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New records of marine tardigrades from Moorea, French Polynesia, with the description of *Styraconyx turbinarium* sp. nov. (Arthrotardigrada, Halechiniscidae)

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Abstract

Five marine arthrotardigrade species are recorded from Moorea, Society Islands, French Polynesia. Four were collected from coral sand; two, *Dipodarctus anaholiensis* Pollock, 1995 and *Florarctus kwoni* Chang & Rho, 1997, are new records for the region, and two, *Halechiniscus perfectus* Schulz, 1955 and *Styraconyx kristenseni kristenseni* Renaud-Mornant, 1981, have been previously reported. The fifth, a new species *Styraconyx turbinarium* **sp. nov.**, is described and was collected from the drifting brown alga *Turbinaria ornata.* The new species is characterized by the presence of peduncles on all digits, an elongate primary clava, and the lateral cirrus *A* arising from a common pedestal and enveloped by a common membrane extending almost to the claval tip. The new species differs from the most similar species, *Styraconyx tyrrhenus* D'Addabbo Gallo, Morone De Lucia & de Zio Grimaldi, 1989, by having longer and differently shaped primary clavae which are elongated in the new species and club-shaped in *S. tyrrhenus*. By having a dorsal cuticle that is coarsely punctated but without folds or other ornamentations, the new species can be easily distinguished from *S. craticulus* (Pollock, 1983), a species with similar primary clavae, but with cuticular dorsal folds ornamented with a grid-like pattern.

Key words: *Dipodarctus, Florarctus*, *Halechiniscus*, *Styraconyx,* meiofauna, Pacific Ocean**,** Tardigrada, *Turbinaria.*

Introduction

Marine tardigrades are present in all oceans, ranging from the intertidal zone to abyssal depths, inhabiting a great diversity of sediments from fine mud to coarse sand, rocks, algae, and in a few cases living as commensals or ectoparasites (Kristensen & Hansen 2005) on larger invertebrates. Nevertheless, our knowledge of the marine tardigrade fauna is still very poor with less than 200 described species and subspecies (Guidetti & Bertolani 2005; Degma *et al.* 2009-2014). French Polynesia (Pacific Ocean) is one of the regions scarcely explored. Until now only six species, *Echiniscoides sigismundi polynesiensis* Renaud-Mornant, 1976, *Florarctus asper* Renaud-Mornant, 1989, *Florarctus stellatus* Renaud-Mornant, 1989, *Halechiniscus perfectus* Schulz, 1955, *Styraconyx kristenseni kristenseni* Renaud-Mornant, 1981, and *Tholoarctus natans natans* Kristensen & Renaud-Mornant, 1983 have been recorded for this region (Salvat & Renaud-Mornant 1969; Renaud-Mornant 1976, 1981, 1989; Kristensen & Renaud-Mornant 1983), and no collections have been made there for over 25 years.

Based on recently collected, shallow marine samples from Moorea Island, we provide a description of *Styraconyx turbinarium*, a species new to science, and present the first French Polynesian records for *Dipodarctus anaholiensis* Pollock, 1995 and *Florarctus kwoni* Chang & Rho, 1997.

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Material and methods

Collections for this study were made by the lead author while on Sea Semester Cruise S250B on the Sailing School Vessel *Robert C. Seamans* (www.sea.edu). Tardigrades were extracted from sublittoral coral sand and washings from the drifting brown alga *Turbinaria ornata* at Moorea Island, Society Islands, French Polynesia. Nine samples each containing 100–200 mls of sediment were collected by hand in jars from the shallow sublittoral zone between 0.5–1.0 m depth at Cook's Bay (17° 29.6' S, 149° 49.6' W) on 11-Jan-2014. These samples were taken by wading just offshore immediately outside the marine protected area at the Richard B. Gump South Pacific Research Station. Twelve bunches of drifting *Turbinaria ornata* were collected by net at Opunohu Bay (17° 30.5' S, 149° 51.2' W) on 13-Jan-2014. To extract the organisms, sand and algae were treated with the freshwater shock method (Kristensen & Higgins 1984). Sand was placed in a 1 litre Erlenmeyer flask with freshwater for one minute, agitated and quickly decanted onto a 63 µm sieve. This process was repeated twice. The algae were washed in a bucket of freshwater, agitated, and the washings were poured through a 333 µm sieve and trapped on a 63 µm sieve. After preservation in 4% buffered formaldehyde solution, tardigrades were sorted under a dissecting microscope. Specimens were transferred to microslides, mounted in polyvinyl alcohol (PVA), and cover slips were sealed with nail polish. Animals were examined, measured (all measurements in micrometers-µm) and photomicrographed under x100 oil immersion, using a Zeiss phase contrast/differential interference contrast (PHC/DIC) microscope equipped with a digital camera and using Axiovision 4.7.1 Imaging System Software or an Olympus BX-60 PHC/DIC microscope with Jenoptiks digital camera and Progress Capture Pro 2.8.8 software. When symmetrical structures were measured, the larger value was recorded if different values were obtained. In order to facilitate the comparison with similar species, the ratio between the primary clavae length and lateral cirri *A* length was assessed for *Styraconyx* specimens (Kristensen 1977; Renaud-Mornant 1981, 1982a). Gender is indicated whenever possible, but in cases listed below as "undetermined gender" improper orientation or poor specimen quality precluded gender determination. Identifications were based on original species descriptions in the literature. For comparison the holotype and a paratype of *Dipodarctus anaholiensis*, kindly loaned by the Smithsonian Institution (National Museum of Natural History), and specimens of *Styraconyx craticulus* (Pollock, 1983), *Styraconyx sardiniae* D'Addabbo Gallo *et al.*, 1989, and *Styraconyx haploceros* Thulin, 1942 were also examined.

Taxonomic accounts

Phylum: Tardigrada Doyère, 1840

Class: Heterotardigrada Marcus, 1927

Order: Arthrotardigrada Marcus, 1927

Family: Halechiniscidae Thulin, 1928

Subfamily: Dipodarctinae Pollock, 1995

Genus: *Dipodarctus* Pollock, 1995

Dipodarctus anaholiensis Pollock, 1995

Fig. 1 A–C

Material examined. Eighteen specimens (1 two-digit larva 75 µm long and 17 adult specimens: 12 females, 3 males and 2 of undetermined gender, body length 82–140 µm), collected in coral sand at Cook's Bay, 0.5–1.0 m depth.

Remarks. According to the original description (Pollock 1995), one of the main features of the genus *Dipodarctus* is the relative size of the digits. Pollock (1995) says that at least three of the four digits are short and of equal length on legs I–III. According to the Pollock (1995) terminology (in which digit 1 is the outermost digit) we noted that the adult specimens collected in Moorea have digit 4 (innermost) slightly but consistently shorter (Kruskal-Wallis test H (3 d.f.; n=111)=39.621; $p<0.001$) (values, in µm, as follows: digit 1: mean=10.8, min–max=8.9–12.6, n=27; digit 2: mean=10.8, min–max=8.9–12.8, n=27; digit 3: mean=10.6, min–max=8.8–12.6, n=28; and digit 4: mean=9.0, min–max=7.0–11.1, n=29). This character has been confirmed by the measurements provided by Pollock (1995) in the original description and also by the examination of type material (Fig. 1A). Another interesting character neglected by Pollock (1995) in the original description is the presence of proximal cuticular folds on external digits, particularly evident on legs IV (Fig. 1B).

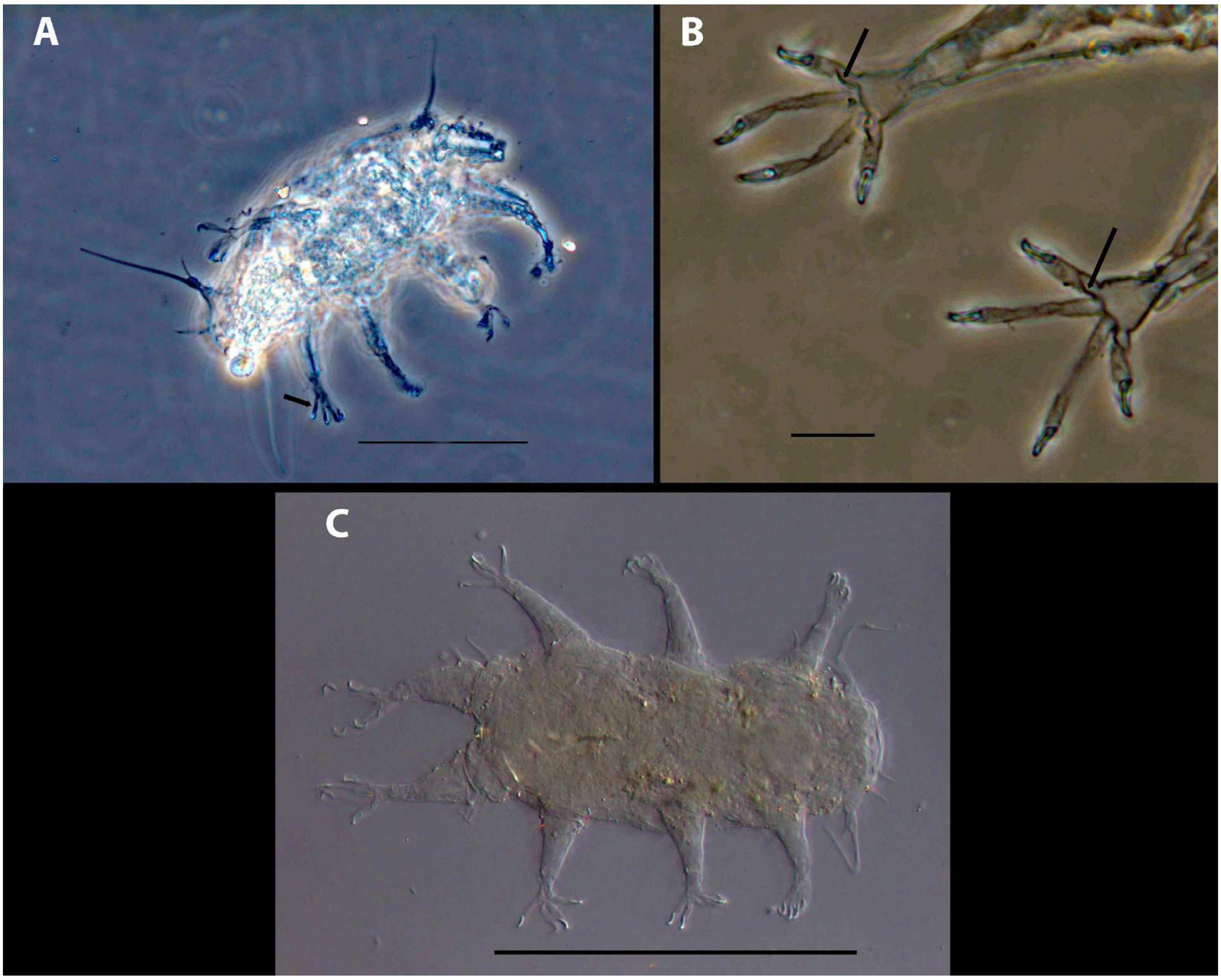

FIGURE 1. *Dipodarctus anaholiensis*. A. Holotype from Hawaii, USA with arrow showing the smaller digit 4 on leg I. Scale bar = 50 µm. B. Specimen from Moorea, French Polynesia. Leg IV with arrow showing the cuticular folds on external digits. Scale bar = 10 µm. C. Specimen from Moorea, French Polynesia. Habitus. Scale bar = 100 µm.

Five species are currently known in this genus, with two recently described species (*Dipodarctus australiensis* Jørgensen *et al.*, 2014 and *Dipodarctus susannae* Jørgensen *et al.*, 2014) from Australian marine caves (Jørgensen *et al.* 2014). Our specimens of *D. anaholiensis* differ from all other species most notably by the lack of an elongate toe on legs I–III (Fig. 1C). Our specimens are most easily distinguished from the new Australian species by the lack of three parallel folds on the digits. In addition, they differ from *D. australiensis* by the lack of lateral processes between legs III and IV; lack of peduncles on legs IV; and lack of cephalic processes and facial plate. Our specimens also differ from *D. susannae* by the lack of a cirrophore on sensory organ IV and fine details of the cephalic cirri. For a more thorough discussion of the taxonomy of this genus, including the junior synonym *Hemitanarctus chimaera* de Zio Grimaldi *et al.,* 1995/96, see Jørgensen *et al.* 2014.

Dipodarctus anaholiensis, primarily a shallow subtidal species, has been found in the Indian Ocean, the Mediterranean (Adriatic Sea, Ionian Sea, Tyrrhenian Sea, Strait of Sicily), and the Pacific Ocean (Pollock 1995; de Zio Grimaldi & D'Addabbo Gallo 2001; de Zio Grimaldi *et al.* 2003; Gallo *et al.* 2007). This is the first record for French Polynesia.

Subfamily: Florarctinae Renaud-Mornant, 1982b

Genus: *Florarctus* Delamare-Deboutteville & Renaud-Mornant, 1965

***Florarctus kwoni* Chang & Rho, 1997**
Fig. 2A, B

Material examined. Four females (121–227 µm long) collected in coral sand at Cook's Bay, 0.5–1.0 m depth.

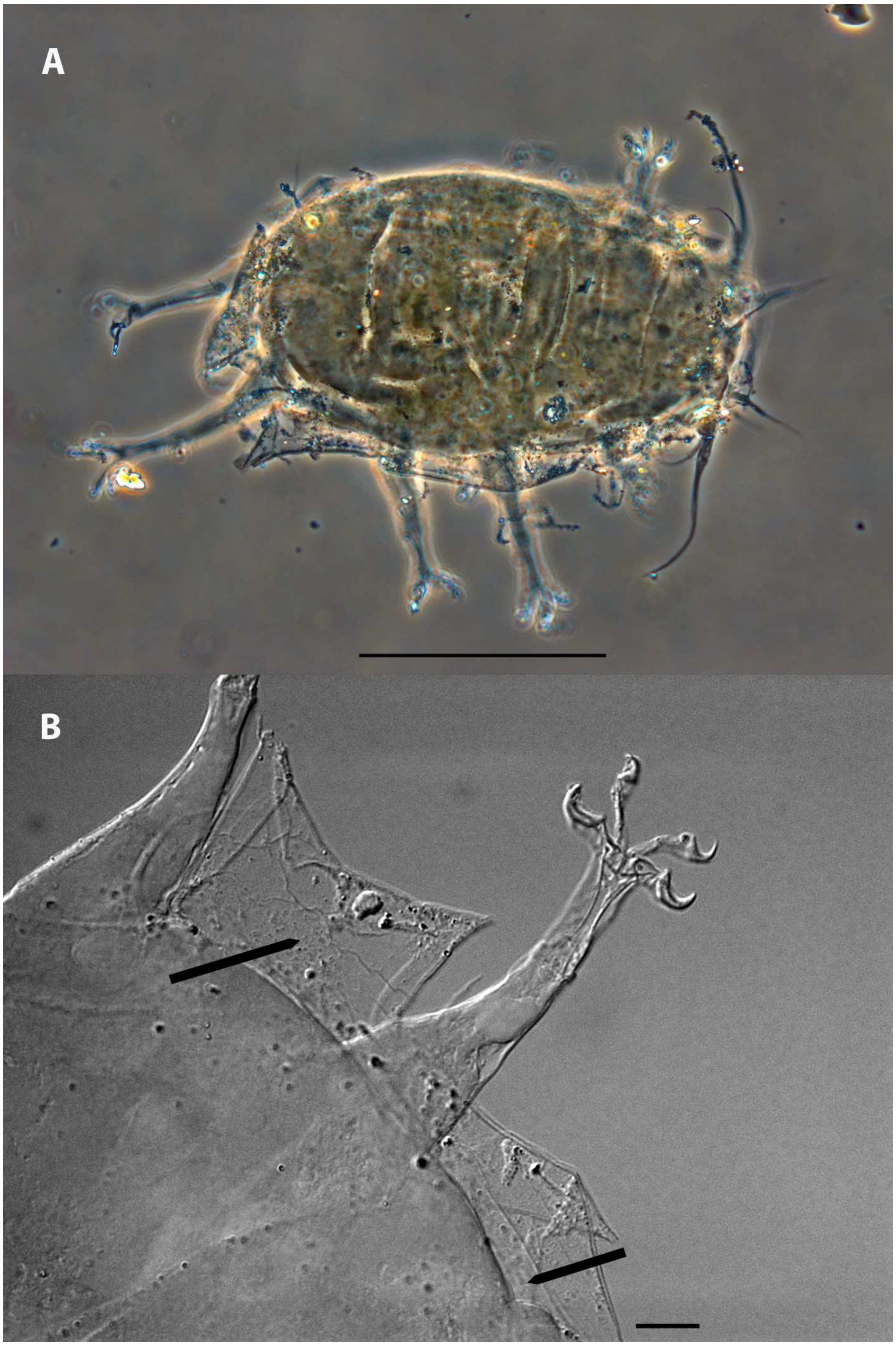

FIGURE 2. *Florarctus kwoni* from Moorea, French Polynesia. A. Habitus showing enlarged posterior margin of right lateral ala making up the right fin of the rocket-shaped alae. Scale bar = 100 µm. B. Second specimen with arrows indicating procuticular supports (*caestus*); leg with foot is leg III, leg to left of photo is leg IV. Scale bar = 10 µm.

Remarks. Of the 14 known species of *Florarctus*, including the recently described *Florarctus wunai* Fujimoto, 2015, only three have undivided lateral alae: *Florarctus salvati* Delamare Deboutteville & Renaud-Mornant, 1965, *Florarctus vulcanis* Renaud-Mornant, 1987, and *F. kwoni*. The alae of the specimens from Moorea, although slightly wider than described by Chang & Rho (1997), are rocket-shaped (Fig. 2A), whereas they are roundish in both *F. salvati* and *F. vulcanis*. Our specimens also clearly show "mammilliform" sculpturing on the dorsal cuticle. Furthermore, in our specimens the procuticular supports (*caestus*) form a continuous belt with ill-defined contours lacking lateral processes (Fig. 2B), fitting the original description of *F. kwoni* (Chang & Rho, 1997). In contrast, in *F. salvati* and *F. vulcanis* the procuticular supports lack the continuous belt, rather forming multiple, individual lateral diverticula. In *F. salvati* these diverticula are digit-shaped while in *F. vulcanis* they are enlarged distally. (Renaud-Mornant 1987). This is the first record of *F. kwoni* for French Polynesia and the first time this species has been found beyond the type locality in Palawan Island, the Philippines.

Subfamily: Halechiniscinae (Thulin, 1928)

Genus: *Halechiniscus* Richters, 1908

Halechiniscus perfectus Schulz, 1955

Material examined. Fifteen specimens (122–196 µm long), 5 females, 2 males, 2 second stage larvae (four clawed) and 6 specimens of undetermined gender collected in coral sand at Cook's Bay, 0.5–1.0 m depth.

Remarks. The specimens perfectly match the description of the species in Ramazzotti & Maucci (1983). This species is widely distributed in both intertidal and subtidal sand, and it has been recorded in the Atlantic Ocean (Brazil, Celtic Sea, Faroe Banks, North Sea, Scotland), Indian Ocean, Mediterranean (Adriatic Sea, Alboran Sea, Balearic Sea, Ionian Sea, Tyrrhenian Sea), and the Pacific Ocean (Coral Sea, French Polynesia, Hawaii) (Schulz 1955; Renaud-Mornant 1967, 1971, 1976; Salvat & Renaud-Mornant 1969; de Zio Grimaldi *et al.* 1980a, b, 1983a; Morgan & O'Reilly 1988; Villora-Moreno & de Zio Grimaldi 1996; Hansen *et al.* 2001; Gallo *et al.* 2007; Moura *et al.* 2009; Jørgensen *et al.* 2010).

Subfamily: Styraconyxinae Kristensen & Renaud-Mornant, 1983

Genus: *Styraconyx* Thulin, 1942

Styraconyx kristenseni kristenseni Renaud-Mornant, 1981

Table 1

Material examined. Three specimens, one female 177 µm long and two specimens of undetermined gender (132–171 µm long), collected in coral sand at Cook's Bay, 0.5–1.0 m depth.

Remarks. This species is known from the Atlantic Ocean (Faroe Banks), Mediterranean (Adriatic Sea, Ionian Sea, Tyrrhenian Sea), Pacific Ocean (New Zealand, French Polynesia, Coral Sea, Tasman Sea), and the Red Sea (Renaud-Mornant 1981; de Zio Grimaldi *et al.* 1983a, b, 2003; Kristensen & Higgins 1984; D'Addabbo Gallo *et al.* 1989; Boesgaard & Kristensen 2001; Hansen *et al.* 2001). *Styraconyx kristenseni* was originally described from Moorea Island, French Polynesia, by Renaud-Mornant (1981), with additional specimens collected from French Polynesia (Reao and Mururoa Atolls, in the Tuomoto Archipelago, previously identified as *Styraconyx sargassi* Thulin, 1942 (Renaud-Mornant 1976)). The subspecies *Styraconyx kristenseni neocaledonensis* Renaud-Mornant, 1981 was also identified from New Caledonia from specimens previously identified as *Styraconyx sargassi* (Renaud-Mornant 1981). The species is characterized by having peduncles on external claws only and short clavae (measuring less than 50% of cirri *A*, Table 1). The two subspecies are distinguished by the leg sense organs: *Styraconyx kristenseni neocaledonensis* Renaud-Mornant, 1981**,** characterized by the presence of minute (just spurs) sense organs on legs I–III from New Caledonia, and *Styraconyx kristenseni kristenseni* Renaud-Mornant, 1981, with normally developed spines on legs I–III, from Polynesia. The specimens examined in this study, although having a larger body size, stronger external peduncles and slightly shorter primary clavae/lateral cirri *A* ratio, otherwise fit the original description of *S. kristenseni kristenseni* (Table 1).

TABLE 1. Measurements (in µm) of some structures of specimens of *Styraconyx turbinarium* **sp. nov.** and *S. kristenseni kristenseni* examined in this study and holotypes (measurements in original descriptions) of *S. tyrrhenus* (D'Addabbo Gallo et al., 1989), *S. craticulus* (Pollock, 1983) and *S. kristenseni* (Renaud-Mornant, 1981).

	***S. turbinarium* sp. nov.**			***S. tyrrhenus***	***S. craticulus***	***S. kristenseni kristenseni***		***S. kristenseni***	
	Holotype 14.9.1	Paratype 14.9.2	Paratype 14.9.3	Holotype	Holotype	Specimen 14-4-2	Specimen 14.7.4	Specimen 14.7.5	Holotype
Locality	Moorea	Moorea	Moorea	Sardinia	Virgin Islands	Moorea	Moorea	Moorea	Moorea
Gender	♀	♀	♂	♀	♀	♀	?	?	♀
Body length	164	152	130	135	111	177	171	132	120
Median cirrus	9.9	9.7	?	4	5.8	13.8	14.7	9.6	9
Internal cirri	12.9	11.7	?	12.5	11.3	14.6	12.2	?	12
External cirri	13.0	13.2	?	11	8.6	15.3	15.6	?	10
Lateral cirri *A*	27.8	23.2	?	28	19.5	26.5	27.6	?	20
Primary clavae	14.4	12.3	?	8.5	9.8	10.9	9.4	7.4	9
Cirri *E*	24.3	23.2	?	38	15.6	34.7	31.5	?	24
1st leg spine	8.5	8.5	?	8	5.9	8.6	5.7	7.7	11
2nd leg spine	9.5	?	12.5	11.5	6.8	9.0	9.2	8.6	11
3rd leg spine	12.5	?	9.7 (?)	14	8.8	10.7	?	9.3	10
4th leg sense organ	10.1	9.8	?	9	11.7	12.9	9.2	?	10
Primary clavae/Lateral cirri *A*	*0.52*	*0.53*	*?*	*0.30*	*0.50*	*0.41*	*0.34*	*?*	*0.45*

Styraconyx turbinarium sp. nov.

Figs. 3A–D; Fig. 4A–J; Table 1

Material examined. Holotype (female) and two paratypes (one female and one male) extracted from drifting *Turbinaria ornata* in Opunohu Bay (17° 30.5' S; 149° 51.2' W).

Type repository. The holotype (slide FP, 14.9.1) and the two paratypes (slides FP, 14.9.2 and 14.9.3*) are deposited in the collection of P. Fontoura at the Department of Biology, Faculty of Sciences, University of Porto, Portugal. [* this is a poor preparation]

Specific diagnosis. *Styraconyx* with subterminal mouth cone, eyespots not visible in specimens mounted in PVA. Elongate primary clavae and lateral cirri *A* situated on a common pedestal and enveloped by a common membrane extending almost to claval tip. Indistinct secondary clavae. Peduncles present on all digits: external, sinuous with two small lateral expansions; internal, rod-shaped. Internal digits with heart-shaped proximal pads. Three pointed claws, with strong basal hook and thin accessory spine. Sense organs present on all legs, spines on legs I–III and club-shaped papilla with terminal spine on leg IV. Cuticle coarsely punctated but otherwise smooth.

Holotype description. Female with slight green colour before mounting, 164 µm long and 78 µm wide (in lateral view) between leg pairs II and III (Fig. 3A). Eye spots not visible in our specimens mounted in PVA. The cuticle coarsely punctated (Fig. 3B), consisting of small pillars (*ca.* 20 pillars/10 µm). The punctation also extends to the ventral cuticle and proximal part of the legs. The dorsal cuticle smooth, without any ridges, folds or other ornamental patterns. Subterminal protruded mouth opening, formed of dome-shaped cuticular annular fold without buccal papillae. Complete set of cephalic sense organs, present. Primary clava elongate (14.4 µm long and 2.2 µm wide); lateral cirrus *A* (27.8 µm); both arise from common dorso-lateral pedestal (about 3.5 µm); both are enveloped by transparent membranous sheath extending almost to the claval tip (Fig. 3C; 4I). The primary clava/ lateral cirrus *A* ratio, 0.52. Van der Land's body present in the base of the primary clavae. The lateral cirri *A* unsegmented, i.e. no visible line separating the scapus and the flagellum. Secondary clavae, indistinct. Dorso-frontal internal cephalic cirri (12.9 µm long), located on short cirrophores (*ca.* 1.8 µm), comprising stout scapus (6.1 µm long) followed by short flagellum (*ca.* 6.8 µm long) telescopically inserted in the scapus (Fig. 3C; 4F). Both ventrally located external cephalic cirri (13.0 µm long) and dorsal medial cirrus (9.9 µm long) lack cirrophores, scapus and flagellum indistinct, however proximal portion of cirri (probably corresponding to scapus) much thicker than sharpened distal portion (probably flagellum) (Fig. 4G; 4H). Dorsal medial cirrus inserted well back on head, not extending beyond front edge of head.

Sense organs on all legs, present. Leg I segmented spine (8.5 µm long) with differentiation of scapus and flagellum (Fig. 4B); legs II (Fig. 4C) and III (Fig. 4D), unsegmented spines, 9.5 µm long and 12.5 µm long, respectively. Leg IV, sense organ (10.1 µm long) consists of smooth papilla (5.3 µm) and terminal spine (4.8 µm), arising on short cirrophore, with basal diffractive structure (Fig. 3A; 4E). This papilla seems to be asymmetrical, having the posterior portion less curved than the anterior, but this character must be evaluated with care because the shape of the structure can be deformed by the slide mounting process.

Cirrus *E* (24.3 µm long) consists of short (3.0 µm long) bell-shaped cirrophore, scapus (*ca.* 7 µm long) with accordion-like appearance, and flagellum (*ca.* 14.3 µm long) (Fig. 4J).

Legs consist of coxa, femur, tibia and tarsus. Four digits on each leg. First three pairs of legs, digits of similar length (leg I: internal digits 4.8 µm long, external digits 3.8 µm long). Leg IV, digits longer (internal digits 7.8 µm long, external digits 4.9 µm long). Heart-shaped proximal pads on internal digits, present. Peduncles present on both internal and external digits. The external hook-shaped peduncles (*ca.* 6.5 µm long on legs IV) attached to the base of the claws and have two small basal lateral processes (*ca.* 4.7 µm distant to the tip). The external peduncles, strongly curved at base and enlarged (about 1.5 µm wide) distal to the lateral processes.

Distal part of external peduncles, hollow; hollow area not extending to peduncle base. The very thin internal rod-shaped peduncles extend from the proximal pads to the claw base (Fig. 3D; 4A).

Claws attached to the peduncle at almost a right angle, not crescent-shaped, with claw sheath. Claw sheath not covering tip of claw hooks, however this character needs to be confirmed. Claws on all legs, internal and external digits of similar size (*ca.* 3.3 µm long). Each claw with three points, comprising thin dorsal spine-like accessory hook, clearly shorter than primary claw hook, and downward directed secondary hook, similar or slightly longer than primary hook (Fig. 3D; 4A).

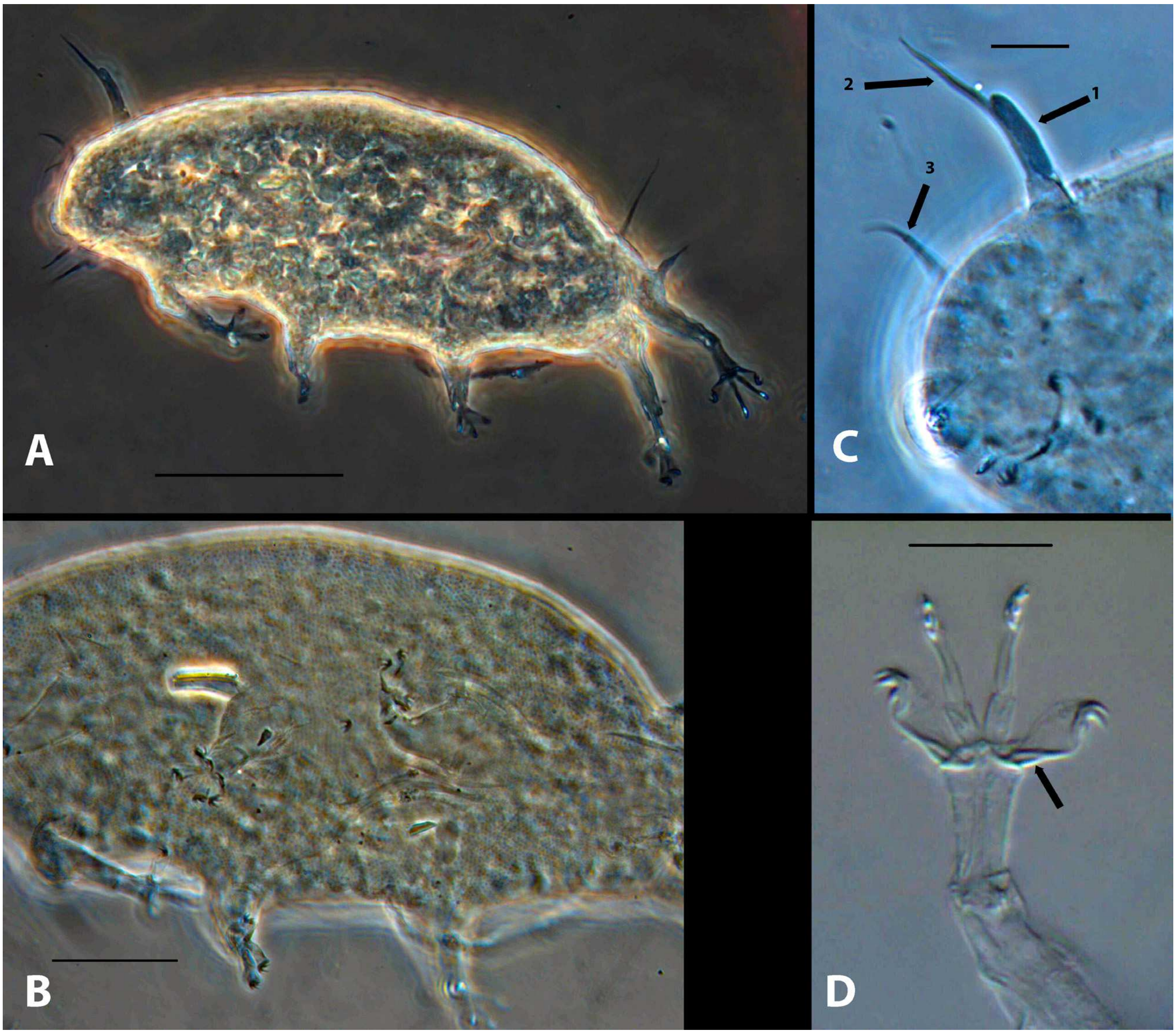

FIGURE 3. *Styraconyx turbinarium* **sp. nov.** Holotype. A. Habitus. Scale bar = 50 µm. B. Cuticular punctations. Scale bar = 25 µm. C. Detail of the primary clava (arrow 1) and lateral cirrus *A* (arrow 2). The segmented internal cephalic cirrus is also visible (arrow 3). Scale bar = 10 µm. D. Leg IV showing claws and peduncles (arrow). Scale bar = 10 µm.

The gonopore consists of a six-cell rosette (9.7 µm from the anus). Seminal receptacles and ducts are not observable in our specimens.

Differential diagnosis. To clearly differentiate *S. turbinarium* **sp. nov.** from similar species we used characters of major taxonomic and phylogenetic value suggested by Kristensen & Higgins (1984) and highlighted by D'Adabbo Gallo *et al.* (1989): namely the type of peduncles and claws and the type of leg sense organs. In addition, the shape of primary clavae (Renaud-Mornant 1982a) and particular characteristics of some species (*e.g.* cuticular characters) were also considered.

Excluding the new species described in this paper, 12 *Styraconyx* species are known as of now. They can be divided into two major groups according the number of peduncles on each foot: seven species constituting the *S. sargassi* group have four peduncles on each foot, and five species of the *Styraconyx hallasi* Kristensen, 1977 group have two peduncles on external digits only. Our new species, *S. turbinarium* **sp. nov.**, has four peduncles on each foot corresponding to the species of the first group: *Styraconyx craticulus*; *Styraconyx craticuliformis* Chang & Rho, 1998; *S. haploceros*; *Styraconyx paulae* Robotti, 1971; *S. sardiniae*; *S. sargassi*; and *Styraconyx tyrrhenus* D'Addabbo Gallo *et al.*, 1989. From this group, *Styraconyx haploceros* with reduced sense organs, and *S. paulae* characterized by having a spine-like primary clavae, can be easily distinguished from all the other species including the new species.

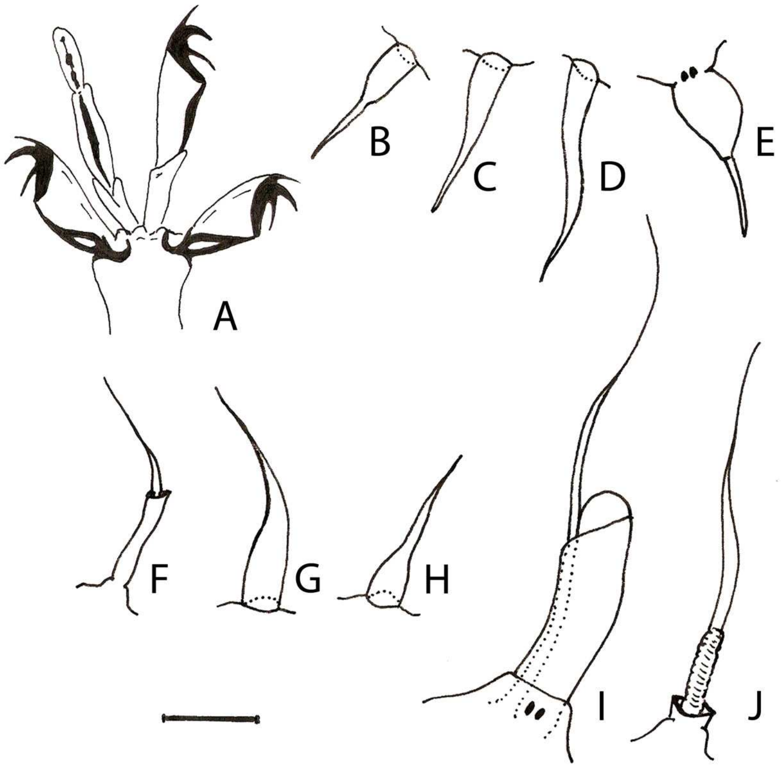

FIGURE 4. Drawings of *Styraconyx turbinarium* **sp. nov.** A. Foot. B. Sense organ leg I. C. Sense organ leg II. D. Sense organ leg III. E. Sense organ leg IV. F. Internal cephalic cirrus. G. External cephalic cirrus. H. Median cirrus. I. Lateral cirrus *A* and primary clava. J. Cirrus *E*. Scale bar = 5 µm.

The new species shares with *S. craticulus* and *S. sargassi* the long sausage-shaped primary clavae, whereas all the other species have a club-shaped or a lanceolate primary clavae. However, unlike *S. sargassi*, the primary clavae and the lateral cirri *A* have a common cirrophore and are enveloped by a common membrane extending beyond the base in both the new species and *S. craticulus*. Additionally, the relative size of claw hooks and especially the external peduncles are very different in *S. turbinarium* **sp. nov.** compared to *S. sargassi*. In the new species, the accessory hook of the claws is thinner and shorter and the external peduncles are much more robust and differently shaped (see figure 45D, page 39 in Kristensen & Higgins 1984, and Fig. 3D). In addition, the lateral cirri *A* are divided in *S. sargassi* and undivided in the new species. The different algal associations of the two species are also important. According to Kristensen & Higgins (1984), *S. sargassi* was found in *Sargassum* (and once on benthic *Dictyota*) whereas our *S. turbinarium* was found in drifting *Turbinaria.*

By having a cuticle without the characteristic grid-like pattern *S. turbinarium* **sp. nov.** differs from *S. craticulus*. In addition, in the new species eye spots were not observed and the sense organs on leg IV have a smooth surface (they are granular, with small tubercles, in *S. craticulus*). The claws of the new species, when compared with the claws of *S. craticulus,* are less curved, the secondary hook is directed downwards, and the accessory hook is smaller and thinner than the other claw hooks. In *S. craticulus* all the cephalic cirri are segmented; in contrast in the new species only the internal cephalic cirrus has a distinct scapus and flagellum. Another very important difference between these two species concerns the shape of the peduncles on the external digits; they are thinner and with the internal hollow area located in the proximal portion in *S. craticulus*. In contrast, in *S. turbinarium* **sp. nov.** the hollow area of the peduncles is restricted to the distal portion following the lateral processes (Fig. 3D, 4A).

Within the *S. sargassi* group, in addition to *S. craticulus* and the new species, only *S. tyrrhenus* has the primary clavae and the lateral cirri *A* situated on common cirrophores and enveloped by a common membrane extending beyond the base. However, in comparison with *S. turbinarium* **sp. nov.**, in *S. tyrrhenus* the primary clavae are shorter and club-shaped as shown by the primary clava/lateral cirrus *A* ratio (Tables 1, 2). Excluding the shape and size of clavae and the presence of segmented external cephalic cirri in *S. tyrrhenus*, all the other features exhibited by the two species are very similar, including the shape of peduncles. Morphologically overall, this makes *S. tyrrhenus* the most similar species to *S. turbinarium* **sp. nov.** Despite the high variability in morphometric data mentioned by Kristensen & Higgins (1984) and the limited number of specimens examined, the membranes enveloping the clavae and lateral cirri *A* and cirri *E* seem to be relatively longer in *S. turbinarium* **sp. nov.**

Etymology. The new species is named after the alga *Turbinaria* with which it is associated. *Styraconyx turbinarium* translates to *Styraconyx* of *Turbinaria*.

Discussion

The genus *Styraconyx* was established by Thulin (1942) and revised by Kristensen (1977). Nevertheless many problems persist concerning the taxonomy of the genus. The reassignment of *Styraconyx* species to the genus *Bathyechiniscus* Steiner, 1926 by Pollock (1983) and the confusion of *S. sargassi* and *S. kristenseni* by Renaud-Mornant (1967, 1981), an indubitable expert on marine tardigrade taxonomy, are examples of those problems. In 1984 the genus was restudied by Kristensen & Higgins. In that study, the authors redescribed the known species of the genus, described two new species, and redefined some important and objective taxonomic characters to distinguish those species. However, they also concluded that the genus is probably paraphyletic which makes its taxonomy very problematic (Kristensen & Higgins 1984). Unfortunately, these difficulties still persist.

The primary clava/lateral cirrus *A* ratio may be a good taxonomic criterion to discriminate *Styraconyx* species (Table 2). Based on these ratios, five sets of species can be discerned: a) species with absent or much reduced clavae, *S. haploceros*; b) species with a very low ratio, *S. hallasi*; c) species with an intermediate ratio (clavae about 1/3 the length of lateral cirri *A*), *S. kristenseni sensu lato, S. nanoqsunguak* Kristensen & Higgins, 1984*, S. qivitoq* Kristensen & Higgins, 1984*, S. sardiniae, S. sargassi, S. testudo* D'Addabbo Gallo *et al.*, 1984*, S. tyrrhenus*; d) species with a high ratio (about 0.50), including the new species and *S. craticulus*; and e) species with a very high ratio, *S. paulae*. This categorization should be viewed as provisional because adequate sample sizes do not exist for statistical analysis and because variation in these values due to preparation needs further study.

Styraconyx haploceros, also in the *S. sargassi* group, was recently studied in the Celtic Sea by Jørgensen & Møbjerg (2014). This species lives in lichens on rocks in the high intertidal zone and it was shown to possess cryptobiotic abilities, surviving desiccation and large changes in salinity. Such capabilities are rare in marine tardigrades and are not known in other members of the genus *Styraconyx*.

According to Renaud-Mornant (1981), *S. kristenseni sensu lato* varies morphologically in different geographic areas, which seems to be corroborated by the specimens examined in this study (larger body size, stronger external peduncles and slightly shorter primary clavae/lateral cirri *A* ratio than the type material). So, it is possible that *S. kristenseni sensu lato* is a complex of cryptic species and, as suggested by Kristensen & Higgins (1984), the probability of describing additional species (or subspecies) is considerable. The same possibility can be extended to other *Styraconyx* species. Pollock (1983) referred to geographic variability concerning *S. craticulus* (see Table 2). For clarification of this subject, more data, including more information about sex and age of the specimens, are needed.

Conclusions

Including the new species, there are now 14 taxa (species and subspecies) in the genus *Styraconyx*. A key to the 12 previously known species (but not the subspecies) can be found in D'Addabbo Gallo *et al.* (1989).

With this study, the total number of marine tardigrade species known from French Polynesia is now nine (*Dipodarctus anaholiensis*, *Echiniscoides sigismundi polynesiensis*, *Florarctus asper*, *Florarctus kwoni, Florarctus stellatus*, *Halechiniscus perfectus*, *Styraconyx turbinarium* **sp. nov.**, *Styraconyx kristenseni kristenseni*, and *Tholoarctus natans natans*). Given that the small amount of material collected for this study yielded two new records and one species new to science, undoubtedly many more species remain to be discovered in this region.

TABLE 2. Ratio (R) between the primary clavae length and lateral cirri *A* length in specimens of *Styraconyx* species (* - mean values).

Species	R	Location	Reference
S. craticulus (Pollock, 1983)	0.50 (holotype, ♀)	Virgin Islands, Atlantic Ocean	Pollock 1983
	0.47 (n=10)*	Virgin Islands, Atlantic Ocean	Pollock 1983
	0.50 (n=1)	Haiti, Atlantic Ocean	Pollock 1983
	0.37 (n=1)	Guadaloupe, Atlantic Ocean	Pollock 1983
	0.36–0.43 (n=4)	Bahamas, Atlantic Ocean	Unpublished data
S. craticuliformis Chang & Rho, 1998	0.41 (holotype, ♀)	Andaman Sea (Thailand), Indian Ocean	Chang & Rho 1998
S. turbinarium **sp. nov.**	0.52–0.53 ♀♀, n=2)	French Polynesia, Pacific Ocean	This study (Table 1)
S. hallasi Kristensen, 1977	0.12–0.18 (n=2)	Greenland	Kristensen 1977
S. haploceros Thulin, 1942	- (clavae absent, ♀♀, n=2)	Portugal, Atlantic Ocean	Unpublished data
S. kristenseni Renaud-Mornant, 1981	0.41–0.45 (♀♀, n=3)	French Polynesia, Pacific Ocean	Renaud-Mornant 1981
	0.34 (gender ?), 0.41 (♀)	French Polynesia, Pacific Ocean	This study (Table 1)
S. nanoqsunguak Kristensen & Higgins, 1984	0.36 (holotype, ♀)	Greenland, Atlantic Ocean	Kristensen & Higgins 1984
	0.33 (♀♀, n=10)*	Greenland, Atlantic Ocean	Kristensen & Higgins 1984
	0.35 (♂♂, n=10)*	Greenland, Atlantic Ocean	Kristensen & Higgins 1984
S. paulae Robotti, 1971	0.69 (n=1)	Stromboli, Italy, Mediterranean Sea	Robotti 1971
S. qivitoq Kristensen & Higgins, 1984	0.36 (holotype, ♀)	Greenland, Atlantic Ocean	Kristensen & Higgins 1984
	0.37 (♀♀, n=25)*	Greenland, Atlantic Ocean	Kristensen & Higgins 1984
	0.45 (♂♂, n=6)*	Greenland, Atlantic Ocean	Kristensen & Higgins 1984
S. sardiniae D'Addabbo Gallo *et al.*, 1989	0.32 (holotype, ♀)	Sardinia, Mediterranean Sea	D'Addabbo Gallo *et al.* 1989
	0.33 (♀♀, n= 46)*	Sardinia, Mediterranean Sea	D'Addabbo Gallo *et al.* 1989
	0.28-0.49 (♀♀, n=2)	Portugal, Atlantic Ocean	Unpublished data
S. sargassi Thulin, 1942	0.40 (n=1)	Sargassum Sea, Atlantic Ocean	Thulin 1942
S. testudo D'Addabbo Gallo *et al.*, 1984	0.18 (holotype, ♀)	Italy, Mediterranean Sea	D'Addabbo Gallo *et al.* 1984
	0.27 (♀♀, n=6)	Italy, Mediterranean Sea	D'Addabbo Gallo *et al.* 1984
S. tyrrhenus D'Addabbo Gallo *et al.*, 1989	0.30 (holotype, ♀)	Sardinia, Mediterranean Sea	D'Addabbo Gallo *et al.* 1989
	0.34 (♀♀, n= 6)*	Sardinia, Mediterranean Sea	D'Addabbo Gallo *et al.* 1989

Styraconyx turbinarium **sp. nov.** and *S. sargassi* are ecologically unique among tardigrades in that they appear to be associates of rafting algae. Very little is known about dispersal in tardigrades (Nelson *et al.* 2015), but it is logical to suppose that these species could be more broadly dispersed and genetically interconnected than other benthic marine tardigrades. Further studies of tardigrades on algal rafts could be fruitful.

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