

HYDROIDS OF THE FAMILY CYTAEIDAE
L. AGASSIZ, 1862

BY
WILLIAM J. REES

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SYNOPSIS

Hydroids of the family Cytaeidae are brought together for the first time in this paper. All medusa-bearing species are placed in the genus *Cytaeis* Eschscholtz, while species with fixed gonophores are placed in *Perarella* Stechow. The problematic genus *Stylactella* Haeckel, 1889, is restricted to the type species *Stylactis vermicola* Allman and retained in the Cytaeidae.

The type specimens of *Stylactis vermicola* Allman, *Stylactella spongicola* Haeckel, *Stylactella abyssicola* Haeckel, *Stylactella niiotha* Pennycuik, *Hydractinia clavata* Jäderholm, *Stylactis indica* Stechow and *Podocoryne nassa* Millard have been examined, and, where possible, re-described. The hydroid *Cytaeis japonica* Komai has been found to be distinct from the medusa *C. japonica* Uchida, 1927 (which is *C. tetrastyla*) and is here re-named *Cytaeis uchidae*. A new species, *Cytaeis nuda*, is described from Japan; this lives in intimate association with a sponge.

To the genus *Perarella* are referred: *Hydractinia clavata* Jäderholm, *Stylactella spongicola*, *S. abyssicola* and provisionally *Stylactis affinis* Jäderholm; the type species of *Perarella* is *Perigonimus schneideri* Motz-Kossowska.

The hydroids *Cytaeis nassa* and *C. niiotha* are distinct despite close resemblances, while *C. uchidae* and *C. nuda* differ from them in having almost mature medusae at liberation. *Cytaeis nuda* lives in a sponge and is noticeably different from *C. uchidae*. *Cytaeis indica* Stechow is an immature colony whose status is uncertain.

I. INTRODUCTION

THE family Cytaeidae was created by Louis Agassiz (1862 : 341) for medusae of the genus *Cytaeis* Eschscholtz. No hydroids belonging to it could be recognized until Komai (1931) found a hydroid and young medusa which he thought belonged to the medusa *Cytaeis japonica*. This discovery was not followed up, except briefly by Rees (1956 : 344), and in this review as many as possible of the type specimens of the species concerned have been re-examined.

Earlier, however, cytaeid hydroids had been described under various genera : *Stylactis*, *Stylactella*, *Hydractinia*, *Perigonimus* and *Perarella*—the genera, other than *Perigonimus*, being usually grouped with the Hydractiniidae. Haeckel (1889) however, recognized the distinctive nature of the *Stylactella* group of hydroids suggesting a family grouping Stylactidae—a suggestion which was never adopted and which cannot now be considered in view of the prior claims of Agassiz's Cytaeidae.

In this paper, the genera *Cytaeis* Eschscholtz, *Perarella* Stechow and *Stylactella* Haeckel are revised and many of the species are re-described either from the type material or from material from the type locality. *Cytaeis* is employed both for cytaeid hydroids and their medusae, *Perarella* for cytaeid hydroids with fixed gonophores and *Stylactella* is restricted to the type species *Stylactis vermicola* Allman, as an insufficiently characterized genus.

2. THE FAMILY CYTAEIDAE

The family Cytaeidae may be defined as follows :

Hydroid (where known). Athecate hydroids with perisarc-covered, anastomosing stolons. Hydranths, naked, tall, columnar, with a group of whorled filiform tentacles around a conical hypostome. Hydranths arising directly from the stolons, often with a short, cup-shaped collar of perisarc. Medusa buds or fixed gonophores borne single on stalks directly from the stolons.

Medusa (where known). Anthomedusae with deep umbrella with four unbranched radial canals and four marginal tentacles. Manubrium, often flask-shaped, with simple mouth with four or more unbranched oral tentacles.¹ Gonads either inter-radial or forming a continuous ring. No ocelli.

As defined here the family includes the following genera : *Cytaeis*, *Perarella* and the problematic genus *Stylactella*.

3. Genus *CYTAEIS* Eschscholtz., 1829*Cytaeis tetrastyla* Eschscholtz, 1829

Cytaeis tetrastyla Eschscholtz, 1829, *System der Acalephen* : 104, pl. 8, fig. 2 (medusa).

Kramp, 1959, *Dana Rep.* 46 : pl. 1, figs. 3-6 (medusa with polypoid buds).

Kramp, 1961, *J. mar. biol. Assoc. U.K.* 40 : 63 (in part).

This well-known circumtropic medusa has not so far been linked with a bottom-living hydroid, although either *C. nassa* (Millard) or *C. niotia* (Pennycuik) could be its hydroid.

¹ In excluding the little known species *Cnidostoma fallax* Vanhöffen, I have followed Picard (in Kramp, 1961 : 444). *Cnidostoma fallax* (syn. *Podocoryne* (*Archaeoceania*) *ournieri*) is placed in the family Clavidae by Picard.

Kramp (1959: 8) has described "polypoid buds on the proximal portion of the stomach wall". They are described as somewhat larger than the medusa buds, cylindrical, with a broad proboscis and a whorl of five to seven short tentacles. The author states that these buds are not fully developed, the tentacles being fairly short and the mouth opening not yet broken through. Sections reveal that the polyps are direct outgrowths from the stomach wall produced by asexual budding. These polyps are too young to enable a comparison to be made with benthic colonies of *Cytaeis*.

There is a possibility that *C. tetrastyla sensu*, Kramp (1961), is an aggregate species (see p. 387).

Cytaeis uchidae nom. nov.

Cytaeis japonica, Komai, 1931, *Annot. zool. jap.* 13: 255, fig. A-C.

The following descriptions are based on colonies kindly sent to me by H.M. The Emperor of Japan. Two fertile colonies were collected at Aburatsubo, Misaki, in Sagami Bay on 28th June, 1960, and it is on these that the main description is based. A further series of 12 shells with fertile colonies were collected in June, 1961, and a batch of newly liberated medusae obtained from them; these were also forwarded to London and the description contains some additional notes on these and on their medusae.

The colonies obtained in 1960 cover the shells of the gastropod *Nassarius livescens* Philippi. The smooth stolons run in the grooves of the shell, frequently anastomosing at intersections (Text-fig. 1).

The very tall columnar polyps arise basally from thin, but well-developed, perisarcular cups; the polyps themselves possess a distal whorl of six to ten hispid tentacles around a bluntly-conical hypostome. Medusa buds are borne singly on long stalks arising directly from the hydrorhiza; they may reach a height of 1.0 mm. Fully-grown medusa buds are about 0.5 mm. long by 0.4 mm. Each medusa bud has four large brownish basal bulbs with equally developed tentacles. There are four capitate tentacles on the manubrium around a single mouth. The manubrium is fusiform reaching to more than half the depth of the bell, and in many examples the ring gonad is well developed.

Medusa buds are plentiful on both shells; in one, the nutritive polyps are as numerous as the medusa buds, but on the other nutritive polyps are few and appear to have been largely resorbed as a result of prolific budding of medusae.

Some typical measurements of the dimensions of the hydroid are given in Table I.

The second series of colonies illustrate the considerable range of variation in the appearance of the colonies (Text-fig. 1); in some, polyps are large and densely crowded on the shell (Pl. 10, fig. 2) and on others less crowded (Pl. 10, figs. 3 and 4). In fact the colonies exhibit much the same diversity as *Hydractinia* both as regards the density of polyps on the shell and as regards reproductive exhaustion (Rees, 1956b).

It will be seen from Table II that the polyps reach a height of nearly 4 mm. in a well-developed colony. The above description agrees well with that of Komai (1931) except that the polyps reach a much larger size in a well-developed colony.

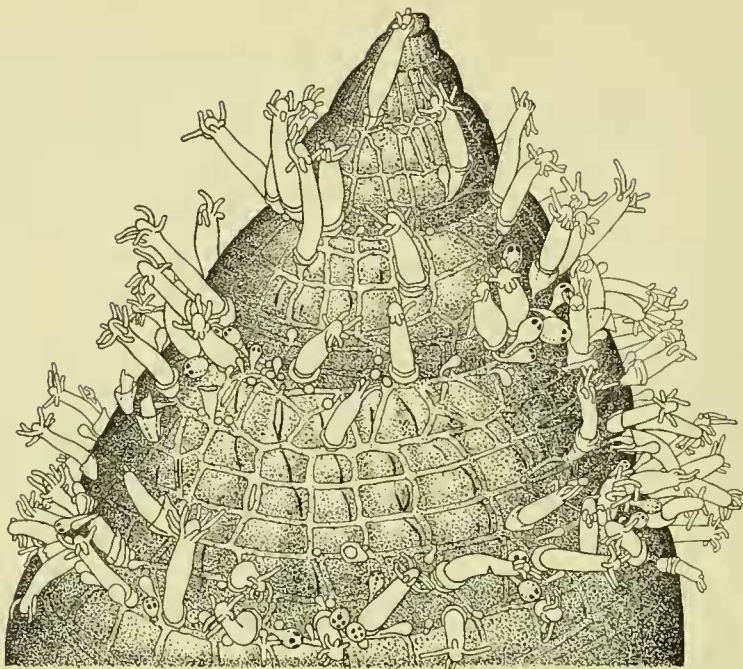


FIG. 1. *Cytaeis uchidae* nom. nov.; general appearance of a colony on the shell of *Nassarius livescens* Philippi from Misaki, June, 1961.

TABLE I.—*The hydroid Cytaeis uchidae* from Sagami Bay, 1960

Measurements in mm.

Height of polyp to hypostome	1.28	1.20	1.24	1.3
Diameter of polyp	0.12	0.12	0.12	0.12
Length of hypostome	0.08	0.12	0.12	0.12
Diameter of basal cup	0.10	0.20	0.23	0.3
Total height of medusa bud	0.88	0.88	0.80	1.0
Length of stalk	0.4	0.44	0.40	0.5
Length of medusa bud	0.48	0.44	0.40	0.5
Diameter of medusa bud	0.36	0.36	0.32	0.4

TABLE II.—*The hydroid Cytaeis uchidae* from Sagami Bay, June 1961

Measurements in mm.

Height of polyp	3.85	2.2	3.9	3.85
Diameter of polyp	0.33	0.38	0.4	0.33
Length of tentacles	0.43	0.45	0.45	0.65
Diameter of basal cup	0.44	0.4	0.45	0.35
Diameter of stolon	0.10	0.12	0.14	0.10
Total height of medusa bud	0.9	0.95	0.95	1.0
Diameter of medusa bud	0.55	0.33	0.35	0.33

Komai also described the newly liberated medusa and it is now possible to confirm his description and to add more details.

The umbrella is deep bell-shaped, approximately as high as wide, being 0.55–0.6 mm. high and 0.5–0.7 mm. wide, depending on fixation (Text-figs. 2 and 3). The jelly is uniformly thick, with scattered nematocysts on its exumbrella surface and there is sometimes a slight apical depression with no indication of an apical plate of cells. The stomach is mounted on a short peduncle and varies from half to three-quarters of the height of the subumbrella cavity in length. The mouth is simple and there are four simple perradial oral tentacles, each armed with a battery of nematocysts. There is a well-developed gonad occupying the greater part of the length of

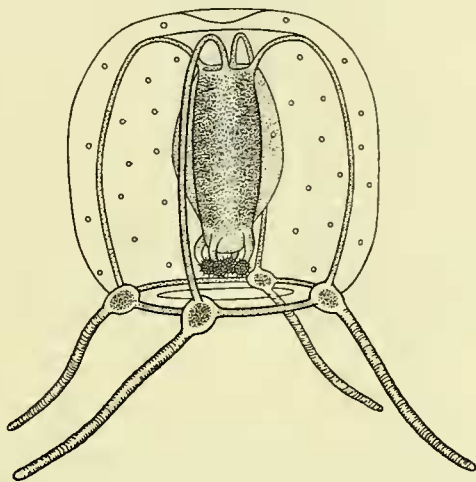


FIG. 2. *Cytæis uchidae* nom. nov.; newly liberated male medusa obtained from the hydroid, Misaki, June, 1961.

the manubrium; in the male it forms a complete ring round the manubrium (Text-fig. 2). In the female the eggs are large and conspicuous (Text-fig. 3).

There are four perradial canals and a ring canal. The four perradial tentacles have well-developed rounded bases with an endoderm of a dark brown colour. The tentacles themselves are rather contracted and heavily armed with nematocysts and there is a suggestion that these tend to be grouped in batteries as in *Cytæis nassa* (see Text-fig. 9). Measurements of typical medusae are given in Table III.

TABLE III.—*Medusae liberated from Cytæis uchidae at Misaki, June, 1961*

Measurements in mm.										
Height of bell	.	.	.	0.60	.	0.55	.	0.55	.	0.6
Diameter of bell	.	.	.	0.55	.	0.5	.	0.7	.	0.55
Length of manubrium	.	.	.	0.30	.	0.30	.	0.35	.	0.5
Diameter of manubrium	.	.	.	0.175	.	0.22	.	0.20	.	0.25
Diameter of tentacle bulb	.	.	.	0.075	.	0.10	.	0.10	.	0.10

The problem presented by this species is whether Komai's identification of this species with *Cytaeis japonica* Uchida is justified. The noteworthy feature about the medusa of this hydroid is that, like *Podocoryne carnea*, it is almost sexually mature at liberation, and probably has only a few days of planktonic existence before spawning and dying.

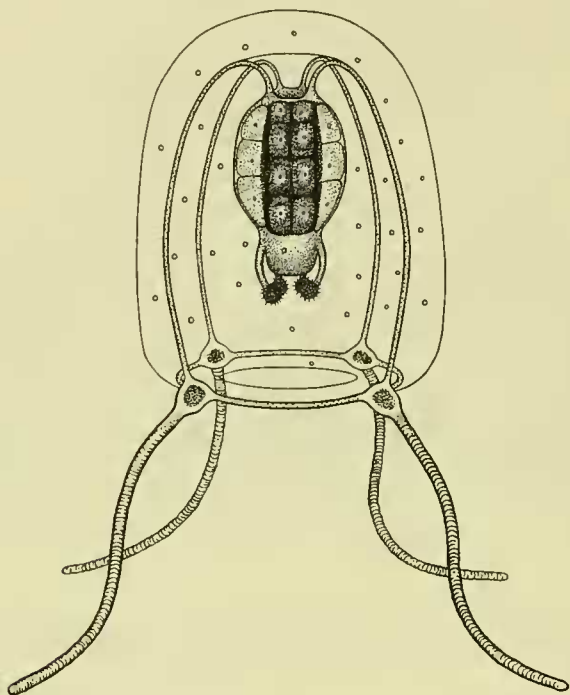


FIG. 3. *Cytaeis uchidae* nom. nov.; newly liberated female medusa obtained from the hydroid, Misaki, June, 1961.

If so, then this medusa probably possesses only the four simple oral tentacles throughout its life.¹ On this assumption it may not be identical with *Cytaeis japonica* Uchida which matures at a much larger size (1.7 mm. \times 1.5 mm.) and possesses 5–12 oral tentacles when mature. Uchida (1927) also indicated that he had found juvenile medusae with medusa buds on the stomach and with only four oral tentacles. It would thus appear that *C. japonica* Uchida passes through an asexual phase in which the stomach may possess only four oral tentacles before reaching

¹ Since this paper was written, Mr. Hatsuki Tsujimura of the Biological Laboratory of the Imperial Household, Tokyo, informs me that in rearing experiments with *C. uchidae* medusae for a period of 40 days, only one medusa increased its oral tentacles to seven. During this period the medusae did not feed and began to shrink after 40 days. The evidence is thus inconclusive but the apparent absence of an asexual budding phase and the presence of a ring gonad justify the retention of *C. uchidae* as a distinct species.

a sexual phase. This is what also takes place in *Cytaeis tetrastyla* Eschscholtz, a species with which *C. japonica* Uchida has been synonymized by Kramp (1961: 64). The asexual budding phase is known to precede sexual reproduction in medusae such as *Sarsia prolifera*, *S. gemmifera*, *Podocoryne minima*, *Rathkea octopunctata*, *Lizzia blondina* and many others. Temperature appears to be the deciding factor which initiates the beginning of the sexual phase in some species (Werner, 1956).

From the above it seems highly probable that *Cytaeis japonica* Komai (*non* Uchida) is a distinct species and this view is strengthened from unpublished evidence from cytaeids collected at Singapore by Mr. J. H. Wickstead. Without going into details, some of the small medusae seen have more than four oral tentacles and the developing gonads are small and inter-radial in position; all this suggests that Kramp (1961: 63-64) has oversimplified the situation in recognizing only three species of *Cytaeis*.

In *Bougainvillia superciliaris* Werner (1961) has recently discovered that female medusae may be able to produce eggs several times successively, but there is no evidence of this known for *Cytaeis*.

In view of the fact that *Cytaeis japonica* Uchida, 1927, has been synonymized with *Cytaeis tetrastyla* Eschscholtz, 1829, Komai's hydroid and medusa must be regarded as distinct, and therefore must be re-named. I have much pleasure in naming it *Cytaeis uchidae* in honour of Professor Tohru Uchida who has done so much to place our knowledge of Japanese medusae on a sound basis.

Cytaeis nuda sp. n.

The following description of a new hydroid is based on two colonies most kindly sent to me by H.M. The Emperor of Japan who also forwarded notes and some of the illustrations given here. The two host snails were collected by means of the *takotsubo* (a small unglazed pot with a small hole through the bottom) used in a kind of long-line fishing for octopus on the sea bottom. The specimens were taken off Hayama, Sagami Bay on 26th and 31st July, 1934.

The colonies are partly embedded in sponges growing on living gastropods of the species *Fusinus perplexus* (A. Adams). The hydrorhiza forms a close reticulate network a little distance below, and parallel with the surface of the sponge. The reticulate network is not annulated and the periderm of the stolons is very thin and not thickened (Text-figs. 4 and 5).

The cylindrical polyps arise at the junctions of the stolons and there is no indication of any cup-like dilation of perisarc at this point. The hydranth is naked with six to eight tentacles arranged in a whorl around a bluntly-conical hypostome. These hydranths are contracted in preservative, measuring 0.5 mm. in height; they sometimes project beyond the surface of the sponge through holes in the substance of the sponge (Pl. 10, fig. 1 & Text-figs. 4 and 5).

Medusa buds, as in other cytaeid hydroids, are oval or pear-shaped and borne on distinct, non-annulated pedicels arising directly from the stolons (Text-fig. 6).



FIG. 4. *Cytæis nuda* sp.n. ; a vertical section of the hydroid colony embedded in the sponge.

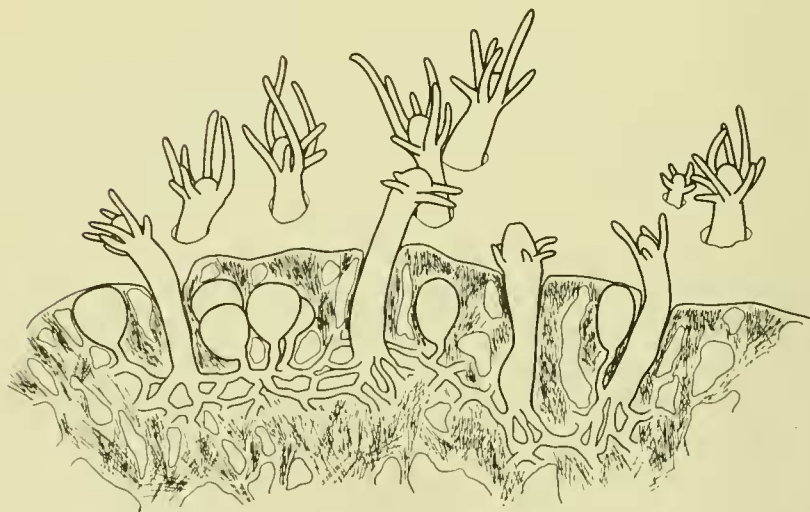


FIG. 5. *Cytæis nuda* sp.n.; a sketch from a micro-preparation of a small section of the colony;
del. H. Daba.

When young the medusa buds are completely enveloped by sponge but with growth the buds push their way to the surface.

A female medusa was obtained from one of the colonies (Text-fig. 7). At liberation this had a deep, bell-shaped umbrella, about 0.3 mm. in height. There were four radial canals, four large perradial bulbs with filiform tentacles of equal size. The tentacles contained reddish brown pigment granules and there were no ocelli. The manubrium, which reached three-quarters of the distance to the bell margin, was fusiform in outline and may have been four-sided in section. The mouth was simple with four, short, capitate oral tentacles. The female gonad appeared to cover

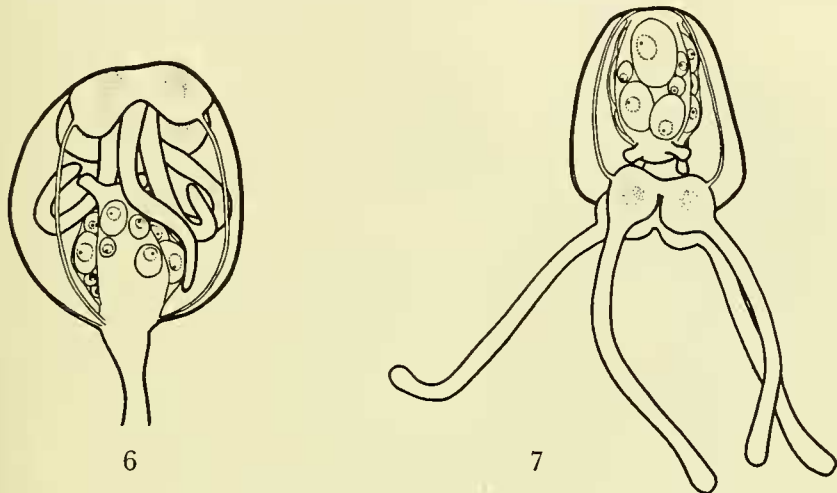


FIG. 6. *Cytaeis nuda* sp. n.; a female medusa bud; del. H. Daba.

FIG. 7. *Cytaeis nuda* sp. n.; a newly liberated female medusa; del. H. Daba.

the manubrium for the greater part of its length and was best developed interradially. At liberation, the medusa was almost mature and the gonad possessed a small number of large eggs with prominent nuclei.

The description can be summarized as follows:

Hydroid. Hydorrhiza, forming a reticulate non-annulated network, with perisarc feebly developed embedded in the tissues of a sponge. Hydranths, cylindrical with six to eight filiform tentacles around a conical hypostome, arising from anastomoses in the hydorrhiza. Hydranths project from surface of sponge and are at least 0.5 mm. long. Medusa buds borne singly on pedicels from the hydorrhiza.

Medusa. Newly-liberated ♀ medusa with deep, bell-shaped umbrella with four radial canals, four perradial bulbs without ocelli and with four filiform tentacles. Stomach fusiform with simple mouth, four simple oral capitate tentacles. Gonad best developed interradially, with a few large eggs, almost mature at liberation.

Type locality. Hayama, Sagami Bay, Japan in a sponge on the gastropod *Fusinus perplexus* (A. Adams).

Holotype. British Museum No. 1962.2.12.1; collected 26 July, 1934. *Paratype*, collected 31 July, 1934 in the collections of the Biological Laboratory of the Imperial Household, Tokyo.

There appear to be distinct differences between this species and *Cytaeis uchidae*. In *C. nuda* the absence of a collar of perisarc and the feebly developed perisarc of the stolons may be linked with the habitat of the species within a sponge. However, the much smaller size of the medusa at liberation, its compressed subumbrella cavity and the smaller number of eggs in the gonad (compare Text-fig. 3 with Text-fig. 7) indicate that *C. nuda* is different from *C. uchidae*.

Cytaeis nassa (Millard, 1959)

Podocoryne nassa Millard, 1959, *Ann. S. Afr. Mus.* 44: 307, fig. 3.

The following description is based on several colonies sent to me by Dr. William Macnae who collected the material between tide levels on Inhaca Island, Lourenço Marques. These colonies are epizooic on the gastropods *Nassa coronata* Brug. and on *Nassa fenestrata* Marratt (Pl. 11).

The perisarc-covered stolons follow the grooves of the shells and the appearance of the colonies which covered the whole of the shells was reminiscent of *Hydractinia* or of *Podocoryne*, but there were differences which indicated that the Inhaca species came nearest to the hydroid described by Komai (1931) as that of the medusa *Cytaeis japonica*.

There are no spines and no encrusting base and the nutritive polyps are fairly evenly distributed at intervals along the stolons as noted by Millard (1959: 308, fig. 3). The stolons are 0.5–0.10 mm. in diameter and are covered by a thin, distinct, non-annulated, hyaline perisarc; they form a reticulate network.

There is only one type of hydranth, the nutritive kind (Text-fig. 8). These are tall, columnar, slightly thicker near the base than distally. There is a double whorl of 8–16 filiform tentacles around a well-developed conical hypostome; these tentacles are smooth and not hispid as those of *C. niotha*. The base of the hydranth narrows sharply and around this there is a sessile or subsessile cup-like dilation of perisarc which fits closely around it when the hydranth is retracted (as in this preserved material). In the colony noted by Millard the hydranths were only 1.4 mm. high with 8–16 tentacles while those noted here are larger (see Table IV).

The medusa buds are borne singly on pedicels, 0.5–0.64 mm. long, arising directly from the stolons, the total height of gonozooid and stalk being 0.84–1.15 mm. These buds are pyriform, becoming almost globular when fully developed; those measured were 0.34–0.5 mm. long by 0.28–0.4 mm. wide.

No newly-liberated medusae were available, but in the fully developed medusa bud, four perradial bulbs with tentacles, four radial canals and a tubular, slightly fusiform, manubrium with four short oral tentacles can be distinguished (Text-fig. 9). The oral tentacles are armed with batteries of nematocysts at their tips. The four perradial tentacle bulbs are well developed and the tentacles themselves are armed with distinct batteries of nematocysts. Gonads are undeveloped.

The following measurements were made from preserved material :

TABLE IV.—*Dimensions of Cytaeis nassa (Millard) from Inhaca Island*

Measurements in mm.						
Total height of polyp	. . .	2.1	. . .	2.45	. . .	2.03
Diameter of polyp	. . .	0.35	. . .	0.35	. . .	0.35
Diameter of stolon	. . .	0.08	. . .	0.10	. . .	0.08
Total height of medusa bud	. . .	0.84	. . .	1.04	. . .	1.05
Length of pedicel	. . .	0.5	. . .	0.64	. . .	0.61
Length of medusa bud	. . .	0.34	. . .	0.4	. . .	0.44
Diameter of medusa bud	. . .	0.3	. . .	0.3	. . .	0.28
						0.4
						0.32

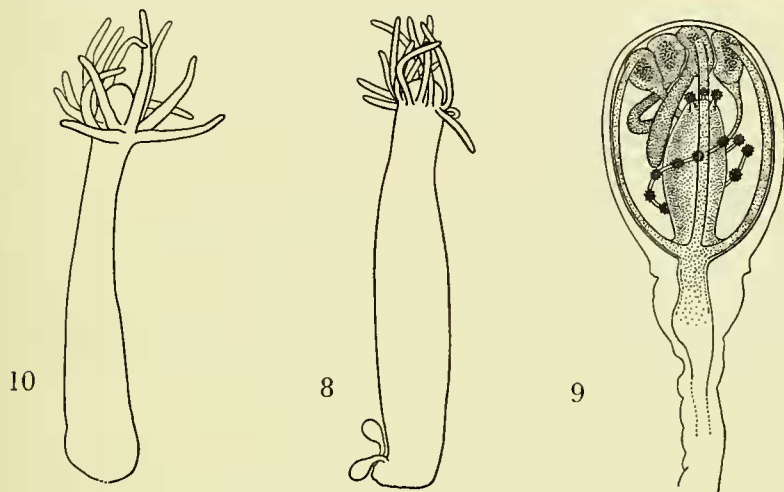


FIG. 8. *Cytaeis nassa* (Millard) ; hydranth.

FIG. 9. *Cytaeis nassa* (Millard) ; medusa bud.

FIG. 10. *Cytaeis niotha* (Pennycuik) ; a hydranth from the holotype colony (Queensland Mus. No. G. 2392).

The form of the hydranth with its cup-like dilation of perisarc at the base and the characters of the medusa, especially the four oral *tentacles* on the manubrium and the four single marginal tentacles identify the species with the genus *Cytaeis*.

As will be noted the species is very similar to *Cytaeis uchidae* but the latter has far fewer tentacles in the polyp and its medusa is almost mature at liberation. It is possible that this East African species belongs to a known *Cytaeis* medusa, such as *C. tetrastyla*.

The following is a summarized description of the species :

Hydroid with creeping, anastomosing, non-annulated stolon covered with thin hyaline perisarc. Hydranths, tall, columnar, with distinct hypostome and a double whorl of 8-16 solid tentacles. Hydranth sessile, or subsessile, supported by a cup-

like dilation of perisarc. Gonozooids borne singly on stalks arising directly from the stolons.

Medusa deep-bell-shaped with four radial canals, ring canal, four perradial marginal bulbs with tentacles armed distally with clusters of nematocysts. Manubrium tubular, with simple mouth, with, at liberation, four oral tentacles armed with nematocyst clusters at their tip. Gonads undeveloped.

Cytaeis niotha (Pennycuik, 1959)

Stylactella niotha Pennycuik, 1959, *Univ. Queensland. Pap. Zool.* 1 (6) : 162, pl. 1, fig. 2.

This species was described from the Great Barrier Reef by Pennycuik. I have been able to re-examine the type colony on the snail *Niotha albescens* Dunker from Heron Island by courtesy of the author and of Mr. George Mack of the Queensland Museum. This colony labelled Queensland Museum G.2392 is here selected as lectotype.

The material is not in very good condition, and although it has not been possible to ascertain some details, it has been possible to establish the relationships of the species with the genus *Cytaeis*.

The hydrorhiza forms a reticulate network running in the grooves of snail's shell and the tall, columnar hydranths arise at short intervals along it, and are, as stated by Pennycuik, more concentrated around the mouth of the shell. In view of the condition of the colony it was not possible to ascertain the existence of perisarcal cups round the bases of the hydranths, although the latter are constricted basally. The hydranths have short pointed hypostomes with double whorls of 14-16 tentacles; the latter are heavily armed with nematocysts and are more hispid than the comparatively smooth tentacles of *C. nassa*. The hypostome, too, seems less developed than in *C. nassa* (Text-fig. 10).

The gonozooids are borne on long stalks arising around the bases of the hydranths. Each is covered by smooth hyaline perisarc and contains a medusa. The latter has four perradial canals, four perradial tentacle bulbs with tentacles equally developed. The slightly-fusiform manubrium has a simple mouth and four, simple, short, capitate tentacles. These are cytaeid characters and the species is therefore referred to *Cytaeis* as *C. niotha*.

It is not possible to unite this species with *C. nassa* in view of the apparent differences in tentacle armature in the hydranths. The species can be distinguished by a greater number of tentacles (14-16 in a double whorl) from *C. uchidae* in which the number is 6-10. There are probably other differences not apparent in this material.

Cytaeis indica (Stechow, 1920)

Stylactis sp., Calman, 1911, *Ann. Mag. nat. Hist.* (8) 8 : 546, text-figs. 1 & 2.

Stylactis indica Stechow, 1920, *Sitz-Ber. Ges. Morph. Phys. München*, 31 : 11.

Stylactella (Stylactaria) indica Stechow, 1923, *Zool. Jb. Syst.* 47 : 63.

In 1911, Calman described a small hydroid with a creeping stolon and polyps of the "*Stylactis*" type from the carapace and legs of a Xanthid crab. This has recently

been re-examined and on one of the stolons, close to a hydranth, a small stalked bud was found. Although the detailed structure of the bud cannot be made out its general appearance (stalked and pear-shaped) strongly recall young medusa buds of *Cytaeis* hydroids. The hydranth, too, has the cup-shaped socket of perisarc at the base as in hydranths of that genus, although this is not immediately obvious because the polyps themselves are much contracted.

Subsequent to Calman's description, Stechow (1920) named this colony *Stylactis indica*, renaming it *Stylactella* (*Stylactaria*) *indica* in 1923. It is now placed in *Cytaeis* as *C. indica*, although better knowledge of *Cytaeis* medusae and their hydroids (as indicated on p. 387) will probably enable the species to be referred to one of the earlier described species of this genus.

The holotype, which is attached to the crab *Xanthias haswelli*, bears the number B.M. (Crustacea) 1911.9.12.36.

4. Genus *PERARELLA* Stechow, 1922

Cytaeid hydroids with fixed gonophores.

In selecting this generic name as the best available name for cytaeid hydroids with fixed gonophores (Rees, 1956 : 344), it was obvious, although not stated then, that the confusion caused by many alterations in generic concepts of *Stylactis*, *Stylactella* *Stylactaria* needed clarifying. The only one of these that concerns this paper is *Stylactella* Haeckel which has been restricted in this paper to an ill-defined type species whose gonosome is unknown.

Haeckel's other *Stylactella* spp. are better defined and can be referred to *Perarella*, although micro-preparations prepared by Haeckel have long dried up and the specimens are no longer recognizable.

The type species of *Perarella* Stechow, 1922, is *Perigonimus schneideri* Motz-Kossowska, 1905.

Other species now referred to the genus are: *Hydractinia clavata* Jäderholm, 1905; *Stylactis affinis* Jäderholm, 1904; *Stylactella spongicola* Haeckel (1889) and *S. abyssicola* Haeckel (1889).

Perarella schneideri (Motz-Kossowska, 1905)

Perigonimus steinachi Jickeli, 1883, *Gegenbaurs Jb.* 8 : 617, pl. 27, figs. 1-9.

Perigonimus schneideri Motz-Kossowska, 1905, *Arch. zool. exp. gén.* (4) 3 : 72, fig. VI.

Clavopsis schneideri, Stechow, 1921, *Arch. Naturg.* 87A : 252.

Perarella schneideri, Stechow, 1922, *Ibid.* 88A : 145.

Rees, 1956, *Bull. Brit. Mus. (Nat. Hist.) Zool.* 3 (8) : 344, 346.

I have not seen this species and the following description is based on the work of Motz-Kossowska and of Stechow.

Definition

Hydrorhiza forming an open network of perisarc-covered stolons. Hydranths long and tubular, with a whorl of 12-14 tentacles around a conical hypostome. Hydranths provided with a basal collar of perisarc.

Gonophores, fixed, oval, borne on short stalks, or almost sessile on the hydro-rhiza. Male gonophore, cryptomedusoid, with four radial canals and four very rudimentary basal bulbs. Manubrium well developed with ring gonad almost completely filling the subumbrella cavity. ♀ gonophore similar, with numerous eggs.

Motz-Kossowska states that the polyps are extremely contractile but when expanded reach a height of 15 mm. (this is apparently a misprint for 1.5 mm.). The ♂ gonophores are said to be milky-white in colour with the radial canals and tentacle bulbs of a vivid red colour.

Picard (1958:190) refers this species to *Perigonimus steinachi* Jickeli, 1883, a species which I regard as insufficiently described (Rees, 1956:344). He identifies Stechow's *Stylactella elsaeoswaldae* from Naples also with the present species; this is probably correct despite the fact that Stechow did not observe the basal collar of perisarc around the base of the hydranth. Stechow gives the height of the hydranths as 0.5–0.75 mm. and the size of the female gonophores as 0.64 mm. by 0.4 mm. The length of gonophore and stalk was 0.96 mm.

Perarella clavata (Jäderholm, 1905)

Hydractinia clavata Jäderholm, 1905, *Wiss. Ergeb. Schwed. Sud-polar Exp.* 1901–05, 5 (8): 5.
Stylactella clavata, Stechow, 1925, *Wiss. Ergeb. Deutsche Tief-sea Exp.* 1898–99, 17 (3): 401.

This hydroid was referred to *Hydractinia* by Jäderholm who found the species growing on shells dredged from a depth of 360 m. off Ludvig Philip Land, Erebus and Terror Gulf, Antarctica (Swedish Sud-polar Expedition, 1901–03, St. 8).

From a preliminary examination of the material in Stockholm in 1954, it was realized that the species could not be retained in *Hydractinia*; it had no basal crust, no spines, no dactylozooids and no reproductive hydranths (all characteristics of *H. echinata*, the type species). Jäderholm's species possessed stalked gonophores arising directly from the basal stolons and together with the basal cup around the proximal end of the hydranth indicated a relationship with hydroids of the family Cytæidae. Apart from the fixed gonophores, the species bore a close resemblance to the *Cytæis* hydroid described by Komai (1931).

This relationship has already been acknowledged by recognizing *Perarella* (Stechow, 1922) as a suitable genus "for cytæid hydroids in which there are fixed gonophores" (Rees, 1956). Accordingly *H. clavata* is referred to the genus *Perarella*.

The following description of *Perarella clavata* is based on a re-examination of the type material in Stockholm in May, 1959.

Description

The basal stolons form a close, reticulate, anastomosing network, but there are no spines, no dactylozooids or other Hydractinian features. The colony is well developed and extensive on its shell base (see Jäderholm, 1905, Taf. 3, fig. 6) so that the network can be assumed to be fully developed.

The hydranths arise from a weakly-chitinized stolon and have thin basal cups of perisarc; the latter has a height of approximately 0.4 mm. The hydranths are

tall, columnar, and are often more swollen distally. There are 10-16 filiform tentacles around a conical hypostome which is not heavily armed with nematocysts.

The gonophores are very characteristic and recall *Cytaeis* rather than *Hydractinia*. They are stalked and arise directly from the stolons (Text-fig. 11). There is, as in the hydranths, a basal ring of perisarc which is only 0.17-0.20 mm. in height. Distal to this, there is a moderately long stalk merging into the gonophore itself, and covered with very thin perisarc. The gonophore is elongate and rather club-shaped in appearance. There were no radial canals described but I have not been able to confirm or deny this from the material. There is a thickening of the wall of the gonophore distally, with apically, a slight protuberance or papilla. The eggs are arranged in a single layer round the well-developed spadix.

Measurements of this type material are given below :

TABLE V.—*Dimensions of the holotype of Perarella clavata (Jäderholm)*

Height of hydranth to hypostome	4.5-6.7
Diameter of hydranth	0.4-1.0
Length of proboscis	0.4-0.6
Diameter of stolons	0.2-0.25
Total height of gonophore	2.15-2.9
Width of gonophore	0.6-0.8
Length of stalk of gonophore	0.4-1.0

The chief difference between this species and the closely related type species of *Perarella*, *P. schneideri* (Motz-Kossowska) lies in the structure of the gonophore. In *P. schneideri* there are four well-developed radial canals and four rudimentary bulbs but in the species *clavata* radial canals are apparently absent and apically there is only a small protuberance.

Perarella spongicola (Haeckel, 1889)

Stylactella spongicola Haeckel, 1889, *Rep. Sci. Res. Challenger Zool.* 32 : 79, pl. 2, figs. 5, 6.

Iwasa, 1934, *J. Fac. Sci. Hokkaido Univ. Zool.* (6) 2 : 254, fig. 5.

Definition

Hydrorhiza consisting of smooth, anastomosing stolons (0.5-0.12 mm. in diameter) forming polygonal or rounded meshes, these giving support to the tissues of the host sponge. Hydranths very small, 0.2-0.3 mm. in diameter, ovate or club-shaped with about eight tentacles around the base of a conical hypostome. Gonophores, fixed, ovate, or club-shaped with distinct stalk. ♀ gonophores are sporosacs with distinct spadix, numerous eggs and no traces of radial canals or of tentacle bulbs (Text-fig. 12a).

This species occurs in association with deep-sea sponges of the genera *Psammophyllum*, *Cerelasma*, and *Psammopemma* in the north and central Pacific at depths of 2,300-2,900 fathoms.

The micro-preparations made by Haeckel have long dried up and no additional information can be given on the species.

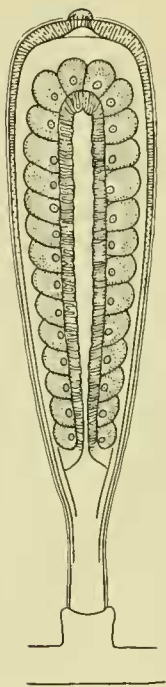


FIG. 11. *Perarella clavata* Jäderholm; a female gonophore from a type slide in the Naturhistoriska Riksmuseum, Stockholm.

***Perarella abyssicola* (Haeckel, 1889)**

Stylactella abyssicola Haeckel, 1889, *Rep. Sci. Res. Challenger Zool.* 32: 81, pl. 2, fig. 7.

Iwasa, 1934, *J. Fac. Sci. Hokkaido Univ. Zool.* (6) 2: 255, fig. 6.

Definition

Hydrorhiza of anastomosing stolons of variable thickness. Hydranths fusiform, with hypostome and oral whorl of 12-16 filiform tentacles, borne on short non-annulated stems. Gonophores, fixed, without radial canals or rudiments of tentacles, with prominent spadix, borne on short stalks (Text-fig. 12*b*).

Haeckel states that the hydranths are 0.5-0.6 mm. in diameter, that is nearly twice the size of those of *P. spongicola*. He draws special attention to the fusiform dilations of the stolons between hydranths and the triangular dilations of the anastomosing tubes at nodal points.

This species, like *P. spongicola*, is associated with deep-sea sponges of the genera *Psammophyllum* and *Stannophyllum* from Challenger stations in the north and central Pacific at depths of 2,300-2,900 fathoms.

Haeckel's preparations are in too poor a condition to yield additional information.

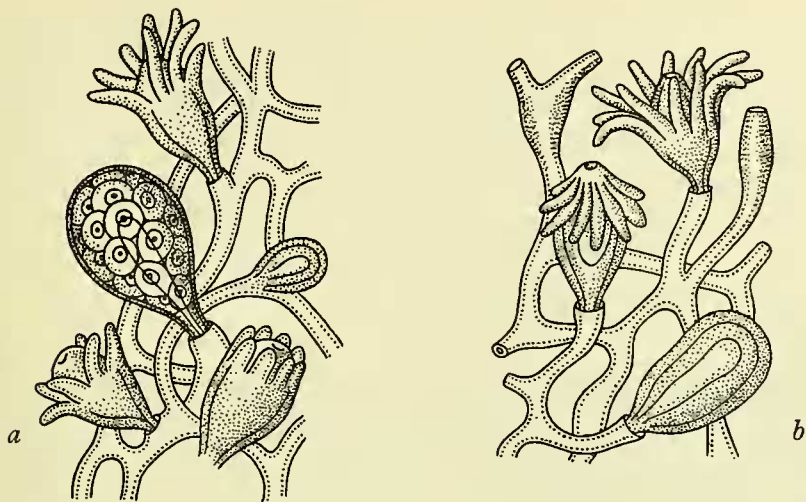


FIG. 12. *a*, *Stylactella spongicola* Haeckel; *b*, *Stylactella abyssicola* Haeckel; both figures redrawn from Haeckel (1889).

Perarella affinis (Jäderholm, 1904)

Stylactis affinis Jäderholm, 1903, *Ark. Zool. Stockholm*, 1: 264, pl. 12, fig. 1.

?*Stylactis affinis* Stechow, 1912, *Z. Jb. (Syst.)* 32 (4): 348, pl. 13, fig. 9.

This small sterile colony cannot be assigned to any other known species. It was re-examined by me at Stockholm in 1954. The salient features of the colony are a creeping, perisarc-covered hydrorhiza formed of anastomosing stolons 0.10–0.12 mm. in diameter. The hydranths are almost sessile, without enlargement of the perisarc stalk at the base. The distal portion of the hydranth is fusiform and there are 10–14 filiform tentacles of about 0.7 mm. each in length grouped around a conical proboscis. The hydranths are 0.7–2.5 mm. long and 0.25–0.4 mm. in maximum diameter. Reproduction is unknown.

Type locality. Romache Bay, Patagonia, on algae from 11 fathoms.

There is no certainty that the small sporosac figured by Stechow (1912: 348, pl. 13, fig. 9) belongs to the same species. It may be noted that Stechow mentions four rudimentary marginal tentacles but his figure suggests more than four. This species is placed provisionally in *Perarella*.

5. Genus *Stylactella* Haeckel, 1889

Stylactella Haeckel, 1889, *Rep. Sci. Res. Challenger Zool.* 32: 79.

In his genus Haeckel included three species *Stylactis vermicola* Allman, 1888 and his new species *Stylactella spongicola* and *Stylactella abyssicola*. He defined his genus as follows:

Tubulariae without hydrocaulus, with a reticular hydrorhiza, from which arise single sessile or pedunculate hydranths, and scattered between them single gonophores. Hydranths claviform, naked, with a single circlet of filiform tentacles, which surround the base of a conical hypostome. Gonophores ovate, naked, with a simple central spadix. Chitinous perisarc investing only the tubular branches of the hydrorhiza.

Stylactis vermicola Allman is here designated as type species of *Stylactella*.

Stylactella vermicola (Allman, 1888)

Stylactis vermicola Allman, 1888, *Rep. Sci. Res. Challenger Zool.* 23 : 2, pl. 1, figs. 2, 2a.

Stylactella vermicola Haeckel, 1889, *Ibid.* 32 : 79.

Stylactella (Stylactella) vermicola Iwasa, 1934, *J. Fac. Sci. Hokkaido Univ. Zool.* (6) 2 : 253, fig. 4.

The following brief description is based on Allman's text and figure : Hydrorhiza branching with smooth perisarc. Hydranths arising at intervals from extremely short stalks from the stolons. Hydranths clavate with distinct conical hypostome and a whorl of about eight tentacles. Gonophores small, oviform on very short stalks springing from the hydranth close to its proximal end or from the stolons.

Type locality. Challenger St. 244, N. Pacific, 35° 22' N., 169° 53' E., 2,900 fathoms on the polychaete *Laetmonice producta*.

A re-examination of the original specimens of the annelid *Laetmonice producta* on which the hydroid was found by Allman, revealed traces of a hydrorhiza and disintegrating fragments of hydranths. There were, however, no other recognizable parts.

Allman thought that the gonophores were adelocodonic (fixed), but in view of their small size there can be no certainty about this, or whether the species is a true cytaeid. Accordingly *Stylactella* (of which *S. vermicola* has already been designated as type species) must be regarded as an insufficiently described genus. It is here restricted to *S. vermicola*, and Haeckel's two species, known to have fixed gonophores, are placed in *Perarella* Stechow.

6. DISCUSSION

It is evident from the above survey that the family Cytaeidae is a well-defined one which can be distinguished from the Hydractiniidae (with which it has been primarily confused), by the complete absence of spines on the hydrorhiza, by the absence of reproductive hydranths, by the direct development of medusa buds on the hydrorhiza and by the characters of the medusa. In the latter the presence of oral tentacles on the manubrium around a simple mouth distinguish it from *Podocoryne* medusae in which the corners of the mouth form oral lips.

The status of those Cytaeid hydroids which liberate medusae cannot be resolved until more is known about the planktonic development of the medusae. In *C. uchidae*, for example, does the medusa shed its gonadial products and die—or does it continue to grow in the plankton and so assume the typical form of *C. tetrastyla* with numerous oral tentacles? The preliminary experiments conducted by Mr. Hatsuki Tsujimura in which one medusa only had increased its oral tentacles to

seven after 40 days are inconclusive, but they (and the work of Werner, 1961) suggest profitable lines for future research.

Cytaeis uchidae and *C. nuda*, both liberating medusae with almost mature gonads, appear to be closely related. Likewise *C. nassa* and *C. niotha* are very similar even in the number of tentacles in the hydranth, but there appears to be a distinct difference in the nematocyst armature of the tentacles in the hydranth.

C. uchidae has much fewer tentacles in the hydranth than *C. nassa* and also differs from it in having an almost mature medusa at liberation. The solution of the *Cytaeis* problem thus depends on careful rearing of the medusae to establish their growth and reproductive pattern.

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30 JUL 1962

PRESENTED