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Leptohelia flexibilis gen. nov. *et* sp. nov., a remarkable deep-sea stylasterid (Cnidaria: Hydrozoa: Stylasteridae) from the southwest Pacific

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Abstract

Leptohelia flexibilis gen. nov. *et* sp. nov., the first stylasterid with a combined calcified and non-calcified skeleton, is described from seamounts and the slope off the islands of New Caledonia, in the southwestern Pacific. The new species is distinguished from all other species of the family Stylasteridae by having a non-calcified organic axis, internal to the basal portion of the calcified corallum. The internal axis is flexible and enclosed by a series of up to 10 calcified annuli, allowing passive lateral bending of the colony. Molecular phylogenetic analyses confirm that *Leptohelia flexibilis* is a stylasterid coral and reveal that the species is closely related to *Leptohelia microstylus* comb. nov., a southwestern Pacific stylasterid that lacks an internal axis.

Key words: evolution, systematics, New Caledonia, Norfolk Ridge, coral

Introduction

Corals are "animals in the cnidarian classes Anthozoa and Hydrozoa that produce either calcium carbonate (aragonitic or calcitic) secretions resulting in a continuous skeleton or as numerous, usually microscopic, individual sclerites, or that have a black, horn-like, proteinaceous axis" (Cairns 2007:312). Whereas the black, horn-like proteinaceous axis of black corals (Anthozoa: Hexacorallia: Antipatharia) and the microscopic calcified sclerites of octocorals (Anthozoa: Octocorallia) are important skeletal elements, it is the continuous calcified skeletons of the so-called 'hard' or 'stony' corals that provide the major building blocks of reef and non-reefal environments worldwide. This polyphyletic assemblage embraces a number of hydrozoans and anthozoans, most notably the families Stylasteridae and Milleporidae (Class Hydrozoa) and the order Scleractinia (Class Anthozoa), the most speciose group of stony corals, with about 1500 species (Cairns *et al*. 1999; Cairns 2007).

Yet, in contrast to the non-calcified or partially calcified colonies of black corals and octocorals that bend with currents, the sturdiness of the continuous calcified colonies of scleractinian and stylasterid corals prevents mobility of colony parts. In this study, we describe the first stylasterid coral with an internal, non-calcified axis. The axis is flexible and enclosed by a series of up to 10 calcified annuli that allow lateral bending of the colony without breakage of the corallum. Molecular phylogenetics and the presence of gastropores, dactylopores and gastrostyles in the calcified portion of the colony confirm that the species is a stylasterid coral (Cnidaria: Hydrozoa: Stylasteridae), the second most diverse group of stony corals with 290 extant species (Cairns *et al*. 1999, Lindner *et al*. 2008).

Material and methods

Colonies of *Leptohelia flexibilis* sp. nov. were collected at depths of 265 to 720 meters off the islands of New Caledonia: off the south and north sides of Grande Terre, off Island of Pines, the Loyalty Islands, and on northern seamounts and banks of the Norfolk Ridge (Table 1). The material has been collected during various cruises,

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mostly in the 'Tropical Deep-Sea Benthos' programme (formerly 'campagnes MUSORSTOM') conducted jointly by Muséum National d'Histoire Naturelle (MNHN) and Institut de Recherche pour le Développement (IRD, formerly ORSTOM), under Claude Lévi (Biocal) and Bertrand Richer de Forges (all other cruises). For the context, see Bouchet *et al*. (2008). Colonies were preserved directly in 70% or 95% ethanol, in formalin (and subsequently transferred to 70% ethanol) or were kept dried. Specimens were studied using methodology as described by Cairns (1983a). The internal axis was studied after colonies were either drilled using an air grinder (Figure 2) or decalcified (Figure 3). The axis was subsequently bleached for 5–10 seconds and immediately rinsed with water and air-dried.

TABLE 1. Collecting stations for *Leptohelia flexibilis*.

Station number	Date	Latitude (south)	Longitude (east)	Depth (meters)
		SMIB2		
DW3	17 Sep 1986	22°56.00	167°14.80	412–428
		Biocal		
DW33	29 Aug 1985	23°09.71	167°10.27	675
DW46	30 Aug 1985	22°53.05	167°17.08	570–610
CP52	31 Aug 1985	23°05.79	167°46.54	540–600
		Musorstom4		
DC168	16 Sep 1985	18°48.20	163°10.80	720
		Musorstom5		
DW274	09 Oct 1986	24°44.83	159°41.00	285
		Musorstom6		
DW391	13 Feb 1989	20°47.35	167°05.70	390
DW397	13 Feb 1989	20°47.35	167°05.17	380
DW407	15 Feb 1989	20°40.70	167°06.60	360
DW459	20 Feb 1989	21°01.39	167°31.47	425
CP464	21 Feb 1989	21°02.30	167°31.60	430
DW487	23 Feb 1989	21°23.30	167°46.40	500
		Lagon8		
Station 444	28 Feb 1985	18°15.30	162°58.80	300–350
		Norfolk2		
DW 2024	21 Oct 2003	23°27.92	167°50.90	370–371
DW 2037	22 Oct 2003	23°40.05	167°40.50	517–570
DW 2117	01 Nov 2003	23°23.95	168°00.43	400
CP 2122	01 Nov 2003	23°21.55	168°00.12	560–577
DW2135	03 Nov 2003	23°01.61	168°21.35	295–330
DW2136	03 Nov 2003	23°00.73	168°22.68	402–410
CP 2140	03 Nov 2003	22°59.85	168°21.80	270–350
DW 2147	04 Nov 2003	22°49.80	167°16.09	496
DW 2156	05 Nov 2003	22°54.19	167°15.13	468–500
DW 2157	05 Nov 2003	22°55.70	167°18.60	553–575
DW 2158	06 Nov 2003	22°41.40	167°14.01	265–283
New records of *Leptohelia microstylus* (Cairns, 1991) on seamounts in the Norfolk Ridge, southern New Caledonia (all *Norfolk2*):				
DW 2066	26 Oct 2003	25°16.90	168°55.11	834–870
DW 2080	27 Oct 2003	25°20.40	168°18.74	764–816
DW 2102	30 Oct 2003	23°55.93	167°44.15	700–715
DW 2113	31 Oct 2003	23°45.17	168°17.99	888–966
DW 2132	02 Nov 2003	23°17.30	168°13.56	405–455

Total DNA was extracted from 95% ethanol-preserved colonies. A total of three gene fragments–large ribosomal subunit of the mitochondrial RNA (lsu-rRNA, 16S), small subunit of the nuclear RNA (ssu-rRNA, 18S), and nuclear calmodulin (CaM)–were amplified and sequenced from two specimens of *Leptohelia flexibilis* (Genbank accession numbers KM886596-KM886601) using primers and techniques as described in Lindner *et al*. (2008). These sequences were aligned using Clustal X (Thompson *et al*. 1997) with the 2638bp dataset of 100 stylasterid species in Lindner *et al*. (2008), and were analysed using Maximum Likelihood and Bayesian analysis with PAUP* (Swofford 1999) and MrBayes (Huelsenbeck & Ronquist 2001), respectively. These analyses also follow methodology as described in Lindner *et al*. (2008). The alignment is available from the first author upon request.

All figured specimens and all specimens of *Leptohelia flexibilis* used for DNA analyses were collected during the 2003 *Norfolk2* cruise (see Table 1 for additional collecting sites). The abbreviations used are: MNHN (Museum National d'Histoire Naturelle, Paris, France); MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil); RMNH (Naturalis, Nationaal Natuurhistorisch Museum, Leiden, the Netherlands); USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.).

Results

Family Stylasteridae Gray, 1847

Leptohelia, new genus

Type-species. ***Leptohelia flexibilis*** Lindner, Cairns & Zibrowius, sp. nov., here designated.

Description. Colonies unbranched and having an internal axis or branched and bushy and lacking an internal axis; branches circular in cross-section and blunt tipped. Base of colonies fully calcified or with internal axis and up to 10 calcified annuli. Coenosteal texture reticulate, sometimes smooth or irregularly granular, white or pink colored. Internal axis dark brown to black, cylindrical, tapering gradually from base to tip. Base of axis several root-like projections, tip of axis a series of coalescing strips and without anchoring projections. Surface of median part of axis (enclosed by annuli) smooth or with projections as if keeping annuli in position. Surface of axis close to base also with small granules. Gastro- and dactylopores uniformly arranged; relatively short (not axial). Gastropores circular or slightly elliptical, flush with coenosteum or with a short lip, and evenly spaced. Gastropore tube double chambered or with a broad basal chamber. Ring palisade absent. Gastrostyles rudimentary. Dactylopores circular, flush with coenosteum or on small mounds. Dactylostyles absent. Female ampullae primarily internal, with slight surface relief; male ampullae entirely internal. Efferent pores opening directly to colony surface or to upper part of gastropore tube. Symbiosis with polynoid polychaetes sometimes present.

Diagnosis. *Leptohelia* is distinguished from other stylasterid genera by the combination of the following characters: (1) having slender branches or corallum; (2) having gastropore tubes double-chambered or with a broad basal chamber; (3) having a small, rudimentary gastrostyle and (4) lacking cyclosystems.

Etymology. *Leptohelia* is formed by combining the Greek *leptos* (meaning 'thin, slender', and referring to the slender, delicate branches and coralla of the species in the genus) and *helios* (meaning 'sun', and referring to the round gastropores), a suffix previously used for stylasterid generic names. Gender: feminine.

Distribution. Southwest Pacific, Kermadec Ridge, Norfolk Ridge, New Caledonia region, 265–1258 m. *Leptohelia flexibilis* sp. nov. is found only in New Caledonia (northern and southern Grande Terre, Island of Pines, northern Norfolk Ridge, and the Loyalty Islands) at depths of 265 to 720 meters. *Leptohelia microstylus* is found in the Norfolk and Kermadec Ridges and off McCauley Island, New Zealand (Cairns 1991). Although *L. microstylus* was previously known from depths of 710 to 1258 meters, a specimen collected during the *Norfolk2* expedition on an unnamed seamount in the Norfolk Ridge, southern New Caledonia (station DW2132: 23°17.30'S, 168°13.56'E, 405–455 meters), provides a shallower–and the northernmost–record of the species. The genus is only known from the Recent.

Remarks. *Leptohelia* is similar to *Lepidopora*, but differs in having short radial (not axial) gastro-and dactylopores, rudimentary gastrostyles, and, in *Leptohelia flexibilis*, an internal flexible axis. Besides *Leptohelia*, the only other stylasterid genus having a small, rudimentary–and also conical–gastrostyle is *Pseudocrypthelia*

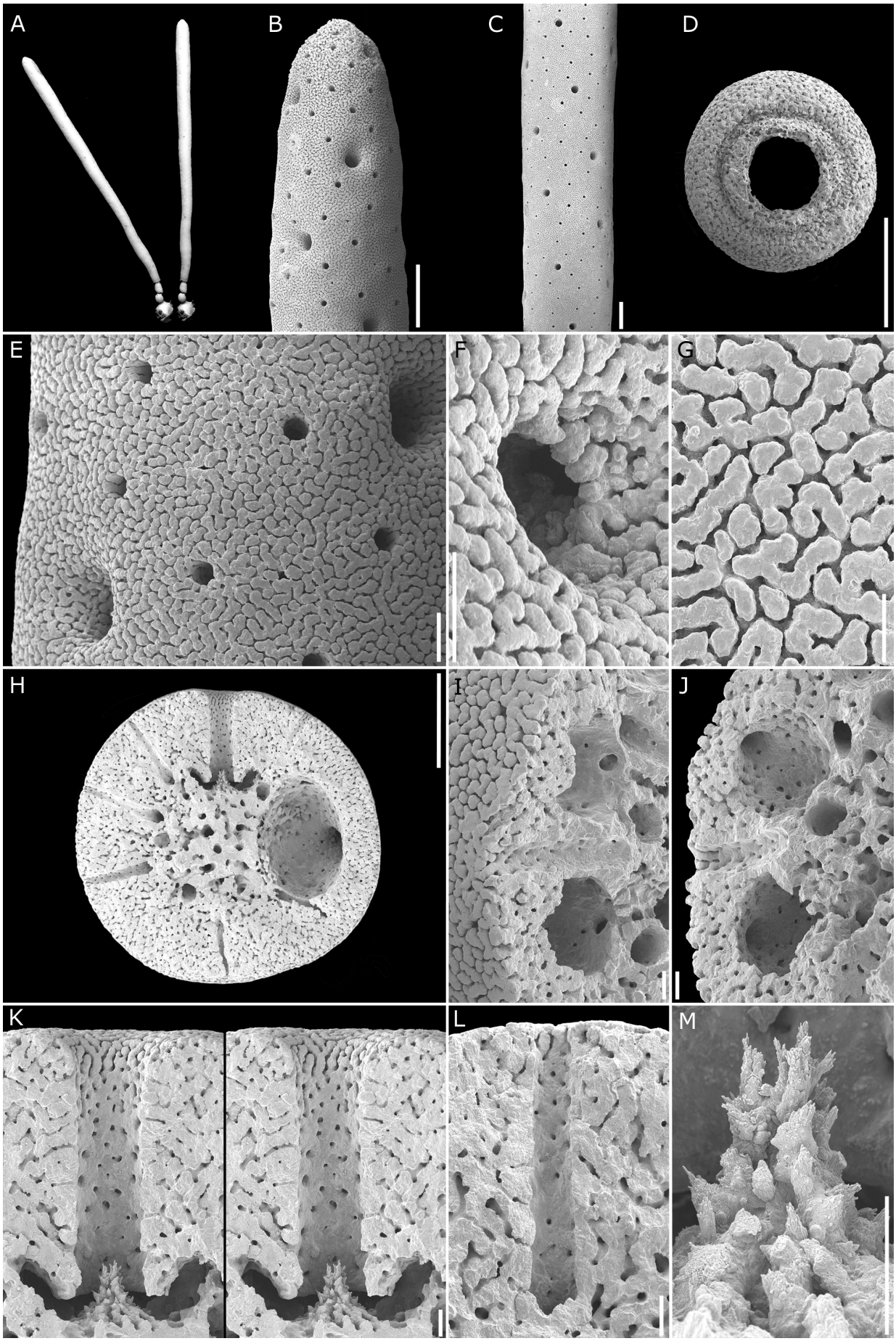
Cairns, 1983b. However, the only species in the genus, *P. pachypoma* (Hickson & England, 1905), has well-developed cyclosytems, not present in colonies of *Leptohelia*, and is distantly related phylogenetically (Figure 4). All other stylasterid genera have either well-developed gastrostyles or lack this structure entirely.

Leptohelia microstylus is here proposed as a new combination for *Lepidopora microstylus* Cairns, 1991 based on three lines of evidence. First, all species of *Lepidopora* have well-developed gastrostyles, but not *L. microstylus*. Second, *L. microstylus* is similar to *L. flexibilis* in several aspects (see Table 1), in particular by also having small, conical gastrostyles (see also Plate 4B in Cairns 1991). Finally, phylogenetic analyses strongly support a monophyletic close relationship between *L. flexibilis* and *L. microstylus* (Figure 4).

***Leptohelia flexibilis*, sp. nov.**
(Figures 1–3; Table 2)

Material examined. Holotype: MNHN-IK-2012-16011, intact colony 3.5cm tall and up to 1.6mm wide, white, with 2 basal annuli, in ethanol 95%. Sex undetermined. *Norfolk2* station DW2117. Type-locality: Antigonia Seamount, Northern Norfolk Ridge, New Caledonia, 23°23.95'S, 168°00.43'W, depth: 400 meters. **Paratypes**: MNHN-IK-2012-16012 (*Biocal1985* station DW33: 1 fragment with basal annuli), MNHN-IK-2012-16013 (*Biocal1985* station CP52: 9 fragments without annuli), MNHN-IK-2012-16014 (*Musorstom6* station CP464: 7 fragments, 4 of which with intact bases), MNHN-IK-2012-16017 (*Musorstom6* station DW459: 11 fragments without annuli), MNHN-IK-2012-16016 (*Musorstom4* station DC168: 5 fragments without annuli), MNHN-IK-2012-16018 (*Musorstom6* station DW391: 1 colony, intact), MNHN-IK-2012-16019 (*SMIB2* station DW3: 1 fragment without annuli), MNHN-IK-2012-16020 (*Musorstom5* station DW274: 1 fragment with basal annuli), MNHN-IK-2012-16021 (*Norfolk2* station DW2158: 1 fragment without basal annuli), MNHN-IK-2012-16022 (*Norfolk2* station DW2157: 2 fragments without basal annuli), MNHN-IK-2012-16023 (*Norfolk2* station DW2117: 1 fragment with basal annuli), MNHN-IK-2012-16024 (*Norfolk2* station DW2117: 1 fragment with basal annuli), MNHN-IK-2012-16025 (*Norfolk2* station DW2117: 2 fragments without basal annuli), MNHN-IK-2012-16026 (*Norfolk2* station DW2147: 2 fragments, one with basal annuli), MNHN-IK-2012-16027 (*Norfolk2* station DW2024: 1 fragment without basal annuli, pink color), MNHN-IK-2012-16028 (*Norfolk2* station DW2156: 3 fragments without basal annuli), MZUSP000968 (*Musorstom6* station DW407: 1 fragment with intact base), MZUSP000969 (*Norfolk2* station DW2140: 7 fragments without basal annuli), MZUSP000970 (*Norfolk2* station DW2117: 2 fragments, one with basal annuli), RMNH Coel. 33540 (*Norfolk2* station DW2147: 5 fragments without basal annuli), RMNH Coel. 33541 (*Norfolk2* station DW2147: 6 fragments, one of which with annuli, USNM1078261 (*Biocal1985* station DW46: 6 fragments, one of which with annuli), USNM1078262 (*Musorstom6* station DW487: 9 fragments without annuli), USNM1078263 (*Musorstom6* station DW407: 2 fragments with intact bases), USNM1078264 (*Musorstom6* station DW487: 4 fragments without basal annuli), USNM1078265 (*Musorstom6* station DW397: 1 colony with intact base), USNM1078266 (*Lagon8* station 444: 4 fragments of same colony, with basal annuli), USNM1078267 (*Norfolk2* station DW2147: 11 fragments, 3 with basal annuli), USNM1078268 (*Norfolk2* station DW2117: 15 fragments, one with intact base and 2 bases mounted in SEM stubs AL.026 and AL.027 and illustrated in Figures 3.2 and 3.3, respectively), USNM1078269 (*Norfolk2* station DW2147: 4 fragments, one with basal annuli), USNM1078270 (*Norfolk2* station CP2122: 5 fragments without basal annuli and SEM stubs AL.029 AND AL.030), USNM1078271 (*Norfolk2* station CP2122: 4 fragments without basal annuli, USNM1078272 (*Norfolk2* station DW2037: 3 fragments without basal annuli), USNM1078273 (*Norfolk2* station DW2037: 4 fragments without basal annuli), USNM1078274 (*Norfolk2* station

FIGURE 1. (next page) *Leptohelia flexibilis* sp. nov. (A) Two views of the holotype, 3.5cm tall and with 2 basal annuli, showing flexibility (left view) of colony; (B) Tip of colony; (C) Median portion of colony with gastropores in spiral arrangement around colony; (D) Upper view of calcified annulus removed from axis illustrated in Figure 2; (E) Detail of colony showing coenosteal texture, gastropores, dactylopores and a small male efferent pore; (F) Gastropore with female efferent pore; (G) Reticulate coenosteal texture; (H) Colony cross-section with gastropore, dactylopores and female ampulla with efferent pore (visible inside ampulla); (I) Edge of colony cross-section showing two male ampullae with their efferent pores opening on coenosteum; (J) Same male ampullae showing efferent pores visible inside ampullae; (K) Double-chambered gastropore tube with gastrostyle (stereo pair); (L) Dactylopore tube; (M) Gastrostyle. (A: Holotype, MNHN; B, E, I, J: Paratype, USNM1078270, SEM stub AL.029; C, F–H, K–M: Paratype, USNM1078270, SEM stub AL.030; D: Paratype, USNM1078268, SEM stub AL.032). Scale Bars: B–D, H, 1mm; E, F, 0.2mm; G, I–M, 0.1mm.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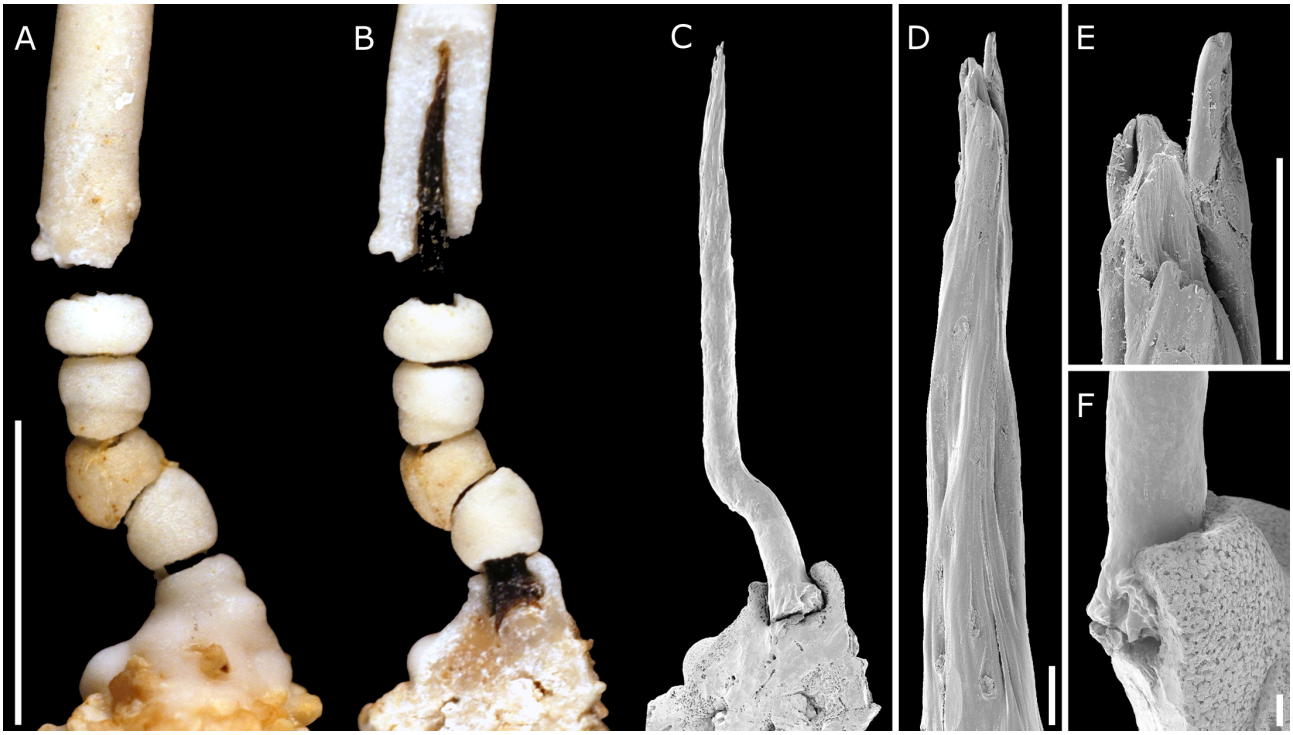

FIGURE 2. *Leptohelia flexibilis* sp. nov. (A) Basal portion of colony with four annuli and encrusting base; (B) Same colony, revealing axis; (C) Scanning electron micrograph of axis and calcified base (annuli and upper calcified part removed); (D) Detail of axis; (E) Tip of axis; (F) Base of colony with axis. (A–F: Paratype, USNM1078268, SEM stub AL.027). Scale Bars: A–C, 5mm; D–F, 0.2mm.

CP2140: 1 fragment without basal annuli), USNM1078275 (*Norfolk2* station CP 1222: 6 fragments without basal annuli and SEM stub AL.028), USNM1078276 (*Norfolk2* station DW2135: 3 colonies without annuli, one of which mounted on SEM stub AL.031), USNM1078277 (*Norfolk2* station DW2136: 2 intact colonies and one fragment).

Description. Colonies with an encrusting base giving rise to a long and unbranched corallum, circular in cross-section and up to 8.7cm long and 3.8mm wide (Figure 1). Width of corallum about equal throughout its length; tip of corallum blunt. Base of colonies with up to 10 adjacent calcified annuli enclosing the median part of an internal flexible axis that confers lateral flexibility to colonies (Figures 1–3; see Remarks). Annuli up to 1.7mm long and 2.5mm wide. Coenosteum reticulate, with smooth, discontinuous and irregularly shaped strips 25–50µm wide, forming a labyrinth of intervening spaces up to 15µm wide (Figure 1E–G). Coenosteum white or rarely pink.

Internal basal axis dark brown to black, cylindrical, up to 16mm long and 0.8mm wide at base, tapering gradually from base to tip (Figures 2–3). Illustrated axis (Figure 2B) located 1.3mm deep into encrusting calcified base of colony; tip of axis 3.5mm into upper calcified part of colony above annuli. Base of axis consists of several root-like projections that attach axis to calcified encrusting base (Figure 3D, G). Tip of axis a series of coalescing strips ~35–120µm wide; anchoring projections absent (Figure 3C). Surface of median part of axis (enclosed by annuli) either smooth - resulting in freely rotating annuli in dry colonies—or with projections into calcified annuli, keeping annuli in position even in dry colonies (Figure 3B, E, F). Surface of axis close to base with granules up to 60µm tall and 80µm wide (Figure 3H).

Gastropores 0.22–0.33mm in diameter, circular or slightly elliptical, the longest axis parallel to colony. Gastropores flush with coenosteum and evenly spaced, usually forming short spiral rows around corallum (Figure 1C). Gastropore tube double chambered, perpendicular to length of corallum (in longitudinal section) or slightly inclined upwards (Figure 1H, K). Upper chamber cylindrical and lower chamber shallow and broad, ~0.7mm wide. Ring palisade absent. Gastrostyles small and conical, illustrated gastrostyle 0.3mm wide at base and 0.23mm tall; tip of style projecting >0.1mm into upper gastropore tube (Figure 1K). Surface of gastrostyle consisting of irregularly shaped, elongated to pointed granules. Dactylopores circular, 50–100µm wide, flush with coenosteum or on small mounds. Basal part of dactylopore tubes forming an axial branch core; distal part of tubes curving

perpendicularly to corallum (in longitudinal section) and gradually tapering towards pore opening (Figure 1H, L). Dactylostyles absent.

Ampullae internal (Figure 1H–J), sometimes producing a slightly undulated colony surface. Female ampullae up to 1.3mm wide, with an efferent pore up to 0.25mm wide and opening at colony surface or at upper part of gastropore tube (Figure 1F). Male ampullae smaller than female, up to 0.44mm wide and with small, 20–30µm wide efferent pores opening at colony surface (Figure 1I, J).

Diagnosis. *Leptohelia flexibilis* is distinguished from all other stylasterids by having an internal non-calcified axis. It is similar to the congener *L. microstylus* (Cairns, 1991), a species with bushy colonies and having polynoid polychaete galls, and lacking the non-calcified axis (Table 2).

TABLE 2. Features of *Leptohelia flexibilis* sp. nov. and *Leptohelia microstylus* (Cairns, 1991).

		Leptohelia flexibilis sp. nov.	*Leptohelia microstylus*
Internal axis		Present	Absent
Colony	Shape	Unbranched	Branched, bushy
	Size	up to 8.7cm tall and 3.4mm wide	up to 1.7cm tall and 2.3cm wide
	Width of branch/corallum	up to 3.4mm	~ 1mm
	Polychaete gall	Absent	Present
Pores	Gastropore	Circular or slightly elliptical, flush with coenosteum	Circular, sometimes with abcauline lip
	Dactylopore	Circular, flush or on small mounds	Circular, on small mounds
	Shape of gastropore tube	Double-chambered	With wide bottom chamber
	Diameter of gastropore tube	0.22–0.33mm	~ 0.18mm
Styles	Gastrostyle	Small, conical	Small, conical
	Dactylostyle	Absent	Absent
Ampullae		Internal	Internal
Coenosteum	Texture	Reticulate (non granular)	Reticulate-granular
	Color	White or pink	White
Distribution	Geographic	New Caledonia: northern and southern Grande Terre, Island of Pines, northern Norfolk Ridge, and the Loyalty Islands	Norfolk and Kermadec Ridges, and McCauley Island, New Zealand
	Bathymetric	265–720 meters	405–1258 meters

Etymology. The specific name *flexibilis* (Latin, bendable) refers to the non-calcified axis that allows the colonies to bend laterally.

Distribution. *Leptohelia flexibilis* sp. nov. is found only in New Caledonia (northern and southern Grande Terre, Island of Pines, northern Norfolk Ridge, and the Loyalty Islands) in depths of 265 to 720 meters.

Remarks. Most colonies of *Leptohelia flexibilis* have a straight cylindrical corallum with up to 10 calcified annuli at the base, but a few small colonies collected off the Loyalty Islands do not have annuli. However, these colonies do have an internal axis, and a narrow separation between the calcified encrusting basal part of the colony and the calcified stem above allows flexibility of the corallum. Some coralla are also S-shaped or slightly curved, and others show regeneration of the corallum, which is inferred by an abrupt change in colony diameter (with a wider basal part) that marks the position of breakage and onset of regeneration. Colonies are able to bend at least 30° without breakage of the axis (Figure 1A).

A specimen of *Pedicularia* Swainson, 1840 (Mollusca: Gastropoda: Ovulidae) was observed on a living colony of *L. flexibilis* collected on station *Norfolk2*-DW2117 (USNM1078268). The gastropod was white (the same color of the colony) and 0.5cm long, and detached after immersion in ethanol 95%. Deep *Pedicularia* scars, as reported by Zibrowius & Cairns (1992) for several North Atlantic stylasterids, were not observed in colonies of *L. flexibilis*.

Phylogenetic analyses indicate that *Leptohelia flexibilis* and *Leptohelia microstylus* are nested within a basal

stylasterid clade that also includes *Conopora, Crypthelia, Pliobothrus* and *Pseudocrypthelia* (Figure 4), genera that embrace species with a double-chambered gastropore tube. *Pseudocrypthelia pachypoma* and the two species of *Leptohelia* are the only stylasterids within this clade with a rudimentary gastrostyle (all other species within this clade lack this structure). The two genera are not closely related within this basal stylasterid clade (Figure 4) and may have evolved the gastrostyle independently.

Sequences obtained from two colonies of *L. flexibilis* (one collected on Munida Bank in the northern Norfolk Ridge and another one off Island of Pines) are considerably divergent (Figure 4) and future studies on the species throughout its range are necessary to determine population structure and possible cryptic speciation.

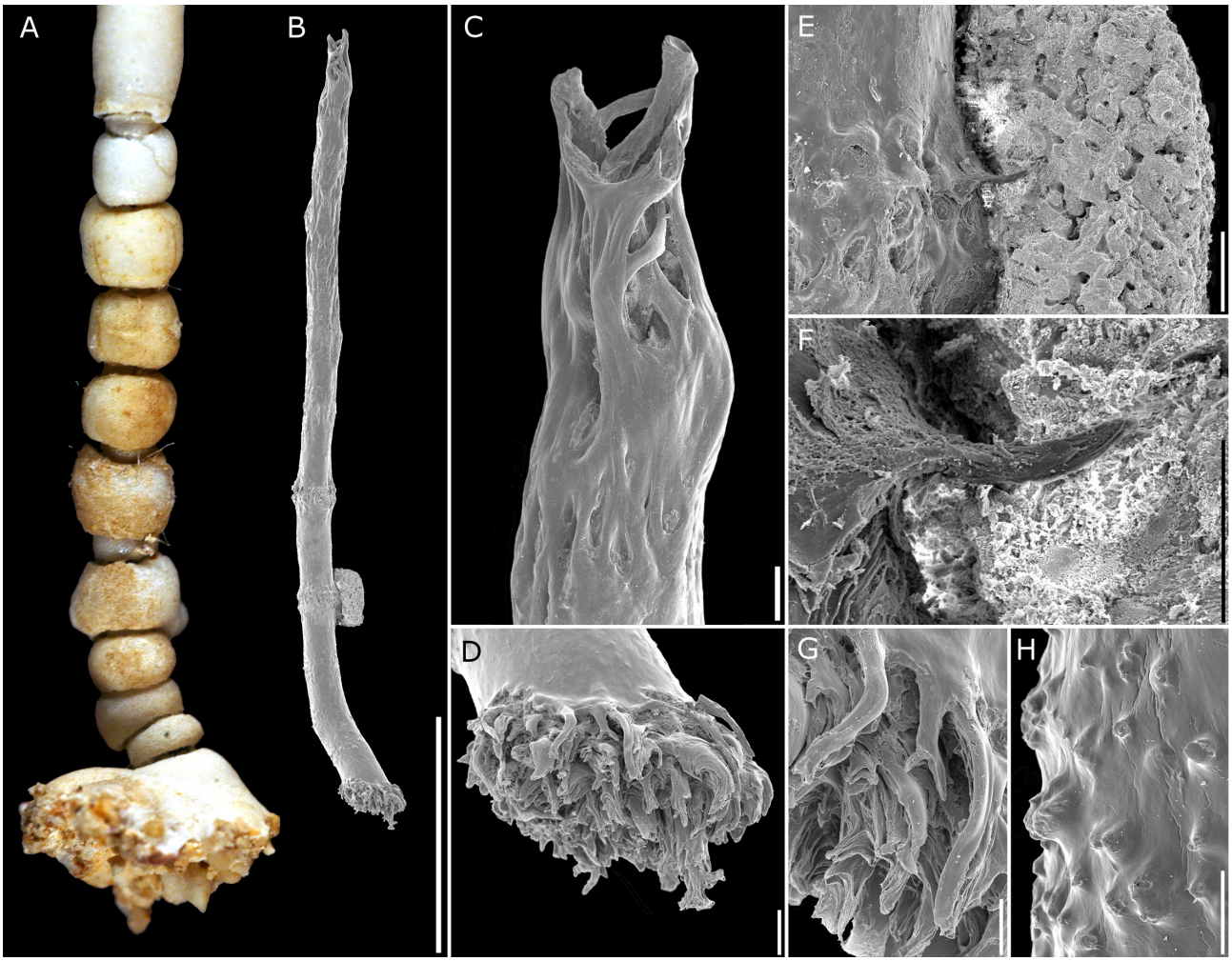

FIGURE 3. *Leptohelia flexibilis* sp. nov. (A) Basal portion of colony with 10 annuli; (B) Scanning electron micrograph of internal axis of same colony, decalcified (except right portion of the 4th annulus from bottom to top); (C) Tip of axis; (D) Base of axis with root-like projections; (E) Axis and broken face of calcified annulus; (F) Detail of projection of axis into calcified annulus; (G) Detail of root-like projections; (H) Detail of surface of axis close to base, with granules. (A–H: Paratype, USNM1078268, SEM stub AL.026). Scale Bars: A, B, 5.0mm; C–E, 0.2mm; F–H, 0.1mm.

Discussion

The only hard coral species previously reported to be able to passively bend the corallum is the fire coral *Millepora alcicornis* (Cnidaria: Hydrozoa: Milleporidae) that may encrust flexible substrates such as sea fans and artificial substrates (e.g., Humann & DeLoach 2002; Lindner, personal observation). Colonies of *M. alcicornis* are able to bend when the substrate that they encrust is thin, and if cracks form in the corallum. However, there is no evidence that colonies of *M. alcicornis* develop a flexible axis themselves. In contrast, in *Leptohelia flexibilis* the axis is always present and is of similar shape and size in all specimens observed. Additionally, in *Leptohelia flexibilis* the organic axis itself is never attached to the substratum; it develops from the basal calcified portion that attaches the

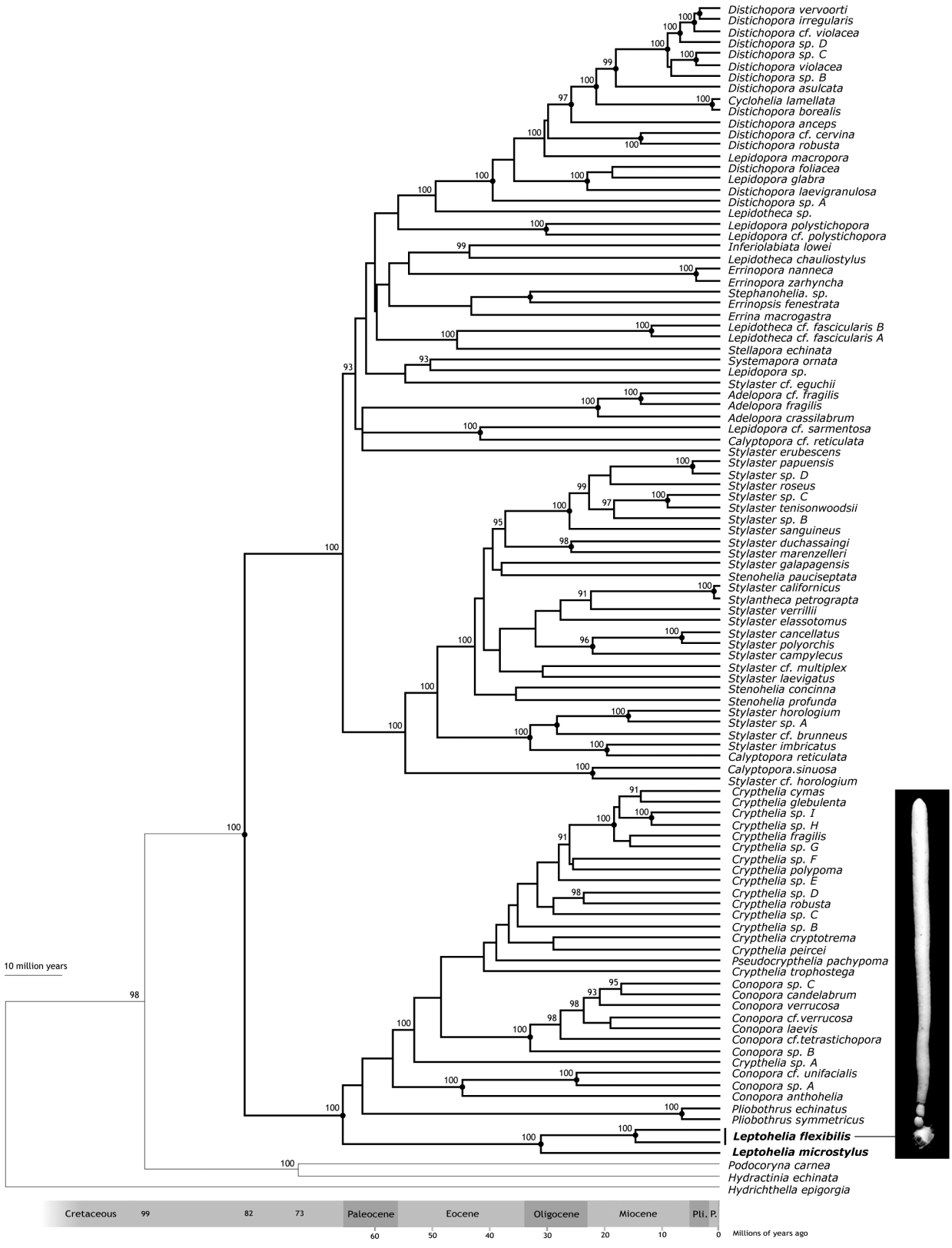

FIGURE 4. Phylogenetic placement of *Leptohelia flexibilis* sp. nov. and *Leptohelia microstylus* within the family Stylasteridae, inferred on the basis of a 2638bp DNA dataset (-ln likelihood 25738.67966). The tree was estimated using maximum likelihood with a GTR+*g*+I model of DNA substitution as determined by the hierarchical likelihood ratio test implemented in Modeltest (Posada & Crandall 1998) and calibrated using the earliest stylasterid fossils, as described in Lindner *et al*. (2008). Numbers are Bayesian posterior probabilities whenever >90%; dots at nodes indicate bootstrap support values whenever >70% for both parsimony and maximum likelihood.

colony (Figure 2B). This strongly indicates that the non-calcified axis is not a foreign structure, but part of the species. The largest colony (USNM1078266) is a broken corallum 8.7cm long with 10 basal annuli and with a maximum diameter of 2.4mm, i.e., the colony is 36 times taller than wide. Both the tip of the corallum and its basal encrusting portion are broken, and the colony was thus certainly taller, possibly up to 10 cm (>40 times taller than wide).

Although not closely related, the hydroid *Hydractinia antonii* Miglietta, 2006 is another hydrozoan species with both flexible and calcified parts, as in *L. flexibilis*. The flexible axis of *Leptohelia flexibilis* is also similar to the chitinous internal skeleton of the capitate hydrozoan *Solanderia* Duchassaing & Michelin, 1846 (Capitata: Solanderiidae) in being smooth surfaced and in having anastomosing threads (Figure 3; Bouillon & Cornelius 1988, Bouillon *et al*. 1992). The axis of *L. flexibilis* is even more similar to the skeleton of *Pseudosolanderia picardi* Bouillon & Gravier-Bonnet, 1987, which is also smooth surfaced and mostly solid, but differs by having ridges and spines on its surface (whereas axes of *L. flexibilis* are only slightly undulated and with short projections; Figure 3C, H). Although further analyses remain to be performed, these morphological similarities indicate that the axis of *L. flexibilis* may be of chitin, the polysaccharide inferred to be synthesized by species of *Solanderia, Pseudosolanderia*, and numerous hydrozoans. *Leptohelia flexibilis* is one more remarkable species discovered in deep-water seamounts and slopes off the islands of New Caledonia (Richer de Forges *et al*. 2000) and the flexible axis is another example of a morphological novelty originating in the deep sea (Lindner *et al*. 2008).

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