

## The taxonomic status of the genus *Stylactaria* Stechow, 1921 (Hydroidomedusae, Anthomedusae, Hydractiniidae), with the description of a new species\*

J. BOUILLON<sup>1</sup>, D. MEDEL<sup>2</sup> and A. L. PEÑA CANTERO<sup>3</sup>

<sup>1</sup>Laboratoire de Biologie Marine, Université Libre de Bruxelles, 50 Ave F. D. Roosevelt, 1050 Bruxelles, Belgium.

<sup>2</sup>Laboratorio de Biología Marina, Facultad de Biología, Universidad de Sevilla, Apdo 1095, E - 41020 Sevilla, Spain.

<sup>3</sup>Departamento de Biología Animal, Facultad de Ciencias Biológicas, Universidad de Valencia, E - 46100 Burjassot, Valencia, Spain.

**SUMMARY:** The status of all the species ascribed in the literature to *Stylactaria* is discussed, that nominal genus is considered a congener of *Hydractinia* and a new species (*Hydractinia calderi* n. sp.) is described. The medusae of the medusa-based genera *Hansiella* and *Tregoubovia*, formerly ascribed to the Hydractiniidae, are shown to be more like the medusae of *Thecocardium*, a genus having ptilocodiid hydroids. Both *Hansiella* and *Tregoubovia* are thus transferred to the Ptilocodiidae. With their removal from the Hydractiniidae, a redefinition of both families is provided. The genus *Fiordlandia* is considered as synonym of *Clavactinia*.

**Key words:** Cnidaria, Hydroidomedusae, Hydractiniidae, Ptilocodiidae, Classification.

**RESUMEN:** TAXONOMÍA DEL GÉNERO *STYLACTARIA* STECHOW, 1921 (HYDROZOA, ANTHOMEDUSAE, HYDRACTINIIDAE) Y DESCRIPCIÓN DE UNA NUEVA ESPECIE. – Se analiza la posición sistemática de todas las especies descritas del género *Stylactaria* que al mismo tiempo se considera sinónimo de *Hydractinia* and, al mismo que se describe una nueva especie (*Hydractinia calderi* n. sp.). Las medusas descritas de los géneros *Hansiella* y *Tregoubovia*, previamente adscritas a la familia Hydractiniidae, se confirma su proximidad sistemática al género *Thecocardium*, un género que tiene hidropólipos ptilocódidos. Los géneros *Hansiella* y *Tregoubovia* se transfieren por tanto a la familia Ptilocodiidae. Con la eliminación de ambos géneros de la familia Hydractiniidae, se aporta una nueva descripción de las dos familias mencionadas. Al mismo tiempo, el género *Fiordlandia* se considera sinónimo de *Clavactinia*.

**Palabras clave:** Cnidaria, Hydroidomedusae, Hydractiniidae, Ptilocodiidae, Taxonomía.

### INTRODUCTION

Only one species of *Stylactaria*, *S. inermis* (Allman, 1872), has been recorded so far from Mediterranean waters (see Boero and Bouillon, 1993). The discovery of several colonies referable to *Stylac-*

*taria* from the Strait of Gibraltar and waters surrounding the Chafarinas Islands led us to review this genus.

The name *Stylactaria* Stechow, 1921a has recently been re-proposed by Calder (1988) as the valid name for *Stylactis* auct. (not *Stylactaria* Allman, 1864). *Stylactaria* assigned to the family Hydractiniidae, is characterized by: a non-encrusting hydrorhiza formed by anastomosing stolonal tubes

\*Received January, 1997. Accepted May, 1997.

surrounded by perisarc, rather than being covered by naked coenosarc. Hydranths sessile and polymorphic: gastrozooids with one or more close whorls of tentacles encircling the hypostome, gonozooids with or without tentacles; occasionally with dactylozooids and spines; gonophores as fixed sporosacs, or either fixed or free eumedusoids with 8 - 10 tentacles. Gonophores borne on gonozooids, originating beneath the tentacles or on the distal part of non-tentacled gonozooids.

The species ascribed to *Stylactaria* have been reviewed three times, by Iwasa (1934), Bouillon (1971) and Namikawa (1991). Hirohito (1988) surveyed the Japanese species. Twenty-nine nominal species and five reports of *Stylactaria* sp. hydroids have been described, the last ones showing the difficulty in identifying these animals at species level (see Table 1).

Calder (1988) noted that characters such as size of gastrozooids, asexual reproduction, tentacle arrangement and presence of spines, could all be "interpreted as nothing more than variations that might be expected within a single species". We agree with Calder (1988) in that most of the characters used to distinguish the species of *Stylactaria* are purely quantitative and, from Table 1 it is evident that most differences could fall within the range of variation of a given character. Many of the 34 described species may prove to be conspecific, but such taxonomic decisions are difficult when based on traditional morphometric characters.

### The diagnostic characters of *Stylactaria*

Characters used to distinguish the species of *Stylactaria* are:

**Size:** in athecate hydroids, size depends on several ecological and biological variables such as: state of contraction, presence of food in the gastrovascular cavity, temperature, salinity etc. (see for instance, Kinne, 1957, 1958; Mc Clary, 1959; Werner, 1963; Arndt, 1965; Nipper-Buscariolli and Moreira, 1983a, b). Even after anesthetization, size may not necessarily correspond to the natural state, in a given colony both size of zooids and tentacle number can vary (for *Stylactaria* see, the figures 2, 8 and 13 in Iwasa, 1934; figures 47a, 48c, 49a and e, 50d in Hirohito, 1988). The taxonomic value of this character must therefore be considered with great caution, and measuring a great number of specimens with a precision of 0,01 mm is meaningless: only the extremes can have some significance.

**Tentacle number:** In the Filifera this feature is often variable and, again, it can change according to ecological factors such as temperature and salinity (Kinne, 1957; Nipper-Buscariolli and Moreira, 1983a, b). Noteworthy and constant differences in tentacle number, however, might allow species distinction more reliably than size.

**Number of tentacle whorls:** the number of tentacle whorls may be linked to tentacle number. When tentacles are numerous, they do not have enough space to grow in a single ring, tend to alternate or to be disposed in 2 or more whorls. More than one tentacle whorl should thus be expected in species with numerous tentacles. This is generally, but not always, the case (see Table 1). Some species with few tentacles have more than one whorl, whereas certain others with numerous tentacles have only one whorl, and, furthermore, species with approximately the same number of tentacles may have either one or more whorls. This character, thus, might be diagnostic, being not only quantitative but also qualitative.

The number of both tentacles and tentacle whorls must of course be counted on fully-grown specimens.

**Dactylozooids** (Tentaculozooids and spiralzooids) (see Bouillon, 1995 for definition): presence, rarity or even absence of dactylozooids is not a reliable character. Daniaud (1951) experimentally demonstrated that the presence of these types of zooids in the hydractiniids is often more linked to host type and activity than to specific features. Colonies of the same species on a crab-inhabited shell and on a living gastropod shell were shown to either have or lack this type of zooid. Namikawa *et al.* (1992) showed that the tentaculozooids of *Stylactaria conchicola* (Yamada, 1947) developed most frequently near or at the colony portion in contact with other sessile animals.

**Hydrorhiza:** the degree of hydrorhizal reticulation depends mainly upon substrate type, colony age, and on key ecological factors, thus being not considered here as having specific value.

**Cnidocysts:** in most *Stylactaria* species the cnidome is composed of microbasic euryteles and desmonemes, but some species also have haplonemes, identified as anisorhizae in *S. inermis* by Boero (1981), and microbasic mastigophores (see Table 1). So cnidome can have some taxonomic importance, especially when other types besides microbasic euryteles and desmonemes are found. Capsule size is very variable within the same nema-

tocyst types (see Vannucci, 1960) and can only have a diagnostic value if size ranges are well separated. Cnidome distribution could be informative, and Namikawa *et al.* (1993) showed that both cnidome composition and distribution in the planulae were potentially useful in the taxonomy of *Stylactaria*. Schuchert (1996) described a thick ring of nematocysts around the hypostome of *Hydractinia otagoensis*, a character also reported by Castric-Fey (1970) for *H. fucicola*.

**Type of gonozooids:** in the three most familiar genera recognized within the Hydractiniidae (*Hydractinia*, *Podocoryna*, *Stylactaria*), the gonozooids are normally tentacled, but tentacles often decrease in number or even disappear during colony growth, the gonozooids resembling blastostyles (see Rees, 1956). This may happen in the same colony, with either tentacled (and with hypostome) or atentaculate (and without hypostome) gonozooids. The same may occur in many other families (e.g. the Zancleidae and the Corynidae) and so the character has little if any systematic value. In some Hydractiniidae the blastostyles are so reduced that the gonophores are almost sessile and appear borne directly from the hydrorhiza, as in the Cytaeidae. In the absence of polymorphism and of a free medusa stage, it is impossible to assign such species to family. In some species it has been suggested that the gonozooids are derived directly from normal gastrozooids. In some cases the gonozooids are even able to redifferentiate into gastrozooids after gonophore liberation (Bouillon, 1995).

**Gonophore type:** the type of gonophores can vary with environmental conditions or with sex (i.e. sexual dimorphism). In the same species, eumedusoids can remain fixed to the gonozooids until planula liberation, or can be liberated with immature eggs and, as remarked by Namikawa *et al.* (1993), "the degree of gonophore reduction alone should not be employed directly to derive a phylogeny of species of the genus".

**Endemicity:** many *Stylactaria* species are reported as endemic, especially from Japanese waters (13 of the 29 nominal species). Most have been found only once, or have been found several times but described under different names, or are considered as substrate-specific.

**Substrate specificity:** some species of *Stylactaria* appear to be strongly substrate-specific (see Namikawa *et al.*, 1993). For instance, *Stylactaria piscicola* (Komai, 1932) has been found only on the stonefish *Erosa erosa*, *S. multigranosi* (Namikawa,

1991) on the gastropod *Nassarius multigranulosus*, *S. conchicola* (Yamada, 1947) on the gastropod *Homalopoma amussitatum*. Such specificity is often inferred from a single or few findings and, furthermore, substrate specificities might result from the habit of distinguishing species on inhabited substrate alone. Since colonies of the same species may have different features according to the inhabited substrate, it is to be expected that different morphologies are encountered in colonies living on different substrates. This is not necessarily an indication of species distinction.

This short review shows that most of the characters heretofore used to distinguish *Stylactaria* species are not reliable. Biochemical and genome analyses will likely be a better tool than morphology for the identification of these animals.

Boero, Bouillon and Piraino (in press) have proposed that the three most familiar nominal hydractiniid genera should be merged into the oldest one, *Hydractinia* van Beneden, 1841. Similar views have been held by several previous authors. Motz-Kossowska (1905) merged *Hydractinia*, *Podocoryna* and *Stylactis* into *Hydractinia*. Broch (1914, 1916) considered that *Stylactaria* (*Stylactis*), *Podocoryna* and *Hydractinia* could not be kept apart and should be included under *Hydractinia*. Stechow (1923) considered *Stylactis* as junior synonym of *Hydractinia*. Kramp (1932) suggested that *Stylactaria* (*Stylactis*) should be placed in the genus *Hydractinia* and that "*Stylactis*" merited no more than subgeneric rank. Naumov (1960-1969) also merged *Podocoryna* into *Hydractinia*. Kramp (1932) assigned *Podocoryna* and *Stylactaria* subgeneric rank within *Hydractinia*, but this is not phylogenetically sound. If *Podocoryna* and *Stylactaria* were monophyletic, they could well be ranked as genera.

A complete revision of *Hydractinia* is outside the scope of this paper. All the species previously referred to *Stylactaria* will be critically reviewed below, including them into *Hydractinia* (Table 1). All *Hydractinia* species heretofore excluded from *Stylactaria* will not be considered here.

## MATERIALS AND METHODS

Specimens of the following nominal species have been examined for the present review:

*Clavactinia gallensis* Thornely, 1904: Seychelles. I.R.S.N.B., IG .27838.

*Clavactinia multitentaculata* Millard, 1975:

TABLE 1. – \* = found only till now in this area; ? = doubtful or unknown; ° = only found on this substrate; A. = algae; An. = anisorhiza; B. = bryozoans; B.I. = basitric-hous isorhiza; Bv. = bivalves; C. = crustaceans; cryp. = cryptomedusoids; D = desmonemes; E. = echinoderms; eum. = eumedusoids; F. = fishes; fix. eum. = fixed eumedusoids; G. = gastropods; Gas: = gastrozooids; Gon: = gonozooids; H. = hydrozoans; Ha. = haplonemes; ht. = heteromedusoids; hydror. = hydrorhizal; M.E. = microbas-ic euryteles; MM = size in millimetres; M.M. = microbasic mastigophores; N°T. = number of tentacles; P.C. = perisarcular cup; R. = rocks; Sg. = sea-grasses; Sp. = sponges; spc. = sporosacs; T. = tunicates; Ts. = tentacle arrangement; w. = whorls; Wo. = worms.

Species	Gastrozooids		Dactylozooids	Spines	Gonozooids		Gonophores		Medusae	Cnidocysts	Substrate	Distribution
	Ts.= 1 whorl N°T.	MM			N°T.	MM	N° types					
1) <i>H. arctica</i> (Jäderholm, 1902)	12-15 P.C.	2-3	-	-	(4?)	1	1-2	?	-	?	<i>Mohnia mohni</i> , <b>F.</b> ; <i>Eudendrium planum</i> , <b>H.</b>	Greenland, Baffin bay (1.200-2.000 M)
2) <i>H. betkensis</i> (Watson, 1978)	8-15	1-2	-	+	8	0,65-0,8 p.e.	1-5, cryp.	-	-	B.I.?, M.E.	<b>G.</b> , <i>Parcannassa burchardi</i> <sup>o</sup>	Australia* (brackish)
3) <i>H. brachyurae</i> (Hirohito, 1968)	14 P.C.	1	-	-	10	-1	10, cryp.	-	-	?	<b>C.</b> , Spider crab <sup>o</sup>	Japan* (80-100 M)
4) <i>H. carcinicola</i> (Hiro, 1939)	12-30	10	usually +	+	2-10	0,5	1-11	eum., 8 tentacles	-	?	<b>G.</b> ; <b>C.</b> ; <b>R.</b>	Japan*
5) <i>H. conchicola</i> (Yamada, 1947)	2 types, 2-5 4-8	1,2-3 0,9-1,9	+	+	0;2-5	0,6-2,5	4-6, ht.	-	-	D., Ha M.E.	<b>G.</b> , <i>Holalopoma amussitatum</i> <sup>o</sup>	Japan*
6) ( <i>H. halecii</i> )= <i>Rhysia halecii</i> (Hickson & Gravely, 1907)												
7) <i>H. hooperii</i> (Sigerfoos, 1899)	15-35	1,5-26	-	+	6-10	8-18	4-5	eum., 8 tentacles	-	?	<b>G.</b> & hermit crabs inhabited shells	USA; Puerto Rico; Brazil
8) <i>H. ingolfi</i> (Kramp, 1932)	15-17 P.C.	2,5	-	-	0	small	1, male?, female cryp.	-	-	D., M.E.	<b>E.</b> , <i>Homalophiura tessellata</i>	Greenland* (2.137-3.229M)
9) <i>H. minoi</i> (Alcock, 1892)	10-40	3,5	scarce	-	0-4	0,5 no mouth	1-7	medusa buds, 8 tentacles	-	?	<b>F.</b> <i>Minous pusillus</i> <sup>o</sup>	Japan, Indian Ocean
10) <i>H. misakiensis</i> (Iwasa, 1934)	10-30	1-4	somet- times +	+	20	1-2	1-5	eum., 8 tentacles	-	?	<b>G.</b> inhabited by hermit crabs	Japan*
11) <i>H. multigranosi</i> (Namikawa, 1991)	8-16	1-1,15	+	-	4-11	0,5-2	1-4, 1-2 w.	-	-	D., Ha.,	<b>G.</b> , <i>Nassarius multigranosus</i> <sup>o</sup>	Japan*
12							fix. eum.	-	-	M.E.		
13) <i>H. otagoensis</i> (Schuchert, 1996)	12-16	2-4	+	+	8	2-4	4-6, spc.	-	-	D., M.E., M.M.	<b>A.</b> , <i>Macrocystis pyrifera</i> ; <b>T.</b> , <i>Pyura pachydermata</i>	New Zealand*
14) <i>H. piscicola</i> (Komai, 1932)	11-30	2-10	-	+	4-12	1,4-3,3	1-3, fix. eum.	-	-	D., M.E.	<b>F.</b> , <i>Erosa erosa</i> , stonefish <sup>o</sup>	Japan*
15) <i>H. pruvoti</i> Motz-Kossowska, 1905	10-14	6-15	somet- times +	+	1-3	4-5	8-9	eum., 4 tentacles	-	?	<b>G.</b> , <i>Cassidaria tyrrhena</i> inha- bited by pagurus <i>Cerithium</i> sp.	Mediterranean*
16) <i>H. reticulata</i> (Hirohito, 1988)	12	5	-	-	10	2,5-3	6, cryp.	-	-	?	<b>R.</b> ; <b>B.</b> ; <b>C.</b>	Japan*
17) <i>H. ?sagamina</i> (Hirohito, 1988)	8-10	0,9	-	+	gonophores on hydrorhiza		-	medusae not fully grown	-	?	<b>G.</b> , inhabited by hermit crabs	Japan*
18) <i>H. sandrae</i> (Welder & Larson, 1986)	11-16	2	-	-	4-11	0,5-1,5	in pairs fix. eum.	-	-	?	<b>T.</b> <sup>o</sup>	Puerto Rico
19) <i>H. siphonis</i>	8-10	0,8	?	-	reproduction		?	?	?	?	<b>G.</b> , <i>Sipho</i>	South Africa*

Species	Gastrozooids		Dactylozooids	Spines	Gonozooids		Gonophores	Medusae	Cnidocysts	Substrate	Distribution
	N°T.	MM			N°T.	MM					
(Stechow, 1921)					unknown					<i>islandicus</i>	
20) <i>H. sp.</i> = <i>H. arge</i> (Crowell, 1947) see Calder, 1988											
21) <i>H. sp.</i> (Welder & Larson, 1986)	9-13	2,3	-	-	5-8	?	1-3, fix. eum.	-	?	<b>G.</b> , <i>Cerithium sp.</i>	Puerto Rico
22) <i>H. sp.</i> (Calder, 1993)	?		?	?	?	?	?	?	?	?	Bermuda
23) <i>H. sp.</i> (Namikawa, 1994)	6-13	1,15- 2,25	-	+	0;6-9	0,8-2,5	1-6, cryp.	-	?	several <b>G.</b>	Japan*
24) <i>H. sp.</i> (Pena Cantero, 1995)	11-16	1,5	-	+	6-8	1	4, oppos- ite 2per2	eum., 8 tentacles	D., M.E.	<b>G.</b> , <i>Cerithium sp.</i>	Mediterranean
25) <i>H. spinipillariss</i> (Hirohito, 1988)	6-12	1,5	+	+	0	0,75	2-3	eum., 4 tentacles	?	<b>G.</b> , <i>Simplicifus graciliformis</i> <sup>o</sup>	Japan*
12) <i>H. nagaensis</i> nom. nov.	6-11	2,0-3,5	+	+	4-6	0,6-2,3	1-16; 1-4 w.; ht.; female = 1 egg	-	D., M.E.	<b>R.;A.:Sp.:Bv.:B.; Wo.; C.</b>	Japan*
26) <i>H. yerii</i> (Iwasa, 1934)	10-14	1,5	-	-	0-4	0,7	4, cryp.	-	?	<b>G.</b> ; <i>Turricula kamakurana, Pseudoetrema fortilirata</i>	Japan*
					<b>Ts. = 2 or more whorls</b>						
27) <i>H. arge</i> (Clarke, 1882)	10-30. till 45 2w.		-	+	5-30	30	4, oppos- ite 2 per 2	eum., 8 tentacles	Gas: D., M.E. Gon: D., <i>M.E., Ha.</i>	<b>A.; Sg.; G.</b> , inhabited by hermit crabs, <i>Cerithium</i>	USA; Bermuda; Puerto Rico
28) <i>H. claviformis</i> (Bouillon, 1965)	18-32	16-50 2-3 w.	+	-	6-10	0,88-2,5	4-8, oppo- site 2- per 2; fem- ale, cryp.	male., eum., 10 tentacles	D. M.E.	<b>A.; Sp.; R.</b>	France Atl., Spain Atl.
29) <i>H. inabai</i> (Hirohito, 1988)	30 or more 1w. or closely alternating w.	+3	rarely+	+	20 or more	3	2-3	eum., 8 tentacles	?	<b>G.</b> , inhabited by hermit crabs; hyd- rorrhiza exceed- ing shell opening	Japan*
30) <i>H. inermis</i> (Allman, 1872)	20	0,6-4,2 several w.; P.C.	somet- imes+	-	12	2	2-6, fix. eum.	-	D., An., M.E.	<b>A.; C.; Sg.; H.</b>	Mediterranean
31) <i>H. mar</i> (Gasca & Calder, 1993)	16-18	3 2 closely w.; large P.C.	+	+	10-12	1,2	3, not ful- ly devel- oped	-	D., Ha., M.E.	<b>Wo.</b> , <i>Pseudopot- amilla reniformis</i> <sup>o</sup>	Mexico, Pacific coast
32) <i>H. monoon</i> (Hirohito, 1988)	8-11	2 almost in 1w. P.C.	+	+	8	1	6; female ht., 1 egg; male?	-	?	<b>Sp.; H.</b> , <i>Euden- drium</i>	Japan; Sea of Okhost?
33) <i>H. spiralis</i> (Goto, 1910)	50	2 closely alternating;	+	rarely+	0-12	0,7	10, cryp.	-	?	<b>G.</b> , inhabited by hermit crabs; hyd- rorrhiza exceed- ing shell opening	Japan*
34) <i>H. calderi</i> n. sp.	20-40	5 3 w.; P.C.	+	+	2-14	1-2,5	1-3, fix. eum.	+?	D., M.E.	<i>Astrea rugosa</i> <b>G.; sp.</b>	Mediterranean

South Africa; FA 501 E, South African Museum H 3446.

*Clavactinia* sp. Peña Cantero, 1995: Chafarinas Islands, Arrastre 5, Spain.

*Hydractinia claviformis* (Bouillon, 1965): Roscoff, France, paratype, I.R.S.N.B., IG. 27838.

*Hydractinia inermis* (Allman, 1872): Villefranche, France. I.R.S.N.B., IG 10262.

*Hydractinia pruvoti* Motz-Kossowska, 1905: Naples, Italy. I.R.S.N.B., IG. 27838.

as *Stylactaria* sp. Medel, 1996, as *H. aculeata* (Wagner, 1833) by Medel *et al.*, 1996: Algeciras Bay, "Crinavis", 24 m depth, Spain.

*Stylactis* sp. Peña Cantero, 1995: Chafarinas Islands, Arrastre Baños de la Reina, Spain.

*Thecocardium quadratum* (Werner, 1965): NE of Mombasa, Kenya; C 10717, 10719, 10720, Zoologisches Institut und Zoologisches Museum der Universität Hamburg.

## SYSTEMATIC ACCOUNT

*Hydractinia arge* (Clarke, 1882). Calder (1988) regarded it as conspecific with *H. hooperii* (Sigerfoos, 1899), considering that their morphological differences were nothing more than variations of the same species and that they had a similar ecology and zoogeographical distribution. Namikawa (1991) did not accept Calder's view because *H. hooperii* differs from *H. arge* in having no eggs developing into planulae within the gonophores, being thus oviparous instead of ovoviviparous. This character could of course be linked to environmental features. But we can also argue that, even if gastrozoid tentacle number falls in the same range (see Table 1), tentacles are in one whorl in *H. hooperii* and in two whorls in *H. arge*. The same difference occurs in the gonozooids, so that we retain this as a valuable specific character (see above). The hydranth of the two species can also attain a very different range of size, and also zoogeographical distributions differ (see Table 1). We thus concur with Namikawa (1991) in keeping the two species as distinct.

*Hydractinia arctica* (Jäderholm, 1902). This species has been found only twice, near Greenland and in Baffin Bay, each time in deep cold waters (1200 to 2000 m) living on gastropods shells and on *Eudendrium*. The gonozooids, observed only once, are smaller than the gastrozooids, have only four tentacles and bear one or two spherical gonophores of unknown structure. The hypostome of the

hydranths is said to be trumpet-shaped (Kramp, 1932; Iwasa, 1934). This seems not to be due to the turning inside out of the hypostomial lips often observed in Filiferan hydranths (see figures and comments in Kramp, 1932), and appears to be a specific feature. The gastrozooids have a basal perisarc cup, a feature recorded also for *H. brachyurae* (Hirohito, 1988), *H. ingolfi* (Kramp, 1932); *H. monoon* (Hirohito, 1988) and *H. inermis* (Allman, 1872). Spines and dactylozooids are absent. Other morphological characters are typical of *Hydractinia* (see Table 1). Kramp (1932) described *Hydractinia ingolfi* from the northern Atlantic, in very deep waters (2137 to 3229 m). Its hypostome is also trumpet-shaped (see also Svoboda *et al.*, 1995), the gastrozooids have a basal perisarc cup and cryptomedusoid gonophores are isolated or borne in couples at the top of reduced gonozooids.

The two species are morphologically similar, their differences in gonozooid structure being currently observed within-colony in other species. They also share the same bathymetric and zoogeographical distribution. Although *H. ingolfi* seems substrate-specific, having been found only on the brittle-star *Homalophiura tessellata* (see *H. multigranosi* for substrate specificity) it is regarded here as conspecific with *H. arctica*.

*Hydractinia brachyurae* (Hirohito, 1988) is very similar to *H. arctica*, and the two might be conspecific (see Table 1). They differ, however, in depth range and zoogeographical distribution. Furthermore, the gonozooids of *H. brachyurae* have more tentacles and have more numerous gonophores (up to ten instead of one or two) distributed in a whorl or on one side almost in the middle of the gonozooid. For these reasons it is maintained here as a separate species.

*Hydractinia betkensis* (Watson, 1978). This is the only species of *Stylactaria* (= *Hydractinia*) recorded from Australia. Watson stated that it resembles both *H. inermis* (Allman, 1872) and *H. yerii* (Iwasa, 1934). Hirohito (1988) suggested some affinities of the species with *H. reticulata*, especially in the lack of spines and dactylozooids. *Hydractinia betkensis* is completely different from *H. inermis*, in which (1) both gastrozooids and gonozooids have two whorls of tentacles, (2) free eumedusoids are produced and (3) dactylozooids may be present. *Hydractinia betkensis*, like *H. reticulata* (= *H. yerii*), has cryptomedusoids but it differs in having a cup-shaped perisarc at the base of the gonozooids. Its cnidome, containing basitrichous isorhizas instead of

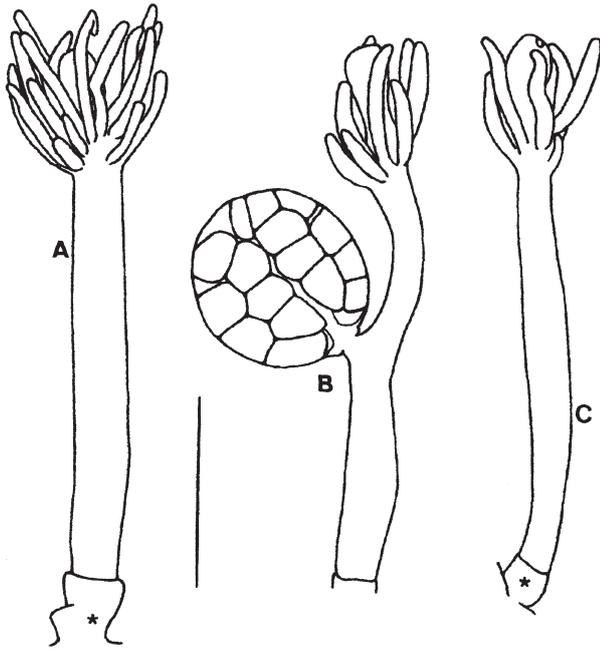


FIG. 1. – *Hydractinia calderi* n. sp. from Chafarinas Islands, Spain. (A) adult gastrozoid; (B) gonozoid; (C) young gastrozoid; \* = basal perisarcal cup; scale bar = 800  $\mu$ m.

desmonemes and euryteles, differs from that of all other species of *Hydractinia*, as far as is known. Furthermore, it occurs in brackish shallow waters. Watson (1978) expressed some doubt about her identification of the nematocysts of *H. betkensis*, but this species is provisionally considered as valid also due to other features, such as the almost capitate tentacles of both gastrozoids and gonozoids. Watson (1978) described the eggs as arranged around the radial canals, but her drawings show that they are on a central spadix.

*Hydractinia brachyurae* (Hirohito, 1988). See *H. arctica* (Jäderholm, 1902).

*Hydractinia calderi* n. sp. (figure 1 A-C, 2 A-D, 3A-B)

Material: one colony on a gastropod shell, Algeciras Bay, “Crinavis”, 24 m depth (reported by Medel, 1996 as *Stylactaria* sp.); one colony on the shell of *Astraea rugosa*, Chafarinas Islands, Arrastre Baños de la Reina (reported by Peña Cantero, 1995 as *Clavactinia* sp.).

**Description:**

Hydrorhiza stolonal, formed by reticular tubes covered with perisarc and adhering to gastropod shells; in the colony growing on *Astraea rugosa* the

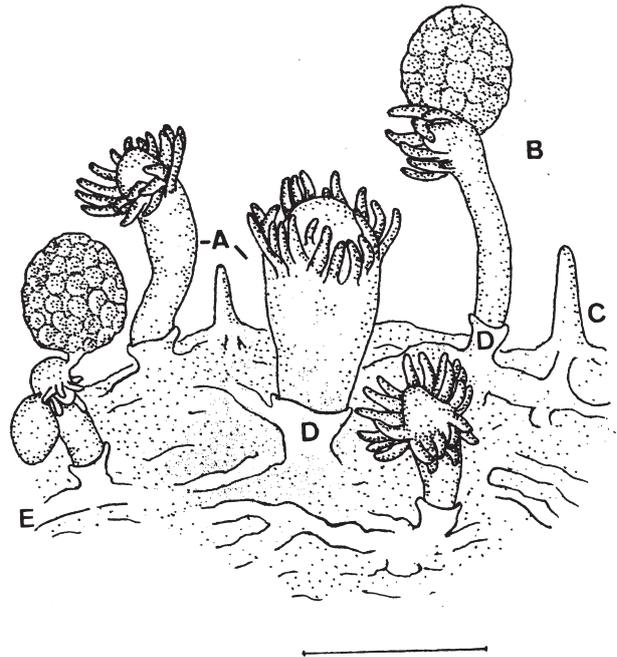


FIG. 2. – *Hydractinia calderi* n. sp. from Algeciras bay, Spain. Part of a retracted colony. (A) gastrozoid; (B) gonozoid; (C) spine; (D) basal perisarcal cup; (E) hydrorhiza; scale bar = 1mm.

hydrorhiza is situated between the shell crests.

Gastrozoids cylindrical, elongated, clavate when contracted, up to 5 mm high, arising from the stolon and with a basal perisarc cup. Hypostome encircled in fully developed zooids by 20 to 40 filiform tentacles in 3 whorls. Gonozoids much shorter, issued from a short basal perisarcal cup, 0,5 to 2,5 mm high, columnar, with a varied number of filiform tentacles (2 to 14) in one whorl. Each gonozoid generally bearing one or two eumedusoids, rarely three, one always well developed, the others juvenile. Eumedusoids with four radial canals and an often reduced subumbrellar cavity with striated muscle, four large bulbs, and four smaller ones. Female eumedusoids with numerous eggs. Dactylozoids (0.5 mm high) and spines (0.38 - 0.55 mm high) present but scarce. Cnidome: microbasic euryteles (8.7-11 x 3.2  $\mu$ m) and desmonemes (6.3-7.5 x 3.2-3.6  $\mu$ m).

**Remarks:**

The presence of striated muscle in the subumbrella indicates that these gonophores might be released as actively swimming eumedusoids. In the group of *Stylactaria* (= *Hydractinia*) with gastrozoids having more than one whorl of tentacles (see table 1) *H. calderi* has close affinities with *H. iner-*

*mis* (Allman, 1872), *H. monoon* (Hirohito, 1988) and *H. spiralis* (Goto, 1910). It differs from *H. inermis* in the presence of a perisarc differentiation at the base of the gonozooids, its gonozooids have only one whorl of tentacles instead of two, its colonies have spines, and the cnidome is different, having only two types of cnidocysts (desmonemes and microbasic euryteles) instead of three (see table 1). *Hydractinia calderi* also resembles *H. monoon* (Hirohito, 1988) having a perisarc cup at the base of the dactylozooids, but *H. monoon* has only 8-11 tentacles disposed in almost one whorl on its gastrozooids, its gonozooids have 6 gonophores which are heteromedusoid in the female and contain only one egg through all development (male gonophores unknown). The gastrozooids of *H. spiralis* (Goto, 1910) have up to 50 closely alternating tentacles, their hydrorhiza forms a gastropod-shell-like crust at the opening of the host shell and may have nematophores, it lacks a basal perisarc cup and the gonozooids bear more than ten cryptomedusoid gonophores.

The above species is thus here considered as new and is dedicated to Dale Calder to honour his eminent work on Hydrozoa.

Holotype material is deposited at the Museo de Ciencias Naturales de Madrid.

Type locality: Chafarinas Islands, Spain.

Diagnosis: Hydrorhiza reticulated, formed by tubes covered with perisarc; polymorphic: gastrozooids with a basal perisarc cup, 20-40 filiform tentacles in three whorls; gonozooids with a short perisarc cup, 2-14 filiform tentacles in 1 whorl; 1-2 rarely 3 fixed eumedusoids, only female known with numerous eggs; dactylozooids and spines present; cnidome comprising desmonemes and microbasic euryteles.

*Hydractinia carcinicola* (Hiro, 1939). This Hydrozoan resembles *H. hooperii* (Sigerfoos, 1899) and, following Hirohito (1988), may be referred to the same species. They differ only in their maximal size, in the usual presence of tentaculozooids in *H. carcinicola* and in the difference in length among the perradial and interradial tentacles of the liberable eumedusoids in the last species. These characters are interpreted here as intraspecific variations and *H. carcinicola* is regarded as conspecific with *H. hooperii*.

*Hydractinia claviformis* (Bouillon, 1965). (see also Ramil *et al.* 1994) This species shows some

affinities with *H. arge* in size, number of tentacles, and number of tentacle whorls of the gastrozooid. It differs by the dimorphism of its gonophores, by having free male eumedusoids with ten tentacles instead of eight and by the cnidome of the gonozooids (see Table 1).

*Hydractinia conchicola* (Yamada, 1947). Namikawa *et al.* (1990) remarked that this species shows great affinities with *H. nagaoensis* {=*Stylactaria uchidai* (Yamada, 1947) see below} differing only by the form of the spadix. This structure is scyphiform with one egg in *H. nagaoensis*, cylindrical and with several eggs in *H. conchicola*. The number of zooid types also reportedly differs but we discount the specific value of that character, especially considering possible different states of gonozooid reduction. *Hydractinia conchicola*, found exclusively on the living gastropod *Homalopoma amussitatum*, has a strong substrate preference, whereas *H. nagaoensis* is a substrate generalist (see Namikawa *et al.* 1992; Namikawa *et al.*, 1993).

Namikawa *et al.* (1993) showed that the cnidome of the planulae of *H. conchicola* consisted only of euryteles, while in *H. nagaoensis* there were euryteles and desmonemes. Namikawa (1995) found haplonemes in *H. conchicola*, a type of cnidocyst absent in *H. nagaoensis*. The two species, although closely related, show differences and should thus be kept separate. The problem of substrate specificity is discussed under *H. multigranosi*.

*Hydractinia halecii* (Hickson and Gravely, 1907). We refer it to the genus *Rhysia* Brinckmann, 1965, family Rhysiidae (see Bouillon, 1985; 1995; Calder, 1988; Brinckmann-Voss *et al.*, 1993).

*Hydractinia hooperii* (Sigerfoos, 1899) see *H. arge*.

*Hydractinia inabai* (Hirohito, 1988). This species is very close to *H. spiralis*. In both species the hydrorhiza forms a gastropod shell-like crust extending beyond the opening of the shell and the gastrozooids possess a great number of tentacles (up to 50) in one or more closely alternating whorls. They differ, however, by the number and the structure of gonophores, these being cryptomedusoid and up to ten per gonozooid in *H. spiralis*, and eumedusoids with two or three per gonozooid in *H. inabai*.

*Hydractinia inermis* (Allman, 1872). This species seems to be endemic to the Mediterranean Sea. It is characterized by gastrozooids with a basal perisarc cup and a relatively small number of tentacles (20) in two or several whorls, by gonozooids with two whorls of tentacles and with fixed eume-

medusoids having eight tentacular bulbs, the females containing many eggs. Picard (1958b) considered it as conspecific with *Podocoryna fucicola* (Sars, 1857) and *Clava nana* Motz-Kossowska, 1905 without giving any further information. *Hydractinia fucicola*, however, is different from *H. inermis* in having an encrusting hydrorhiza covered by naked coenosarc; both gastrozooids and gonozooids have a characteristic ring of large microbasic euryteles surrounding the hypostome above the single tentacle whorl (of 4-12 tentacles); and, finally, the hydrorhiza is armed by numerous spines (Castric-Fey, 1970). *H. fucicola* is not endemic to the Mediterranean, being found also in the Glenan Archipelago (Atlantic Coast of France).

*Hydractinia ingolfi* (Kramp, 1932) see *H. arctica* (Jäderholm, 1902).

*Hydractinia mar* (Gasca and Calder, 1993). This species resembles *H. arctica*, *H. calderi*, *H. inermis* and *H. monoon* in having gastrozooids with a basal perisarc cup. Like *H. inermis* it has a cnidome comprising three types of cnidocysts instead of two in *H. arctica* and *H. calderi* (see Table 1); it differs nevertheless from *H. inermis* by the presence of spines and in having gonozooids with only one whorl of tentacles. *H. mar* is close to *H. monoon* having a perisarc cup on all types of zooids; the latter species however has a female gonophore with a single egg and a particular type of dactylozoid (see below). Pending further knowledge on the development of *Hydractinia mar*, which is not fully known, we provisionally consider this species as valid.

*Hydractinia minoi* (Alcock, 1892). This species was originally assigned to *Stylactis*, then to *Podocoryna* by Stechow (1909) because its anstomosing hydrorhiza was covered by a common perisarc. Later Stechow 1921b, referred it to *Podocorella*, because it presumably produces free medusae (and not eumedusoids) which, unlike *Podocoryna*, are deprived of oral tentacles. No liberated medusae, however, have been observed and this feature has been described from only medusa buds. As a matter of fact, *Podocoryna* medusae lack oral tentacles but have oral lips armed with clusters of nematocysts, these lips can be more or less developed according to the species, and might be not evident in medusa buds. Like *H. minoi*, *Hydractinia bella* (Hand, 1961) lives on fish, and its medusa is a *Podocoryna*, even though the drawings of the medusa buds do not show oral "tentacles" (Hand, 1961). We propose to merge *Podocorella* into *Hydractinia*, hypothesizing that the medusa of *H. minoi* might be a "*Podocoryna*".

*Hydractinia misakiensis* (Iwasa, 1934). It differs from *H. carcinicola* only in gastrozoid size and in having marginal tentacles of the eumedusoids of identical length. Hirohito (1988) pointed out that the two might be identical, and that *H. misakiensis* resembled *H. hooperii*. We consider *H. carcinicola* and *H. misakiensis* as conspecific with *H. hooperii*.

*Hydractinia monoon* (Hirohito, 1988). Hirohito noticed that this species resembles *H. nagaoensis*, which is said by Namikawa *et al.* (1990) to be close to *H. conchicola* (see above). *Hydractinia monoon* differs from *H. nagaoensis* and *H. conchicola* by having a perisarc cup at the base of all its zooids (see Table 1). Its female gonophores contain a single egg and are heteromedusoid instead of styloid as in the two other cited species. Finally, its dactylozooids have a hollow base (being intermediate between tentaculozooids and spiral zooids). This species is based on sound specific characters and is considered valid.

*Hydractinia multigranosi* (Namikawa, 1991). According Namikawa (1991), this species differs from *H. conchicola* and *H. nagaoensis* in having fixed eumedusoids instead of styloid gonophores and from *H. piscicola*, *H. sandrae* and *H. arctica* by host species.

The above characters are not convincing by themselves, but Namikawa's (1991) intensive investigation showed that *H. multigranosi* was substrate-specific, being only found on the gastropod *Nassaricus multigranosus* and, for this reason, he kept it as a distinct species. Buss and Yund (1989) reported on a group of sibling species of *Hydractinia* that, in spite of being largely indistinguishable by traditional morphometric characters, were customarily associated with a single host species of hermit crab. Namikawa *et al.* (1993) remarked that a similar situation was possible in some species of *Stylactaria* (= *Hydractinia*) namely: *H. piscicola*, *H. conchicola* and *H. multigranosi*. The presence of closely morphologically related species of substrate-specific *Hydractinia* could partly explain the large number of species described from Japanese waters, although nothing comparable apparently happens in other areas of the world. *Hydractinia multigranosi* has a different cnidome from *H. piscicola*, having also haplonemes, besides the typical microbasic euryteles and desmonemes (see Table 1).

*Hydractinia nagaoensis*, nom. nov. Nagao (1961) described a new hydractiniid, *Hydractinia uchidai* which is morphologically different from *Stylactaria* (= *Hydractinia*) *uchidai* (Yamada, 1947)

which new combination becomes a junior homonym of *Hydractinia uchidai* Nagao, 1961 and must be replaced. *Hydractinia nagaoensis* is proposed here as replacement name for Yamada taxon.

*Hydractinia otagoensis* (Schuchert, 1996). Its distinguishing characters are the presence of microbasic mastigophores and a ring of microbasic euryteles surrounding the hypostome of both gastro- and gonozooids. It appears also very close to *H. fucicola* (Sars, 1857), this also having a ring of microbasic euryteles around the hypostome (Castric-Fey, 1970), but this species has an encrusting hydrorhiza and is apparently devoid of microbasic mastigophores.

*Hydractinia piscicola* (Komai, 1932). This species has been recorded only twice and only from Japanese waters, each time on the stonefish *Erosa erosa*. This species does not have any unique morphological characters, but we agree with Kubota (1991) and Namikawa (1991) in considering it a valid substrate-specific species (see remarks for *H. conchicola* and *H. multigranosi*).

*Hydractinia pruvoti* Motz-Kossowska, 1905. This species was described as *Hydractinia pruvoti* by Motz-Kossowska (1905), referred to *Stylactis* by Behner (1914), who showed that the hydrorhiza was stolonal, placed by Stechow (1921a) who considered it as a pandeid; in the genus *Hydractomma* Stechow, 1921a and replaced in the genus *Stylactis* by Iwasa (1934) and Bouillon (1971). Picard (1958b) called it *Podocoryna pruvoti*. Calder (1988) removed it from *Stylactaria* because its hydrorhiza "is encrusting rather than reticular" and "Moreover its medusa is campanulate instead of sac-shaped, and four tentacles are present instead of eight". Hirohito (1988), describing a new species of *Stylactis*, *S. spinipapillaris*, with four-tentacled eumedusoids, and discussing the affinities between the two species, maintained Motz-Kossowska's species in the genus *Stylactis*. In the discussion he stated that the eumedusoids of *S. pruvoti* lack a velum. Behner (1914) and Neppi (1917), however, showed that a velum is present. *Hydractinia pruvoti* and *H. spinipapillaris* are nevertheless distinct, the first being characterized by one-tentacled gonozooids (and occasional 2-3 tentacled ones), the second by original papillary dactylozooids and by sharp gonozooid reduction.

*Hydractinia pruvoti* apparently may have either a stolonal or an encrusting hydrorhiza, being a perfect example of the confusion and muddle existing at a generic level in the Hydractiniidae.

*Hydractinia reticulata* (Hirohito, 1988). This species is deprived of both spines and dactylozooids, being similar in this feature to *H. yerii* (Iwasa, 1934). The two species are distinguished on insufficient ground and are here considered as conspecific (see *H. yerii*).

*Hydractinia ? sagamiensis* (Hirohito, 1988). This species lacks both gonozooids and dactylozooids, whereas spines are present. The gonophores are inserted on the hydrorhiza. They have four radial canals and four large tentacular bulbs. Hirohito (1988) reported that the gonads were undeveloped and oral tentacles were absent. This means that these gonophores are not eumedusoid, since they have no sign of sex cells (very evident since the beginning of the formation of this kind of gonophore). Hirohito (1988) kept this species in *Stylactis* but remarked that if the development of the medusae proceeds further, this species should be included in the genus *Perigonella* Stechow, 1921b. We agree with Hirohito (1988) in provisionally maintaining this species within *Stylactaria* (= *Hydractinia*), pending further knowledge on gonophore structure and further development.

*Hydractinia sandrae* (Wedler and Larson, 1986). The authors remarked that "owing to the difference in size and shape of the hydranth, number of tentacles, arrangement of gonophores, absence of thorns and existence of a red circle (between the tentacle whorl and the sporosacs)" this species is definitely different from *H. hooperii* and seems to be more closely related to *H. arge*. The differences between *H. hooperii* and *H. arge* have been defined above. *H. sandrae* is distinguished on characters falling within the intraspecific variations of *H. hooperii* and so does the *Stylactaria* sp. described by Wedler and Larson (1986).

? *Hydractinia siphonis* (Stechow, 1921c). This species has been rightly considered as doubtful by Millard (1975). It was briefly described by Stechow (1921c) from South Africa.

*Hydractinia spinipapillaris* (Hirohito, 1988). The eumedusoids of this species possess, like those of *H. pruvoti* and *H. minoi*, four tentacles instead of eight or ten, as reported for the other species of the genus. See discussion of *H. pruvoti*. It is here considered as valid.

*Hydractinia spiralis* (Goto, 1910). This species is characterized by the great number of tentacles of the gastrozooids (up to 50) distributed in alternating whorls, by the great number of gonophores (more than ten per gonozooid) and by its hydrorhiza, form-

ing a gastropod-shell-like crust exceeding the host shell inhabited by hermit crabs. This last feature exists also in *H. inabai* (Hirohito, 1988) but *H. spiralis* possesses free eumedusoids instead of cryptomedusoids. Some colonies also have peculiar nematophore bodies in the inner side of the hydrorhiza. It is here considered as valid.

*Hydractinia uchidai* (Yamada, 1947) see *Hydractinia nagoensis*.

*Hydractinia yerii* (Iwasa, 1934). This species lacks spines and dactylozooids. It has been distinguished from *H. reticulata* by its smaller size and moreover, its gonophores can contain more than 4 eggs (Hirohito, 1988). Such differences are interpreted here as intraspecific variations and we consider the two species as conspecific, the name *H. yerii* having priority.

*Hydractinia* sp. (Crowell, 1947) considered by Calder (1988) as identical with *H. arge*.

*Hydractinia* sp. (Wedler and Larson, 1986), see above, under *H. sandrae*.

*Hydractinia* sp. (Calder, 1993) not identifiable due to insufficient description (believed to be a new and as yet undescribed species).

*Hydractinia* sp. (Namikawa, 1994), not identifiable due to insufficient description.

*Hydractinia* sp. (Peña Cantero, 1995). Examination of Table 1 shows that this Mediterranean form is identical with *H. hooperii*. This species has been recorded from the western Atlantic, the Caribbean sea and Brazilian waters (Moreira *et al.* 1979) where it has been found on different living gastropods and hermit crab-inhabited shells. This is the first record from the Mediterranean Sea.

## DISCUSSION

The following species of *Stylactaria* (= *Hydractinia*) retained as valid here are:

1. *Hydractinia arge* (Clarke, 1882)
2. *Hydractinia arctica* (Jäderholm, 1902)
3. *Hydractinia betkensis* (Watson, 1978)
4. *Hydractinia brachyurae* (Hirohito, 1988)
5. *Hydractinia calderi* n. sp.
6. *Hydractinia claviformis* (Bouillon, 1965)
7. *Hydractinia conchicola* (Yamada, 1947)
8. *Hydractinia hooperii* (Sigerfoos, 1899)
9. *Hydractinia inabai* (Hirohito, 1988)
10. *Hydractinia inermis* (Allman, 1872)
11. *Hydractinia mar* (Gasca & Calder, 1993)
12. *Hydractinia minoi* (Alcock, 1892)

13. *Hydractinia monoon* (Hirohito, 1988)
14. *Hydractinia multigranosi* (Namikawa, 1991)
15. *Hydractinia nagoensis*, nom. nov.
16. *Hydractinia otagoensis* (Schuchert, 1996)
17. *Hydractinia piscicola* (Komai, 1932)
18. *Hydractinia pruvoti* Motz-Kossowska, 1905
19. *Hydractinia sagamiensis* (Hirohito, 1988)
20. *Hydractinia spinipapillaris* (Hirohito, 1988)
21. *Hydractinia spiralis* (Hirohito, 1988)
22. *Hydractinia yerii* (Iwasa, 1934)

The present revision of *Stylactaria* by no means resolves all the taxonomic problems of the group. A critical analysis has resulted in a considerable reduction in the number of recognizable species (from 34 to 22) in the future, other may be found to be conspecific, especially some of the Japanese species (11 of the 22 retained as valid). Several may be based on only young colonies of *Hydractinia* s.str. (Broch, 1916). Biochemical genome analyses will apparently be the best tool for the differentiation of these animals (see Cunningham and Buss, 1993).

Nominal genera included in the synonymy of the genus *Hydractinia* van Beneden, 1841 here include: *Archaeoecania* Picard and Rham, 1954; *Cionistes* Wright, 1861; *Corynopsis* Allman, 1864; *Halerella*, Stechow, 1922; *Halorhiza* Stechow, 1962; *Hydrissa* Stechow, 1921a; *Hydractomma* Stechow, 1921a; *Hydronema* Stechow, 1921a; *Oorhiza* Merechkowsky, 1877; *Nuttingia* (*Hydrodendrium*) Stechow, 1909; *Podocoryna* Sars, 1846; *Rhizocline* Allman, 1864; *Stylactaria* Stechow, 1921a; *Stylactis* Allman, 1864.

## REMARKS ON THE GENERIC COMPOSITION OF THE HYDRACTINIIDAE AND PTILOCODIIDAE

*Clavactinia* Thornely, 1904. (figure 3C).

In the course of our investigations on *Hydractinia calderi* we examined several specimens of the genus *Clavactinia*. This genus proposed by Thornely (1904), is characterized as having gastrozooids with tentacles scattered on the distal half of the hydranth, reduced gonozooids with fixed gonophores and an encrusting hydrorhiza with spines. Besides the type species *C. gallensis* Thornely, 1904, this genus currently accommodates another species: *C. multitentaculata* Millard, 1975. The gastrozooids of *Clavactinia multitentaculata* have, however, several closely-set tentacle verticils

concentrated around the hypostome, much resembling a *Hydractinia* hydranth, whereas *C. gallensis* has distinctly *Clava*-like hydranths. *Clavactinia multitentaculata*, furthermore, has less reduced gonozooids than *C. gallensis* and has also dactylozooids, a feature lacking in *C. gallensis*. Millard (1975) regarded *Hydractinia* as having a single row of tentacles or rarely two alternating ones, so she ascribed her material to *Clavactinia* due to tentacle arrangement. But many *Hydractinia* species have several closely set tentacle whorls {e.g. *H. sodalis* Stimpson, 1859; *H. epiconcha* Stechow, 1907 and, even, *H. echinata* Fleming, 1828 as reported by Allman, (1872)}, thus, not falling within the scope of the genus as defined by Millard (1975).

The type specimen of *C. gallensis* deposited at the Natural History Museum of London is deprived of hydranths and is of little help for a taxonomic revision. After the examination of part of Millard's material and colonies of *C. gallensis* from the Seychelles (fig. 3C), we consider that *C. multitentaculata* cannot be included into *Clavactinia*, being referred instead to *Hydractinia*.

Hansiella Bouillon, 1980 and Tregoubovia Picard, 1958a.

The genus *Hansiella* was founded to accommodate the medusa-based species *Hansiella fragilis* Bouillon, 1980, characterized by having (1) a well developed cnidocyst ring on the exumbrellar margin, (2) up to 28 didermic centripetal processes, (3) four radial canals, (4) four stiff marginal tentacles from which only the tips are studded with cnidocysts, (5) short mesenteries and (6) adradial gonads. Bouillon (1985) provided further detail, figuring a specimen with a non-contracted umbrella and with a more developed marginal ring at the base of the centripetal structures, forming what could be interpreted as reduced marginal bulbs.

*Hansiella fragilis* was included in the Hydractiniidae by Bouillon (1980) because of its four simple oral lips armed with cnidocyst clusters, but the presence of mesenteries and adradial gonads required modification of the definition of the family.

A medusa similar to *H. fragilis* is *Thecocodium quadratum* (Werner, 1965) family Ptilocodiidae Coward, 1909, as illustrated and briefly described by Jarms (1987). Its re-examination allowed us to compare the two species and determine their systematic position.

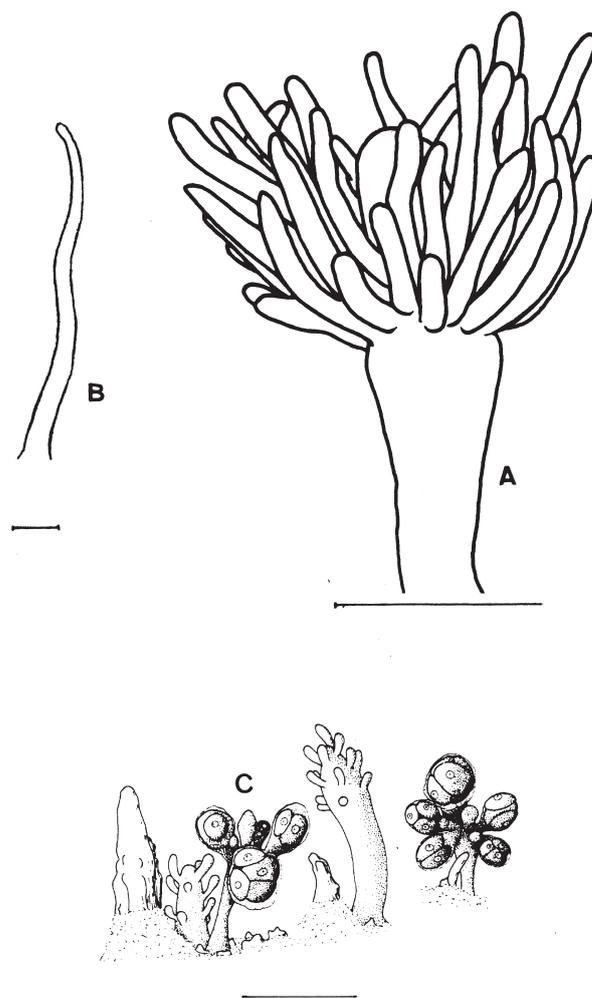


FIG. 3. — (A & B) *Hydractinia calderi* n.sp. from Chafarinas Islands, Spain. (A) apical part of an adult gastrozooid; (B) dactylozooid. (C) Part of a colony of *Clavactinia gallensis* Thornely, 1904 showing the scattered position of the gastrozooid tentacles (After Millard & Bouillon, 1973); scale bar: A = 800  $\mu$ m, B = 300  $\mu$ m, C = 400  $\mu$ m.

The features of *T. quadratum* medusae are: umbrella pyriform; manubrium cylindrical not reaching beyond umbrella margin; mouth with four lips armed with cnidocyst clusters; four stiff tentacles with tips armed with cnidocysts and situated in exumbrellar furrows; a marginal cnidocyst ring with many didermic exumbrellar centripetal processes; short mesenteries; interradial gonads; medusa buds on manubrium. It is clear from the above descriptions that *H. fragilis* and *T. quadratum* share many key characters, the main differences being the presence of exumbrellar furrows in *Thecocodium* and the position of the gonads, adradial in *Hansiella* and interradial in *Thecocodium*.

The medusa-based species *Tregoubovia atentaculata* Picard, 1958a has close affinities with the above mentioned genera, having 8 to 16 exumbrel-

lar didermic centripetal processes issuing from a marginal ring, short mesenteries and a mouth with four arms, no marginal bulbs or tentacles and interradial gonads. Picard (1958a) included it in the Hydractiniidae (see also Goy, 1973).

Picard (1958a; Goy, 1973) considered the exumbrellar processes of *Tregoubovia* as marginal tentacles developed inside the exumbrellar mesoglea. Jarms (1987) gave a similar interpretation to the centripetal processes of *Thecocardium quadratum*, and this must be the case also for *Hansiella fragilis*.

The medusae of *Hansiella*, *Tregoubovia* and *Thecocardium* are clearly similar and deserve the inclusion in the same family. An essential clue for inferring the systematic position of these genera is found in the hydroid stage of the only species with a known life cycle. The hydroid of *Thecocardium quadratum* clearly indicates that the three genera, pending knowledge of the life cycles of *Hansiella* and *Tregoubovia*, must be included into the Ptilocodiidae.

The diagnosis of the Ptilocodiidae is modified here as follows: Hydractinoidea with stolonar reticular hydrorhiza or with encrusting hydrorhiza covered by naked coenosarc. Hydranths sessile, naked and polymorphic. Gastrozooids without tentacles; dactylozooids with 4 or more capitate tentacles, sometimes filiform; gonophores on gonozooids or gastrogonozooids. Reproduction by fixed sporosacs, eumedusoids or free medusae. Medusae more or less bell-shaped; with or without radial exumbrellar furrows; with didermic centripetal tracks or exumbrellar rows of refringent spots; with a marginal cnidocysts ring; when present, marginal tentacles solid, with tips armed with cnidocysts; four radial canals; manubrium tubular or bottle-shaped, with mouth lips armed with cnidocyst clusters; with adradial or interradian gonads.

The family Ptilocodiidae accommodates the following genera: *Hansiella* Bouillon, 1980; *Hydractella* Stechow, 1909; *Ptilocodium* Coward, 1909; *Thecocardium* Bouillon, 1967, *Tregoubovia* Picard, 1958a.

#### *Fiordlandia* Schuchert, 1996

Schuchert (1996) proposed a new hydractiniid genus, *Fiordlandia*, based on two main characters: the structure of the hydrorhiza supporting the gonophores, where staghorn tubes form a protection for the reproductive structures, and the presence of scattered tentacles on the gastrozoid. This last fea-

ture, however, is not a good character for a new hydractiniid genus, being the key feature of *Clavactinia*. The only distinctive feature of *Fiordlandia*, thus is the development of the protective tubes. Many hydroids produce protective structures around their gonophores. These are given generic rank in the Aglaopheniidae, whereas they are not in several serulariid genera in which some species have an apical chamber (marsupium) to accommodate the acrocyst, and some have not. Also, in the Haleciidae the presence of a glomulus is not considered as a good generic character, so that *Halecium* and *Hydrodendron* comprises both species with and without this protective structure. Whether a stolonar protection of the gonophores is enough for the recognition of a new genus is a matter of character weighting and is subjective. No other species of hydractiniid is known to have such feature, so *Fiordlandia protecta* might be the ancestor of a future clade deserving generic rank. Maybe this clade exists already and comprises undescribed hydractiniids with stolonar protection of the gonophores. Of course one cannot foresee what evolution will lead to (or what will be the structure of unknown species) and it seems premature to propose a new genus (accommodating a single species) based on a single character which might have no relevance in the evolution of the genus *Clavactinia* (see above), of which *Fiordlandia* should be considered, in our opinion, a synonym.

The family Hydractiniidae Agassiz, 1862 currently includes the following genera (fossils excluded): *Clavactinia* Thornely, 1904; *Hydractinia* van Beneden, 1841; *Hydrocorella* Stechow, 1921d; *Janaria* Stechow, 1921d; *Kinetocodium* Kramp, 1921.

The removal of both *Hansiella* and *Tregoubovia* from the Hydractiniidae requires modification of the diagnosis provided by Bouillon (1985, 1995): hydrorhiza either stolonar and reticular, formed by tubes covered with perisarc, sometimes forming protective tubes, or encrusting, covered with naked coenosarc, or forming a calcareous skeleton, frequently with spines, sometimes forming branches. Hydranths sessile, naked, polymorphic. Gastrozooids with one or more whorls of oral filiform tentacles, or with scattered tentacles on the distal half of the body; gonozooids with one or more whorls of oral tentacles, or without tentacles and mouth; dactylozooids, when present, with no tentacles. Vesicles of unknown function present or not. Reproduction by fixed sporosacs, eumedusoids, or free medusae generally borne on gonozooids, exceptionally on hydrorhiza.

Medusae more or less bell shaped; with or without slight apical process; four, eight or more solid, simple marginal tentacles; ocelli present or absent; with or without gastric peduncle; with four radial canals; manubrium tubular or sac-shaped not extending beyond umbrella margin; gonads on manubrium interradial, sometimes extending along the proximal portions of the radial canals; mouth with four simple or branched lips armed with terminal clusters of cnidocysts (exceptionally mouth rim simple and armed with a cnidocyst ring).

## ACKNOWLEDGEMENTS

We gratefully thank the Institutions mentioned in the list of material examined for their generous loan of material. We wish to thank Professor F. Boero and Dr. D. Calder who read and commented on the manuscript, providing valuable suggestions. This work was supported by the F.N.R.S., Belgium (grant n° 1.5.144.97).

## REFERENCES

- Agassiz, L. – 1862. *Contributions to the Natural History of the United States of America*, Boston, Little, Brown, 4: 1-380.
- Alcock, A. – 1892. A case of commensalism between a gymnoblastic anthomedusoid and scorpaenoid fish, *Ann. Mag. Nat. Hist.*, 10: 207-214.
- Allman, G. J. – 1864. On the construction and limitation of genera among the Hydroida, *Ann. Mag. Nat. Hist.*, 13: 345-380.
- Allman, G. J. – 1872. *A monograph of the Gymnoblasic or Tubularian Hydroids. I. – The Hydroida in general. II. – The genera and species of the Gymnoblastea*. Ray Society, London. pp: 450.
- Arndt, E. A. – 1965. Ueber die Fauna des sekundären Hartbodens der Martwa Wisla und ihres Mündungsgebietes (Danziger Bucht), *Wiss. Zeits., Univ. Rostock*, 14: 645-653.
- Behner, A. – 1914. Beitrag zur Kenntnis der Hydromedusen, *wiss. Zool.*, 111: 381-427.
- Boero, F. – 1981. Systematics and ecology of the hydroid population of two Posidonia oceanica meadows, P. S. Z. N.I., *Mar. Ecol.*, 2: 181-197.
- Boero, F. and Bouillon J. – 1993. Zoogeography and life cycle patterns of Mediterranean hydromedusae (Cnidaria), *Biol. J. Linn. Soc.*, 48: 239-266.
- Boero, F., Bouillon, J. and Piraino, S., – (in press). Heterochrony, generic distinction and phylogeny in the Family Hydractiniidae (Hydrozoa, Cnidaria)
- Bouillon, J., – 1965. Diagnose préliminaire de trois hydroides de Roscoff, in: G. Teissier, (ed), *Inventaire de la faune de Roscoff*, p. 54.
- Bouillon, J., – 1967. Révision de la famille des Ptilocodiidae avec la description d'un nouveau genre et d'une nouvelle espèce, *Bull. Acad. Belg.*, 53: 1106-1131.
- Bouillon, J. – 1971. Sur quelques hydroides de Roscoff, *Cah. Biol. mar.*, 12: 323-364.
- Bouillon, J. – 1980. Hydroméduses de la mer de Bismarck (Papouasie Nouvelle- Guinée). Partie III: Anthomedusae Filifera (Hydrozoa-Cnidaria), *Cah. Biol. mar.*, 21: 307-344.
- Bouillon, J. – 1985. Essai de classification des Hydropolypes - Hydroméduses (Hydrozoa-Cnidaria), *Indo-Malayan Zool.*, 2: 29-243.
- Bouillon, J. – 1995. *Classe des Hydrozoaires*, in: P. P. Grassé and D. Doumenc (eds), *Traité de Zoologie*, 3, (2), Masson, Paris, pp. 29-416.
- Brinckmann, A. – 1965. The biology and development of *Rhysia autumnalis* gen. n., sp.n. (Anthomedusae/Athecatae, Rhysiidae fam. n.), *Can. J. Zool.*, 43: 941-952.
- Brinckmann- Voss, A., Lickey, D.M., and Mills, C.E. – 1993. *Rhysia fletcheri* (Cnidaria, Hydrozoa, Rhysiidae), a new species of colonial hydroid from Vancouver Island (British Columbia, Canada) and the San Juan Archipelago (Washington, U.S.A.), *Can. J. Zool.*, 71: 401-406.
- Broch, H. – 1914. *Hydrozoa benthonica*, in: W. Michaelsen, (ed), *Beiträge zur Kenntnis der Meeresfauna Westafrikas*, 1: 19-50. Friederichsen, Hamburg.
- Broch, H. – 1916. Hydroida (part 1), *Danish Ingolf-Expedition*, 5 (6): 1-66.
- Buss, L. and Yund, P. – 1989. A sibling species group of *Hydractinia* in the north-eastern United States, *J. mar. biol. Ass. U.K.*, 69: 857-874.
- Calder, D. – 1988. Shallow water hydroids of Bermuda. The Athecatae, Life Sciences Contributions, *Royal Ontario Museum*, 148: 1-107.
- Calder, D. – 1993. Local distribution and biogeography of the Hydroids (Cnidaria) of Bermuda, *Caribbean J. Sci.* 29: 61-74.
- Castric-Fey, A. – 1970. Sur quelques hydroides de l'Archipel de Glénan (Sud-Finistère), *Vie Milieu*, 21: 1-23.
- Clarke, S. F. – 1882. New and interesting hydroids from Chesapeake Bay, *Mem. Boston Soc. Nat. Hist.*, 3: 135-142.
- Coward, W. – 1909. On *Ptilocodium repens* a new gymnoblastic hydroid epizoic on a Pennatulid (Siboga Exp.), *Koninkl. Acad. Wetens. Amsterdam*, 22: 729-735.
- Crowell, S. – 1947. A new form of the hydroid *Stylactis*, *Biol. Bull.*, 93: 206.
- Cunningham, C. and Buss, L. – 1993. Molecular evidence for multiple episodes of paedomorphosis in the family Hydractiniidae, *Bioch. Syst. Ecol.* 21: 57-69.
- Daniaud, J. M. – 1951. Sur la morphogénèse des dactylozoïdes d'*Hydractinia echinata* Flem., *C. r. hebd. Séanc. Acad. Sci.*, Paris., 233: 758-759.
- Fleming, J. – 1828. *A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca and Radiata of the United Kingdom*, Edinburgh, Bell and Bradfute.
- Gasca, R. and Calder, D. – 1993. *Stylactaria mar* (Cnidaria,Hydractiniidae), una nueva especie de hidroide atecado de la costa del Pacífico de México, *Revi. Biol.Tropi.*, 41: 215-218.
- Goto, S. – 1910. On two species of *Hydractinia* living in symbiosis with a Hermit Crab, *J. Exp. Zool.*, 9: 469-496.
- Goy, J. – 1973. Les Hydroméduses de la mer Ligure, *Bull. Mus. Nat. Hist. nat. Paris*, 3, (83), *Zool.*, 62: 965-1008.
- Hand, C. – 1961. A new species of athecate hydroid, *Podocoryne bella* (Hydractyniidae) living on the pig-fish *Congiopodus leucopaecilus*, *Trans. R. Soci. N. Zeal.*, 1: 91-94.
- Hickson, S.J. and Gravely, F.H. – 1907. Hydroid Zoophytes, in: *National Antarctic Expedition 1901-1904, Natural History, Vol. 3. Zoology and Botany. The Trustees of the British Museum*, London: 1-34.
- Hiro, F. – 1939. Notes on the animals found on *Macrocheira kaempferi* de Haan. III. Hydroids, *Annot. Zool. Jap.*, 18: 167-176.
- Hirohito -1988. *The Hydroids of Sagami Bay. Part I. Athecata*, Biological Laboratory, Imperial Household, Tokyo.
- Iwasa, M. – 1934. Revision of *Stylactis* and its allied genera, with description of *Stylactella (Stylactis) yerii* n. sp., *J. Facul. Sci., Hokkaido Imp.Univ.*, 2: 241-277.
- Jäderholm, E. – 1902. Neue oder wenig bekannte ostasiatische Hydroiden, *Bih. Kungl. Sv. Vetensk. Akad. Hand.*, 28: 1-7.
- Jarms, G. – 1987. *Thecocardium quadratum* (Werner 1965) redescribed, *T. penicillatum* sp. nov., and a method for rearing hydrozoans, in: J. Bouillon, F. Boero, F. Cicogna and P.F.S. Cornelius, (eds), *Modern trends in the Systematics, Ecology and Evolution of Hydroids and Hydromedusae*, Clarendon Press, Oxford, pp. 57-66.
- Kinne, O. – 1957. Adaptation and temperature in a euryhaline hydroid, *Biol. Bull.*, 113: 330.
- Kinne, O. – 1958. Ueber die Reaktion erbgleichen Coelenteratengewebes auf verschiedene Salzgehalts- und Temperaturbe-

- dingungen. II. Mitteilungen über den Einfluss des Salzgehaltes auf Wachstum und Entwicklung mariner, brackischer und limnischer Organismen, *Zool. Jahr., Allg. Zool. Phys.*, 67: 407-486.
- Komai, T. – 1932. On two species of Athecate hydroids associated with Scorpaenoid fishes, *Annot. Zool. Jap.*, 13: 445-458.
- Kramp, P. L. – 1921. *Kinetocodium danae*, n. g., n. sp. a new gym-noblastic hydroid, parasitic on a pteropod, *Vidensk. Med. Dansk Natur. Foren.*, 74: 1-21.
- Kramp, P. L. – 1932. Hydroids, in: The Godthaab expedition 1928, *Med. Grönland*, 79: 1-86.
- Kubota, S. – 1991. Second finding of *Stylactaria piscicola* (Komai, 1932) comb. nov. (Hydrozoa: Hydractiniidae) from off Atsumi Peninsula, Japan, *Publ. Seto Marine Biol. Lab.*, 35: 11-15.
- Mc Clary, A. – 1959. The effect of temperature on growth and reproduction in *Craspedacusta sowerbii*, *Ecology*, 40: 158-162.
- Medel, M.D. – 1996. *Hydrozoos del Estrecho de Gibraltar y areas próximas*, Ph. Doc.Thesis, Univerisdad de Sevilla.
- Medel, M.D. and López González, P.J. – 1996. Updated Catalogue of hydrozoans of the Iberian Peninsula and Balearic Islands, with remarks on Zoogeography and affinities. *Sci. Mar.*, 60: 183-209.
- Merechkowsky, C. – 1877. On a new genus of hydroids from the White Sea, with a short description of other new Hydroids, *Ann. Mag. Nat. Hist.*, 20: 220-229.
- Millard, N. A. H. – 1975. Monograph on the Hydroida of southern Africa, *Ann. S. Afr. Mus.*, 68: 1-513.
- Millard, N. A. H. and Bouillon, J. – 1973. Hydroids from the Seychelles (Coelenterata), *Annl. Mus. r. Afr. Centr., Sci. Zool.*, 206: 1-106.
- Moreira, G.S., Nipper, M.G. and Leite, L.R. – 1979. On *Stylactis hooperi* Sigerfoos, 1899 (Hydrozoa, Hydractiniidae) a new addition to the fauna of southern Brazil, in: *Proceedings international Symposium on marine biogeography and evolution in the southern hemisphere*, 2: 679-689.
- Motz-Kossowska, S. – 1905. Contribution à la connaissance des hydriaires de la Méditerranée occidentale. I.- Hydriaires Gym-noblastiques, *Arch. Zool. exp. gén.*, 3: 39-88.
- Nagao, Z. – 1961. On a new athecate hydroid, *Hydractinia uchidai*, n.sp. from Akkeshi, Hokkaido, *Jap. J. Zool.*, 13: 1-5.
- Namikawa, H. – 1991. A new species of the genus *Stylactaria* (Cnidaria, Hydrozoa) from Hokkaido, Japan, *Zool. Sci., Japan*, 8: 805-812.
- Namikawa, H. – 1994. Four species of Hydractiniid Hydroids from off Kushiro, Hokkaido, Japan, *Mem. Nat. Sci. Mus., Tokyo*, 27: 79-86.
- Namikawa, H. – 1995. Nematocysts of thirteen species of athecate hydroids from Onagawa Bay, Japan, *Mem. Nat. Sci. Mus., Tokyo*, 28: 91-98.
- Namikawa, H., Kubota, S. and Mawatari, S.F. – 1990. Redescription of *Stylactaria uchidai* (Yamada, 1947), comb. nov. (Hydrozoa: Hydractiniidae) in Hokkaido, Japan, *Proc. Jap. Soc. Syst. Zool.*, 42: 2-9.
- Namikawa, H., Kubota, S. and Mawatari, S.F. – 1992. Redescription of *Stylactaria conchicola* (Yamada, 1947), comb. nov. (Hydrozoa: Hydractiniidae) from Hokkaido, Japan, *Hydrobiologia*, 231: 69-76.
- Namikawa, H., Mawatari, S.F. and Calder, D.R. – 1992. Role of the tentaculozooids of the polymorphic hydroid *Stylactaria conchicola* (Yamada) in interactions with some epifaunal space competitors, *J. exper. mar. Biol. Ecol.*, 162: 65-75.
- Namikawa, H., Mawatari, S.F., and Calder, D.R. – 1993. Reproduction, planula development, and substratum selection in three species of *Stylactaria* (Cnidaria: Hydrozoa) from Hokkaido, Japan, *J. nat. Hist.* 27: 521-533.
- Naumov, D. – 1960-1969. *Gidroidi i gidromedusy morskikh, solonovatovodnykh i presnovodnykh basseinov SSSR. Opredelitel' po faune SSSR. Izdavaemye Zoologicheskim Institutom Akademii Nauk SSSR.*, 70: 1-626 (English translation by Israel Program for scientific translations, cat. no. 5108, as "Hydroids and Hydromedusae of the USSR": 1- 631).
- Neppi, V. – 1917. Osservazioni sui polipi idroidi del Golfo di Napoli, *Pubbl. Staz. Zool. Napoli*, 2: 29-65.
- Nipper-Buscariolli, M. and Moreira, G.S. – 1983a. Combined effects of temperature and salinity on *Stylactis hooperi* Sigerfoos, 1899 (Hydrozoa, Hydractiniidae). 1. Colony growth development of medusa buds and hydranth degeneration, *Stud. Neotropical Fauna and Environment*, 18: 111-120.
- Nipper-Buscariolli, M. and Moreira, G.S. – 1983b. Combined effects of temperature and salinity on *Stylactis hooperi* Sigerfoos, 1899 (Hydrozoa, Hydractiniidae). 2. Polyp growth and tentacle development, *Bol. Fisiol. Ani.*, Univ. Sao Paulo, 7: 41-48.
- Peña Cantero, A. L. – 1995. *Hydrozoos bentónicos de las Islas Canarias: faunística, ecología, biocenología y biogeografía*, Thesis. University of Valencia, Spain.
- Picard, J. – 1958a. *Tregoubovia* n. gen. *atentaculata* n. sp. Nouvelle Anthoméduse, dépourvue de tentacules récolté dans le plancton profond de Villefranche-sur-mer, *Rapp. P.-v. Réunion, Com. internat. Explor. Scient. Mer Méditerranée*, 14: 185-186.
- Picard, J. – 1958b. Origines et affinités de la faune d'hydropolypes (Gymnoblastes et Calyptoblastes) et d'hydroméduses (Anthomédues et Leptomédues) de la Méditerranée, *Rapp. P.-v. Réunion, Com. internat. Explor. Scient. Mer Méditerranée*, 14: 187-199.
- Picard, J. and Rham, U. – 1954. *Archaeoceania* n. gen. *ournieri* n. sp. Une nouvelle Anthoméduse de la famille des Oceaniidae de la lagune Ebrié (Côte d'Ivoire), *Acta Tropica*, 11: 303-307.
- Ramil, F., Ansón, J.A. and Pulpeiro, E.F. – 1994. Aportaciones al conocimiento de *Stylactaria claviformis* (Bouillon, 1965) (Cnidaria, Hydrozoa, Anthomedusae), Galicia, España, *Bol. R. Soci. Españ. Hist. Nat.*, 91: 103-107.
- Rees, W.J. – 1956. On three northern species of *Hydractinia*, *Bull. Br. Mus. Nat. Hist.*, 3: 351-362.
- Sars, M. – 1846. *Fauna Littoralis Norvegiae oder Beschreibung und Abbildungen neuer oder wenig bekannten Seethiere, nebst Beobachtungen über die Organisation, Lebensweise und Entwicklung derselben*. Heft. I. Christiania, Johann Dahl: 1-93.
- Sars, M. – 1857. Bidrag til kundskaben om Mittelhavets littoral-fauna, Reisebemaerkninger far Italien, *Nyt Mag. Naturvid.*, 9: 110-164.
- Schuchert, P. – 1996. Athecate hydroids and their medusae (Cnidaria, Hydrozoa), *N. Zeal. Oceanogr. Inst. Mem.*, 106: 1-159.
- Sigerfoos, C. P. – 1899. A new hydroid from Long Island Sound, *Am. Nat.*, 33: 801-807.
- Stechow, E. – 1907. Neue japanische Athecata und Plumularidae aus der Sammlung Dr. Doflein, *Zool. Anz.*, 32: 192-200.
- Stechow, E. – 1909. Hydroidpolyphen der japanischen Ostküste. I. Teil: Athecata und Plumularidae, *Abh. Math. Physik. Klas. Kön. Bayer. Akad. Wissens.*, suppl., 6: 1-111.
- Stechow, E. – 1921a. Neue Genera und Species von Hydrozoen und anderen Evertebraten, *Arch. Naturg.*, 87: 248-265.
- Stechow, E. – 1921b. Neue Ergebnisse auf dem Gebiete der Hydroidenforschung, II. *Münch. Mediz. Woch.*, 68: 30.
- Stechow, E. – 1921c. Über Hydroiden der Deutschen Tiefsee-Expedition nebst Bemerkungen über einige andere Formen, *Zool. Anz.*, 53: 223-236.
- Stechow, E. – 1921d. Neue Gruppen skelettbildender Hydrozoen und Verwandtschaftsbeziehungen rezenter und fossiler Formen, *Ver. zool. Ges.*, 26: 29-31.
- Stechow, E. – 1922. Zur Systematik der Hydrozoen, Stromatoporen, Siphonophoren, Anthozoen und Ctenophoren, *Arch. Naturg.*, 88: 141-155.
- Stechow, E. – 1923. Zur kenntnis der Hydroidenfauna des Mittelmeeres, Americas und anderer Gebiete. II, *Zool. Jb. Syst. Okol. Geogr. Tiere*, 47: 29-270.
- Stechow, E. – 1962. Ueber skelettbildende Hydrozoen, *Zool. Anz.*, 169: 416-428.
- Stimpson, W. – 1859. Prodromus descriptionis animalium evertbratorum, quae in Expeditione ad oceanum pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit W. Stimpson. P. VII, Crustacea Anomura, *Proc. Acad. Nat. Sci. Philadelphia* (1858), 10: 225-252.
- Svoboda, A., Stepanjants, S. and Smirnov, I. – 1995. Zwei polare Hydractiniden -Arten (Hydroida, Cnidaria) als Symbionten nahe verwandter Schlangensterne (Ophiolepididae, Echinodermata)-ein ökologisches Beispiel für Bipolarität, *Ber. Polar.*, 155: 86-89.
- Thornely, L. R. – 1904. Report on the Hydroida collected by professor Herdman, at Ceylon, in 1902, *Ceylon Pearl Oyster Fisheries - Supplementary Reports*, 8: 107-126.
- van Beneden, P. J. – 1841. Recherches sur la structure de l'oeuf dans un nouveau genre de polype (Genre Hydractinie), *Bull.*

- Acad. Roy. Sci. Belles-Lettres, Belgique*, 8: 1-6.
- Vannucci, M. – 1960. On the intraspecific variation and biology of *Merga tergestina* (Anthomedusae Pandeidae), *Pubbl. Staz. Zool. Napoli.*, 31: 393-420.
- Wagner, R. – 1833. Neue im Adriatischen Meere gefundene Art von nacktem Armpolypen, *Isis*, 3: 256.
- Watson, J.E. – 1978. New species and new records of Australian athecate hydroids, *Proc. R. Soc. Victoria*, 90: 301-314.
- Wedler, E. and Larson, R. – 1986. Atecate hydroids from Puerto Rico and the Virgin Islands, *Stud. Neotropical Fauna and Environment*, 21: 69-101.
- Werner, B. – 1963. Effect of some environmental factors on differentiation and determination in marine Hydrozoa, with a note on their evolutionary significance, *Ann. N. Y. Acad. Sci.*, 105: 461-488.
- Werner, B. – 1965. Die Nesselkapseln der Cnidaria, mit besonderer Berücksichtigung der Hydroida. 1. Klassifikation und Bedeutung für die Systematik und Evolution, *Helgol. wiss. Meeresunt.*, 12: 1-39.
- Wright, T. S. – 1861 Observations on British Protozoa and zoophytes, *Ann. Mag. Nat. Hist.*, 8: 120-135.
- Yamada, M. – 1947. On two new species of athecate hydroid *Stylactis* from Hokkaido, *J. Fac. Sci., Hokkaido Univ.*, 9: 383-387.

Scient. ed.: J.M. Gili