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

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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 medusae denera *Ransiella* and *Tregoubovia*, formerly ascribed to the Hydractinidae, are shown to be more like the medusae of *Thecocodium*, a genus having ptilocodiid hydroids. Both *Hansiella* and *Tregoubovia* are thus transferred to the Ptilocodiidae. With their removal from the Hydractinidae, 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 géneroStylactaria que al mismo tiempo se considera sinónimo de Hydractinia and, al mismo que se describe una nueva especie (Hydractinia calderi n. sp.). Las medusas descrtas de los géneros Hansiella y Tregoubovia, previamente adscritas a la familia Hydractiniidae, se confirma su proximidad sistemática al género Thecocodium, un género que tiene hidropólipos pilocódidos. Los géneros Hansiella y Tregoubovia es transfieron 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 referrable to *Stylac*-

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*taria* from the Strait of Gibraltrar 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 hydror-hiza formed by anastomosing stolonal tubes 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 necessarly 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, futhermore, 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 Table1). 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-

TABLE 1. – \* = found only till now in this area; ? = doubtfull or unknown; ° = only found on this substrate; A. = algae; An. = anisorhiza; B. = bryozoans; B.I. = basitrichous 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. = microbasic euryteles; MM = size in millimetres; M.M. = microbasic mastigophores; N°T. = number of tentacles; P.C. = perisarcal cup; R. = rocks; Sg. = sea-grasses; Sp. = sponges; spc. = sporosacs; T. = tunicates; Ts. = tentacle arrangement; w. = whorls; Wo. = worms.

Species	Gastrozooids Ts.= 1 whorl N°T. MM	Dactylo- zooids	Spines	Gonozooids	Gono- <b>phores</b>	Medusae	Cnido- cysts	Substrate	Distribution
				N°T. MM	N° types				
1) H. arctica 👌 (Jäderholm, 1902)	12-15 2-3 P.C.			(4?) 1	1-2 ?	-	?	Mohnia mohni, F.; Eudendrium planum, H.	Greenland, Baffin bay (1.200-2.000 M
2) H. betkensis (Watson, 1978) <sup>4</sup>	8-15 1-2		+	8 0,65-0,8 p.e.	1-5, cryp.	-	B.I.?, M.E.	<b>G.,</b> Parcannassa burchardi°	Australia* (brackish)
3) H. brachyurae (Hirohito, 1968)	14 1 <b>P.C</b> .	-	-	10 -1	10, cryp.	-	?	C., Spider crab <sup>o</sup>	Japan* (80-100 M)
4) H. carcinicola (Hiro, 1939)	12-30 10	usually +	+	2-10 0,5	1-11	eum., 8 tentacles	?	G; C.; R.	Japan*
5) H. conchicola (Yamada, 1947)	2 types, 2-5 1,2-3 4-8 0,9-1,9	+	+	0;2-5 0,6-2,5	4-6, ht.		D., Ha M.E.	<b>G.,</b> Holalopoma amussitatum°	Japan*
6) (H. halecii)=Rhysia halecii (Hickson & Gravely, 1907)									
7) H. hooperii (Sigerfoos,1899)	15-35 1,5-26		+	6-10 8-18	4-5	eum., 8 tentacles	?	G. & hermit crabs inhabited shells	USA; Puerto Rico; Brazil
8) <i>H. ingolfi</i> (Kramp, 1932)	15-17 2,5 P.C		2	0 small	1, male?, female cryp.		D., M.E.	<b>E.,</b> Homalophiura tesselata	Greenland* (2.137-3.229M)
9) H. minoi (Alcock ,1892)	10-40 3,5	scarce	3	0-4 0,5 no mouth	1-7	medusa buds, 8 tentacles	?	F. Minous pusillus"	Japan, Indian Ocean
10) H. misakiensis & (Iwasa, 1934)	10-30 1-4	some- times +	+	20 1-2	1-5	eum., 8 tentacles	?	G. inhabited by hermit crabs	Japan*
11) H. multigranosi (Namikawa, 1991)	8-16 1-1,15	+		4-11 0,5-2	1-4, 1-2 w.		D., Ha.,	<b>G.,</b> Nassarius multigranosus°	Japan*
12					fix. eum.		M.E.		
13) H. otagoensis (Schuchert,1996) F	12-16 2-4	+	÷	8 2-4	4-6, spc.		D., M.E., M.M.	<b>A.,</b> Macrocystis pyriferea; <b>T.,</b> Pyura pachydermata	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	some- times +	+	1-3 4-5	8-9	eum., 4 tentacles	?	<b>G.,</b> <i>Cassidaria</i> <i>tyrrhena</i> inha- bited by pagurus <i>Cerithium</i> sp.	Mediterranean*
16) H. reticulata (Hirohito, 1988)	12 5		-	10 2,5-3	6,cryp.		?	R.; B.; C.	Japan*
17) H. ?sagamina ⅓ (Hirohito, 1988)	8-10 0,9		+	gonophores on hydrorhiza		medusae not fully grown	?	G., inhabited by hermit crabs	Japan*
18) <i>H. sandrae</i> (Welder & Larson, 1986)	11-16 2		1	4-11 0,5-1,5	in pairs fix. eum.		?	Τ.º	Puerto Rico
19) H. siphonis	8-10 0,8	?		reproduction	?	?	?	G., Sipho	South Africa*

X

Species	Gastrozooids Ts.= 1 whorl N°T. MM	Dactylo- zooids	Spines	Gonozooids	Gono- phores		Cnido- cysts	Substrate	Distribution
				№T. MM	№ types				
Stechow, 1921)				unknown				islandicus	
20). <i>H.</i> sp. = <i>H. arge</i> Crowell, 1947) see Calder, 1988									
21) <i>H.</i> sp. Welder & Larson, 1986)	9-13 2,3			5-8 ?	1-3, fix eum.		?	G., Cerithium sp.	Puerto Rico
22) H. sp. Calder, 1993)	?	ŋ	?	9	?	?	?	?	Bermuda
23) <i>H</i> . sp. Namikawa, 1994)	6-13 1,15- 2,25		+	0;6-9 0,8-2,5	1-6, cryp.	-	?	several G.	Japan*
24) H. sp. Pena Cantero, 1995)	11-16 1,5		+	6-8 1	4, oppos- ite 2per2	eum., 8 tentacles	D., M.E.	<b>G.,</b> Cerithium sp.	Mediterranean
25) <i>H. spinipalpillaris</i> (Hirohito, 1988)	6-12 1,5	+ papillary	+	0 0,75	2-3	eum., 4 tentacles	?	<b>G.,</b> Simplicifus graciliformis°	Japan*
2) H. nagaoensis nom. nov.	6-11 2,0-3,5	Ŧ	+	4-6 0,6-2,3	1-16; 1-4 w.; ht.; female = 1 egg	-	D., M.E.	R.;A.;Sp.;Bv.;B.; Wo.; C.	Japan*
26) H. yerii (Iwasa, 1934)	10-14 1,5			0-4 0,7	4, cryp.	-	?	G.; Turricula kamakurana, Pseudoetrema fortilirata	Japan*
	Ts. = 2 or more whorls								
27) H. arge (Clarke, 1882)	10-30. till 45 2w.		+	5-30 30 2w.	4, oppos- ite 2 per 2	eum., 8 tentacles	Gas: D., M.E. Gon: D., <i>M.E.,</i> <i>Ha</i> .	A.; Sg.; G., inhabited by hermit crabs, <i>Certhium</i>	USA; Bermud Puerto Rico
28) <i>H. claviformis y</i> (Bouillon, 1965)	18-32 16-50 2-3 w.	+		6-10 0,88-2,5	4-8, opp- osite 2- per 2; fem ale, cryp.	male,. eum., 10 - tentacles	D. M.E.	A.; Sp.; R.	France Atl., Spain Atl.
29) H. inabai ə (Hirohito, 1988)	30 or +3 more 1w. or closely alternating w.	rarely+	+	20 3 or more	2-3	eum., 8 tentacles	?	G., inhabited by hermit crabs; hyd- rorhiza exceed- ing shell opening	Japan*
30) <i>H. inermis</i> (Allman, 1872)	20 0,6-4,2 several w.; P.C.	some- times+		12 2 2w.	2-6, fix eum.		D., An., M.E.	А.; С.; Sg.; Н.	Mediterranean
31) H. mar 🔥 (Gasca & Calder, 1993)	16-18 3 2 closely w.; large P.C.	+ P.C.	+	10-12 1,2 P.C.	3, not ful- ly devel- loped	-	D., Ha., M.E.	<b>Wo.,</b> Pseudopot- amilla reniformis°	Mexico, Pacifi coast
32) <i>H. monoon</i> & Hirohito, 1988)	8-11 2 almost in 1w. P.C.	+ P.C.	+ scare	8 1 P.C.	6; female ht., 1 egg; male?	-	?	<b>Sp.; H.</b> , Euden- drium	Japan; Sea of Okhost?
33) <i>H. spiralis</i> 50 Goto, 1910)	50 2 closely alternating;	+ hydror. nemat- phores	rarely+	0-12 0,7	10, cryp.	-	?	G., inhabited by hermit crabs; hyd- rorhiza exceed- ing shell opening	Japan*
34)H. calderi 🍯	20-40 5 3 w.; P.C.	+ scare	+ scare	2-14 1-2,5 P.C.	1-3, fix. eum.	+?	D., M.E	Astrea rugosa G.; sp.	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.

*Thecocodium 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 where 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 gastrozooid tentacle number falls in the same range (see Table1), 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 Table1). We thus concur with Namikawa (1991) in keeping the two species as distinct.

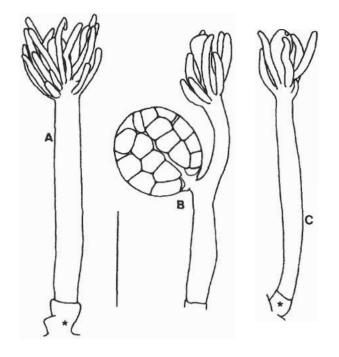
*Hydractinia arctica* (Jäderholm, 1902). This species has been found only twice, near Greenland and in Baffin Bay, each time in deep cold waters (1200 to 2000 m) living on gastropods shells and on *Eudendrium*. The gonozooids, observed only once, are smaller than the gastrozooids, have only four tentacles 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 nothern 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-strar *Homalophiura tesselata* (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



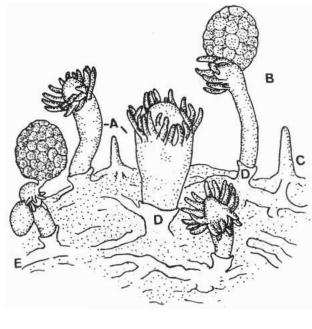


FIG. 1. – *Hydractinia calderi* n. sp. from Chafarinas Islands, Spain. (A) adult gastrozooid; (B) gonozooid; (C) young gastrozooid; \*= basal perisarcal cup; scale bar = 800 µm.

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

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 gastrozooids and gonozooids. 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 hydrorhiza is situated between the shell crests.

Gastrozooids 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. Gonozooids 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 gonozooid 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. Dactylozooids (0.5 mm high) and spines (0.38 - 0.55 mm high) present but scarce. Cnidome: microbasic euryteles (8.7-11 x 3.2 µm) and desmonemes (6.3-7.5 x 3.2-3.6 µm).

## 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 gastrozooids having more than one whorl of tentacles (see table1) *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 perisarcal 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 perisarcal 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 perisarcal cup, 20-40 filiform tentacles in three whorls; gonozooids with a short perisarcal 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 subtrate 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-

dusoids 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 ressembles H. arctica, H. calderi, H. inermis and H. monoon in having gastrozooids with a basal perisarcal 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 perisarcal cup on all types of zooids; the latter species however has a female gonophore with a single egg and a particular type of dactylozooid (see below). Pending futher 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 gastrozooid 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 substratespecific, being only found on the gastropod Nassarius 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 gastroand 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-Kosswska (1905), referred to Stylactis by Behner (1914), who showed that the hydrorizha 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<sup>#</sup>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 nagaoensis.

*Hydractinia yerii* (Iwasa, 1934). This species lacks spines and dactylozooids. It has been distinguished from *H. reticulata* by its smaller size and moeover, 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 nagaoensis, 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: *Archaeoceania* 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 PTILOCODI-IDAE

Clavactinia Thornely, 1904. (figure 3C).

In the course of our investigations on *Hydrac*tinia 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 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 centripedal 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) familly 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.

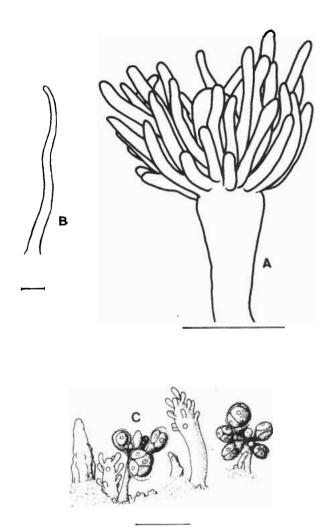


FIG. 3. – (A & B) *Hydractinia calderi* n.sp. from Chafarinas Islands, Spain.(A) apical part of an adult gastrozooid; (B) dactylozooid. (C) Part of a colony of *Clavactinia gallensis* Thornely, 1904 showing the scattered position of the gastrozooid tentacles (After Millard & Bouillon, 1973); scale bar: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

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 centripedal 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 exumbrellar 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 *Thecocodium quadratum*, and this must be the case also for *Hansiella fragilis*.

The medusae of *Hansiella, Tregoubovia* and *The*cocodium 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 *Thecocodium 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 stolonal 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 interradial gonads.

The familly Ptilocodiidae accommodates the following genera: *Hansiella* Bouillon, 1980; *Hydrichtella* Stechow, 1909; *Ptilocodium* Coward, 1909; *Thecocodium* 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 gastrozooid. This last feature, 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 sertulariid 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 stolonal 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 stolonal 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 stolonal 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 sporosarcs, 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).

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