the hydrotheca: where Jarvis described a sort of groove visible only in profile, Millard in contrast noted a small tooth. Further observation is necessary to resolve this point.

Comparison with *G. aglaopheniaformis* was difficult because there were only two descriptions available at the time of this study, and they were not strictly comparable. Mulder & Trebilcock (1909: 32) described the species for the first time; then Shepherd & Watson (1970: 140) collected fertile colonies but they did not describe them, and later Watson (1973: 186) gave a brief description in which she noted differences from the original one. Mulder & Trebilcock regarded as important the relation of the peduncle of the lateral nematotheca to the hydrothecal margin: "The most peculiar structure ... is the peduncle ... It is produced onwards, past the base of sarcotheca, in the form of a spine which rises well above the margin of the hydrotheca. The margin terminates at the front of this, and at right angles with it, about half-way between the base of the sarcotheca and the top of the spine, and commencing again at the summit of the spine behind curves downwards and then upwards to the summit of the corresponding spine on the opposite side of the hydrotheca."; before they also noted: "margin sinuate, interrupted at each side by a prolongation of the peduncle". Watson did not describe or figure these characters and did not refer to a spine on the peduncle; but she stated (1973: 186): "the marginal projections differ from those of *P. aglaopheniaformis* figured by Mulder & Trebilcock", and in its description she mentioned: "Hydrotheca deep (lateral view), with broadly lobed margin, the anterior and posterior lateral projections curving inwards over the aperture". From these data it has been possible to deduce: 1) that *G. aglaopheniaformis* has no adcauline tooth (which agrees with the two descriptions), but in contrast has an adcauline groove as in *G. trebilcocki*, another Australian species the identity of which has been questioned by Schuchert (1997: 147). This deduction is supported by the recent redescription of the species by Schuchert (1997: 143, fig. 49); 2) that the "spine" described by Mulder & Trebilcock on the peduncle of the lateral nematotheca and the "posterior lateral projection curving inwards over the aperture" of Watson are the same thing and are similar to the lateral tooth of *G. wimleni*. This is also confirmed by the good description and illustration published by Schuchert, who moreover considered the hydrothecal margin as having five teeth. *Gattya wimleni* would then differ from *G. aglaopheniaformis* in the following ways: four teeth with one adcauline; a deep emargination on the whole face of the lateral nematotheca (instead of only on the upper chamber as in the Australian species, according to the single figure available); and a greater number of superior and of median superior nematothecae (1 + 1 only in *G. aglaopheniaformis*).

Beside several common characters, *G. tropicalis* differs from *G. wimleni* in the number of lateral teeth (6), the absence of superior nematothecae, the abcauline situation of the peduncle of the lateral nematothecae with regard to the median line in profile view (adcauline in each of the other species), and the shape (emarginate on the distal chamber only) and reduction (basal chamber very small) of this nematotheca (Millard & Bouillon, 1973: 80). The second pair of lateral nematothecae described by these

authors in *G. tropicalis* might be considered as median superior nematothecae because they are borne at the base and on the middle of the free part of the adcauline hydrothecal wall (Millard, 1978: 328, fig. 106): a second lateral pair would be set laterally and not on the median line.

Finally, compared with *G. wimleni*, *G. conspecta* has different hydrothecae according to their general shape (more dumpy, adcauline wall concave at base) and margin (adcauline tooth less prominent than abcauline, abcauline very sharp, lateral margin sinuate but without teeth), and is typically strictly homomerously segmented.

Remarks: Several authors have cited lateral teeth in a similar position as those of *G. wimleni*, but drawings are rare. Warren (1908: 326) noted, as a monstrosity of *Paragattya intermedia*, the exceptional presence of "two pairs of lateral teeth" instead of one, the second being just behind the lateral nematotheca (fig. 27-2a, pl. 47), a normal shape in *G. wimleni*. In contrast, in *G. balei* several authors have recorded lateral teeth. Bartlett (1907: 65) noted without further detail the presence of "four marginal teeth", and we can suppose from his figure that he referred to the small undulations of the margin, undulations of the same size as in the two small anterior and posterior teeth. Later, Mulder & Trebilcock (1909: 29-30) wrote "margin undulated, peaked at back and front", and, more precisely: "the margin of the cell being raised into a tooth-like projection beyond the termination of the peduncle"; but they did not give a figure of this important character, which recalled the "spine" that they described several pages later in *G. aglaopheniaformis*. Slightly later, Briggs (1918: 41) noted "a small lateral tooth-like projection opposite the peduncle of the supracalycine sarcotheca"; and Bale (1919: 345) "a small, narrow lobe behind each lateral sarcotheca". According to these descriptions, and although the teeth described are small, *G. balei* is grouped here with the other species provided with lateral teeth set one on each side behind the lateral nematothecae: *G. aglaopheniaformis*, *G. tropicalis* and *G. wimleni* spec. nov.

Identification key to the species of *Gattya*

This key has been compiled from the literature. It takes into account the characters of the hydrothecal internodes considered as the most stable among all those of the trophosome. It should be used provisionally, pending further data on the gonosomes of the species included.

1. Peduncle of the lateral nematotheca short; nematotheca under or at the level of the hydrothecal margin 2
- Peduncle of the lateral nematotheca long; nematotheca extending clearly above the level of hydrothecal margin 4
2. Hydrothecal margin with one adcauline tooth; distal chamber of the lateral nematotheca bivalve; segmentation typically homomerous 3
- Hydrothecal margin with an adcauline groove between two lobes; distal chamber of the lateral nematotheca chamfered; heteromerous segmentation *G. trebilcocki* Watson, 1973.
3. Hydrothecal margin with four regular and similar teeth; abcauline wall of the hydrotheca straight; stem polysiphonic *G. heurteli* (Billard, 1907).
- Hydrothecal margin with four irregular teeth, the abcauline prominent; abcauline

- wall of the hydrotheca convex; stem monosiphonic *G. humilis* Allman, 1886.
4. Hydrotheca having intra- abcauline septum *G. balei* (Bartlett, 1907).
 - Hydrotheca lacking septum 5
 5. Hydrothecal margin with no adcauline tooth or one of a small size 6
 - Hydrothecal margin with an adcauline tooth as large as the other teeth 8
 6. Hydrothecal margin with no lateral tooth, margin sinuate 7
 - Hydrothecal margin with one lateral tooth, or spine, just behind the lateral nematotheca; having an adcauline groove *G. aglaopheniaformis* (Mulder & Trebilcock, 1909).
 7. Hydrocladial hydrothecae as high as wide; segmentation typically homomerous ..
 - Hydrocladial hydrothecae less wide than high; segmentation typically heteromerous *G. conspecta* (Billard, 1907).
 - Hydrothecal margin with one pair of lateral teeth *G. multithecata* (Jarvis, 1922).
 8. Hydrothecal margin with one pair of lateral teeth *G. wimleni* spec. nov.
 - Hydrothecal margin with three pairs of lateral teeth *G. tropicalis* Millard & Bouillon, 1973.

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