

New records of *Swiftia* (Cnidaria, Anthozoa, Octocorallia) from off the Pacific Costa Rican margin, including a new species from methane seeps

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Abstract

Exploration of the deep sea off the Pacific margin of Costa Rica has resulted in the discovery of a number of new species and reports for the region. Here, we report on the occurrence of the octocoral genus *Swiftia*, and describe a new species collected by the *Alvin* submersible off the Pacific coast of Costa Rica. The new species has been observed at around 1000 m depth, growing on authigenic carbonates near methane seeps. *Swiftia sahlingi* sp. nov. is characterised by having bright red colonies that are with limited branching, with slightly raised polyp-mounds, thin coenenchyme mainly composed of long warty spindles, and conspicuous plates. A molecular phylogenetic analysis supports the differences between this new taxon and the closest *Swiftia* species. The new species represents the first record of the genus from Costa Rica and in fact for the Eastern Tropical Pacific.

Key words: Carbonate mounds, gorgonian, methane seeps, Plexauridae, *Swiftia*, taxonomy

Introduction

The Pacific margin of Costa Rica has been explored a number of times since the late 1990s and early 2000s, mainly with a chemical and geophysical focus, and over 100 fluid seeps have been reported in the area (Sahling *et al.* 2008). In 2009 and 2010, studies began on the biota and microbiological processes at some of those cold methane seeps and ‘hydrothermal seeps’ including the diversity of macrofauna inhabiting authigenic carbonates (Levin *et al.* 2012, 2015). The first species described from those expeditions was a new species of black coral, *Lillipathes ritamariae* (Opresko & Breedy 2010). Also among the organisms observed and collected was an octocoral of the genus *Swiftia* Duchassaing and Michelotti, 1860 (Fig. 1F in Levin *et al.* 2015).

In 2017, the Human Occupied Vehicle (HOV) *Alvin* on the RV *Atlantis* was used to further explore the methane seeps and the deep-sea carbonate mounds off the Pacific coast of Costa Rica. During this expedition, the previously noted *Swiftia* was commonly observed growing on authigenic carbonate ledges at depths of 996 to 1002 m at one of the methane seep sites, called Mound 12 (Sahling *et al.* 2008). Herein, we describe this species using an integrative taxonomic approach, evaluating morphological characters and two mitochondrial genes (*mtMutS* and *igr1+COI*). We also report the occurrence of another *Swiftia* species found on a seamount further offshore. *Swiftia sahlingi* sp. nov. represents the first species of the genus *Swiftia* described from Costa Rica, and the first report of the genus in the Eastern Tropical Pacific.

Material and methods

Study Site and Collection Methods. The specimens were collected with the HOV *Alvin* (Fig. 1A) during the R/V

Atlantis Expedition AT37-13, between 996–1002 m, at Mound 12, approximately 50 km off the mainland on the Pacific margin of Costa Rica (08°55.845'N, 084°18.768'W). Mound 12 is characterized by methane seeps on the western flank and abundant authigenic carbonate on the sides and crest of the mound. The coral colonies were photographed *in situ* (Figs. 2A–D), collected, and once retrieved, they were kept alive for photographs (Figs. 1A–C) and preliminary analyses. The specimens were preserved dried and/or in 96% ethanol. The holotype and paratypes are deposited in the Museo de Zoología, Universidad de Costa Rica, San Jose, Costa Rica (MZUCR) and subsamples of some specimens are housed in the Benthic Invertebrate Collection at the Scripps Institution of Oceanography, La Jolla, California (SIO-BIC).

Morphological analysis. For microscopic study, the specimens were prepared according to Breedy and Guzman (2002) and observed using optical and scanning electron microscopy (Olympus LX 51 and Hitachi N-3700) at the Research Center of Microscopic Structures (CIEMic) of the University of Costa Rica (UCR). Optical micrographs of unsorted samples of sclerites were presented for color observation and relative abundance. Electron micrographs of the sclerites show sculptural details. The taxonomic evaluation was based on Nutting (1909), Deichmann (1936), Madsen (1970), Breedy *et al.* (2015) and Williams and Breedy (2016). The terminology used in descriptions mostly follows Bayer *et al.* (1983).

DNA sequence acquisition and phylogenetic analysis. Subsamples were taken from each specimen at sea and stored in 95% EtOH. Total genomic DNA (gDNA) was extracted from tissue samples (3–6 polyps, size dependent) using Qiagen DNeasy Blood & Tissue Kit, according to the manufacturer's protocol. Two mitochondrial gene fragments (COI, ~900bp; MutS, ~700bp) were amplified using standard PCR protocols and sequenced. For COI amplification, primers COII8068xF (McFadden *et al.* 2004) and COIOCTr (France & Hoover, 2002) were used to amplify a fragment encompassing the 'Folmer region' of COI and part of the adjacent intergenic region (igr1). For MutS, the primers ND42599F (France and Hoover, 2002) and MUT3458R (Sánchez *et al.* 2003) were used. PCR reactions were carried out in 25 µl reactions containing 2.5 µl 10X Econo Taq Buffer, 2 µl MgCl₂ (25 nM), 1 µl BSA, 2.5 µl dNTPs (10 µM), 1 µl per primer (10 µM), 0.25 µl Econo Taq polymerase, 1–3 µl gDNA and 13.75 µl molecular grade water. COI and MutS polymerase chain reaction (PCR) were run using an Eppendorf Mastercycler with an initial denaturation step of 94°C for 5 minutes and a final extension at 72°C for 10 minutes, under the following conditions, respectively: 32 x (94°C:30 s; 60°C:90 s; 72°C:60 s); 32 x (94°C: 30 s; 51°C:45 s; 72°C:60 s). Negative controls were included in each PCR to check for contamination. PCR products were resolved on a 1.5% agarose gel stained with SYBR safe DNA gel stain. Amplified products were cleaned and sequenced in an automated sequencer by Genewiz (South Plainfield, NJ).

The COI and MutS sequences were aligned in BioEdit (Hall, 1999) against other *Swiftia* and outgroup sequences retrieved from the NCBI GenBank database. Outgroups were chosen based on the placement of *Swiftia* in the phylogenetic analysis of Octocorallia in McFadden *et al.* (2006). A maximum likelihood tree was generated in RAxML 8 (Stamatakis, 2014) using partitioned gene fragments and the GTR+G+I substitution model and support as assessed via 1000 thorough bootstrap pseudoreplicates. Bayesian analyses were also performed using the Beast2 program package (Bouckaert *et al.* 2014) where the HKY site model (based on JModeltest2; Darriba *et al.* 2012) was used. Sequences were partitioned and three separate MCMC analyses with 10 million generations were run, the output of which were checked in Tracer (Rambaut *et al.*, 2018) for convergence and stationarity. A majority rule consensus tree was generated using TreeAnnotator from the Beast2 package and visualized in FigTree v1.4.3 along with posterior probabilities.

Results

Systematics

Subclass Octocorallia

Order Alcyonacea Lamouroux, 1816

Family Plexauridae Gray, 1859

***Swiftia* Duchassaing & Michelotti, 1864**

Swiftia Duchassaing & Michelotti, 1864:13; Kükenthal, 1924: 236; Deichmann, 1936: 185–186; Bayer, 1956: F206; Bayer, 1981: 945; Harden, 1979: 109–110; Breedy, *et al.*, 2015: 329; Williams & Breedy, 2016: 3.
Stenogorgia Verrill, 1883: 29 (see Kükenthal, 1924: 347 for *Stenogorgia* synonymy).
Platycaulos Wright & Studer, 1889: 61; Bayer, 1981: 945.
Callistephanus Wright & Studer, 1889: 62; Bayer, 1981: 945.
Allogorgia Verrill, 1928: 7; Bayer, 1981: 945.

Diagnosis (modified from Breedy *et al.* 2015, Williams & Breedy 2016). Growth form variable, whip-like, fan-like or bushy. Colonies branching in one or several planes, lateral, fan-like, dichotomous, pinnate-like, or unbranched. Branches mostly free or with some anastomoses. Axis horny with non-mineralised organic fibers filling the axial chambers. Polyp mounds low-rounded to cylindrical or conical, slightly raised to prominent, scattered, or crowded, usually biserial or present on all sides of polyp-bearing branches, giving, in some cases, a zigzag outline characteristic of some *Swiftia* colonies. Coenenchyme usually thin. Coenenchymal sclerites mostly capstans and spindles many of which are modified to a lesser or greater degree as discs, eight-radiates, and irregular spindles. Wart clubs and/or plates present in some species. Anthocodiae with point arrangements of straight to curved bar-like rods, and frequently elongate tuberculated spindles and warty clubs. Collaret absent or of a few bar-like rods transversely arranged. Polyp-neck zone nude or with plates or scales. Colour of the colonies red, orange, pink or white.

Type species: *Swiftia exserta* (Ellis & Solander, 1786)

Distribution. The genus has been reported for the western and northeast Atlantic, Indo-Pacific, and in the Pacific from Californian and northern Patagonia in the Magellanic Province, Chile, and from the Gulf of Alaska and Aleutian Islands (Breedy *et al.* 2015) with about 23 species considered as valid according to the World Register of Marine Species 2019 (WORMS).

***Swiftia sahlingi* sp. nov.**

Figures 1–4

Material examined. *Holotype:* MZUCR 2725, SIO-BIC Co2917, ethanol preserved, Mound 12, 1000 m, HOV *Alvin* Dive 4908, pilot Jefferson Grau, R/V *Atlantis* Expedition AT37-13, 23 May 2017.

Paratypes: MZUCR 1967, ethanol preserved, Mound 12, AT15-44, HOV *Alvin*, Dive 4501, pilot M. Spear, 1000 m, 22 February 2009. MZUCR 2726, 2 specimens, ethanol preserved, as the holotype; MZUCR 2647, 3 specimens, ethanol preserved, as the holotype; MZUCR 2648, SIO-BIC Co2916, ethanol preserved, Mound 12, 999 m, HOV *Alvin*, Dive 4907, pilot J. Patrick Hickey, 22 May 2017. MZUCR 2727, 5 specimens; MZUCR 2650 (CR-AV-4909-4), 2 specimens; MZUCR 2730 (CR-AV-4909-5), ethanol preserved; MZUCR 2727, ethanol preserved; MZUCR 2731, fragment, ethanol preserved, Mound 12, 996–1000 m, HOV *Alvin*, Dive 4909, pilot Mike Skowronski, 24 May 2017. MZUCR 2732, SIO-BIC Co2935, dry, Mound 12, 1002 m, HOV *Alvin*, Dive 4917, pilot Jefferson Grau, 1 June 2017. MZUCR 2729, 2 specimens; MZUCR 2733, SIO-BIC Co2945, 3 specimens, Mound 12, 996 m, HOV *Alvin*, Dive 4922, pilot Mike Skowronski, 5 June 2017.

Type locality: Mound 12 (08°55.845'N, 084°18.768'W), 996–1002 m, Costa Rica Pacific margin.

Description. The holotype is an erect, sparsely branched colony, 9 cm tall, and about 10 cm wide (Figs. 1A, 2A). It is attached to a 15-cm long rock together with a smaller colony (7 cm tall). The two colonies are about 2.5 cm apart, and arise from incrusting holdfasts about 1 cm in diameter each (Figs. 1A, 2A–B). The main stem of the holotype is 3 mm in diameter at the base, and extends 7 mm tall, subdividing in 4 main branches that subdivide 2–3 times, branching up to five times (Fig. 1A). Branching is lateral and irregular in different planes. The branches are stout, and reach up to 2 mm in diameter including the polyp-mound. Unbranched terminal ends reach up to 8 cm in length. The flexible horny axis is light brown and somewhat translucent, with non-mineralised organic fibers. The main stem is devoid of polyps. The polyps are translucent (Figs. 1B–C), and are about 1 mm apart. Polyp mounds are alternating, about 6 polyp mounds/cm at the end branchlets (n=8 branches) (Fig. 1A). The polyp mounds are perpendicular to the branches, raised up to 1 mm tall (Figs. 1B–C) and about the same in width. The anthocodiae are preserved exsert, reaching up to 1 mm tall, and fully expanded, in life, up to 3 mm (Figs. 1B–C, 2A–C).

The coenenchyme is thin. Coenenchymal sclerites consist of long, thin, warty spindles, mostly straight, 0.26–

0.60 mm long and 0.04–0.09 mm wide (Figs. 3A, 4A). Conspicuous plates with sparse tubercular sculpture, 0.153–0.315 mm long and 0.05–0.08 mm wide (Figs. 3A, 4C) are surrounding the polyp mound, at the neck zone of the anthocodiae and also occur in the external layer. The sclerites in the axial sheath are mostly tuberculated spindles, straight and curved; and immature sclerites (Figs. 3A, 4B). The anthocodial armature is arranged “en chevron” with points consisting of bar-like rods, straight or slightly bent, 0.28–0.44 mm long, and 0.04–0.08 mm wide (Fig. 4D), warty clubs with tuberculated or bifurcated heads, 0.19–0.39 mm long, and 0.034–0.075 mm wide (Fig. 4E), and irregular flattened rods around the peristome and along the tentacles, up to the tips, 0.10–0.19 mm long and 0.022–0.049 mm wide (Figs. 3B, 4E). Tentacular sclerites are colourless (Fig. 3B).

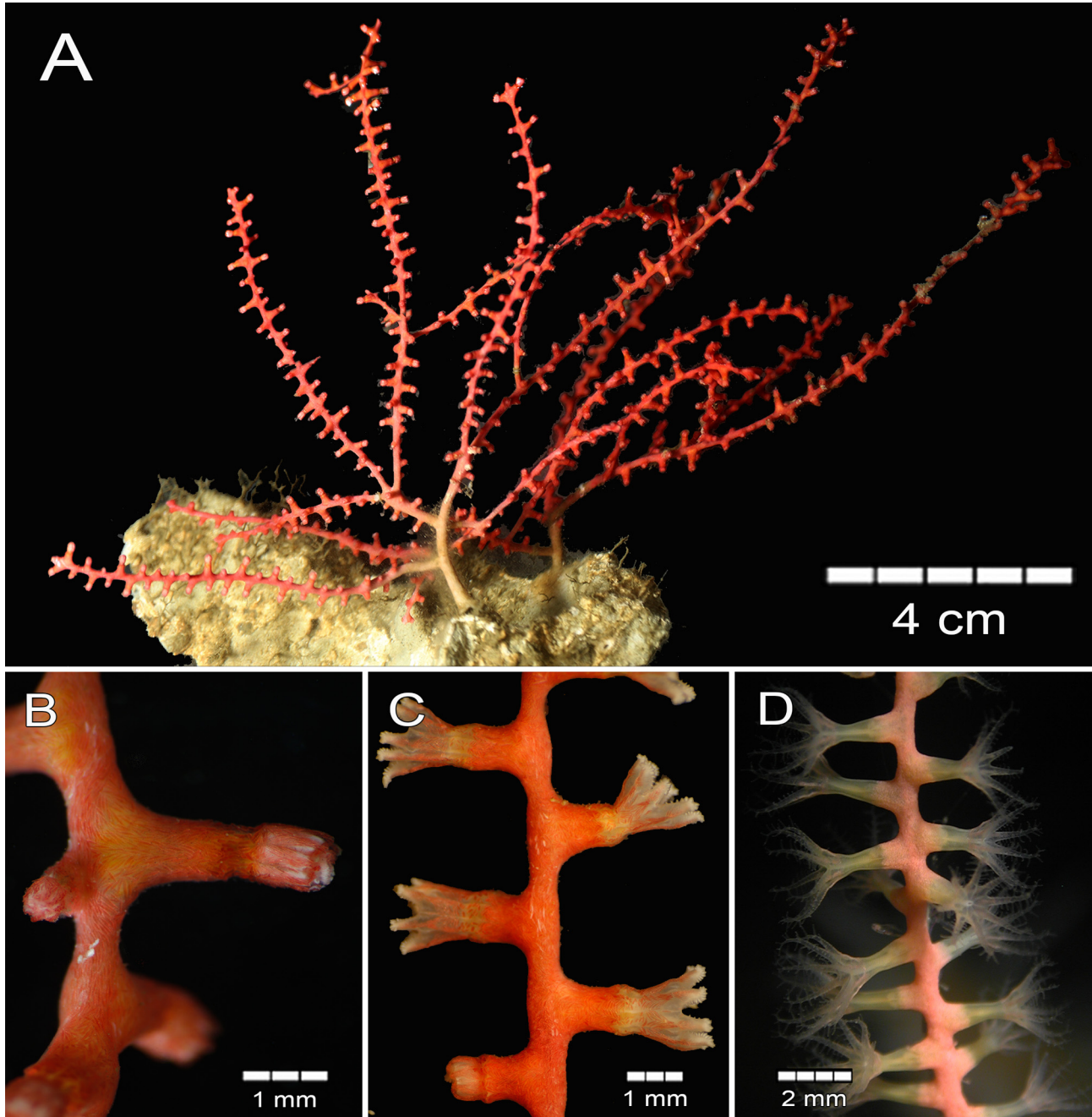


FIGURE 1. *Swiftia sahlingi* sp. nov. MZUCR 2725, holotype; (A) entire colony; (B) detail of branches and polyp mounds; (C) MZUCR 2729, paratype, polyp detail; (D) *Swiftia comauensis*, polyp detail (photograph: Verene Häussermann).

The colour of the colony is red, and preserves the colour after fixation, sclerites are red, orange and of lighter hues (Figs. 1A, 3A).

Variability. The paratypes are from 8 to 17 cm long (the largest MZUCR 2730). Specimens have up to 9 main branches that subsequently subdivide up to 8 times (MZUCR 1967). Unbranched terminal ends reach up to 8.5

cm (MZUCR 2729). Polyps are distributed as in the holotype, but more closely spaced, in some cases, i.e., 5–5.3 polyps/cm ($n=20$ branches); but they could be more distant at the base of the colonies, up to 2 mm apart (MZUCR 2729). Stems are normally devoid of polyps. In some cases, the lateral branches of neighbouring colonies could stick together forming a loose braid (e.g. MZUCR 1967, MZUCR 2650). The sclerite types, colours and sizes of the paratypes are similar to those of the holotype.

Habitat. The species was found living in dense clusters on top of flat authigenic carbonate ledges (Figs. 2A–D). Many of the observed and collected colonies were close to active methane seepage, and a colony was even observed on a tube of the polychaete *Lamellibrachia* (Siboglinidae). Nearby the collection location were clusters of mussels (*Bathymodiolus* spp.), bacterial mats and branching Foraminifera.

Etymology. The species is named in memory of Heiko Sahling, a distinguished marine geologist who discovered and named Mound 12, the type locality of the new species.

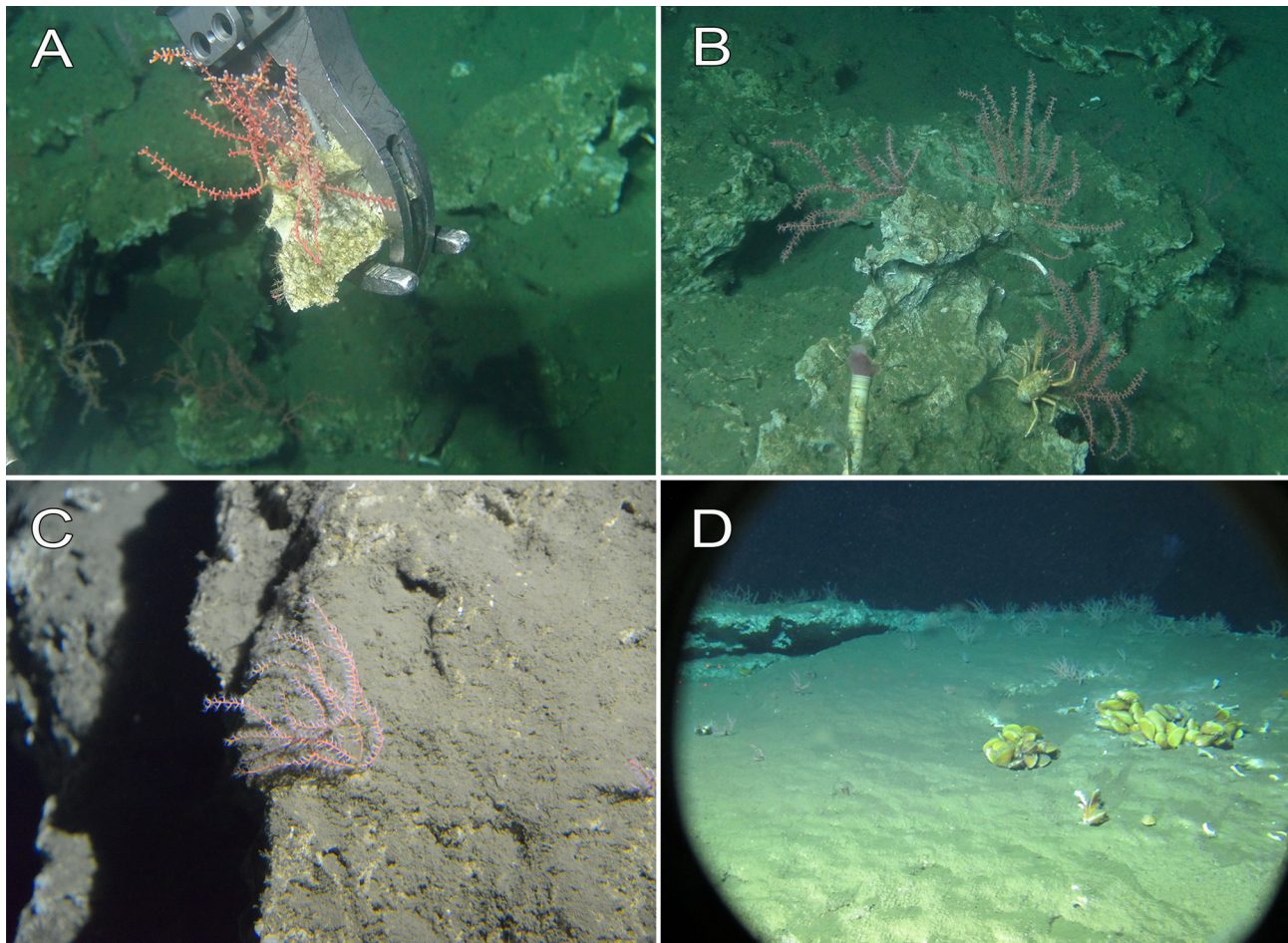


FIGURE 2. *Swiftia sahlingi* sp. nov. (A) MZUCR 2725, holotype; (B–D) colonies *in situ*, at the type locality, Mound 12.

Swiftia sp.

Material examined. MZUCR 2772, AD 4927-1, SIO-BIC Co2969, ethanol preserved, Seamount 1, 2270 m, HOV *Alvin*, Dive 4927, pilot Jefferson Grau, 10 June 2017. MZUCR 2773, SIO-BIC Co3046, ethanol preserved, Seamount 1, 2089 m, HOV *Alvin*, Dive 4983, pilot Jefferson Grau, 29 October 2018.

Diagnosis. Colony subflabellate, branching irregularly pinnate and in one plane. Main stem up to 2.8 mm, branchlets thin, 0.5–1.7 mm in diameter. Coenenchyme thin, with predominance of spindles in outer layer. Spindles with scarce warts and ornamentation, up to 0.18 mm long, and tuberculate radiates up to 0.12 mm long. Polyp mounds prominent, 1.5–2.23 mm tall, and 1.5–2 mm wide and well spaced, about 4–5 polyps/cm. Anthocodial armature strong, “*en chevron*” with bar-like rods, up to 0.2 mm long, and with warty clubs up to 0.12 mm long.

Sclerites colour pale orange. Colony colour brownish red.

Remarks. The phylogeny shows that this species matches sequences from GenBank for what is called *S. simplex* from the NE Pacific (Everett *et al.* 2016). However, the morphology does not match *S. simplex* sensu Nutting 1909 (Breedy pers. obs). Therefore, further work is needed on the NE Pacific *Swiftia* species to resolve this problem and we leave the specimen simply as *Swiftia* sp.

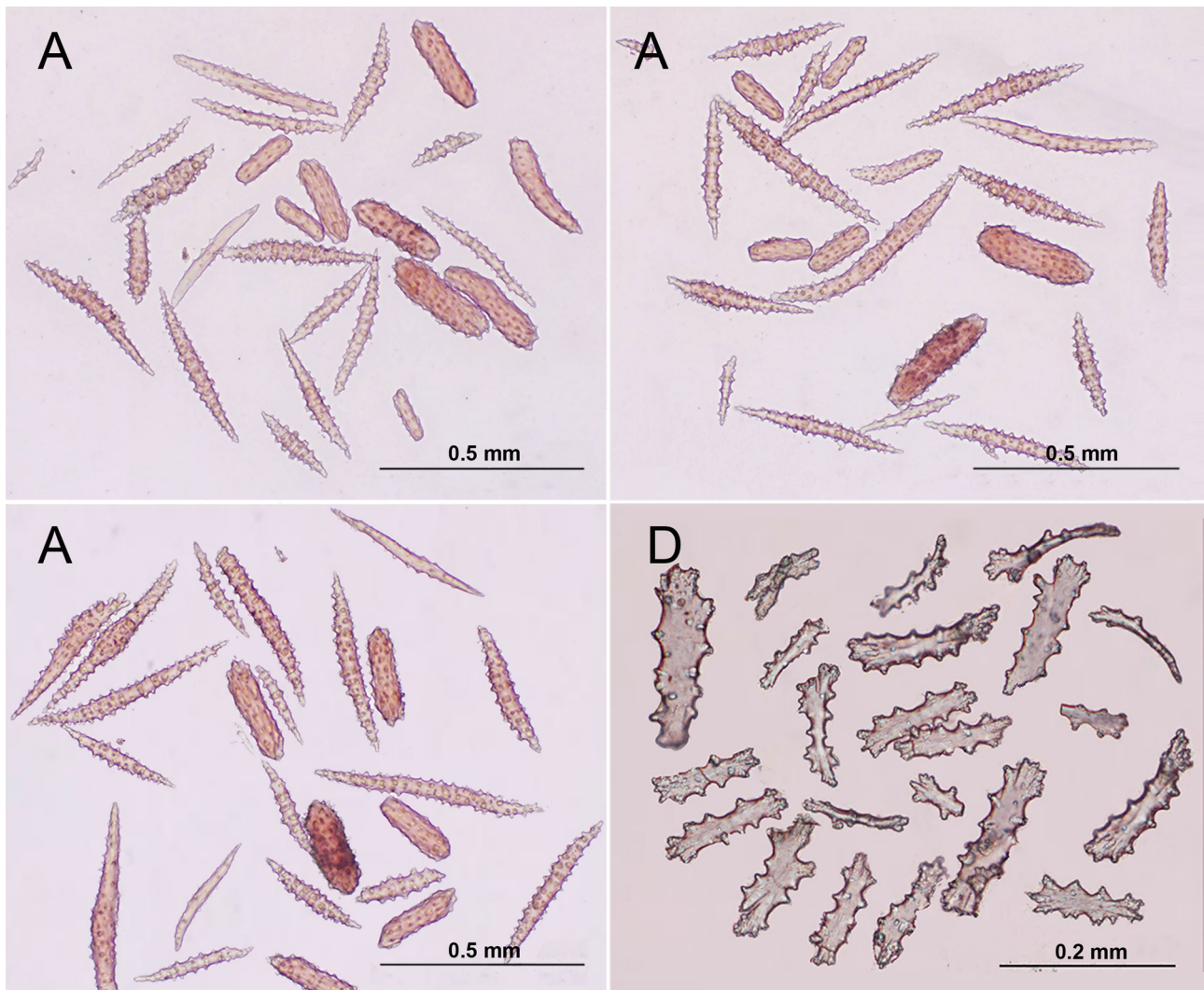


FIGURE 3. *Swiftia sahlingi* sp. nov., MZUCR 2725 (holotype). (A–C) coenenchymal sclerites; (D) tentacular rods (optic micrographs).

Key to *Swiftia* species reported from California, USA to Chile

(based on Nutting 1909, Breedy *et al.* 2015, Williams and Breedy 2016)

- 1a. Colony unbranched (flagelliform, whip-like) or Y-shaped 2
- 1b. Colony multiple-branched 3
- 2a. Colony white; polyp mounds low (less than 1 mm tall), wider than tall; coenenchymal sclerites without plates *S. farallonesica* Williams and Breedy, 2016
- 2b. Colony pink; polyp mounds slightly raised (more than 1 mm tall), taller than wide; coenenchymal sclerites with plates *S. simplex* (Nutting, 1909)
- 3a. Colony flabellate, densely branched 4
- 3b. Colony sparsely branched 6
- 4a. Colony irregularly pinnate; polyp-mounds prominent (more than 1.5 mm tall) and sparsely spaced (more than 2 mm) 5
- 4b. Colony mostly dichotomous; polyp-mounds slightly raised (less than 1.5 mm tall) and closely spaced (less than 1.5 mm) *S. spauldingi* (Nutting, 1909)
- 5a. Colony red with deep-red polyp mounds; branches not anastomosing, branching irregularly pinnate, polyp mounds more than 2.5 mm apart *S. kofoidi* (Nutting, 1909)
- 5b. Colony dark purplish red; branches frequently anastomosing in a loose reticulation, polyp-mounds less than 2.5 mm apart

-*S. torreyi* (Nutting, 1909)
- 6a. Branches dropping and flexible, anthocodiae with naked neck zone; outer coenenchyme and polyp-mound rims without plates, mostly composed of spindles *S. comauensis* Breedy *et al.*, 2015
- 6b. Branches stout, anthocodiae with plates at neck zone; outer coenenchyme and polyp-mound rim with plates and spindles *S. sahlingi* **sp. nov.**

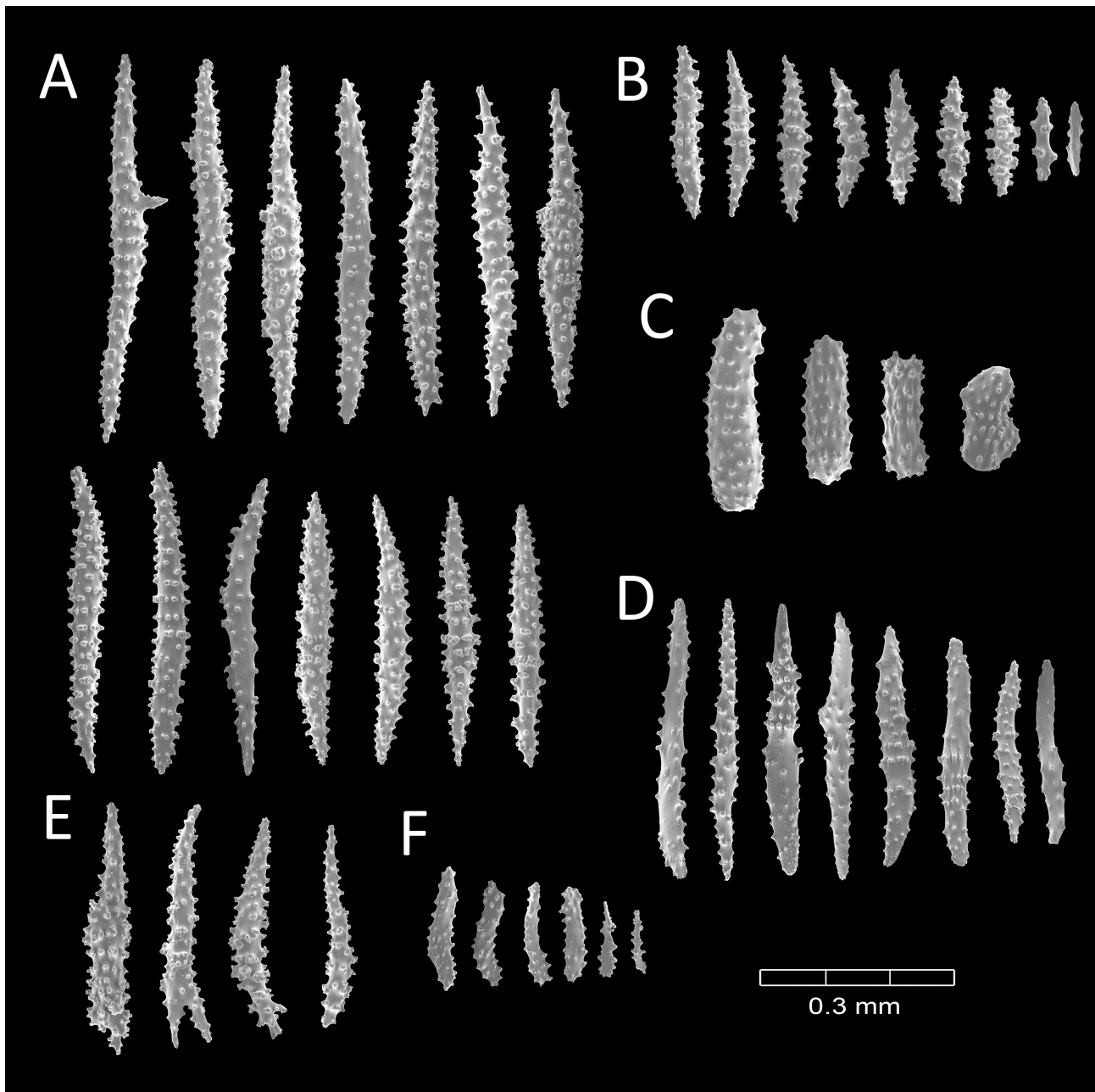


FIGURE 4. *Swiftia sahlingi* **sp. nov.**, MZUCR 2725 (holotype) SEM micrographs. (A) spindles; (B) spindles and radiates; (C) plates; (D) points sclerites; (E) warty clubs; (F) polyp rods.

Species comparison. *Swiftia* is currently placed in the octocoral family Plexauridae (Williams and Cairns 2015, Williams and Breedy 2016). Differences among *S. sahlingi* **sp. nov.** and the former described species appear in the Key of *Swiftia* species above. *Swiftia simplex* and *S. farallonesica* are usually unbranched or with a few branches forming Y-shaped colonies; *S. farallonesica* is white and with low polyp-mounds, 0.8–1 mm tall, and about 2 mm wide (Williams and Breedy 2016); *S. simplex* is of a light pink colour and slightly raised polyp-mounds, about 1 mm (Nutting 1909) taller than wider; while *S. sahlingi* **sp. nov.** is of a bright red colour, branches several times, and the polyp mounds are about 1 mm tall and of about the same in width. *Swiftia spauldingi* is a bright red colony, similar to *S. sahlingi* **sp. nov.** but it has a mostly dichotomous branching pattern and slightly raised and closely placed polyp

mounds, different from the new species. *Swiftia torreyi* and *S. kofoidi* are red flabellate colonies, with prominent polyp-mounds, taller and more separated distributed than the ones in *S. sahlingi* **sp. nov.** *Swiftia torreyi* has characteristically dense anastomosing branches, relative to other species in the genus, forming a loose net-like colony, which is different from the sparse, ascending branching pattern of the new species. *Swiftia kofoidi* and *S. torreyi* lack the characteristic plates in the polyp-mound rims and outer coenenchyme of *S. sahlingi* **sp. nov.** *Swiftia comauensis*, with a sparse branching colony, is the most similar species morphologically (Breedy *et al.* 2015), but the *S. sahlingi* **sp. nov.** colony form is stouter and more ramified than in the former. The structure of the anthocodiae is different, being weaker in the *S. comauensis*, which has an almost naked neck zone (Figs. 1B–D). Sclerites differ in types and relative abundances, but differ little in size, with the main difference being the absence of plates in coenenchyme and anthocodiae of *S. comauensis*. Colonies and sclerites are red in both species, but brighter in the new one.

Phylogenetic relationships. Mitochondrial DNA sequences were successfully obtained from 16 individuals identified as *Swiftia*. PCR and sequencing yielded ~890 bp fragments of COI and ~670 bp fragments of MutS for individuals from both locations: 15 for Mount 12 and one from Seamount 1 (see Table 1 for accession numbers). There was no intraspecific sequence variation observed in the COI or MutS fragments among any of the 15 specimens of *Swiftia sahlingi* **sp. nov.** sequenced. However, the single specimen collected from Seamount 1 showed marked differences in both loci from *Swiftia sahlingi* **sp. nov.** The *Swiftia* sp. specimen from Seamount 1 was 1.1% divergent on COI and 2.4% on MutS (uncorrected pairwise distance) from *Swiftia sahlingi* n. sp. It was the sister taxon a *Swiftia* ‘simplex’ terminal from the NE Pacific (Fig. 5) and these likely represent the same species (not *S. simplex*) with less than 0.2% on both COI and MutS distance between them. *Swiftia sahlingi* n. sp., was 1.2% and 3.1% divergent respectively from its sister taxon *S. spauldingi* (Fig. 5). This specimen also showed morphological differences with *S. sahlingi* **sp. nov.** and other previously described species within this genus. Phylogenetic results using Bayesian and ML methods produced similar topologies, but only the ML result is shown here (Fig. 5). *Swiftia* was recovered as a clade in both analyses with reasonable support. *Swiftia sahlingi* **sp. nov.** was found to be the sister taxon to *S. spauldingi* in each analysis. However, the support values for this relationship were low. The second specimen type from Seamount 1 was recovered, with high support from both methods, as a sister taxon to specimens referred to as *Swiftia simplex* from the NE Pacific (Everett *et al.* 2016). However, this species likely needs to be revised as current descriptions vary considerably (Cairns *et al.* 2017).

TABLE 1. DNA sequences from GenBank used in assessing the placement of *Swiftia* specimens collected from Costa Rica. Sequences in bold are new.

Species	COI	MUTS
<i>Swiftia pallida</i>	FJ264905	KC984598
<i>Swiftia pacifica</i>	KF874210	MF319963
<i>Swiftia spauldingi</i>	KF874183	MF319940
<i>Swiftia koreni</i>	KC984632	KC984596
<i>Swiftia exserta</i>	KC984618	KC984582
<i>Swiftia kofoidi</i>	KX904960	MF319961
<i>Swiftia simplex</i>	KX904978	MF319965
<i>Swiftia sahlingi</i> sp. nov.	MK775491	MK775493
*<i>Swiftia</i> sp.	MK775492	MK775494
OUTGROUPS		
<i>Leptogorgia virgulata</i>	MH235899	AY126418
<i>Plexaurella nutans</i>	GQ342451	HG917026
<i>Pacifigorgia stenobrochis</i>	HG917078	HG917026

(*) This specimen matches the sequences of the species reported in the GenBank as *Swiftia simplex* (KX904978 and MF319965) but because the taxonomic status of *S. simplex* needs revision, we keep the species as *Swiftia* sp. (MK775492 and MK775494).

Geographic distribution. *Swiftia* has not been reported from the Eastern Pacific in the area between Baja California and Perú, but is known from California to the north and from the Chilean fjords to the south (Table 2). *Swiftia comauensis* Breedy *et al.*, 2015, is known from Chile, while *Swiftia kofoidi* (Nutting, 1909), *Swiftia spauldingi* (Nutting, 1909), *Swiftia simplex* (Nutting, 1909), *Swiftia torreyi* (Nutting, 1909) and *Swiftia farallonesica* Williams

& Breedy, 2016 are known from California, USA. Most of the species were collected in shallow waters (Table 2), with the exception of *S. torreyi*, *S. simplex* and the new species (Table 2) (Nutting 1909, Williams and Breedy 2016). However, the geographic distribution and depth range of the genus as a whole needs to be revised because many of the museum specimens that have been identified as *Swiftia* belong to other genera (Breedy pers. obs.).

TABLE 2. Geographic distribution and bathymetry of the *Swiftia* species reported from California, USA to Chile (After Nutting 1909, Breedy *et al.* 2015, Williams & Breedy 2016).

Species	Location	Depth (m)
<i>S. farallonesica</i>	Greater Farallones, National Marine Sanctuary, off Bodega Bay	181–190
<i>S. simplex</i>	Channel Islands, Santa Barbara, Santa Cruz	817–933
<i>S. spauldingi</i>	Monterey Bay	no data
<i>S. torreyi</i>	Monterey Bay	48–1942
<i>S. kofoidi</i>	Monterey Bay	110–135
<i>S. comauensis</i>	Comau Fjord, Chilean fjords	15–59
<i>S. sahlingi</i> sp. nov.	Costa Rica Pacific margin	996–1002

Conclusion

Morphological characters of gorgonians, growth form of the colony, axial structure, size and arrangements of polyps, size, shape, and arrangement of sclerites must be considered together in establishing taxonomic boundaries of species (Bayer 1991). In this sense, *S. sahlingi* **sp. nov.** showed clear differences with the most closely related species, and therefore should be considered as a separate taxon. In some cases, the application of these morphological characters, especially in problematic groups, involves the analysis of large suites of specimens in order to obtain reliable results. Deep-water octocorals are difficult to obtain and in some cases only few fragments of species are available for taxonomists.

The identification of octocorals is increasingly facilitated by the use of molecular tools, such as DNA barcoding (McFadden *et al.* 2014, Herbert *et al.* 2003). In some cases, the application of sequence data can resolve cryptic species, and assist with the discovery of new species (DeSalle *et al.* 2005, Rubinoff *et al.* 2006, Will *et al.* 2005). Within Octocorallia, many phylogenetic relationships remain unresolved and our general taxonomic understanding remains relatively poor. Many deep-sea species are yet to be described and those that have been will likely need revisions, consequently an integrative approach utilizing morphological and phylogenetic data is essential (McFadden *et al.* 2006). In our phylogenetic analyses, both ML and Bayesian trees gave very similar results, placing *S. sahlingi* **sp. nov.** as a sister taxon to *S. spauldingi*, however, this relationship was not well supported. There are 21 accepted species of *Swiftia* in addition to *S. sahlingi* **sp. nov.**, but there is sequence data in Genbank for only seven of these species (Table 1). Until sequences for additional species are available, the relationships within *Swiftia* and even its monophyly, as shown in Figure 5, must be regarded as preliminary. Furthermore, it is known that mitochondrial genomes in deep-sea octocorals have slow evolutionary rates compared to those of other taxa (Shearer *et al.* 2002). This is most likely due to the efficiency of the mismatch repair gene *mtMutS* (Bilewitch & Degnan 2011) and potentially why we see low support for some of the nodes in Figure 5. The low divergence within the octocoral mitochondrial genome can limit the use of barcoding for species identification, which highlights the importance of combined morphological analyses as in the present study.

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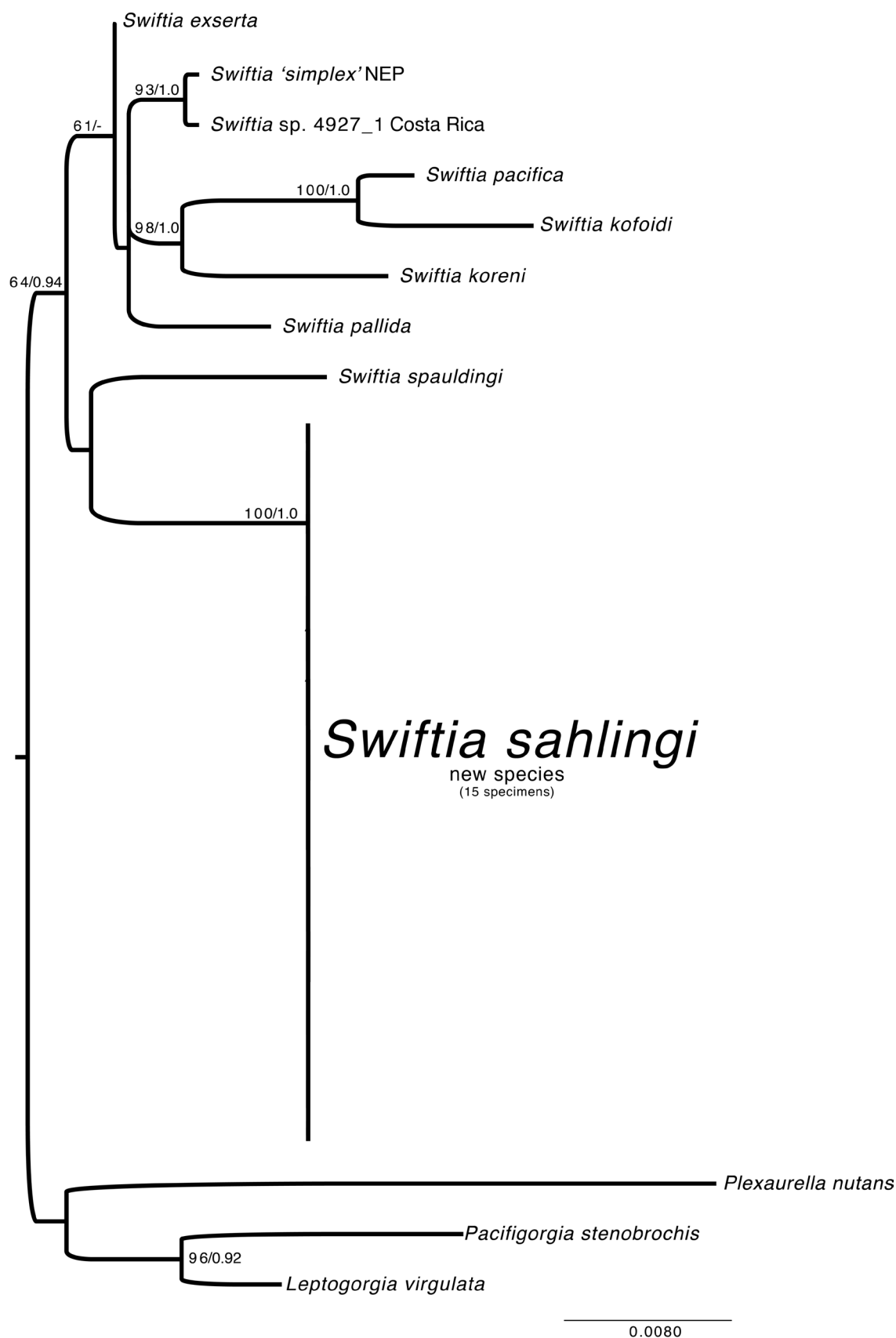


FIGURE 5. *Swiftia* phylogenetic analysis. Maximum likelihood tree of the combined analysis of COI and MutS. Numbers above nodes are bootstrap support percentages (BS) from RAxML, followed by Bayesian posterior probabilities (PP). Nodes with no numbers indicate support was less than 50% BS and 0.7 PP. A dash ‘-’ indicates the node was not found in the Bayesian analysis.

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