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Research Article

A new family of soft corals (Anthozoa, Octocorallia, Alcyonacea) from the aphotic tropical eastern Pacific waters revealed by integrative taxonomy

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(Received 2 April 2012; revised 17 June 2012; accepted 25 June 2012)

The new family Aquambridae is described based on distinct morphological characters and supported by a molecular phylogenetic analysis. Aquambridae is similar to Nidaliidae, Nephtheidae and Alcyoniidae in having arborescent colonies and lacking axis structure or stolons, but differs from them in having very different sclerite composition and having conspicuous transparent jelly-like lobes. Phylogenetic analysis of two mitochondrial genes, ND2 and mtMutS, strongly supports its placement in a separated clade. Herein we describe *Aquambr klapferi* sp. nov., gen. nov. in the new family. The organisms were obtained from the seamounts, ridges and canyons out of the insular shelf of Isla del Coco, Costa Rica, down to 400 m depth. The new species represents the first discovery of a soft coral in an eastern Pacific oceanic island, and provides hints of the biodiversity of the largely unexplored deep waters of the tropical eastern Pacific.

Key words: Alcyonacea, eastern Pacific, Isla del Coco, Octocorallia, sea mounts, soft coral

Introduction

Octocorals are sessile, mostly colonial Anthozoa having polyps invariably containing eight tentacles, which are almost always pinnate. Most species have a calcium carbonate skeletal structure consisting of numerous microscopic sclerites embedded in an organic matrix, the coenenchyme. Among the three recognized octocorallian orders, Alcyonacea constitutes the most diverse in terms of species and body-plans and includes soft corals and gorgonians. Soft corals, once included in the polyphyletic Suborder Alcyoniina, represent an artificial group that contains corals of several different structural types: thick incrusting colonies with tough and leathery texture, profuse branching colonies from bush-like to tree-like, some soft and others rough to the touch, or others that have thick stalks with abundant soft upright lobes (Fabricius & Alderslade, 2001), yet they invariably lack the proteinaceous/calcified axis characteristic of gorgonians.

The taxonomy of the Alcyonacea is mainly based on the structure, colour and arrangement of the sclerites. Most of these characters have been shown to be of little phylogenetic value by molecular studies of the subclass, which have demonstrated the polyphyly of all non-monotypic families within Alcyonacea (e.g. McFadden *et al.*, 2006). Octocorals can be found in nearly all marine environments, and they constitute the dominant fauna of many benthic communities. Soft corals, especially the families Alcyoniidae and Nephtheidae, are the most common octocorals in the tropical Indo-Pacific and the western Pacific waters and can be found from low tide to the abyss (Van Ofwegen & Groenenberg, 2007). Interestingly, to date, soft corals have not been recorded in the tropical eastern Pacific. However, octocoral biodiversity research in this region has been mainly focused on the bathymetric range from sea level down to 40 m depth, and until present the surveys have only yielded gorgonian species (Williams & Breedy, 2004; Breedy & Guzman, 2008; Guzman & Breedy, 2008; Breedy & Cortés, 2011). Consequently, the deep-water octocorals of the tropical eastern Pacific region are poorly known.

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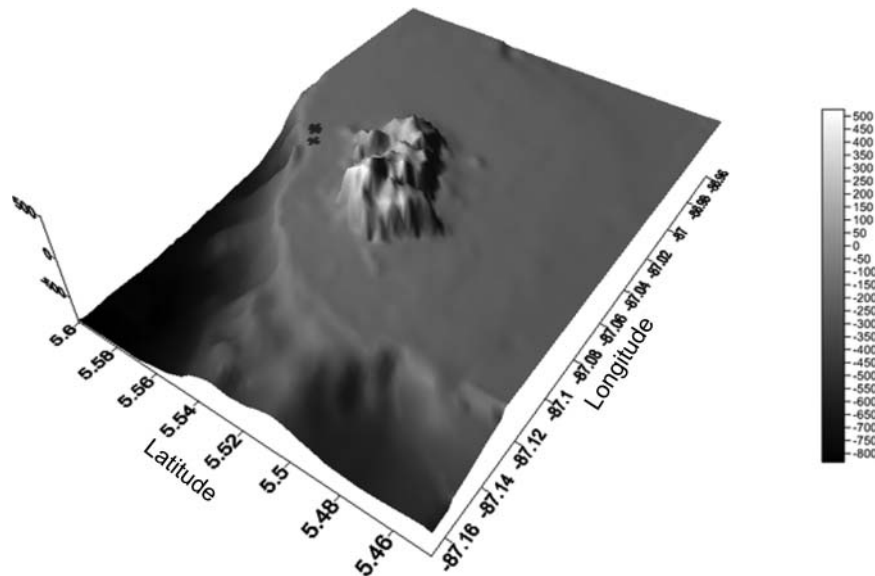


Fig. 1. Study sites out of the insular shelf of Isla del Coco, Pacific Costa Rica. Map made by O. Lizano (UCR).

Recently, a rich octocoral fauna has been photographed and obtained from seamounts, ridges and canyons out of the insular shelf of the Isla del Coco, Pacific Costa Rica (Breedy & Cortés, 2008; Cortés & Blum, 2008). Isla del Coco represents a biodiversity and endemism hot-spot for marine organisms (Wehrtmann *et al.*, 2009).

Herein we describe a new family of soft corals from the deep waters of Isla del Coco, Pacific Costa Rica. The new species represents the first discovery of a soft coral in an eastern Pacific oceanic island and along the eastern Pacific waters in general, and provide hints of the biodiversity of the largely unexplored deep waters of the tropical eastern Pacific.

Materials and methods

Sample collection

Isla del Coco is an oceanic island located 500 km S–SW from the Pacific coast of Costa Rica (Cortés, 2008); the island represents the only emerged summit of the Cocos ridge (Alvarado-Induni, 2000). The species described here was observed and photographed during many dives of the submersible *DeepSee* (UnderSea Hunter Group) to nearby seamounts, ridges and canyons of the Isla del Coco insular shelf: Wall 0475, 05°34.691'N, 087°03.469'W, 200–450 m depth; Piedra Drop, 05°34.640'N, 087°03.557'W, 200 m depth, and Canyons, 05°34.383'N, 087°03.909'W, 233–450 m depth (Fig. 1).

Specimens were collected at two of these points, Wall 0475 and Canyons (Fig. 1), using a mechanical arm (Model Orion, Shilling Robotics USA). When recovered, they were deck-photographed and preserved in 95% ethanol.

Morphological study

Polyps were dissected and treated with xylene and Permunt® to study the arrangement of the sclerites. For sclerite examination, fragments of different parts of the colony (base, polyp and wall) were treated with sodium hypochlorite for dissociation, washed, air-dried, mounted with silver paint on aluminium stubs, and coated with 80-nm gold layers in an Eiko IB-3 (Breedy & Guzman, 2002), and then examined with an electron microscope (N-2360 Hitachi and a S-570 Hitachi) operated at 15 kv, at the Centro de Investigación en Estructuras Microscópicas, Universidad de Costa Rica.

Molecular methods

Polyps of ethanol-preserved specimens were extracted using a Qiagen's DNeasy Blood and Tissue kit, and the resulting DNA was used to amplify a fragment of the mitochondrial ND2 and mtMutS genes according to the methods in McFadden *et al.* (2006). Bands of the expected size were excised from a 1.5% agarose gel and sequenced in both directions with the same primers used for amplification. Sequences were assembled and edited in CodonCode Aligner (CodonCode Corporation), and the resulting contigs were deposited in the European Nucleotide Archive, EMBL, under accession numbers HE819888–HE819891.

Phylogenetic analysis

The obtained ND2 and mtMutS sequences were aligned together with a comprehensive sample of other octocoral genera deposited at the NCBI, GenBank. The taxonomic sampling for the present analysis is similar to that of McFadden *et al.* (2006), including representatives of most octocoral families. For the phylogenetic analysis, the two molecular markers were concatenated into a supermatrix that was used to infer a maximum likelihood (ML; RAxML 7.2.8; Stamatakis, 2006) and Bayesian (MrBayes, 25 000 000 generations, sample frequency = 500 generations, only the last 15 000 trees were used for the consensus; Ronquist & Huelsenbeck, 2003) phylogenetic hypotheses under the GTR model. Among-site rate variation was modeled using a discrete gamma distribution with four categories. Each partition was modelled independently in both analyses. In the resulting phylogenies, the Holaxonia-Alcyoniina was rooted using the Calcaxonia-Penatulacea + *Anthomastus*-*Corallium* clade. Clades with a bootstrap support value > 70 in the ML analysis and a posterior probability > 0.95 in the Bayesian phylogeny were considered supported. Additionally, we estimated the distance between the proposed new family and selected soft-corals clades using PAUP* 4.0 (Swofford, 2003).

Results

Taxonomy

Class Anthozoa Ehrenberg, 1831
Subclass Octocorallia Haeckel, 1866
Order Alcyonacea Lamouroux, 1812
Family Aquaumbriidae fam. nov.

Diagnosis. Soft corals with an arborescent colony form, lobes transparent, jelly-like, arising from a basal stalk. Colonies flabby. Polyps with collaret and points. Sclerites are colourless rods and needles, of similar shape in all parts of the colony.

Type genus. *Aquaumbra* gen. nov., here designated.

Genus *Aquaumbra* gen. nov.

Type species. *Aquaumbra klapperi* sp. nov., by original designation.

Etymology. *Aqua* (L) = water (n)+*Umbra* (L) = ghost (n). The name meaning water ghost is an allusion to the transparency of the colony and to evoke fearful legends about pirates and treasures lost in the Island long time ago.

Diagnosis. Aquaumbriidae with laterally branched colonies with polyps arranged along the lobes, fewer present on the primary branches, and lacking on the stalk. Polyps contractile. Azooxanthellate.

Aquaumbra klapperi sp. nov.

Figs 2–13

Holotype. MZUCR 2177 (Canyons, Dive 1245, 17.12.2010).

Paratype. MZUCR 2178 (Wall 0475, Dive 939, 25.9.2009).

Type locality. Isla del Coco, 268–308 m.

Distribution. Observed and photographed at Piedra Drop, Wall 0475 and Canyons, from 268 to 320 m in depth. Only known for the type locality, seamounts of Isla del Coco.

Habitat. Colonies attached to basaltic substrata, living in clusters or solitary (Figs 8–13) in between other organisms that cover the rocks, sponges, hydroids, hydrocorals, tunicates, black corals and cup corals among others.

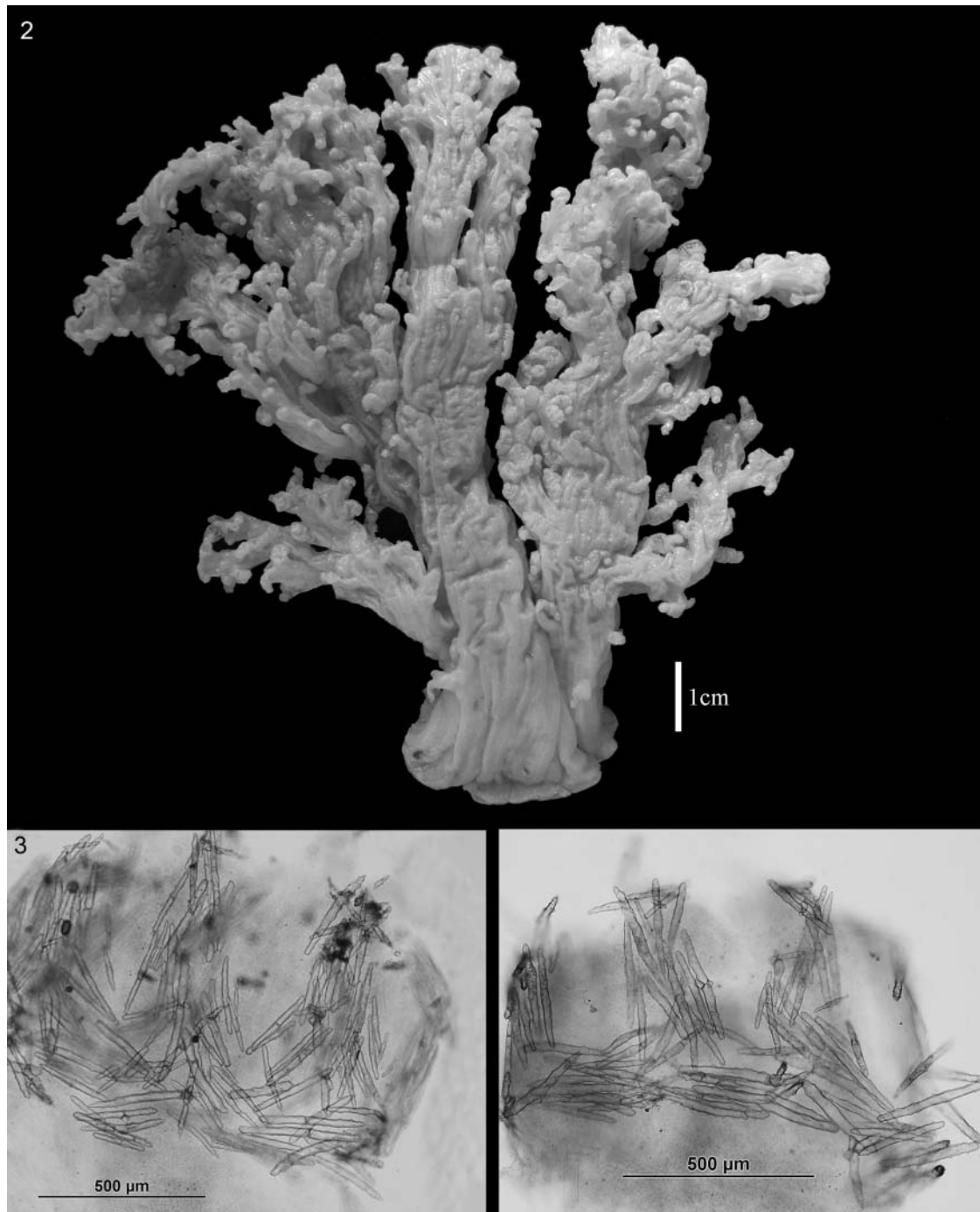
Etymology. The new species is named after Avi Klapper, owner of the UnderSea Hunter Group, for his constant curiosity and interest in the ocean deep environment. He collected and photographed the new species for the first time.

Description

Growth form. The preserved, contracted holotype is 10.5 cm in length and 9.4 cm in width at the distal end (Fig. 2). The colony is erect and arborescent, consists of a basal stalk measuring approximately 30 mm in width at proximal portion of holdfast. Lateral branching begins about 25 mm above the holdfast into two primary lateral lobes. The primary lobes each give rise to several secondary lobes that subdivide 2–3 times toward their distal ends. Holdfast is oval, 30 mm long and 15 mm wide. The colony is very flabby, almost translucent; the texture of the branches is jelly-like (Figs 2, 8–13).

Polyps. They are arranged laterally along the lobes and in clusters of 3–5 at the distal ends of lobes. Some polyps also occur on the primary lobes, they sprout in groups of two or more. Polyps are not retractile but tentacles are folded into the polyp body. Polyps are colourless, bulbous, mostly 1.5–4 mm long, and 1.5–3 mm wide at the base of anthocodia. Polyps have a collaret and points at the base of the tentacles. Eight, distinct *en chevron* points composed of several sclerites and a weak collaret of 2–3 rows of sclerites (Fig. 3).

Sclerites. Sclerites are basically rods and needles covered by short, sparsely placed acute tubercles. There is not a clear difference between sclerites from every part of the colony. Polyp sclerites are needles up to 0.45 mm long and 0.032 mm wide, rods up to 0.42 mm long and 0.08 mm wide (Fig. 4). Tentacle sclerites are mostly lobed rods up to 0.36 mm long and 0.07 mm wide, mostly with a median widening. Some boomerang-shaped rods up to 0.44 mm long and 0.10 mm wide (Fig. 5). Lobes and upper stalk



Figs 2–3. Holotype of *Aquaumbra klapferi* sp. nov. (MZUCR 2177): **2**, complete preserved colony; **3**, sclerite arrangement of polyps.

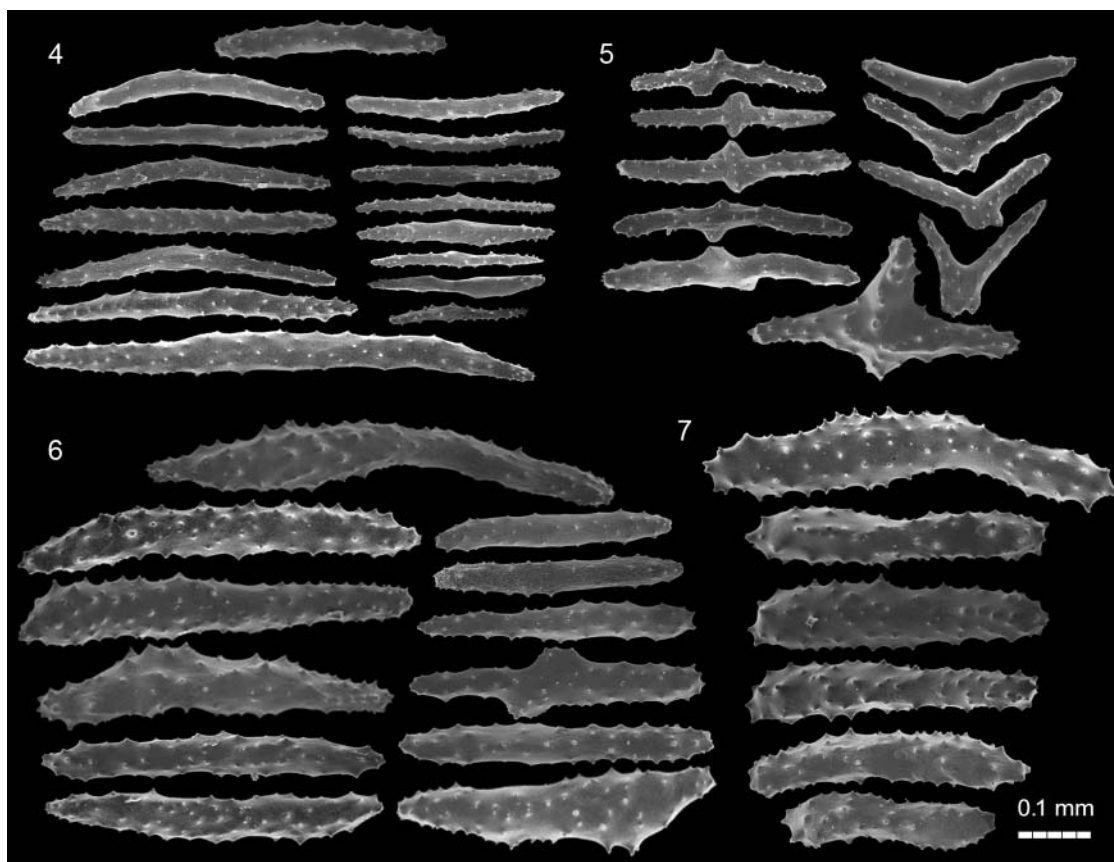
contain rods up to 0.70 mm long and 0.12 mm wide (Fig. 6). At the base of the stalk the sclerites are mostly rods, up to 0.58 mm long and 0.14 mm wide (Fig. 7).

All sclerites are colourless.

Results and discussion

In the literature three families have been described having arborescent colonies and lacking axis structure or stolons.

The Nidaliidae genera *Chironephthya* Wright & Studer, 1889 and *Siphonogorgia* Kölliker, 1874 have such colonies, but both genera always have brittle stiff colonies which easily break, quite different from the flabby Aquaumbridae. Moreover, these two genera have big spindles as sclerites instead of the needles and rods of the Aquaumbridae. In the Alcyoniidae only the genus *Klyxum* Alderslade, 2000 resembles the Aquaumbridae in having flabby colonies, contractile polyps, and sclerites similar to those of the

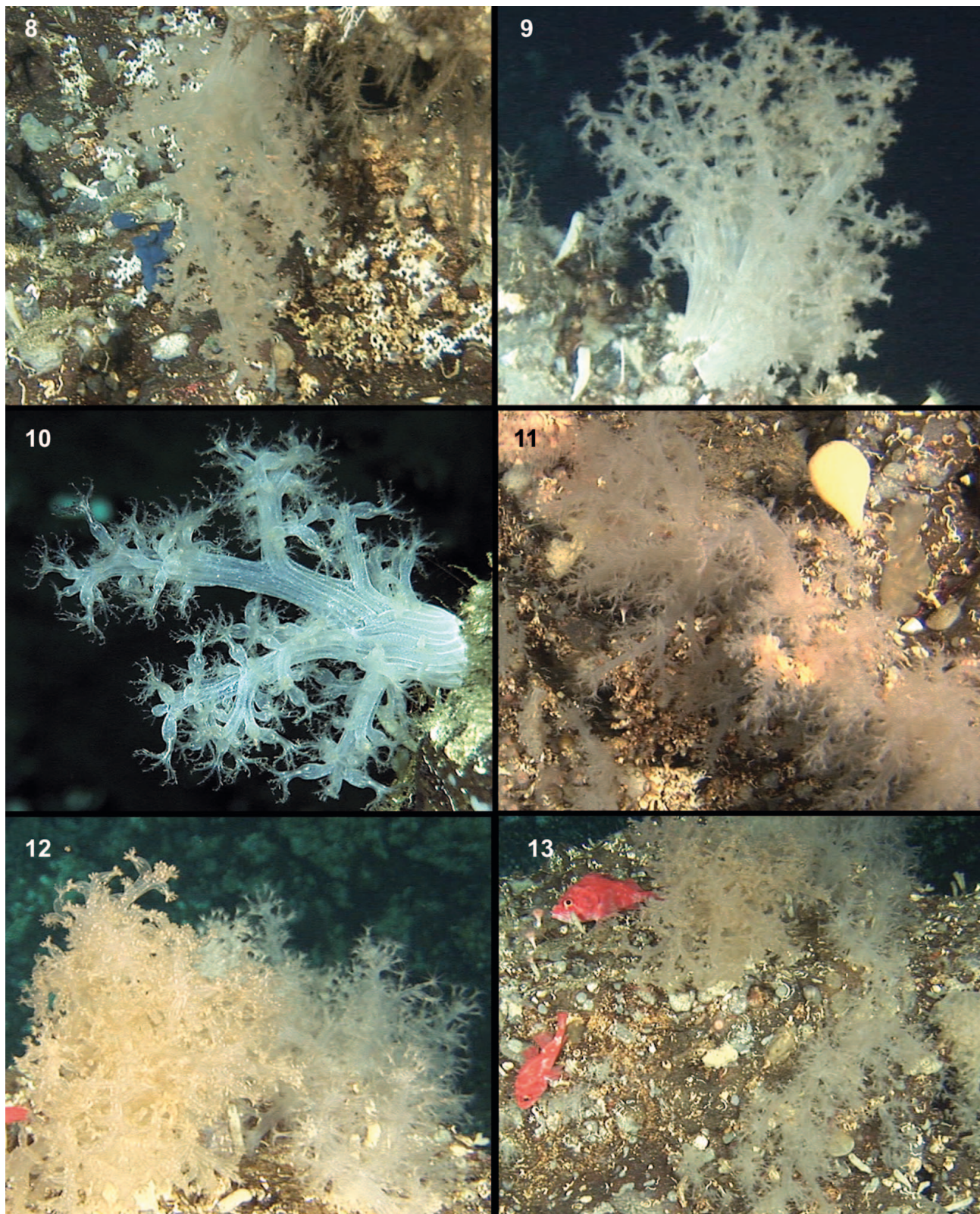


Figs 4–7. SEM photographs of *Aquaumbra klapferi* sp. nov., holotype (MZUCR 2177): **4**, sclerites of polyp; **5**, sclerites of tentacles; **6**, sclerites of lobes and upper stalk; **7**, sclerites of base of stalk.

Aquaumbridae. However, *Klyxum* has characteristic minute granular disks and flattened rods in the polyps, and it is zooxanthellate. The Nephtheidae resemble the Aquaumbridae most. Several genera have an arborescent colony shape and contractile polyps in common with the Aquaumbridae, but all these genera have distinctly different sclerites. Besides, the transparent jelly-like nature of the lobes in Aquaumbridae is unique, being denser and opaque in the other families.

In the molecular phylogeny inferred, all above-mentioned genera show up in different clades. The Bayesian (Fig. 14) and ML analyses (see supplementary material, which is available on the Supplementary tab of the article's Taylor & Francis Online page at <http://dx.doi/10.1080/14772000.2012.707694>) resulted in similar phylogenetic trees showing several highly supported clades collapsed to the backbone of the tree (Bayesian analysis) or which phylogenetic relationships were poorly supported (ML phylogeny). Specimens of the new family Aquaumbridae formed a clade sister to the plexaurid *Alaskagorgia aleutiana*, Sánchez & Cairns, 2004, however the phylogenetic relationship between *A. aleutiana* and Aquaumbridae was not supported ($P = 0.56$). Aquaumbridae was not closely related to any soft coral taxa included in the analysis. In the

ML tree, Aquaumbridae branched basal to Nephtheidae, however this relation was unsupported. In this respect, following the Bayesian phylogeny, the relationships of Aquaumbridae must be considered unsettled pending a better resolution of the molecular phylogenies. Other soft coral genera having arborescent colonies included in the molecular phylogenetic analyses were spread over the tree. *Chironephthya* and *Siphonogorgia* formed a clade basal to most other Holaxonia–Alcyoniina genera. *Nidalia* Gray, 1835 was related to *Iciligorgia* Duchassaing, 1870 and *Malacacanthus* Thomson, 1910, the alcyoniid *Klyxum* was sister to *Cladiella* Gray, 1869, and these genera formed a marginally supported clade with *Pterogorgia* Ehrenberg, 1834–*Muriceopsis* Aurivillius, 1931 in the Bayesian analysis. *Gersemia* Marenzeller, 1878 was related to species of *Alcyonium* Linnaeus, 1758, and several members of the family Nephtheidae were included in a large, highly supported clade together with sequences from the families Alcyoniidae, Nidaliidae, Paralcyoniidae and Xenidiidae. The genetic distance (uncorrected P-distance) between the new family Aquaumbridae and other clades containing tree-like soft corals ranged between 4.367% and 7.862% (see Table 1 for details), well in the range between these clades.



Figs 8–13. *In situ* photographs of the new species. Photographs by A. Klapfer and S. Blum.

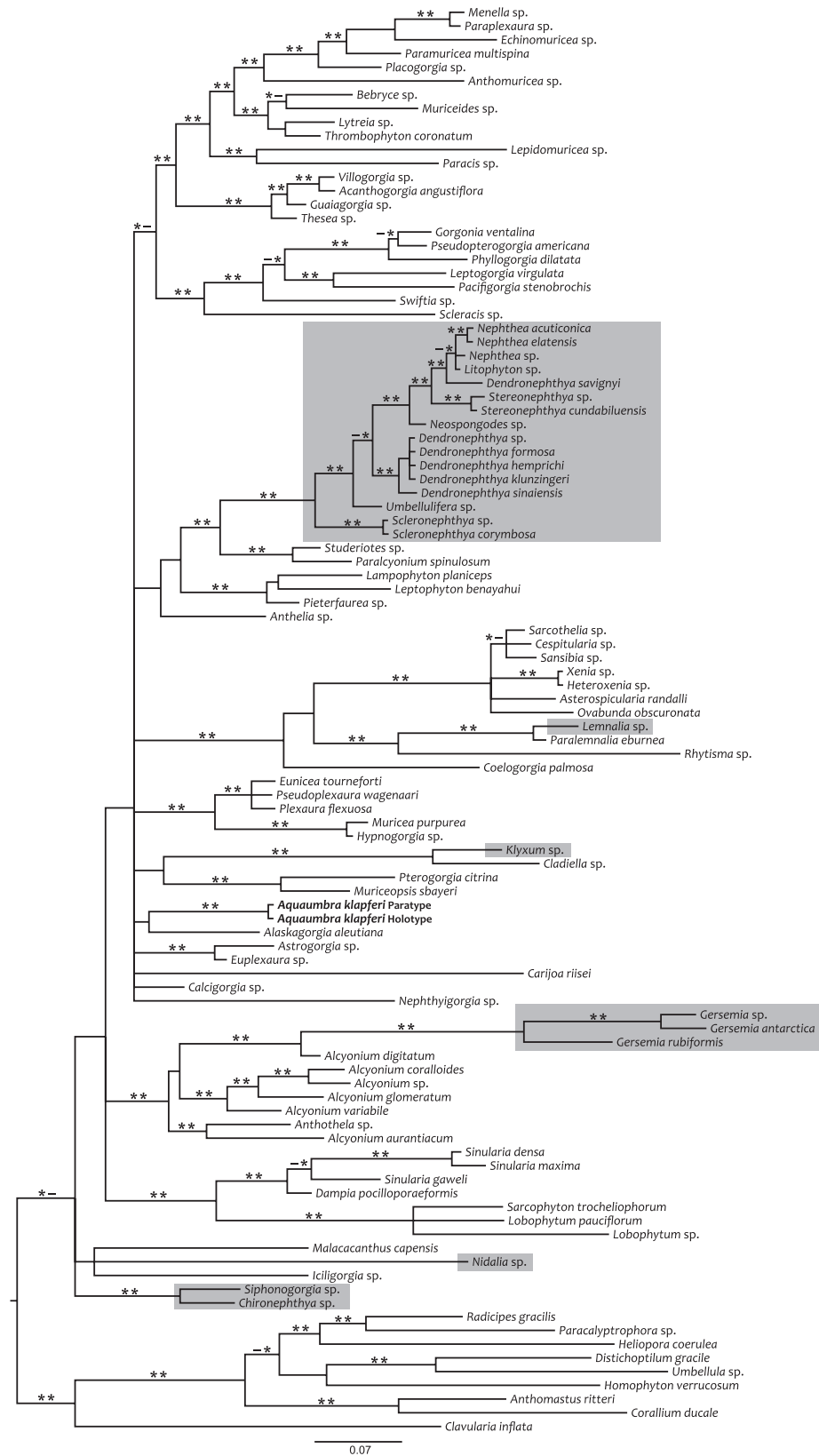


Fig. 14. Bayesian phylogenetic analysis of the Alcyonacea including the new family Aquaumbridae (in bold). Highlighted in grey are octocorals with tree-like colonies. Support values are given only for branches with posterior probability > 0.95. The asterisks over the branches represent posterior probability values > 0.95 (left asterisk) and bootstrap values > 70% (right asterisk); unsupported branches in the ML bootstrap analysis are annotated with a minus (-) sign.

Table 1. Uncorrected P-distance (minimum–maximum) between clades containing selected tree-like soft-coral genera.

Clade	<i>Siphonogorgia</i> + <i>Chironephthya</i>	<i>Klyxum</i> sp.	Nephthidae (partial)*	Aquaumbridae
<i>Siphonogorgia</i> + <i>Chironephthya</i>	0–0.01849	—	—	—
<i>Klyxum</i> sp.	0.07130–0.07922	0	—	—
Nephthidae	0.05722–0.08965	0.08891–0.12551	0–0.03862	—
Aquaumbridae	0.04367–0.04841	0.07576–0.07834	0.04813–0.07862	0

*Nephthidae refers to the genera highlighted in Figure 14: *Nephthea*, *Litophyton*, *Dendronephthya*, *Stereonephthya*, *Neospongodes*, *Umbellulifera*, *Scleronephthya*.

Although new soft coral genera are still being described frequently all families seemingly were already known many years ago; in 1977 Bayer & Muzik added the Lithotelestidae, and 33 years later Ofwegen & McFadden (2010) described the Acanthoaxiidae from shallow waters of tropical Cameroon. Molecular analyses have revealed that most families of octocorals are polyphyletic and that morphologically unrelated taxa are more closely related than hitherto thought. This contribution demonstrates that the integration of molecular and morphological information can reveal new lineages that morphology alone would classify as aberrant members of existing families; Nephthidae in the case of *Aquaumbra*. We can expect more families will be described in the near future using such an integrative approach to the study of octocorals. The description of the Aquaumbridae shows still much can be discovered about octocoral taxonomy and systematics in obviously under-examined tropical regions. In our opinion the description of these taxa is the only way to resolve the still incomplete phylogenetic classification of Octocorallia.

Acknowledgements

We are grateful to anonymous reviewers for critical review of the manuscript. We thank Jorge Cortés (CIMAR) who has promoted the deep water research at Isla del Coco. Gert Wörheide provided laboratory space and computational resources for SV during part of the realization of this study. We acknowledge the following people and institutions for their help and interest: Alex Rodríguez (CIEMIC); Rita Vargas (MZUCR); personnel of the Área de Conservación Marina Isla del Coco (ACMIC), Ministerio de Ambiente y Energía for allowing our research in Cocos Island National Park and the rangers. Finally, we thank; Avi Klapfer, Yosy Namaan and Shmulik Blum, owners of the *DeepSee* submersible (UnderSea Hunter Group), and the crew members of the MV *Argo*. Samples were collected under the 0890 permit.

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Associate Editor: Peter Hayward