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Redescription of the type material of *Clavularia* de Blainville, 1830 (Anthozoa: Octocorallia), with descriptions of new taxa and a new family

Stefano Borghi[A,B,C,*], Catherine S. McFadden[D], Tom C. L. Bridge[A,B], Andrew H. Baird[A], Merrick Ekins[E], Michela L. Mitchell[A], James D. Reimer[C,F] and Peter F. Cowman[A,B,G]

For full list of author affiliations and declarations see end of paper

***Correspondence to:**
Stefano Borghi
College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia
Email: stefano.borghi@my.jcu.edu.au

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ABSTRACT

The taxonomy of soft corals with a stoloniferous growth form is challenging. The family Clavulariidae and, more specifically, the genus *Clavularia* have acted as a repository for most stoloniferous corals that could not systematically be differentiated with morphology. In addition, the lack of morphological and genetic data for the type species of *Clavularia*, *Clavularia viridis*, has made a revision of the genus impossible. In this study, we use an integrative taxonomic approach combining morphological examinations and novel molecular methods to revise the taxonomy and systematics of Clavulariidae within Octocorallia. We re-describe key species of *Clavularia*, including *C. viridis*, *C. inflata* and *C. koellikeri*, resolve the position of Clavulariidae within Octocorallia, and present a revised taxonomy of the tropical, zooxanthellate species of *Clavularia* that includes morphological characters of each species. We further confirm the polyphyly of Clavulariidae, and resurrect the genus *Hicksonia* and family Hicksoniidae (Malacalcyonacea) to accommodate a new species with connecting tubes on multiple levels (*H. tohrui* sp. nov.). We also describe a new genus and species of Clavulariidae from Japan *Bairdium iriomotejimaensis* gen. nov., sp. nov. and a new *Clavularia* species from the Great Barrier Reef (*C. brunafolia* sp. nov.). This study resolves the fundamental taxonomy of *Clavularia*, and provides the necessary baseline for future works.

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Keywords: Clavulariidae, identification key, new genus, new species, Octocorallia, phylogenomics, species boundaries, systematics, taxonomy, ultraconserved elements, Western Pacific.

Introduction

The octocoral genus *Clavularia* was introduced by de Blainville in Levrault (1830, p. 464), who established the genus for specimens collected by Quoy and Gaimard during the voyage of the Astrolabe between 1826 and 1829. The genus originally included two species known only from dry specimens: *Clavularia viridis* Quoy & Gaimard, 1833 and *C. violacea* Quoy & Gaimard, 1833, both collected in Vanikoro (Solomon Islands) (de Blainville in Levrault 1830) (Fig. 1). Both species were described as cylindrical animals, characterised by pinnate tentacles that emerge from elongate and striated tubes, which are densely packed and connected at the base by a membranous stolonic structure (de Blainville in Levrault 1830; Quoy and Gaimard 1833). Today, *C. viridis* is considered the type species of the genus (Hickson 1930), whereas *C. violacea* was subsequently transferred to the genus *Briareum* Blainville, 1834 (Gohar 1940; Verseveldt 1960; Samimi-Namin and van Ofwegen 2016). The taxonomic placement of *C. viridis* within Octocorallia, however, remains subject to debate, as we do not have morphological or genetic data from the type material.

Historically, the taxonomic identity of the genus *Clavularia* and its placement within Octocorallia have been the subject of considerable debate. Originally, the genus *Clavularia* was compared to the pre-existing genus *Cornularia* Lamarck, 1816 and placed

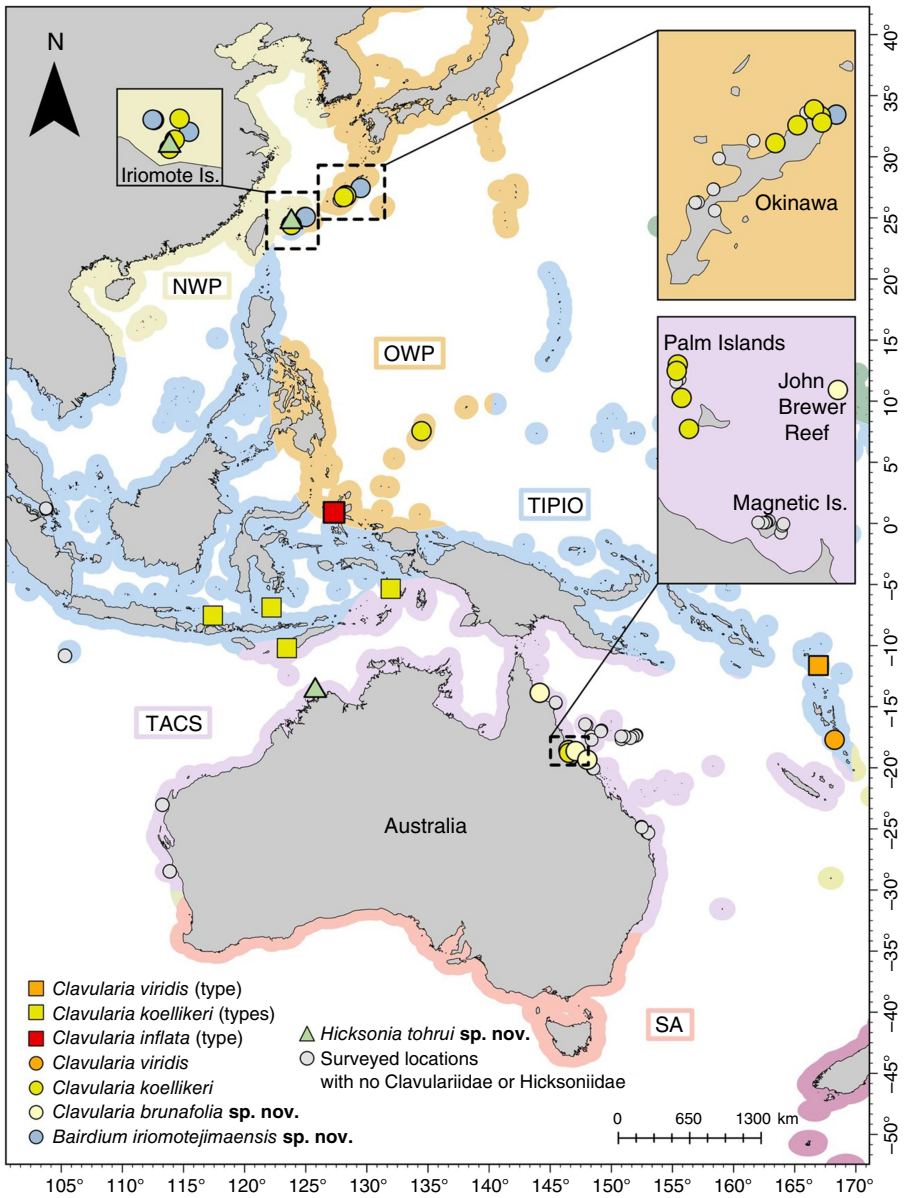

Fig. 1. Type localities of the three key species of *Clavularia* here examined: *C. viridis* (Quoy and Gaimard 1833; orange square), *C. inflata* (Schenk 1896; red square) and *C. koellikeri* (Dean 1927; yellow squares). Species of Clavulariidae included in this study and their distribution are shown as circles, and Hicksoniidae as triangles. Grey dots show locations where no colonies were observed. Colour shades indicate distinct marine biogeographic realms (see Costello *et al.* 2017). NWP, N W Pacific; OWP, Offshore W Pacific; TIPIO, Tropical Indo-Pacific and coastal Indian Ocean; OIO, Offshore Indian Ocean; TACS, Tropical Australia and Coral Sea; and SA, Southern Australia.

within the family Cornulariidae Dana, 1846 due to similarities in their gross morphology (de Blainville in Levrault 1830). Hickson (1894) subsequently introduced the family Clavulariidae as an alternative to Cornulariidae, and included in it the genera *Clavularia*, *Cornularia* Lamarck, 1816, *Stereosoma* Hickson, 1894 and *Sympodium* Ehrenberg, 1834. He justified using Clavulariidae as an alternative to Cornulariidae based on *Cornularia* lacking of sclerites – a morphological characteristic too uncommon within the family for a species of *Cornularia* to represent the type species of the group. Hickson's decision was also based on the fact that the genus *Clavularia* was more speciose than the genus *Cornularia*.

Hickson (1894) also noted that *C. viridis* was the only species that matched the description of the genus as given by Quoy and Gaimard (1833). Consequently, he expanded the description of the genus by Quoy and Gaimard (1833) to include characteristics found in other *Clavularia* species at the time, but failed to officially designate any species as the type species of the genus (Hickson 1894). Based on his new definition of the genus *Clavularia*, Hickson (1894) added 16 species to the 23 described at the time. Of these 16 additional species, 6 were originally described within the genus *Anthelia* Lamarck, 1816. Additionally, Hickson also synonymised 5 genera with *Clavularia*: *Cornulariella* Verrill, 1874 (1 species), *Gymnosarca* Saville Kent, 1870 (1 species), *Sarcodictyon* Forbes, 1847 (2 species), *Sympodium* Ehrenberg, 1834 (1 species), and *Rhizoxenia* Ehrenberg, 1834 (5 species). The reason behind Hickson's (1894) decision was the acknowledgement that some of these genera were imperfectly described and figured, and species were erected ignoring the original characters of those genera. For

instance, Hickson (1894) noted that the genus *Rhizoxenia* was erected for species similar to previously described species in *Clavularia* and *Cornularia* apart from with the presence of non-retractile polyps. However, additional species of *Rhizoxenia* were later described for specimens with retractile polyps (e.g. *Rhizoxenia primula* Dana, 1846). Consequently, the defining character of the genus was lost, and therefore Hickson (1894) synonymised the genus with *Clavularia* until more informative characters were found.

Hickson (1894) designated *C. viridis* as the type species of *Clavularia* but re-described the species based on a specimen he collected from North Celebes (Sulawesi, Indonesia) without re-examining the type material from Vanikoro Island. By doing this, Hickson (1894) reported morphological details that were absent or differed from the original description of Quoy and Gaimard (1833), including an intricate stolonal network of connecting tubes that extend from one polyp to another and at multiple levels, similar to members of the genus *Tubipora* Linnaeus, 1758. Of the 39 species included within *Clavularia* by Hickson (1894), these connecting tubes were present only in the specimen of *C. viridis* collected in Indonesia (Hickson 1894). Delage and Hérouard (1901) later transferred the Indonesian specimen into the new family Hicksoniidae Delage & Hérouard, 1901 and genus *Hicksonia* Delage & Hérouard, 1901 as *Hicksonia viridis*. Kükenthal (1906) caused further confusion by questioning the taxonomic placement of the Quoy and Gaimard specimen within *Clavularia* based on the limited retractility of the polyps into the calyx, and suggested the specimen might belong to the genus *Anthelia*. Kükenthal (1906) noted that the genus *Clavularia* could therefore be considered invalid, but highlighted the need for further research. Ultimately, Kükenthal (1906) placed the genus *Clavularia* within Cornulariidae like many other contemporary authors (Thomson and Henderson 1906) and ignored the proposed alternative representation of the family by Hickson (1894).

Despite the debate surrounding the placement of *C. viridis*, the type specimen of Quoy and Gaimard from Vanikoro was never officially transferred to the genus *Anthelia*, and therefore the genus *Clavularia* remained valid. However, uncertainty continued regarding the assumption that the specimens of Quoy and Gaimard and Hickson were the same species, and therefore whether the transfer of *C. viridis* to the genus *Hicksonia* was valid. Dean (1927) accepted the genus *Hicksonia* and described a new species (*H. koellikeri* Dean, 1927), whereas Hickson (1930) proposed a more systematic approach. Hickson (1930) first designated *C. viridis* as the type species of *Clavularia*, highlighting how the species must not be separated from the genus, and proposed to keep *Hicksonia* as a subgeneric name. Hickson (1930) also acknowledged that his previous decision to lump both *Cornularia* and *Clavularia* into Clavulariidae as an alternative representation of the pre-existing family Cornulariidae was not appropriate. Consequently, he recognised Clavulariidae and Cornulariidae as distinct families. Since then, the species *C. viridis* has been acknowledged to be the type species of the genus *Clavularia* and of the family Clavulariidae. Despite this, the broader application of the genus *Clavularia* to encompass numerous other stoloniferous corals presents additional taxonomic challenges.

Most species with a stoloniferous growth form were provisionally assigned to the genus *Clavularia* in revisions and species descriptions from the mid-late 20th Century (Madsen 1944; Bayer 1981), but recent molecular work using hundreds of nuclear markers has suggested that both the family Clavulariidae and genus *Clavularia* are polyphyletic (McFadden *et al.* 2022). Based on molecular evidence, Clavulariidae includes only three genera (*Hanabira* Lau, Stokvis, Imahara & Reimer, 2019, *Knopia* Alderslade & McFadden, 2007 and *Clavularia*), the last of which includes only tropical zooxanthellate species with large polyps (McFadden *et al.* 2022). However, the family Clavulariidae remains unresolved taxonomically because the holotype of *C. viridis* has never been re-described and also due to a lack of molecular data for the species (McFadden *et al.* 2022). Additionally, a specimen from Brazil that matched Dean's (1927) description of *H. viridis* fell outside of the Clavulariidae clade in a recent phylogenomic analysis (McFadden *et al.* 2022).

The two species of tropical zooxanthellate *Clavularia* with large polyps included in the molecular phylogeny of McFadden *et al.* (2022) were identified as *C. viridis* and *C. inflata*. *Clavularia viridis* is thought to be widespread throughout the eastern Indian Ocean and West Pacific, and has been recorded from the southern Ryukyu Archipelago, Japan (Benayahu 2002), Indonesia (Hickson 1894), the Andaman and Nicobar Islands (Raghunathan and Yogesh Kumar 2024), and tropical Western Australia (Bryce *et al.* 2018). A species resembling *C. viridis* was also reportedly introduced to the southwestern Atlantic coast of Brazil (Mantelatto *et al.* 2018). In the absence of a comprehensive morphological description and sequence data representative of *C. viridis*, other species of *Clavularia* considered to be morphologically similar to *C. viridis* have been used to represent the genus in recent phylogenomic reconstructions. For instance, McFadden *et al.* (2022) established the currently accepted clade for the family Clavulariidae based on a specimen attributed to *C. inflata* Schenk, 1896 from Palau; although the species was originally described from Ternate, Indonesia (Schenk 1896) (Fig. 1), it is considered to be geographically widespread across the West Pacific. *Clavularia inflata* has been reported from Indonesia (Subhan *et al.* 2022*a*), the Ryukyu Archipelago, Japan (Benayahu 2002), the Great Barrier Reef (Alino and Coll 1989) and southern Taiwan (Benayahu *et al.* 2004). Another species of *Clavularia* considered to be morphologically similar to *C. viridis* is *C. koellikeri* (Dean, 1927). However, although the holotype of *C. inflata* fits the definition of *Clavularia* given by Quoy and Gaimard (1833), *C. koellikeri* was originally described in the genus *Hicksonia* due to its similarities to the specimen of

C. viridis collected by Hickson (1894) in Indonesia. *C. koellikeri* was originally described based on eight specimens collected from four Indonesian reefs (Dean 1927) (Fig. 1), but it has also been reported along the Great Barrier Reef (Bastidas *et al.* 2002).

The aim of this study is to clarify the taxonomic status of Clavulariidae based on an integrated taxonomic approach combining morphological analysis of type material and newly collected specimens with molecular phylogenomic data. Specifically, we examine original type material and additional specimens identified as the type species of the genus *Clavularia*, *C. viridis*, as well as two additional nominal species, *C. inflata* and *C. koellikeri*. These represent the only three nominal species currently included in *Clavularia* that are zooxanthellate, have large polyps and are from the tropical Indo-Pacific. We then compare *C. viridis* from the Pacific to *C.* cf. *viridis* collected from Brazil and included in McFadden *et al.* (2022), as well as with other specimens from the Queensland Museum collection that have been identified and registered as *C. viridis*. Although the specimen from Brazil reportedly matches the description of *C. viridis* from Indonesia by Hickson (1894), we could not test this morphologically as we could not establish the current location of the Indonesian specimen. Species boundaries identified through morphological analysis were then tested using molecular analysis of previously published and freshly collected specimens, which were used to reconstruct the phylogeny of Clavulariidae. Based on this integrated approach, we resolve the position of the genus *Clavularia* within Octocorallia, describe a new genus and two new species of Clavulariidae, and reinstate the genus *Hicksonia* and family Hicksoniidae to accommodate material erroneously assigned to *Clavularia viridis*.

Materials and methods

Abbreviations

BMNH, British Museum of Natural History, London, England; GBR, Great Barrier Reef; MNHN, Muséum national d'Histoire naturelle, Paris, France; NTM, Museum and Art Gallery of the Northern Territory, Darwin, Australia; QM, Queensland Museum, Brisbane, Australia; QMT, Queensland Museum Tropics, Townsville, Australia; RMNH, Naturalis Biodiversity Center, Leiden, Netherlands; SMF, Senckenberg Nature Museum, Frankfurt, Germany; SMNHTAU, Steinhardt Museum of Natural History at Tel Aviv University, Tel Aviv, Israel; WAM, Western Australia Museum, Perth, Australia.

We examined the type material of *C. viridis* Quoy & Gaimard, 1833 deposited at MNHN; the type specimen of *C. inflata* Schenk, 1896 deposited at SMF; and all eight specimens from the type series of *C. koellikeri* (Dean, 1927) deposited at RMNH; and the material of *C.* cf. *viridis* and *C. inflata* included in the systematic revision of Octocorallia by McFadden *et al.* (2022). For comparison, additional specimens registered in museum collections as *C. viridis* were also examined, including QM G334154 and QMT G84405. To include a representative of *C. viridis* in our molecular phylogeny, we used a topotype collected in Vanuatu and preserved at the California Academy of Sciences (CASIZ 307254). With the term topotype, we refer to a specimen collected from or very near the type locality that resembles the name-bearing type specimen morphologically (see Bonito *et al.* 2021; Bridge *et al.* 2024).

For this study, additional specimens were collected from locations within the known distribution of *C. viridis*, *C. koellikeri* and *C. inflata*, to better delineate these species and further assess their geographic distribution. We surveyed 75 different dives sites at three locations across the Western Pacific, including subtropical reefs south of the GBR (Hervey Bay), Okinawa Is. (Ryukyu Archipelago) and Singapore (Fig. 1). Specimens were photographed in the field and collected on SCUBA (Supplementary Table S1). Voucher specimens were initially fixed in 95% ethanol within 2 h after collection. The ethanol was changed twice in a 48-h period, and its concentration lowered to 80%. Two additional polyps were taken from the voucher specimens and preserved in 100% ethanol for subsequent morphological and molecular analyses. All freshly collected vouchers were later curated and deposited at QM and QMT (see https://collections.qm.qld.gov.au/explore).

Morphological analyses

We recorded the shape and size of preserved specimens and sub-samples. We noted the colour of the preserved material, contractility or retractility of the anthocodia and their preservation status. We measured the length of the polyps, the breadth of their upper and lower calyx sections, and the thickness of the stolon using *ImageJ* software (ver. 1.54K, W. S. Rasband, US National Institutes of Health, Bethesda, MD, USA, see https://imagej.net/ij/; Schneider *et al.* 2012), and calculated the mean, the median and the range over those measurements.

For the examination of the sclerites, five distinct regions of the colony were analysed independently, when possible: the pinnules, tentacles, collaret or points, calyx and stolon. We noted when any of these regions were missing due to age of the specimens or preservation. Tissue from each region was independently dissolved in 4% sodium hypochlorite (household bleach), rinsed twice in de-ionised water and finally two more times in 95% ethanol. After, we mounted the sclerites on stubs and coated them with Pd or Au before viewing them under a Hitachi TM4000Plus scanning electron microscope (SEM). During the analysis on the SEM, the shape and size of sclerites was recorded. When possible, a minimum of 10 and maximum of 30 sclerites were measured per region and per sclerite shape, and the mean, median and range calculated.

Molecular phylogenetic analyses

To resolve the phylogenetic placement of *Clavularia* species within Octocorallia and understand their relationships, we extracted DNA from the lectotype and one of the paralectotypes of *C. koellikeri*, as well as from additional museum specimens obtained through intra-museum loans. For both freshly collected and museum specimens, DNA was extracted using the Qiagen DNEasy Blood and Tissue Kit following the manufacturer's recommended protocol. The DNA samples were quantified using a Qubit fluorometer, and their quality checked with a NanoDrop spectrophotometer. We sent 19 DNA samples to Arbor Biosystems for library preparation, target-enrichment and sequencing (Ann Arbor, MI, USA), using myBaits Custom DNA-Seq protocol (ver. 5.03). For the target-enrichment of UCEs/exons, we used the octocoral baitset (ver. 2; Erickson *et al.* 2021). In addition to targeted capture sequencing, DNA from 23 samples were sent to the Australian Genome Research Facility (AGRF) for library preparation and genome skimming (e.g. low coverage shotgun-sequencing). Library preparation was carried out viby adaptor ligation, and samples were processed under 5Gbp Prep M bundle for which sequencing was performed on the illumina NovaSeq X platform using 300 cycle or 150-bp PE reads with a read target of 20 million paired end reads (see https://www.agrf.org.au/).

We combined our new sequences with published UCE/exon data for 14 octocorals (9 families) from the study by McFadden *et al.* (2022) from the BioProjects PRJNA588468, PRJNA822352 and PRJNA413622 from GenBank (Erickson *et al.* 2021; McFadden *et al.* 2022). We processed paired end reads using *phyluce* (ver. 1.7.2, see https://github.com/faircloth-lab/phyluce; Faircloth 2016). We performed quality control and pre-processing of reads using *fastp* (ver. 0.32.2, see https://github.com/OpenGene/fastp; Chen *et al.* 2018) before assembling using *SPAdes* (ver. 3.15.5, see https://github.com/ablab/spades; Bankevich *et al.* 2012), outside of *phyluce*. Assembled contigs were mapped and corrected (https://phyluce.readthedocs.io/en/latest/daily-use/daily-use-4-workflows.html), before being matched in *phyluce* to the octocoral baitset (Erickson *et al.* 2021) to find loci with a minimum identity and coverage of 70% using phyluce_assembly_match_contigs_to_probes. We then created an incomplete data matrix and extracted the loci into a FASTA file by running phyluce_assembly_get_match_counts and phyluce_assembly_get_fastas_from_match_counts respectively. Loci were aligned using *MAFFT* (ver. 7.505, see https://mafft.cbrc.jp/alignment/software/; Katoh *et al.* 2002) and internally trimmed using phyluce_align_seqcap_align with the 'no trim' option followed by phyluce_align_get_gblocks_trimmed_alignments_from_untrimmed (Castresana 2000). Alignment matrices were then created for loci represented by 60% sample occupancy using phyluce_align_get_only_loci_with_min_tax.

Maximum likelihood analysis was performed in *IQ-TREE* (ver. 2.2.2.2, see https://github.com/iqtree/iqtree2; Minh *et al.* 2020). The *ModelFinder* algorithm in *IQ-TREE* (see http://www.iqtree.org/ModelFinder/) was used to select the best substitution model and partitioning scheme for the UCE/exon loci (Kalyaanamoorthy *et al.* 2017), with the '-m MFP + MERGE --merge-model GTR --merge-rate G --rclusterf 10' parameters. Ultrafast Bootstrap support was estimated from 1000 bootstrap replicates (Hoang *et al.* 2018).

To investigate topological concordance among overall site patterns and independent gene trees, site concordance factors (sCF) and gene concordance factors (gCF) were computed using *IQ-TREE*. Both site and gene concordance factors are different from statistical measures of support (e.g. parametric bootstrap) and more accurately describe topological variation related to biological parameters (Lanfear and Hahn 2024). The gene concordance factor (gCF) quantifies the percentage of individual UCE loci whose inferred trees contain a specific branch found in the reference (e.g. species) tree; thus, a higher gCF indicates that a larger proportion of UCE loci agrees with that particular branch (Minh *et al.* 2020). Low gCF values, potentially reaching zero, indicate that individual gene trees conflict with the species tree topology for a given branch. Such discordance is often attributed to insufficient phylogenetic signal in gene alignments or to biological factors like incomplete lineage sorting (ILS), the latter being particularly common along short branches (Minh *et al.* 2020). Site concordance factors (sCF) measure the percentage of phylogenetically informative sites in an alignment that support a specific branch in a reference tree. Because there are three possible unrooted quartet topologies for any given set of four taxa, an sCF value close to 33.3% for a branch indicates substantial conflict among sites, suggesting that the three alternative resolutions receive nearly equal support (Minh *et al.* 2020). Consequently, a sCF value notably exceeding this level of conflict is generally interpreted as stronger evidence for that branch.

Species delimitation

For species delimitation, we used an integrated approach that relies on multiple lines of evidence. We adopted the unified species concept proposed by De Queiroz (2007), which considers being 'independently evolving metapopulation lineages' as the only property necessary to define a species. Accordingly, this approach allows evolutionarily distinct lineages to be distinguished even in the absence of clear morphological differences (De Queiroz 2007; Bridge *et al.* 2024). This also addresses a major issue in Octocorallia, as species that are genetically distinct are known to have identical or overlapping morphological features (e.g. cryptic species) and biogeography (Concepcion *et al.* 2008; McFadden *et al.* 2017).

We generated species hypotheses using two species delimitation methods. These are standard genetic clustering

methods called principal coordinate analysis (PCA) and *STRUCTURE* (ver. 2.3, see https://web.stanford.edu/group/pritchardlab/structure.html; Pritchard *et al.* 2000), and an unsupervised machine learning method known as t-distributed Stochastic Neighbour Embedding (t-SNE; van der Maaten and Hinton 2008). Both methods were applied to a SNPs dataset generated from the UCE data. SNPs were extracted using the following pipeline: https://github.com/Lavarchus/SNP-calling-GATK4. Briefly, the sample with the highest number of UCE contigs was selected as reference sample for SNP calling. For 21 samples, UCEs were bioinformatically obtained from genome skimming data, and therefore had longer contigs. Consequently, we selected the sample with the highest number of UCE contigs manually from the log file phyluce_assembly_match_contigs_to_probes.log from targeted sequencing data. Clean and trimmed reads for all samples were mapped using *bwa* (ver. 0.7.17, see https://github.com/lh3/bwa) to the reference (Li 2013), sorted using *Samtools* (ver. 1.20, see https://github.com/samtools/samtools; Li *et al.* 2009), and duplicates were marked and removed using *Picard* (ver. 3.1.1, Broad Institute, Cambridge, MA, USA, see http://broadinstitute.github.io/picard/). The Genome Analysis Toolkit (*GATK4*, ver. 4.5.0.0, see https://gatk.broadinstitute.org/hc/en-us; Van der Auwera *et al.* 2013) was used for initial haplotype calling (gatk HaplotypeCaller), consolidation (gatk CombineGVCFs), joint genotyping (gatk GenotypeGVCFs) and SNPs and indels extraction (gatk SelectVariants). Later, *GATK4* was also used to filter and select variants that passed filtering to improve call set, using '–filter-expression SOR' (gatk VariantFiltration and gatk SelectVariants). Then, we ran the first calibration step on unrecalibrated data (gatk BaseRecalibrator), created new bam files with adjusted base quality scores (gatk ApplyBQSR) and recalibrated the resulting adjusted bam files (gatk BaseRecalibrator). Before and after recalibration plots were produced to assess the effects of the first recalibration on the original data. We repeated the pipeline until the plots showed convergence. All plots are available in the Supplementary Fig. S3.

STRUCTURE employs a Bayesian clustering approach to assign samples in the form of multilocus genotypes (SNPs) into a defined number of genetic clusters (referred to as K populations). We transformed the vcf file obtained from the SNP pipeline into a genlight object using the package *adegenet* (ver. 2.1.1, function 'vcfR2genlight', see https://CRAN.R-project.org/package=adegenet; Jombart 2008) in *R* (ver. 2024.12.1, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/). Then, we ran *STRUCTURE* also in *R* using the function 'gl.run.structure' (package *dartR*, ver. 1.0.5, see https://CRAN.R-project.org/package=dartR; Gruber *et al.* 2018; Mijangos *et al.* 2022) using 100,000 generations and a burnin of 50,000. We did 5 runs for each number of *K*, with a maximum *K* of 6. The most likely number of genetic clusters was then determined from the Evanno DeltaK plot (Evanno *et al.* 2005) in *R*, using the function gl.evanno. The *STRUCTURE* output was then fed to *StructureSelector* (see https://lmme.ac.cn/StructureSelector/) to test the possibility of *K* being 1 (Li and Liu 2018).

t-SNE is a non-linear and randomised approach that reduces the dimensionality of the data. In a low dimensional embedding, the method maintains the probability distribution of distances within a cluster that was in the original high-dimensional space. Simultaneously, it repels points that were distant in the high-dimensional space, which are then interpreted as being from different clusters (Derkarabetian *et al.* 2019). Following PCA results, we performed the t-SNE analysis in *R*, using the package *Rtsne* (ver. 0.17, J. Donaldson, see https://github.com/jdonaldson/rtsne/), function 'tsne'. We specified a perplexity = 7.

Systematics

Order **MALACALCYONACEA** McFadden, van Ofwegen & Quattrini, 2022

Family **CLAVULARIIDAE** Hickson, 1894

Clavularia de Blainville, 1830

Type species: *Clavularia viridis* Quoy & Gaimard, 1833.

Diagnosis (translated and amended from de Blainville in Levrault 1830, with changes or additions in bold)

Octocorals with no skeletal axis. Individual polyps arise from a basal ribbon-like or membranous stolon. Polyps monomorphic and clavate, occasionally with very tall calyces. **Pinnules free,** often arranged in multiple rows. **Sclerites of pinnules are minute plates, often peanut shaped or oval, sometimes tuberculated on both ends. Calyx with long and fusiform spindles or shorter rods. Stolon with highly tuberculated rods, often fused together or interlocked. Zooxanthellate.**

Key to the genera of Clavulariidae and Hicksoniidae

1. Basal stolon only.....2
   Stolons form bridges connecting polyps on multiple levels.....***Hicksonia***
2. Pinnules fused forming pseudopinnules.....3
   Pinnules free.....***Clavularia***
3. Fused sclerites in the stolon.....***Hanabira***
   Sparse scale-like sclerites.....***Knopia***

Key to the species of *Clavularia*

1. Plates with tubercles on both ends.....**2**
   No tubercles on plates.....***C. brunafolia* sp. nov.**
2. Stolon sclerites are highly tuberculated rods.....3
   Stolon sclerites are smooth rods with tuberculated ends.....
   .....***C. inflata***
3. Tentacles folded over mouth.....***C. viridis***
   Tentacles occasionally folded over mouth, mostly retracted in calyx.....***C. koellikeri***

Clavularia viridis Quoy & Gaimard, 1833

(Fig. 2, 3, 16.)

Not *Clavularia viridis*: Hickson (1894), pp. 335–344, plate 49.

Not *Hicksonia* (*Clavularia*) *viridis* Delage & Hérouard, 1901, pp. 386–387, fig. 506.

Not *Hicksonia viridis*: Dean (1927), pp. 115–118, fig. 2 & 4.

Not *Clavularia viridis*: Hickson (1930).

Not *Clavularia viridis*: Fujiwara *et al.* 2003 (listed only).

Not *Clavularia* cf. *viridis*: McFadden *et al.* 2022 (listed only).

Type material examined

LECTOTYPE (here designated). MNHN-IK-2000-184, Solomon Islands, Island of Vanikoro (Santa Cruz group), South Pacific, 1829, coll. Quoy & Gaimard.

Additional material

Vanuatu, CAS_IZ307254, North Mele Bay, Efate, Vanuatu, South Pacific Ocean, 1.5 km offshore (17°42.36′S 168°15.80′E), 17 November 2000, SCUBA, coll. Coral Reef Research Foundation.

Description

The specimen MNHN-IK-2000-184 is well preserved and all sections were present for morphological analyses. The specimen consists of three fragments assumed to be of the same colony (Fig. 2*a*). The stolon is a spreading membrane, 0.50–0.67 mm thick ($\bar{x}$ = 0.58 mm, s.d. = 0.08, n = 5). Polyps have prominent longitudinal striations and are spaced close together. The height of the polyps preserved in ethanol ranges from 1.76 to 2.36 cm depending on the degree of contraction of the upper portion ($\bar{x}$ = 2.13 cm, s.d. = 0.22, n = 15). Polyps are clavate; the diameter of the base of the calyx is wider, 1.17–2.35 mm ($\bar{x}$ = 2.08 mm, s.d. = 0.21, n = 10), whereas the distal end is ~3.40–4.61 mm ($\bar{x}$ = 3.70 mm, s.d. = 0.36, n = 9). Tentacles are folded over the mouth (Fig. 2*d*).

The sclerites are abundant, highly diverse in size, shape and ornamentation, and densely aggregated throughout the entire lectotype. The sclerites from the pinnules are mostly elongated plates, occasionally tri-lobed (Fig. 3*a*), 0.03–0.07 mm in length ($\bar{x}$ = 0.05 mm, s.d. = 0.01, n = 31). They have small tubercles at the ends.

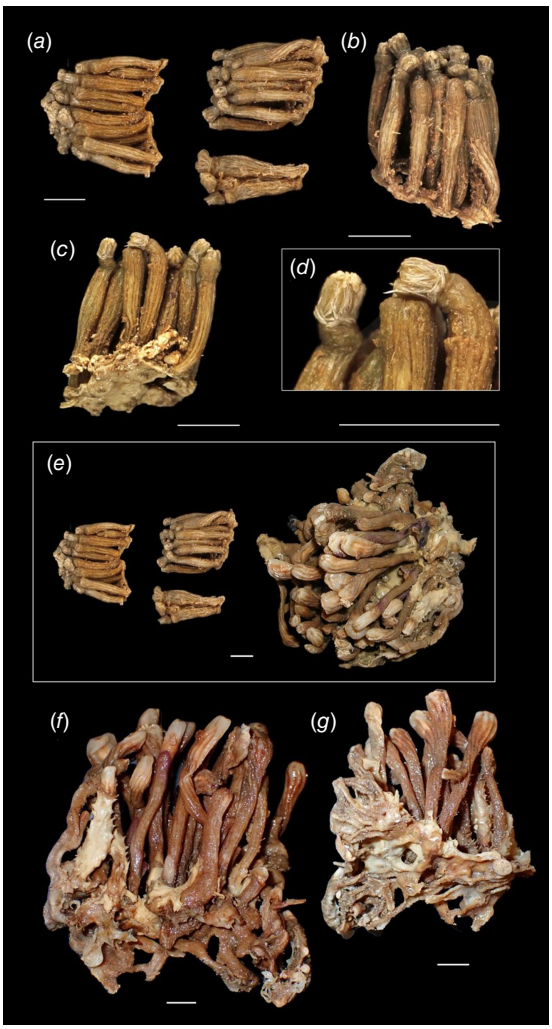

Fig. 2. *Clavularia viridis* Quoy & Gaimard, 1833. (*a*) The lectotype preserved at the Muséum national d'Histoire naturelle in Paris (MNHN-IK-2000-184) consists of three fragments. (*b*) Magnification of one of the fragments, with related (*c*) stolonic structure at the base and (*d*) polyps; (*e*) Size comparison between *C. viridis* Quoy & Gaimard, 1833 (left) and *Hicksonia tohrui* **sp. nov.** holotype (SMNHTAU Co_38221). (right), (*f*) photograph of SMNHTAU Co_38221 and (*g*) its stolonic structure at the base. Scale bar: 1 cm.

Different sclerite shapes and sizes are found in the tentacles. Small plates with smooth margins like the ones from the pinnules were observed, often with tuberculated ends, 0.04–0.06 mm in length ($\bar{x}$ = 0.05 mm, s.d. = 0.01, n = 31) (Fig. 3*a*). Small rods, smooth and with tuberculated ends, can also occur, 0.04–0.18 mm in length ($\bar{x}$ = 0.10 mm, s.d. = 0.03, n = 31) (Fig. 3*a*). Sclerites from the tentacles are tuberculated and often bifurcated rods, 0.20–0.57 mm in length ($\bar{x}$ = 0.30 mm, s.d. = 0.11, n = 35) (Fig. 3*b*). Polyp sclerites are arranged as points and collaret. The points consist of long and bent spindles, 0.57–1.52 mm in length ($\bar{x}$ = 0.90 mm, s.d. = 0.36, n = 13) (Fig. 3*c*). The collaret is made up of three rows of sclerites. They consist of long spindles ($\bar{x}$ = 0.88 mm, s.d. = 0.35, n = 11), occasionally

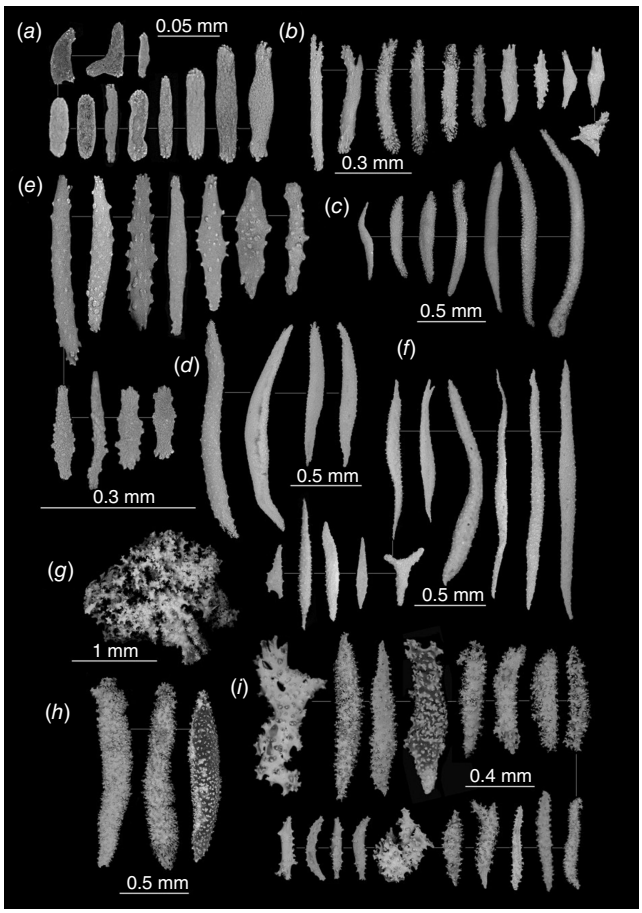

Fig. 3. Scanning electron micrographs of sclerites of the lectotype of *Clavularia viridis* Quoy & Gaimard, 1833 (MNHN-IK-2000-184). Sclerites from (*a*) the pinnules and tentacles, (*b*) only tentacles, (*c*) points, (*d*, *e*) collaret, (*f*) calyx and (*g*–*i*) stolon.

bent or forked on one end, and with simple tubercles (Fig. 3*d*). Rods are also found in the collaret, 0.10–0.37 mm in length ($\overline{x}$ = 0.20 mm, s.d. = 0.08, n = 18). The majority of these rods have large and sparse tubercles, but some of the smaller rods appear unornamented and smooth (Fig. 3*e*).

Sclerites in the calyx are a combination of rods, 0.09–0.79 mm ($\overline{x}$ = 0.40 mm, s.d. = 0.21, n = 16), with small and sparse tubercles, and slender spindles, 0.55–1.84 mm ($\overline{x}$ = 1.15 mm, s.d. = 0.44, n = 13) (Fig. 3*f*), also with sparse and small tubercles. Sclerites from the stolon are highly tuberculated stout spindles, and are interlocked (Fig. 3*g*–*i*). These rods can be bifurcated at one end and stouter, ranging in size between 0.31 and 1.65 mm ($\overline{x}$ = 0.85 mm, s.d. = 0.38, n = 30). Occasionally, sclerites in the stolon have smooth and palmate projections similar to antlers (Fig. 3*i*).

Colour

The anthocodiae of the type material preserved in 75% ethanol are light cream. The rest of the colony is light brown. Quoy and Gaimard (1833) describe the species to be green. *In situ* images of the topotype show the species to be white in colour (Fig. 16*a*).

Variations

The morphology of the topotype (CAS_IZ307254) is mostly consistent with that of the lectotype (Fig. 16*b*). The preserved specimen comprises six polyps, 1.63–2.60 cm long ($\overline{x}$ = 2.01 cm, s.d. = 0.45, n = 6). Polyps are set close together, touching each other in most cases. Polyps are clavate, although both the diameter of the top and bottom of the calyx is wider than in the lectotype; the breadth at the top of the calyx is 6.41–10.20 mm wide ($\overline{x}$ = 8.23 mm, s.d. = 1.26, n = 6), whereas the bottom diameter is smaller, 3.90–5.65 mm wide ($\overline{x}$ = 4.99 mm, s.d. = 0.61, n = 6).

Remarks

This study is the first to re-examine the holotype of *C. viridis* since its designation by Quoy and Gaimard (1833). Quoy and Gaimard described the gross morphology of the species, but our current findings are not consistent with the original description. Firstly, we reveal that an incorrect unit of measurement was used when the size of the polyps was stated. Quoy and Gaimard (1833) reported the length of the polyps to be ~2 inches (~5 cm). By contrast, our measurements suggest an average length of ~2 cm.

Secondly, Quoy and Gaimard did not show the differences in sclerite shapes and sizes between different sections of the polyps. Our SEM images of the lectotype's sclerites are the first to show the diversity of shapes and sizes between different polyp regions. In the original taxonomic plate of the type, Quoy and Gaimard (1833) only sketched long spindles with sparse and simple tubercles. Similar spindles can be found in the calyx, collaret or even the aboral side of the tentacles. Spindles from the collaret and tentacles, however, are shorter and not the predominant shape. The collaret and points mainly feature rods with sparse and simple tubercles. The sclerites from the tentacles are mostly highly tuberculated and often bifurcated rods. In both tentacles and pinnules, small and unornamented plates also occur. Finally, the sclerites of the membranous stolon are highly tuberculated stout spindles that occasionally have smooth and palmate projections similar to antlers.

Differences are also seen compared to the specimens of *C. viridis* collected and published by Hickson (1894) and Dean (1927) (Table 1). Indeed, the average length of the polyps reported in their accounts matches the size reported in the original description of the Quoy and Gaimard specimen. However, those measurements were based on the wrong unit of measurement, and our re-description of the type material revealed the species to be smaller than previously thought. Additional differences are in the shape and distribution of sclerites in the colony. Hickson (1894) reported the anthocodia

to be devoid of sclerites in his Indonesian specimen, but Dean (1927) described small multi-rayed platelets. Additionally, neither author described the sclerites from the stolon, although the irregular sclerites described by Dean (1927) from the calyx are a close match to the ones found in the type. Therefore, Hickson's and Dean's specimens are likely not of *C. viridis*. Overall, our re-description of the type revealed a complexity of shapes and sizes never reported before across specimens identified as *C. viridis*.

Living features

Polyps in the field white in colour (Fig. 16*a*). Pinnules arranged in a single row and long. Pinnules longer when closer to the oral section.

Clavularia inflata Schenk, 1896

(Fig. 4.)

Clavularia inflata: Schenk (1896), pp. 48–49, fig. 1, 24–26.

Clavularia (*Hicksonia*) *inflata*: Hickson (1930) (listed only).

Not *Clavularia inflata*: McFadden *et al.* (2021) (listed only).

Not *Clavularia inflata*: McFadden *et al.* (2022), pp. 8–12 (listed only).

Not *Clavularia inflata*: Subhan *et al.* (2022*a*), fig. 2, 3.

Not *Clavularia inflata*: Subhan *et al.* (2022*b*) (listed only).

Type material examined

LECTOTYPE (here designated). SMF37, Indonesia, Moluccas, coll. Kükenthal, 1894.

Description

The specimen SMF37 consists of two small fragments assumed to be from the same colony (Fig. 4*a*). The stolon appears to be a spreading membrane, although its thickness could not be accurately measured since part of the structure in the subsample here examined turned out to be an encrusting sponge (Fig. 4*b*). Based on the photographic record provided, the lectotype consists of approximately six short polyps in total, 0.20–1.51 cm long ($\bar{x}$ = 0.67 cm, s.d. = 0.45) depending on the degree of contraction. Polyps are cylindrical and stiff, and not equally distant from each other. The polyps' bodies have vertical striations, but the surface appears smooth compared to the striated polyps of the type of *C. viridis*. The anthocodia is fully retracted within the calyx. From the subsample it was not possible to observe structures such as points and collaret.

The sclerites are abundant and densely packed throughout the colony. The pinnule sclerites comprise small platelets with medial constrictions, 0.01–0.03 mm in length ($\bar{x}$ = 0.02 mm, s.d. = 0.01, n = 10) (Fig. 4*c*). Tentacles have smooth rods with tubercles at the ends, 0.03–0.09 mm ($\bar{x}$ = 0.06 mm, s.d. = 0.02, n = 7) (Fig. 4*d*). From the fragment here analysed, it was not possible to identify whether sclerites are organised as collaret or points. The calyx sclerites comprise smooth rods often forked and with

Table 1. Morphological comparison between the type material of *Clavularia viridis* Quoy & Gaimard, 1833, here examined, with the morphology of the unexamined specimens of Hickson (1894) and Dean (1927).

	Clavularia viridis **Hickson (1894), pp. 335–344, plate 49.**	***Hicksonia viridis*** **Dean (1927), pp. 115–118, fig. 2, 4.**	***Clavularia viridis*** **Lectotype. MNHN-IK-2000-184 (this study)**
Collection location	Celebes, Indonesia.	Saleyer and Karakelang Island, Indonesia.	Vanikoro, Solomon Islands.
Length of the polyps	Average = ~5 cm Max. = ~10 cm	Average = NA Max. = 5 cm	Average = ~2 cm Max. = ~2.5 cm
Breadth of top of calyx	Average = NA Max. = NA	Average = 3.5 mm Max. = NA	Average = 3.7 mm Max. = 4.6 mm
Sclerites of the anthocodia	Absent	Numerous small plates, multi-rayed. Average diameter 0.03 mm	(a) Small plates (0.05 mm long) (b) Small and unornamented rods (c) Larger and often bifurcated rods (d) Long and pointed spindles that run along the tentacles (0.9 mm long)
Sclerites of the calyx	Long spindles with numerous tubercles. Average length is 2.3 mm	(a) Long spindles with simple tubercles (2.5 mm long) (b) Large spindles, highly tuberculated and with branched ends. Variable in size (0.8–2.5 mm long) (c) Irregular and interlocked, ~0.4 mm long	(a) Rods with small and sparse tubercles (0.4 mm long) (b) Slender spindles with sparse and small tubercles (1.2 mm long)
Sclerites of the stolon	NA	NA	Stout spindles, often bifurcated (0.8 mm long)

NA indicates information not provided. Max., maximum.

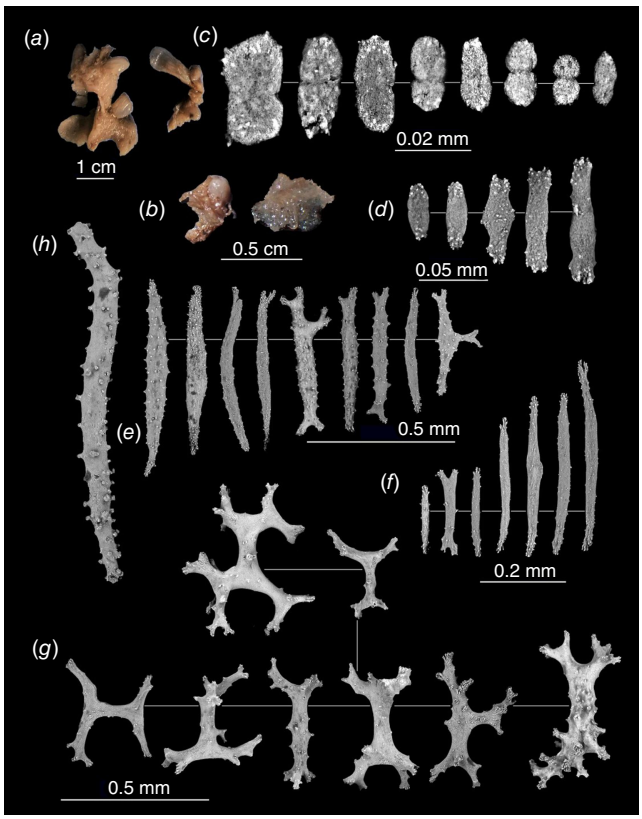

Fig. 4. (*a*) Lectotype of *Clavularia inflata* (Schenk, 1896) (SMF37) and (*b*) fragments sub-sampled from the lectotype and examined. (*c*, *d*) Scanning electron micrographs of sclerites from the pinnules and tentacles. Sclerites from the (*e*, *f*) calyx, and (*g*) stolon. (*h*) Long rod from the calyx base.

sparse, small and simple tubercles, especially clustered at the ends, 0.16–0.82 mm ($\overline{x}$ = 0.47 mm, s.d. = 0.16, n = 30) (Fig. 4*e*, *f*). Occasionally, rods can be branched (Fig. 4*e*, *f*). Where the calyx merges with the stolon, we observed three long rods, all with damaged tips (Fig. 4*h*). All three rods were >1 mm long, and were not observed in any other part of the sub-sample. Finally, the stolon sclerites consist of smooth branched rods with tuberculated ends, 0.17–0.53 mm long ($\overline{x}$ = 0.37 mm, s.d. = 0.09, n = 30) (Fig. 4*g*).

Colour

The polyps preserved in 70% ethanol are brown. The stolon is a darker shade of brown.

Remarks

This study is the first to re-examine part of the syntype series of *C. inflata* since its designation by Schenk (1896). A detailed analysis of the gross morphology of the lectotype (here designated) was complicated due to the small size of the fragments, but our measurements of the length of the polyps are consistent with the original description. We also confirm the polyps are stiff, as sclerites are abundant and densely packed across all regions of the colony. Based on the material loaned, however, the stolon was not evident or measurable. Indeed, we found the stolon was covered by a sponge, which was also encrusting the lower section of the calyx. Although the presence of the sponge was acknowledged by Schenk (1896), he sketched the sponge spicules in the original description when showing the arrangement of the sclerites of the calyx section. Our analyses of the sclerites from the tentacles and polyp body are consistent with the original description, although our measurements of the sclerites from the calyx show slightly shorter sclerites than previously reported. Finally, our SEM images of the lectotype stolon are the first to show the shape and size of its sclerites. *C. inflata* differs from *C. viridis* and *C. koellikeri* in both gross morphology and sclerites. Indeed, the polyps in *C. inflata* are the shortest among the three species. The smooth and branched rods with tuberculated ends from the stolon are also a unique feature of *C. inflata*. Some specimens of *C. koellikeri* do have similar sclerites in the stolon, but they are never the main shape and are often covered in small and simple tubercles not just at the ends (Fig. 11*g*).

Additional syntypes of *Clavularia inflata* are preserved at the Museum für Naturkunde in Berlin (ZMB 3593) and at the Senckenberg Nature Museum in Frankfurt (SMF36). These syntypes should be considered as paralectotypes, although they were not analysed in this study. The specimen ZMB 3593 has additional information attached; specimen was collected in Ternate (0°53.864′N 127°18.998′E). The specimen was acquired from Kükenthal on 19 January 1897. Data from SMF36 is as per lectotype (here designated). No molecular data were obtained from this species.

Living features

The species is known only from the preserved specimens and no *in situ* photographs are available.

Distribution

The species does not seem to occur on the GBR or in Japan (Okinawa and Iriomote Is.). Therefore, it is possible the species is confined to the type locality of Indonesia.

Clavularia koellikeri (Dean, 1927)

(Fig. 5–14.)

Hicksonia köllikeri Dean, 1927, pp. 118–120, fig. 1, 3.

Clavularia koellikeri: Hickson (1930) (listed only).

Clavularia koellikeri: Bastidas *et al.* (2002) (listed only).

Clavularia koellikeri: Fujiwara *et al.* (2003) (listed only).

Clavularia inflata: McFadden *et al.* (2021) (listed only).

Clavularia inflata: McFadden *et al.* (2022) (listed only).

Material examined

LECTOTYPE (here designated). Indonesia. ZMA.COEL.2683, Lesser Sunda Islands, Timor, Samau Island, Haingsisi (10°12′18.0″S, 123°27′32.8″E), 27 April 1899. **PARALECTOTYPES (here designated).** Indonesia. ZMA.COEL.2693, Lesser Sunda Islands, Paternoster Islands, Sailus Ketjil, close to reef (7°32′39.8″S, 117°24′06.1″E), 30 March 1899; Indonesia. ZMA.COEL.2695, Lesser Sunda Islands, Paternoster Islands, Sailus Ketjil, close to reef (7°32′39.8″S, 117°24′06.1″E), 30 March 1899; Indonesia. ZMA.COEL.2699, Lesser Sunda Islands, Timor, Samau Island, Haingsisi (10°12′18.0″S, 123°27′32.8″E), 27 April 1899; Indonesia. ZMA.COEL.2688, Maluku, Kur Island, anchorage off Kilsuin (5°21′04.7″S, 131°57′10.4″E), 6 December 1899; Indonesia. ZMA.COEL.2687, Sulawesi, 1300 m distant from the North point of Kabia Island reefpoint (6°52′49.4″S, 122°12′10.8″E), 28 September 1899; Indonesia, ZMA.COEL.2694, Maluku, Kur Island, anchorage off Kilsuin (5°21′04.7″S, 131°57′10.4″E), 27 April 1899; Indonesia. ZMA.COEL.2702, Lesser Sunda Islands, Timor, Samau Island, Haingsisi (10°12′18.0″S, 123°27′32.8″E), 27 April 1899.

Additional material

Palau. QMT G84672, West Channel, Palau (7°32′29.76″N, 134°28′20.82″E), 20 May 2010, 10–20 m, coll. Catherine McFadden; Australia. QMT G84386, Snapper Point, Orpheus Island, Queensland (18°39′35.032″S, 146°30′29.128″E), 4 October 2022, 2.1 m, coll. Stefano Borghi; Australia. QMT G84387, Snapper Point, Orpheus Island, Queensland (18°39′35.032″S, 146°30′29.128″E), 4 October 2022, 2.4 m, coll. Stefano Borghi; Australia. QMT G84388, North Pelorus Island, Queensland (18°32′14.381″S, 146°29′38.198″E), 4 October 2022, 4.8 m, coll. Stefano Borghi; Australia, QMT G84392, Seabird Islet, Lizard Island (14°41′33.3″S, 145°28′04.6″E), Queensland, 6 m, 11 April 2022, coll. Stefano Borghi; Australia, QMT G84393, Seabird Islet, Lizard Island (14°41′33.3″S, 145°28′04.6″E), Queensland, 6 m, 11 April 2022, coll. Stefano Borghi; Australia, QMT G84394, Pelorus Island (18°33′38.293″S, 146°29′24.432″E), Queensland, 4 m, 3 November 2022, coll. Stefano Borghi and Augustine Crosbie; Australia, QMT G84395 to QMT G84399, South Pelorus Island (18°33′38.293″S, 146°29′24.432″E), Queensland, 4 m, 3 November 2022, coll. Stefano Borghi; Australia, QMT G84401- G84402, G84408 and QM G339835, Falcon Island (18°37′49.357″S, 147°4′51.902″E), Queensland, 5 m, 23 November 2022, coll. Stefano Borghi, Merrick Ekins and Thomas Bridge; Australia, QMT G84494 and QMT G84496, North of Corbett Reef (13°51′42.768″S, 144°8′9.758″E), Queensland, 5 m, 29 March 2024, coll. Andrew Baird; QM G309080, Fantome Island (18°39′48″S, 146°30′30″E), Queensland, 7 m, NCIQ66C0398-W, 19 February 1987, coll. Australian Institute of Marine Sciences; QM G309099, Orpheus Island (18°34′00.0″S, 146°29′24″E), Queensland, 5 m, NCIQ66C0465-U, 20 February 1987, coll. Australian Institute of Marine Sciences; Japan, QMT G84478 to QMT G84480, Nakano Beach (24°25′0.8″N, 128°49′44.778″E), Iriomote Island, 25 m, 16 September 2023, coll. Stefano Borghi and James D. Reimer; Japan, QMT G84460, QMT G84462 and QMT G84463, Oku Beach (26°51′7.83″N, 128°16′59.455″E), Okinawa, 4 m, 5 September 2023, coll. Stefano Borghi; Japan, QMT G84465, Jashiki, Kunigami district (26°46′56.133″N, 128°12′38.38″E), Okinawa, 9 m, 10 September 2023, coll. Stefano Borghi; Australia, BMNH 1946.1.14.101, Maer Island (9.9172°S, 144.0516°E), Torres Strait Island Region, Queensland, Great Barrier Reef Expedition 1928–1929, Professor S.J. Hickson Collection.

Description

The lectotype consists of numerous fragments with more than 40 polyps in total, presumably from the same colony and species. A fragment with four polyps was analysed morphologically from the lectotype (ZMA.COEL.2683) (Fig. 6*a*). The polyps are variable in size, 0.31–1.10 cm ($\bar{x}$ = 0.82 cm, s.d. = 0.29, n = 6), and not rigid. The anthocodia is often not fully retracted within the calyx, and tentacles are seen folded over the mouth. Polyps are clavate, with a wider diameter in the upper calyx region, 0.29–0.43 cm ($\bar{x}$ = 0.35 cm, s.d. = 0.06, n = 9), compared to the base being 0.15–0.28 cm ($\bar{x}$ = 0.19 cm, s.d. = 0.05, n = 6). Most fragments comprise individual polyps and therefore it is uncertain how close the polyps are in living colonies. Based on the few fragments with multiple polyps, the polyps are set close together. The stolon is fragmented but appears ribbon-like and rigid.

Sclerites are abundant across all sections of the specimen. The sclerites from the pinnules are small plates densely packed. These plates are sometimes ornamented with tubercles at both ends, and sometimes unornamented and often peanut-shaped (Fig. 6*b*), 0.02–0.06 mm in length ($\bar{x}$ = 0.04 mm,

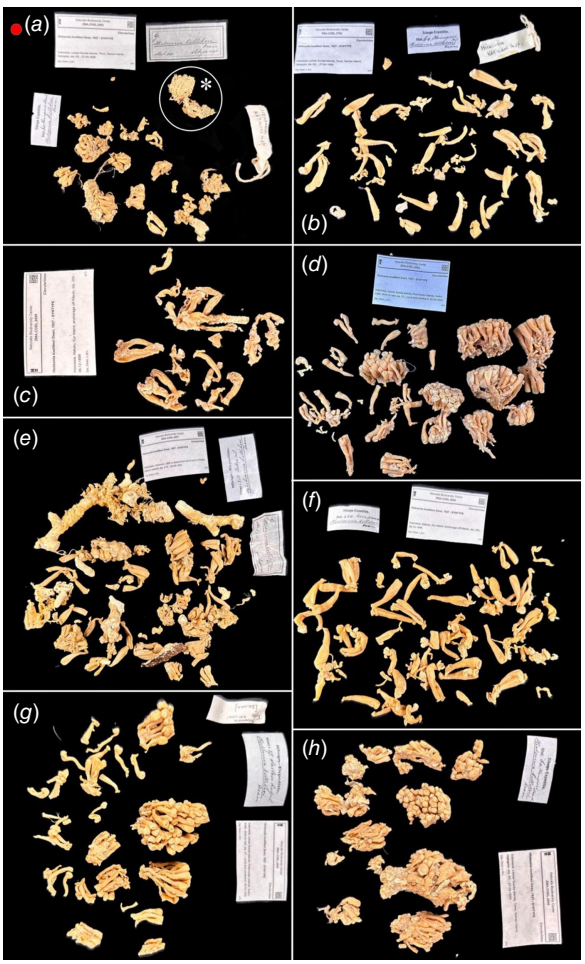

Fig. 5. Syntype series of *Clavularia koellikeri* (Dean, 1927). (*a*) Lectotype (ZMA.COEL.2683; red dot) here designated and paralectotypes. The asterisk ('*') indicates a fragment preserved with the lectotype that belongs to a different family (presumably Xeniidae). (*b*) ZMA.COEL.2702, (*c*) ZMA.COEL.2688, (*d*) ZMA.COEL.2693, (*e*) ZMA.COEL.2687, (*f*) ZMA.COEL.2694, (*g*) ZMA.COEL.2695, (*h*) ZMA.COEL.2699. Barcodes on museum labels are 0.5 cm for scale.

s.d. = 0.01, n = 30). Sclerites from the tentacles and points are rods with sparse and simple tubercles, occasionally slightly bent, 0.14–0.59 mm ($\bar{x}$ = 0.36 mm, s.d. = 0.18, n = 40) (Fig. 6*c*). Sclerites from the neck are also a combination of rods and spindles with small and sparse tubercles, 0.15–0.80 mm long ($\bar{x}$ = 0.36 mm, s.d. = 0.20, n = 20) (Fig. 6*d*, *e*). The calyx has rods with small, sparse and simple tubercles, 0.17–0.42 mm ($\bar{x}$ = 0.28 mm, s.d. = 0.04, n = 30) (Fig. 6*f*). The stolon consists of tuberculated rods (Fig. 6*g*), often bifurcated, 0.22–0.48 mm ($\bar{x}$ = 0.36 mm, s.d. = 0.08, n = 15).

Colour

The ethanol-preserved specimen is light brown. Pinnules are cream in colour.

Variation between lectotype and paralectotypes

Gross morphology

Size of polyps varies among the paralectotypes (Fig. 5). Polyps in ZMA.COEL.2699 ($\bar{x}$ = 1.13 cm, s.d. = 0.32, n = 5) are the most similar to the lectotype, and the shortest among paralectotypes. The largest polyps were observed in the paralectotype ZMA.COEL.2702 ($\bar{x}$ = 2.65 cm). The diameter of the upper and lower calyx, however, was consistent across all specimens (Supplementary Table S2). We also note differences in the appearance and structural arrangement of the stolonic base. The basal stolon is irregular and ribbon-like in most specimens, sometimes giving the appearance of bridges connecting polyps on multiple levels. These connections, however, are only visible in the lower half of the calyx in some of the preserved specimens, including ZMA.COEL.2695 and ZMA.COEL.2699. The stolon in ZMA.COEL.2693 is more like a spreading membrane rather than tubular and ribbon-like.

Pinnule sclerites

Sclerites are found in pinnules in all preserved specimens, but often differ in shape and size (Fig. 7–12). The pinnule sclerites of the paralectotypes are similar in size to the those of the lectotype, but smaller plates can be found in ZMA.COEL.2688, 0.02–0.06 mm long ($\bar{x}$ = 0.03 mm, s.d. = 0.01, n = 30) (Fig. 11*b*). All specimens, however, have similar sclerites with medial constrictions, which can also occasionally be three lobed (e.g. ZMA.COEL.2687 and ZMA.COEL.2683) (Fig. 6*b* and 9*b* respectively). Pinnule sclerites from the specimen ZMA.COEL.2699 are the most similar in size to the lectotype, 0.02–0.05 mm long ($\bar{x}$ = 0.04 mm, s.d. = 0.01, n = 30) (Fig. 10*b*), although some differ in shape for they are never three lobed.

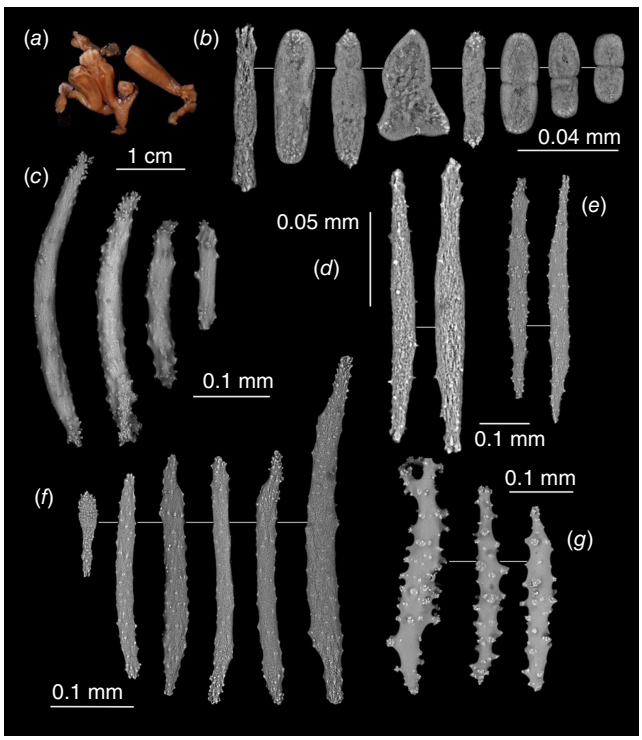

Fig. 6. (*a*) Fragment of the lectotype of *C. koellikeri* (ZMA.COEL.2683) and examined in this study. Sclerites from (*b*) pinnules, (*c*) tentacles, (*d*) anthocodia but magnified (*e*) anthocodia section, (*f*) calyx and (*g*) stolon.

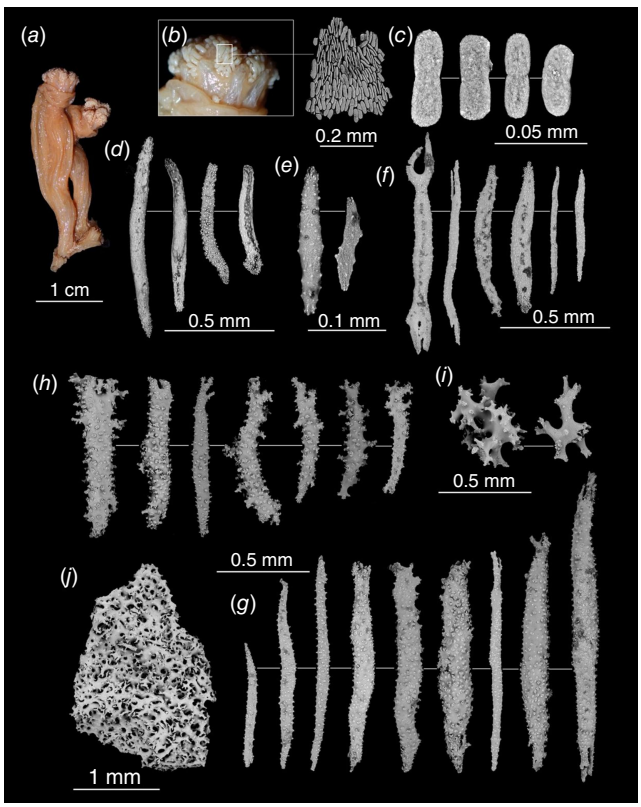

Fig. 7. (*a*) Fragment of the paralectotype of *C. koellikeri* (ZMA.COEL.2702) and examined in this study. (*b*) sclerite arrangement in the pinnules. Sclerites from (*c*) pinnules, (*d*,*e*) tentacles and points, (*f*) anthocodia, (*g*) calyx and (*h*–*j*) stolon.

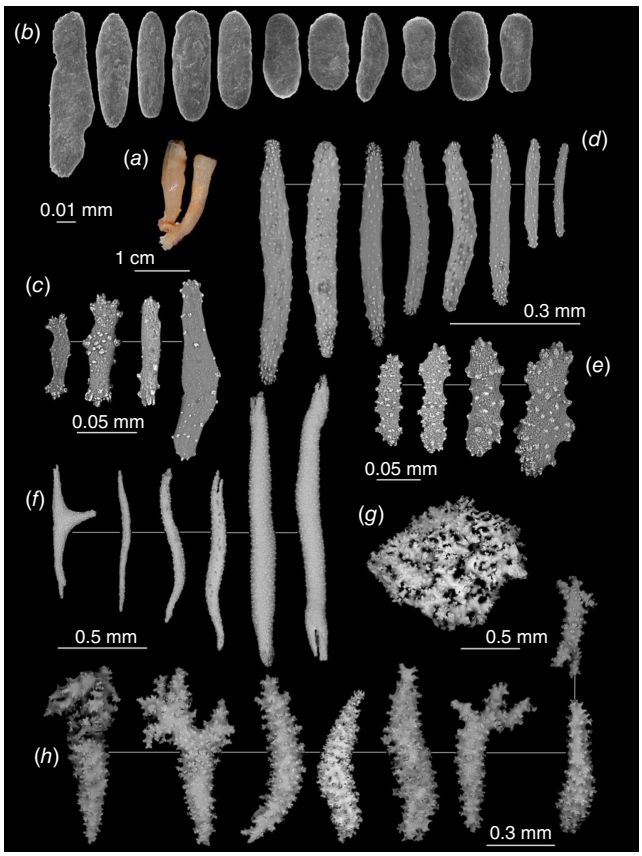

Fig. 8. (*a*) Fragment of the paralectotype of *C. koellikeri* (ZMA.COEL.2693) examined in this study. Sclerites from (*b*) pinnules, (*c*, *e*) tentacles, (*d*) anthocodia, (*f*) calyx and (*g*, *h*) stolon.

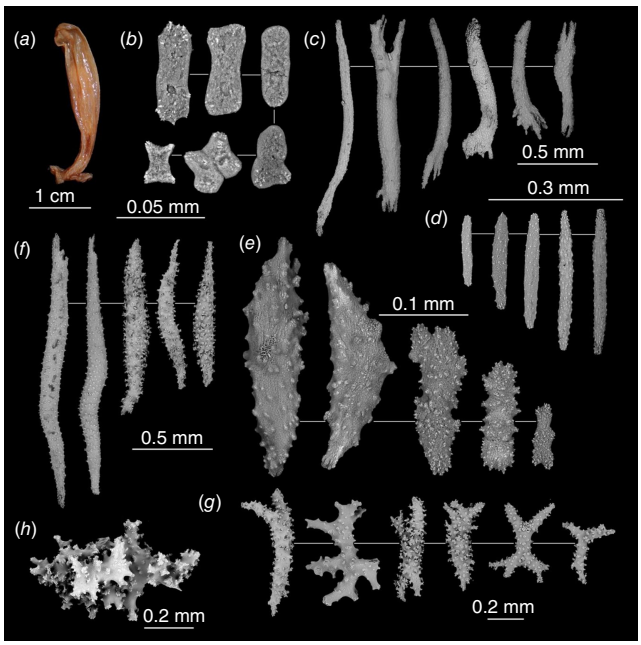

Fig. 9. (*a*) Fragment of the paralectotype of *Clavularia koellikeri* (ZMA.COEL.2687), and examined in this study. Sclerites from (*b*) pinnules, (*c*, *d*) tentacles, (*e*) anthocodia, (*f*) calyx and (*g*, *h*) stolon.

Tentacle sclerites

In all the types, rods are the dominant shape of sclerites within the tentacles. Rods mostly have simple tubercles and can be of similar size to the lectotype, such as in ZMA.COEL.2699 (0.34–0.71 mm long; $\bar{x}$ = 0.55 mm, s.d. = 0.11, n = 16) (Fig. 10*d*), ZMA.COEL.2707 (0.17–0.71 mm long; $\bar{x}$ = 0.45 mm, s.d. = 0.26, n = 9) (Fig. 7*d*), ZMA.COEL.2693 (0.06–0.15 mm long; $\bar{x}$ = 0.09 mm, s.d. = 0.02, n = 14) (Fig. 8*c*) and ZMA.COEL.2695 (0.15–0.54 mm long; $\bar{x}$ = 0.36 mm, s.d. = 0.13, n = 8) (Fig. 12*c*, *d*). Small and unornamented rods, however, can also occur, such as in ZMA.COEL.2699 (0.03–0.19 mm long; $\bar{x}$ = 0.10 mm, s.d. = 0.06, n = 20) (Fig. 10*c*).

The shape and size of sclerites from the tentacles in ZMA.COEL.2687 and ZMA.COEL.2693, however, differ from the other types. The rods found in ZMA.COEL.2687 are doubled in size, ranging between 0.64 and 1.52 mm in length ($\bar{x}$ = 0.90 mm, s.d. = 0.25, n = 25) (Fig. 9*c*). Moreover, we observed small, flat and tuberculated plates in both ZMA.COEL.2687 (0.06–0.27 mm long; $\bar{x}$ = 0.18 mm, s.d. = 0.05, n = 19) and ZMA.COEL.2693 (0.07–0.18 mm long; $\bar{x}$ = 0.14 mm, s.d. = 0.03, n = 14) (Fig. 8*e* and 9*e* respectively). These tuberculated plates are missing in all other types analysed. In the paralectotypes, we were not able to determine the arrangement of sclerites as points or collaret, as the polyps received on loan had the upper anthocodia fully retracted within the calyx. Therefore, we are now referring to sclerites between the calyx and tentacles as part of the anthocodial section, ignoring their arrangement.

Anthocodial sclerites

The anthocodial sclerites in the paralectotypes are similar in size to the lectotype. The shape is consistently that of rods with simple tubercles. Among types, ZMA.COEL.2683 had the shortest rods on average (0.10–0.80 mm long; $\bar{x}$ = 0.36 mm, s.d. = 0.20, n = 20) (Fig. 6*d*, *e*), followed by ZMA.COEL.2693 (0.20–0.65 mm long; $\bar{x}$ = 0.43 mm, s.d. = 0.13, n = 21) (Fig. 8*d*) and ZMA.COEL.2687 (0.17–0.95 mm long; $\bar{x}$ = 0.49 mm, s.d. = 0.24, n = 18) (Fig. 9*d*). The specimens ZMA.COEL.2695 (0.52–0.96 mm long; $\bar{x}$ = 0.74 mm, s.d. = 0.19, n = 4) (Fig. 12*e*) and ZMA.COEL.2702 (0.43–1.14 mm long; $\bar{x}$ = 0.80 mm, s.d. = 0.22, n = 11) (Fig. 7*f*) are the only exceptions, for their rods are on average longer in size relative to the lectotype's.

Calyx sclerites

The paralectotypes exhibit variation in the shape and size of the sclerites from the calyx. This variation also exists between the paralectotypes and the lectotype. The predominant sclerite shape among the types is the spindle, which can be stouter (Fig. 11*e*) or long and slender, and occasionally bifurcated (Fig. 8*f*). Spindles similar in size can be found

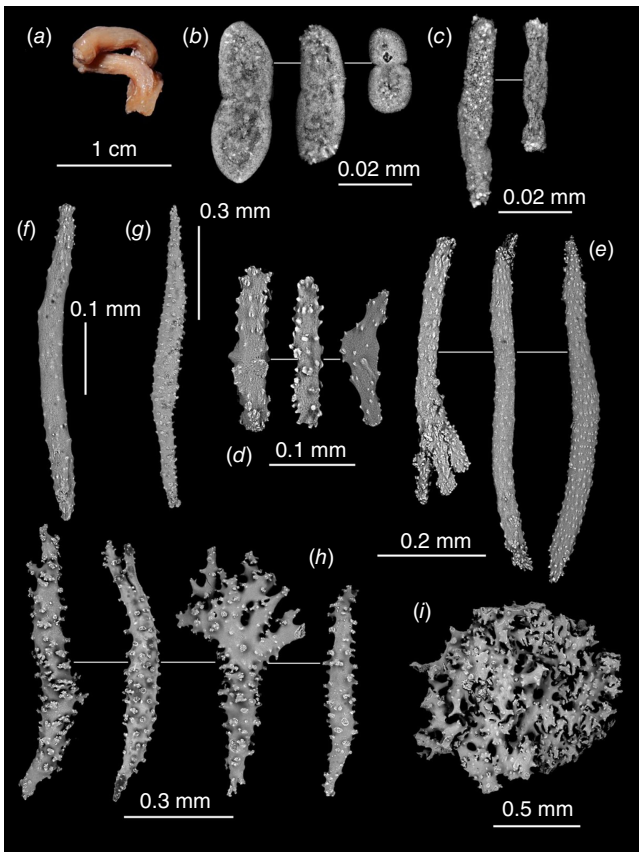

Fig. 10. (*a*) Fragment of the paralectotype of *Clavularia koellikeri* (ZMA.COEL.2699) examined in this study. Sclerites from (*b*) pinnules, (*c*, *e*) tentacles, (*f*) anthocodia, (*g*) calyx and (*h*, *i*) stolon.

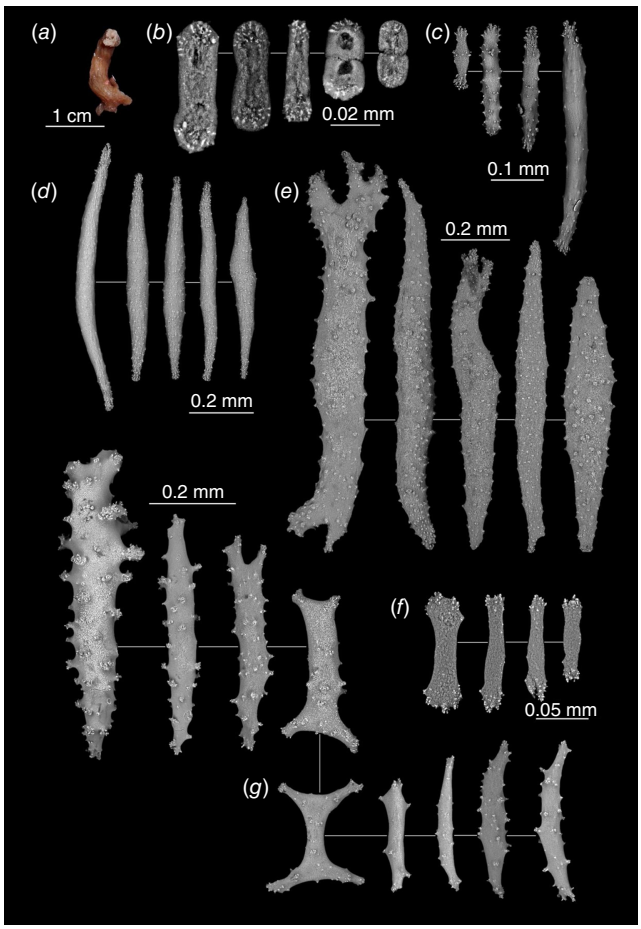

Fig. 11. (*a*) Fragment of the paralectotype of *Clavularia koellikeri* (ZMA.COEL.2688) examined in this study. Sclerites from (*b*) pinnules, (*c*) tentacles, (*d*) anthocodia, (*e*, *f*) calyx and (*g*) stolon.

in ZMA.COEL.2687 (0.78–1.65 mm long; $\bar{x}$ = 1.29 mm, s.d. = 0.28, n = 19) (Fig. 9*f*), ZMA.COEL.2693 (0.59–1.79 mm long; $\bar{x}$ = 1.12 mm, s.d. = 0.36, n = 23) (Fig. 8*f*), ZMA.COEL.2695 (0.52–1.97 mm long; $\bar{x}$ = 1.26 mm, s.d. = 0.36, n = 5) (Fig. 12*f*) and ZMA.COEL.2702 (0.70–1.77 mm long; $\bar{x}$ = 1.15 mm, s.d. = 0.23, n = 17) (Fig. 7*g*). Smaller spindles seem to occur in ZMA.COEL.2699, although only one spindle was found fully intact, 0.97 mm in length (Fig. 10*g*).

In addition to the spindles, we also found small and smooth rods from the paralectotype ZMA.COEL.2688, 0.08–0.18 mm ($\bar{x}$ = 0.11 mm, s.d. = 0.03, n = 10) (Fig. 11*f*). The lectotype ZMA.COEL.2683 is the only one that lacks spindles, as all sclerites are more similar to short rods 0.17–0.42 mm in length ($\bar{x}$ = 0.28 mm, s.d. = 0.04, n = 30) (Fig. 6*f*).

Stolon sclerites

All paralectotypes have a rigid stolonic structure, but the level of rigidity of the stolon appears to be determined by the shape of its sclerites. For instance, the stolons in ZMA.COEL.2695 and ZMA.COEL.2688 are similar to that of the lectotype, and comprise highly tuberculated rods that are often branched but never form a compact structure (Fig. 11*g*, 12*g* respectively). Contrastingly, rods in other specimens from the type series are more irregular in shape and branched, forming densely packed structures that maintain their rigidity after bleach treatment. These highly irregular rods are normally long, especially in ZMA.COEL.2699 (0.58–0.81 mm long; $\bar{x}$ = 0.69 mm, s.d. = 0.08, n = 8) (Fig. 10*h*, *i*), ZMA.COEL.2693 (0.55–0.87 mm long; $\bar{x}$ = 0.73 mm, s.d. = 0.11, n = 27) (Fig. 8*g*, *h*) and ZMA.COEL.2702 (0.49–0.90 mm long; $\bar{x}$ = 0.71, s.d. = 0.15, n = 9) (Fig. 7*h–j*). These sclerites, however, are normally smaller in size when they do not form densely packed aggregates, such as in ZMA.COEL.2688 (0.26–0.78 mm long; $\bar{x}$ = 0.46 mm, s.d. = 0.15, n = 23) (Fig. 11*g*).

Stolon sclerites in ZMA.COEL.2688 differ from the others (Fig. 11*g*). We observed smooth and branched rods more similar to the sclerites from the type of *C. inflata* (Fig. 4*e*). Similarly, the stolon in the specimen ZMA.COEL.2694 differs in rigidity and sclerites to the point we originally presumed the specimen belonged to a distinct species. In ZMA.COEL.2694, the stolon is flaccid, and comprises sparse

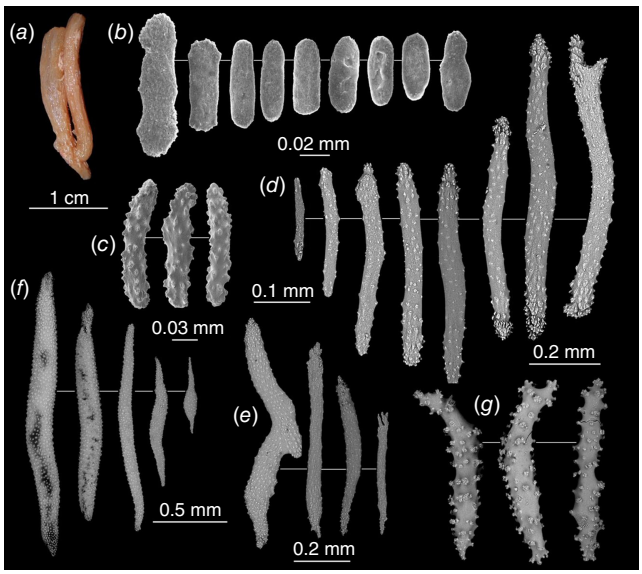

Fig. 12. (*a*) Fragment of the paralectotype of *Clavularia koellikeri* (ZMA.COEL.2695) examined in this study. Tentacles from (*b*) pinnules, (*c*, *d*) tentacles, (*e*) anthocodia, (*f*) calyx and (*g*) stolon.

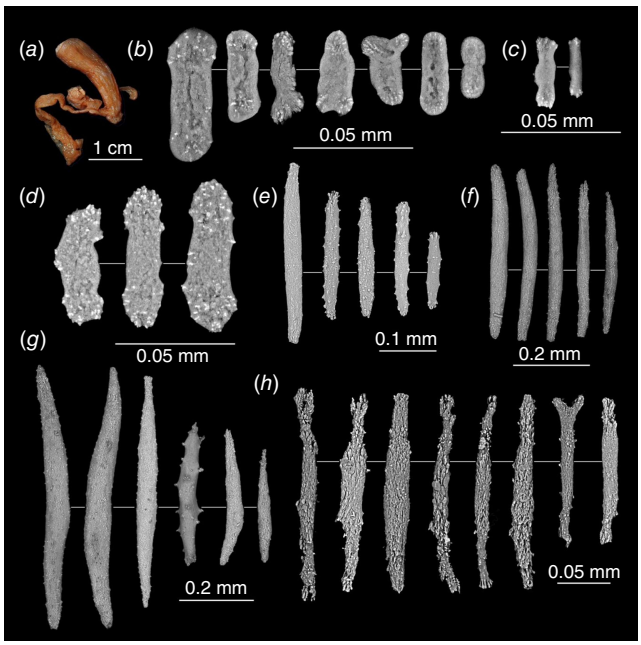

Fig. 13. (*a*) *Clavularia koellikeri*, fragment of the paralectotype ZMA.COEL.2694 examined in this study. Sclerites from (*b*, *c*) pinnules, (*d*, *e*) tentacles, (*f*) anthocodia, (*g*) calyx and (*h*) stolon.

rods that measure between 0.13 and 0.20 mm in length (M = 0.16 mm, s.d. = 0.02, n = 21) (Fig. 13*h*). These rods lack tubercles, can be bifurcated and have a granulated surface. Molecular evidence, however, suggests that ZMA.COEL.2694 and the lectotype of *C. koellikeri* belong to the same species, highlighting the significant morphological variation of the species.

Variation in freshly collected specimens

Our phylogenomic reconstruction (Fig. 24) includes specimens of *Clavularia koellikeri*. These were collected from the central and north GBR, Japan, Indonesia and Palau from ~2–30-m depth. They show variability in their gross morphology and sclerites not only between geographic regions, but also between adjacent collecting sites, similar to what is observed in specimens from the original syntype series. Preserved specimens can have short calyces (Fig. 14*a*, *c*), sometimes showing as small bulbous protuberances that barely stand out from the stolon (QMT G84393) (Fig. 14*e*). Others have calyces up to 3.5 cm long (e.g. QMT G84394, QMT G84395 or QMT G84396) (Fig. 14*g*). This variability in calyx size is not as evident in the field, where the variability is largely in the colour of the tentacles, ranging from pink to cream. The only exception is in the specimen collected from 30-m depth in Iriomote Is. (QMT G84476, QMT G84477, QMT G84478 and QMT G84479) (Fig. 14*h*). Indeed, we originally considered these specimens to belong to a distinct species, based on the long calyx size in the field, being greater than 5 cm in length. However, morphological examination showed a variability in size congruent with what was observed in the syntype series; plates in the pinnules are consistently small, smooth and peanut-shaped. In the tentacle, anthocodia and calyx, different combinations of smooth rods or spindles occur, often bifurcated. Sclerites from the stolon are tuberculated rods. Within the stolon, some specimens have branched rods similar to the lectotype of *C. inflata* (e.g. QMT G84672 from Palau and QMT G84396 from the GBR) (Supplementary Fig. S1). However, *C. inflata* has only branched rods in the stolon (Fig. 4*g*), but they are rare in the *C. koellikeri* specimens.

Colour

The ethanol-preserved specimens are light brown. Pinnules are cream in colour. Living specimens can have cream- to pink-coloured tentacles. Living specimens can have cream- to yellow- to pink- to off-white-coloured tentacles, with a white mouth. In life when contracted the polyp is white and retracts into a white stolonic base, which is often obscured by epibionts. On deck the tentacles are grey, the polyps are a grey purple with maroon-red bases and stolons.

Remarks

The current study is the first to re-examine the specimens of the syntype series of *Hicksonia koellikeri* Dean, 1927. In the original description of the species, the shapes and sizes of the sclerites are shown for all specimens combined, without any specific reference to the intra-specific differences between them. Our current study is the first to present SEM images of the sclerites from each specimen individually. There are numerous morphological differences in sclerites

between specimens. This variability is particularly evident in the tentacles, where small and tuberculated plates can occur (Fig. 8*e* and 9*d*). Although we acknowledge these variants could represent different species, genetic data suggests the high morphological variability is a characteristic of the species.

It is worth noting that the specimen ZMA.COEL.2694 consistently differs in sclerite shapes and sizes from the other paralectotypes, especially in stolonic sclerites (Fig. 13*h*). Specimens in our phylogeny also show significant morphological variability in both their gross morphology and sclerites. Therefore, our phylogeny clusters both ZMA.COEL.2694 and the lectotype together with GBR and Japanese samples, but the inclusion of additional samples from regions such as Papua New Guinea, Timor-Leste, Palau and the Philippines could potentially reveal a greater species diversity than our data suggest.

Living features

Living colonies have polyps cream to pink in colour (Fig. 14). Colonies are locally abundant, often found overgrowing rubble beds. Polyps of different colour can occur within a single colony.

Clavularia brunafolia Borghi, Ekins & Cowman, 2026, sp. nov.

(Fig. 15, 16.)

ZooBank: urn:lsid:zoobank.org:act:39540BC6-5535-44C0-9D0E-258CC871CD7B

Material examined

HOLOTYPE. Australia, QMT G84400, John Brewer Reef, off Townsville (18°45′48.017″S, 146°31′56.258″E), central GBR, 3.4 m, 22 November 2022, coll. Stefano Borghi and Merrick Ekins. **PARATYPES.** Australia, QM G339823 same details as holotype; Australia, QMT G84495, North of Corbett Reef (24°25′0.8″S, 123°49′44.778″E), 5 m, 24 March 2022, coll. Andrew Baird.

Additional material

Australia, QMT G132855, Old Reef (19°20′13.2″S, 148°2′2.4″E), off Ayr, central GBR, 10 m, 16 October 2001, coll. Australian Institute of Marine Science.

Description

The holotype consists of ~30 polyps, connected at the base by a ribbon-like stolon, 0.30–0.44 mm thick ($\bar{x}$ = 0.38 mm, s.d. = 0.05, n = 4) (Fig. 16*d*). Polyps are set close together, a few millimetres apart or fully touching at the base. Preserved polyps are visibly clavate, 0.77–0.84 mm wide in the diameter of the upper calyx section ($\bar{x}$ = 0.80 mm, s.d. = 0.03, n = 4) and 0.26–0.30 mm wide in the lower calyx ($\bar{x}$ = 0.27 mm, s.d. = 0.02, n = 4). Polyps are tall, 1.95–2.96 cm long ($\bar{x}$ = 2.31 cm, s.d. = 0.44, n = 5), and with numerous longitudinal striations. Tentacles can fully retract inside the calyx, but are mostly folded over the mouth.

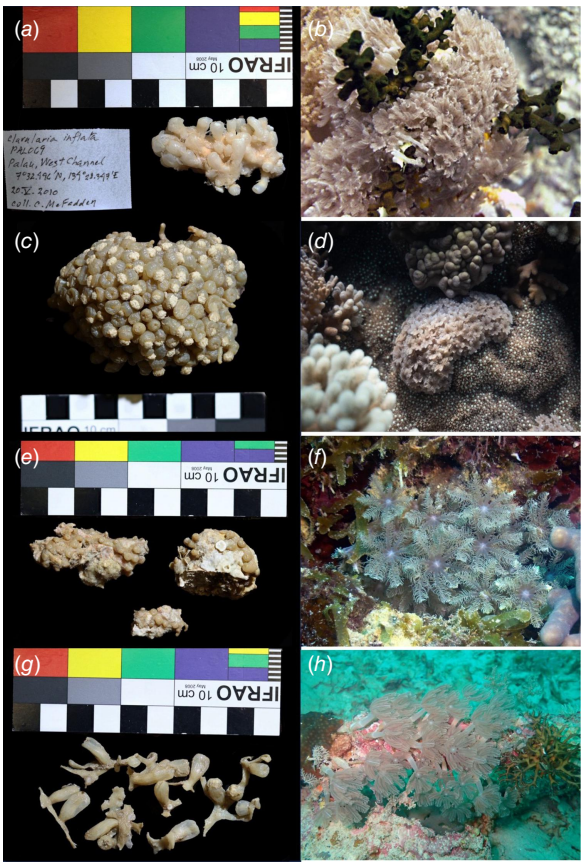

Fig. 14. Morphological variability of *Clavularia koellikeri*. Museum and *in situ* images of (*a*, *b*) QMT G84672, (*c*, *d*) QMT G84399, (*e*, *f*) QMT G84393, (*g*, *h*) QMT G84478.

Sclerites are abundant across all anatomical regions of the colony. Pinnule sclerites are small plates with no fine structuring on them and smooth margins, 0.03–0.06 mm long ($\bar{x}$ = 0.04 mm, s.d. = 0.01, n = 7) (Fig. 15*a*). Sclerites from other sections are particularly long. Smooth and slender rods run along the length of the tentacles, 1.10–1.42 mm long ($\bar{x}$ = 1.27 mm, s.d. = 0.14, n = 5) (Fig. 15*b*). Tentacle rods are occasionally bent. Even longer spindles but with sparse and simple tubercles are in the calyx, 1.47–2.26 mm long ($\bar{x}$ = 1.89, s.d. = 0.33, n = 8) (Fig. 15*c*). Calyx spindles can be bifurcated at one end or bent. Most spindles terminate with an S pattern rather than straight, occasionally at both ends. Stolonic sclerites are highly tuberculated rods, often branched or bifurcated, 0.69–1.13 mm long ($\bar{x}$ = 0.94 mm, s.d. = 0.15, n = 6) (Fig. 15*d*). These sclerites can fuse together to form a more rigid structure, but are mostly interlocked and easy to separate in bleach.

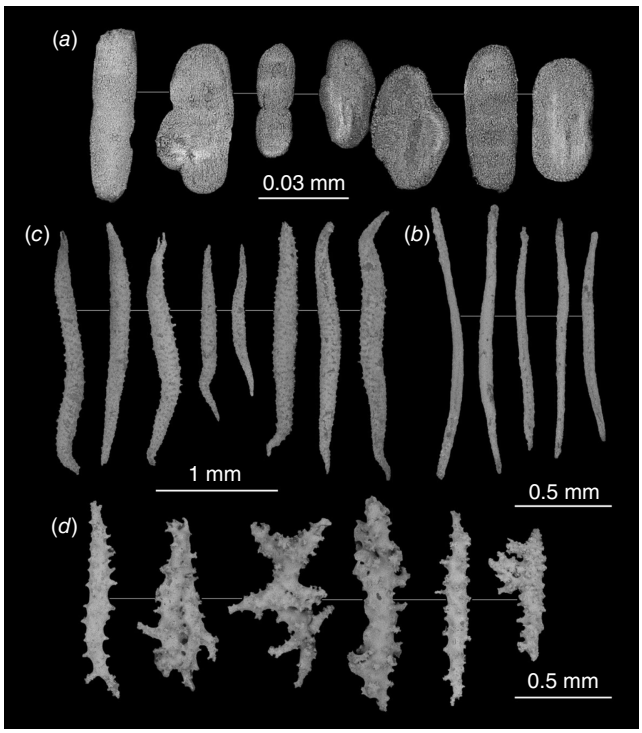

Fig. 15. Scanning electron micrographs of sclerites of *Clavularia brunafolia* **sp. nov.** holotype (QMT G84400). Sclerites from (*a*) pinnules, (*b*) tentacles (points), (*c*) calyx and (*d*) stolon.

Etymology

The species name *brunafolia* (from the Latin words *bruna*, meaning 'brown', and *folia*, meaning 'leaf') refers to the characteristic brown colour of the living polyps of the holotype here designated.

Living features

Colonies cream to light brown in colour, with a white mouth and the central rib on the underside of the tentacle is also white (Fig. 16*c*). On deck the tentacles are a dark purplish grey and the polyps are distally a lighter purplish grey fading through a deep red to a cream base and stolons. They were observed growing on rocky coral reef substrate rather than rubble beds, often adjacent to other corals. Uncommon, only a few colonies were observed or collected.

Variations

Measurements from the paratypes are consistent with the holotype. The only exception in gross morphology is in specimen QMT G132855, which has the upper anthocodiae fully retracted into calyces that are never >2 cm tall (Fig. 16*g*). Sclerite shapes and sizes are also congruent.

Remarks

Clavularia brunafolia sp. nov. represents the first species of *Clavularia* (and of Clavulariidae) ever described from the GBR (Fig. 16). We originally identified specimens of *C. brunafolia* sp. nov. as *C. koellikeri*. Indeed, we observed calyces in *C. koellikeri* specimens (e.g. QMT G84395 and QMT G84394) of similar size to those of *C. brunafolia* sp. nov. However, most of the tentacles in *C. koellikeri* specimens are fully retracted within the calyx, whereas the new species has most of the tentacles folded over the mouth, similar to what is observed for the lectotype of *C. viridis* (Fig. 2*d*, 16*d*, *f*). Additionally, the uniform brown colour of the polyps appears to be a distinct feature of *C. brunafolia*, as all living colonies of *C. koellikeri* observed ranged from cream to pink colours only. In contrast to the three other species of *Clavularia*, *C. brunafolia* sp. nov. always lacks pinnule sclerites with tubercles on one or both ends, but they are rather smooth and often three lobed (Fig. 15*a*).

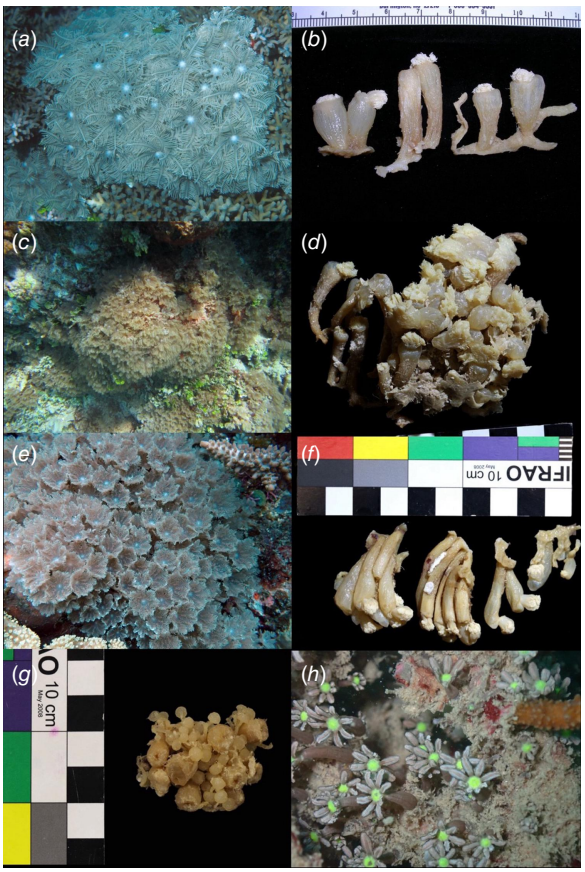

Fig. 16. *Clavularia viridis*, *C. brunafolia* **sp. nov.** and *Knopia octocontacanalis*; *in situ* and voucher images of specimens of the topotype of *Clavularia viridis* CAS IZ308254 (*a*). *In situ* photograph of *C. viridis* provided by Patrick L. Colin and Lori J. Bell Colin (Coral Reef Research Foundation). (*b*) Preserved specimen, CAS IZ308254 (photograph taken by Catherine S. McFadden). *In situ* and voucher images of specimens of *C. brunafolia* **sp. nov.**; (*c*, *d*) QMT G84400, (*e*, *f*) QMT G84495 and (*g*) QMT G132855. (*h*) *In situ* image of *Knopia octocontacanalis* from the GBR (QMT G84389).

Hanabira Lau, Stokvis, Imahara & Reimer, 2019

Type species: *Hanabira yukibana* Lau, Stokvis, Imahara & Reimer, 2019.

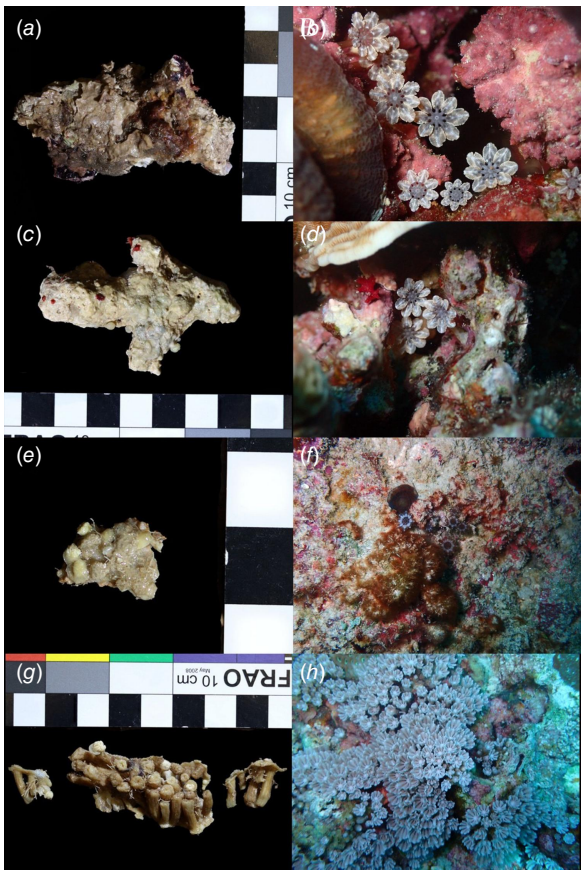

Fig. 17. Voucher specimens (left) and *in situ* photographs (right) of the topotype specimens of *Hanabira yukibana* Lau, Stokvis, Imahara & Reimer, 2019 examined in this study: (*a*, *b*) QMT G84472, (*c*, *d*) QMT G84473 and (*e*, *f*) QMT G84486. (*g*, *h*) *Bairdium iriomotejimaensis* **gen. nov., sp. nov.** from Okinawa Island (QMT G84487).

Hanabira yukibana Lau, Stokvis, Imahara & Reimer, 2019

(Fig. 17.)

Hanabira yukibana: Lau *et al.* (2019), pp. 62–68, fig. 3, 4.

Material examined

Japan, QMT G84472, Nakano Beach, Iriomote Is. (24°25′0.8″N, 123°49′44.778″E), 14 September 2023, 8 m, coll. Stefano Borghi & James Reimer; QMT G84473, Nakano Beach, Iriomote Is. (24°25′0.8″N, 123°49′44.778″E), 14 September 2023, 8 m, coll. Stefano Borghi & James Reimer; QMT G84486, Nakano Beach, Iriomote Is. (24°25′0.8″N, 123°49′44.778″E), 16 September 2023, 15 m, coll. Stefano Borghi & James Reimer.

Remarks

All three specimens examined were collected from Iriomote Is. (off Nakano Beach, NE side), which is the type locality of the species *Habanira yukibana* Lau, Stokvis, Imahara & Reimer, 2019 (Fig. 17*a*–*f*). The freshly collected specimens were identified and used in this revision as topotypes for the species.

Knopia Alderslade & McFadden, 2007

Type species: *Knopia octocontacanalis* Alderslade & McFadden, 2007.

Knopia octocontacanalis Alderslade & McFadden, 2007

(Fig. 16*g*, *h*.)

Knopia octocontacanalis: Alderslade and McFadden (2007), pp. 35–42, fig. 5–10.

Material examined

PARATYPE. NTM C015392, Thousand Islands (5°42.77′S 106°33.675′E), Kotok Is., Indonesia, 16 July 2002, 15–22 m, Daniel Knop.

Additional material

Australia, QMT G84389, North Pelorus Is., North-east Queensland (18°32′14.4″S, 146°29′38.2″E), 11 April 2022, 7.6 m, coll. Stefano Borghi.

Remarks

This species was previously known only from Malaysia and Indonesia. However, our molecular phylogeny confirms that the species also occurs on the GBR (Fig. 16*h*).

Bairdium Borghi, Reimer & Cowman, 2026, gen. nov.

Type species: *Bairdium iriomotejimaensis* Borghi, Reimer & Cowman, **sp. nov.**

ZooBank: urn:lsid:zoobank.org:act:8C137CC3-8DFE-496E-B809-222C1C21DEF6

Diagnosis

Polyps connected basally by ribbon-like stolons or thin membranes, colony without a skeletal axis. Polyps monomorphic. Anthocodiae retractile into clavate calyces. Pinnules free and arranged in single rows. Sclerites of pinnules are small plates with granular surface. Sclerites of calyces and stolons are tuberculated spindles, often interlocked.

Etymology

The genus is named after Prof. Andrew Baird, who collected specimens of the genus in Iriomote Is., and facilitated the collection of additional specimens.

Remarks

The specimens are here described as a new genus within Clavulariidae on both morphological and genetic basis. Morphologically, pinnule sclerites in *Bairdium* specimens have a rather coarse granular surface (Fig. 19*g*) compared to the granulation of plates found in *Clavularia* (Fig. 19*f*). Tentacles thicker than in species of *Clavularia*, and rather cylindrical. Genetic data show the genus as sister to *Knopia* and *Hanabira* rather than *Clavularia*.

Bairdium iriomotejimaensis Borghi, Reimer & Cowman, 2026, sp. nov.

(Fig. 17–19.)

ZooBank: urn:lsid:zoobank.org:act:AF4C598F-7AD5-4471-8C98-DDFC3117814C

Material

HOLOTYPE. Japan, QMT G84403, Nata (24°25′41.52″N 123°47′43.8″E), Iriomote Island, 4th July 2022, 6 m, coll. Andrew Baird. **PARATYPES.** Japan, QMT G84458, Sosu (26°47′39.062″N 128°19′6.301″E), Okinawa, 2 m, 12 September 2023, coll. Stefano Borghi and James D. Reimer; QMT G84483, Nakano Beach (24°25′0.8″N 123°49′44.778″E), Iriomote Island, 15 m, 16 September 2023, coll. Stefano Borghi and James D. Reimer.

Additional material

Japan, QMT G84459, Sosu (26°47′39.062″N 128°19′6.301″E), Okinawa, 2 m, 12 September 2023, coll. Stefano Borghi and James D. Reimer; QMT G84475 and QMT G84487, Nakano Beach (24°25′0.8″N 123°49′44.778″E), Iriomote Island, 10 m, 16 September 2023, coll. Stefano Borghi and James D. Reimer.

Description

The holotype consists of a small fragment of less than 10 polyps encrusting a rock 2.36 cm wide (Fig. 18*c*, *d*). Polyps grow on a flat membranous stolon. Polyps with clear longitudinal striations and set close together. The height of the polyps preserved in ethanol ranges from 1.20 to 1.39 cm ($\bar{x}$ = 1.29 cm, s.d. = 0.09, n = 5). Polyps are cylindrical, with the diameter of the upper and lower section ranging from 0.27 to 0.32 cm ($\bar{x}$ = 0.30, s.d. = 0.02, n = 5) and

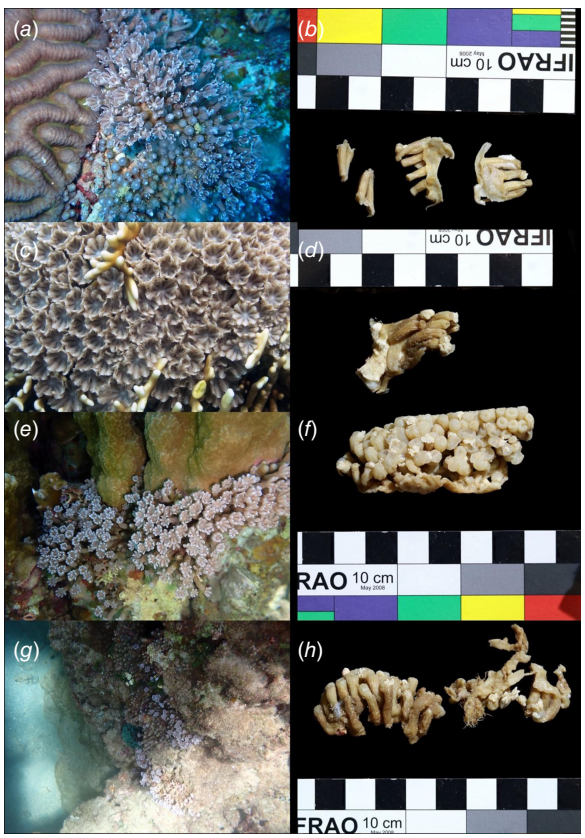

Fig. 18. *Bairdium iriomotejimaensis* **sp. nov.** with field images (left) and preserved specimens (right); (*a*, *b*) QMT G84483, (*c*, *d*) QMT G84403, (*e*, *f*) QMT G84459 and (*g*, *h*) QMT G84458.

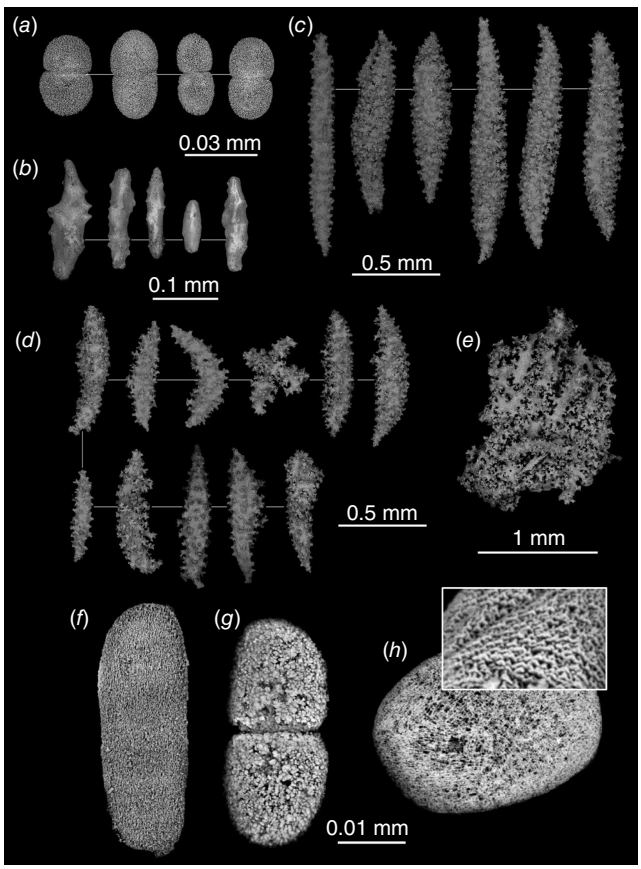

Fig. 19. Scanning electron micrographs of sclerites of *Bairdium iriomotejimaensis* **gen. nov., sp. nov.** holotype (QMT G84403). Sclerites from (*a*) pinnules, (*b*) tentacles, (*c*) calyx and (*d*, *e*) stolon; comparison of pinnule sclerites between (*f*) *Clavularia*, (*g*) *Bairdium* and (*h*) *Hicksonia*.

0.26–0.34 cm ($\bar{x}$ = 0.29, s.d. = 0.03, n = 4) respectively. Tentacles fully retractile into the calyx. Pinnules free and mostly arranged in a single row of 14–20 on each side of the tentacle.

Sclerites are abundant across all sections except around the pharynx. Pinnule sclerites are small plates with medial constrictions and granular surface, 0.03–0.04 mm long ($\bar{x}$ = 0.03 mm, s.d. = 0.01, n = 4) (Fig. 19*a*). Tentacle sclerites are short and smooth rods, occasionally with few and simple tubercles, 0.08–0.19 mm in length ($\bar{x}$ = 0.14 mm, s.d. = 0.04, n = 5) (Fig. 19*b*). Sclerites from the calyx are long and highly tuberculated spindles, 0.98–1.41 mm long ($\bar{x}$ = 1.20 mm, s.d. = 0.16, n = 6) (Fig. 19*c*). Sclerites from the stolon also are highly tuberculated stout spindles, but shorter and interlocked, 0.48–0.81 mm long ($\bar{x}$ = 0.68 mm, s.d. = 0.11, n = 11) (Fig. 19*d*).

Etymology

The species name *iriomotejimaensis* refers to the type locality of the species: Iriomote Island.

Living features

Colonies pale pink to creamy brown in colour. They were observed growing on rocks rather than rubble beds, often adjacent to other corals. Common in the shallows, between 2- and 15-m depth. Specimens from Okinawa were collected in turbid waters near an estuary, whereas specimens from Iriomote Is. inhabited clear and deeper waters.

Variations

Both preserved paratypes have slightly smaller polyps than the holotype; QMT G84483 comprises four small fragments from the same colony and has the shortest polyps, 0.85–1.13 cm long ($\bar{x}$ = 0.98 cm, s.d. = 0.10, n = 5) (Fig. 18*a*, *b*). QMT G84458 has polyps more similar in size to the holotype, 1.10–1.42 cm in length ($\bar{x}$ = 1.24 cm, s.d. = 0.11, n = 6) (Fig. 18*e*, *f*). Polyps are always cylindrical, and measurements of the upper and lower diameter of the polyps are consistent across specimens. Sclerite shape is consistent between specimens, but sclerites differ in size in the calyx. For instance, QMT G84458 has shorter sclerites in the calyx, 0.64–0.91 mm long ($\bar{x}$ = 0.78 cm, s.d. = 0.12, n = 6).

Remarks

The species was originally identified as *C. viridis* because of the rigidity of the calyx and the characteristic of often having the tentacles folded over the mouth. Additionally, *C. viridis* was considered to inhabit subtropical waters of Japan. Indeed, Fujiwara *et al.* (2003) sequenced large-polyped *Clavularia* from Japan, which were identified as *C. koellikeri* and *C. viridis*. However, as shown by comparing material here examined with the lectotype of *C. viridis*, the polyp length is consistently shorter in the Japanese material and sclerites differ in shape across all anatomical regions. Our phylogeny (Fig. 23) places the Japanese material sister to *Knopia* and *Hanabira* rather than *Clavularia*, hence we consider the specimens to belong to a distinct new genus within the Clavulariidae clade. The coarse granular surface of the plates found in the pinnules, which is a key characteristic of this new genus (Fig. 19*g*), is also not a feature found in the lectotype of *C. viridis*.

Distribution

The species is currently known only from Okinawa and Iriomote islands, Japan.

Family **HICKSONIIDAE** Delage & Hérouard, 1901

Diagnosis (translated and amended from Delage and Hérouard 1901, with changes or additions in bold)

Octocorals lacking a skeletal axis. Polyps connected basally by ribbon-like stolons or thin membranes, which also connect polyps on multiple levels along the calyx region. Polyps monomorphic. **Anthocodiae retractile into clavate calyces.** Calyces normally very tall. Pinnules free. **Sclerites of tentacles minute plates of calcite rods radially arranged. Sclerites of calyx long rods or spindles. Sclerites of stolon highly tuberculated rods, often interlocked to form rigid structure. Zooxanthellate.**

Type genus: ***Hicksonia*** Delage & Hérouard, 1901.

Remarks

In this study, we resurrect the family Hicksoniidae proposed by Delage and Hérouard (1901) (as Hicksoninae), which they established for one specimen identified by Hickson (1894) as *C. viridis*, and we amend the diagnosis of the family to include additional morphological features. One of the specimens here analysed (SMNHTAU Co_38221) was initially identified as *C.* cf. *viridis*, a species of Clavulariidae originally described from the Solomon Islands that was recently reported to have been introduced to the southwest Atlantic coast of Brazil (Mantelatto *et al.* 2018). The resurrection of the genus *Hicksonia* is based on matching morphology to the literature description of the species, as the Indonesian specimen collected and described by Hickson (1894) is considered lost. However, molecular data from the Brazilian specimen (SMNHTAU Co_38221) identified as *C.* cf. *viridis* suggest it is in a different clade from the *C. viridis* topotype. Hence, we here designate a new species to accommodate such differences. We also remove the genus *Hicksonia* Delage & Hérouard, 1901 from synonymy.

Hicksonia Delage & Hérouard, 1901

Type species: *Hicksonia hicksoni*, sp. nov.

ZooBank: urn:lsid:zoobank.org:act:6852C70F-45BE-48C2-B890-B7A1D534CBD4

Diagnosis (translated and amended from Delage and Hérouard 1901, with changes or additions in bold)

Soft corals with clavate polyps, which arise from a rigid ribbon-like stolon. Stolons form bridges connecting polyps on multiple levels. Polyps are monomorphic and fully retractile. Sclerites are abundant in all parts of the colony, but differ in shapes and sizes. **Pinnules feature small plates**, bent rods are found in the anthocodia, and the calyx and stolon are dominated by an intricate structure of irregular and highly tuberculated sclerites.

Remarks

The genus *Hicksonia* and family Hicksoniidae were established for a specimen considered to be *Clavularia viridis*. *C. viridis* would have been the type species of the genus *Hicksonia* by monotypy (see Delage and Hérouard 1901). However, it is now apparent that the Indonesian specimen for which *Hicksonia* was established is not *C. viridis*. A replacement name is needed for this species.

Key to the species of *Hicksonia* (status revised)

1. Anthocodia free of sclerites.....***H. hicksoni.***
   Small plates in pinnules, with fibrils like little triangles (calthrops).....***H. tohrui.***

Hicksonia hicksoni Borghi, 2026, sp. nov.

ZooBank: urn:lsid:zoobank.org:act:1C4C5C76-7E18-4236-9B75-45614333DF2A

Clavularia viridis: Hickson (1894), pp. 343–344, plate 49.

Hicksonia viridis: Delage and Hérouard (1901), pp. 386–387, fig. 506.

Hicksonia viridis: Dean (1927), pp. 115–122, fig. 2 and 4.

Description (after Hickson 1894)

Shallow tropical species, forming large clumps 12–15 cm in height and over 30 cm in diameter. Stolon is ribbon-like and never extended enough to form a membranous structure, and consists of a network of tubes connecting calyces on multiple levels. Polyps are variable in height, 2–5 cm long, the longest measuring ~10 cm. Polyps fully retractile inside the calyx, which is rigid and remains firm even when the colony is dried under the sun. Tentacles olive brown or green in colour. Sclerites absent in the pinnules, tentacles and anthocodia. In the calyx, long spindles with simple tubercles and occasionally thorned occur, ~2.3 mm long.

Distribution

The species is only known from shallow coral reefs of North Celebes, Indonesia.

Etymology

The species name *hicksoni* is given after Professor Hickson, who first described the specimen from Indonesia as *C. viridis* (1894).

Remarks

The specimen collected and presented by Hickson from Indonesia (1894) is most likely in the British Museum, but upon enquiring the specimen was not found and therefore is to be considered missing. Hickson (1894) actually failed to explain the number of specimens identified as *C. viridis* he collected and examined from North Celebes. Although he figured only one (Hickson 1894), there are two specimens at BMNH he may have included in his analysis: BMNH 1897.6.16.4 and BMNH 1897.6.16.3, both of which are registered with Talisae as the nearest named place. If these specimens are found and can be shown to be the ones described by Hickson (1894), they should be considered the holotype and paratype for *H. hicksoni*. Three slides of *C. viridis* specimens from Celebes are also registered at BMNH (1961.3.23.20, 1961.3.23.21 and 1961.3.23.22) but also appear to be missing. Hickson (1894) mentioned additional specimens collected by Wallace from Aru Island, Indonesia, identified as *C. viridis* and also deposited in the British Museum. However, he does not say whether these Indonesian specimens collected by Wallace were examined by him or if they matched his specimen from North Celebes.

In establishing the genus *Hicksonia*, Delage and Hérouard (1901) also do not clarify whether Hickson (1894) examined one or multiple specimens. In addition, Delage and Hérouard (1901) did not re-examine Hickson's *C. viridis* or the Quoy and Gaimard specimen, but rather re-used Hickson's description and figures to establish a new family and genus. Later, Dean (1927) claimed specimens from Saleyer and Karakelang Island (Indonesia, no depth recorded) were similar in gross morphology to Hickson's *C. viridis* and provided additional morphological information on the species while supporting the taxonomic placement of *C. viridis* within the genus *Hicksonia*. The specimens examined by Dean (1927) had shorter polyps than Hickson's material, maximum 5 cm long, and numerous minute plates in the anthocodiae, sometimes two, four or multi-rayed, 0.03 mm long. However, Dean also did not re-describe Hickson's specimen, and therefore it remains unknown whether Hickson failed to report sclerites from the anthocodiae or if Dean's specimens are possibly of a different species.

Despite the confusion surrounding the morphology of the specimen from North Celebes, the stolon connecting polyps on multiple levels is a unique feature of the genus *Hicksonia* and not observed in the Quoy and Gaimard lectotype of *C. viridis*. Therefore, we name Hickson's specimen *Hicksonia hicksoni* to acknowledge it to be a different species than *C. viridis*. We retain *H. hicksoni* as distinct from *H. tohrui* (see below) based on morphology; polyps in *H. tohrui* are generally shorter, and numerous plates and rods are observed in the anthocodiae.

Hicksonia tohrui Borghi, McFadden, Baird, Ekins & Cowman, 2026, sp. nov.

(Fig. 2, 19–22.)

ZooBank: urn:lsid:zoobank.org:act:960A4C28-6F32-4548-B058-4149C49FB947

Clavularia cf. *viridis*: Mantelatto *et al.* (2018) (listed only).

Clavularia cf. *viridis*: McFadden *et al.* (2022), p. 35 (listed only).

Material examined

HOLOTYPE. Japan. QMT G84405, Channel Marker (24°24′29.16″N 123°49′27.12″E), Iriomote Island, 4 July 2022, 22 m, coll. Andrew Baird. **PARATYPES.** Australia. QM G334154, off Cassini Island (13°57′12.024″S 125°46′58.368″E), Kimberley, Western Australia, 18 November 2010, coll. Merrick Ekins and Monika Schlacher, intertidal reef; Australia, QM G334058, off Cassini Island (13°55′55.56″S 125°37′5.628″E), Kimberley, Western Australia, 9–15 m, 16 October 2010, coll. Merrick Ekins and Monika Schlacher; QM G334101, off Cassini Island (13°55′32.772″S 125°38′13.272″E), Kimberley, Western Australia, 10–14 m, 19 October 2010, coll. Merrick Ekins and Monika Schlacher; WAM Z59819, same collection details as QM G334154.

Additional material

Brazil, SMNHTAU Co_38221, Vermelha rocky reefs (23°01′33.6″S 44°30′03.6″W), Ilha Grande Bay, Rio de Janeiro State, October 2017, coll. Joel Creed.

Description

The holotype consists of one fragment comprising nine polyps (Fig. 20*a*). The tentacles retract into the polyps that range in height from 1.04 to 1.21 cm ($\bar{x}$ = 1.13 cm, s.d. = 0.06, n = 5), which in turn sit on an intricate series of stolonic bridges that connect the polyps to one another on multiple levels (Fig. 20*a*, *d*). These 'bridges' are densely packed with sclerites, making this formation more rigid than the stolonic structures seen in Clavulariidae. Polyps are cylindrical, as the diameter of the upper calyx matches the lower portion, ~3.4 mm wide.

Sclerites are abundant in all anatomical sections. Sclerites in the pinnules are small plates with rounded edges, 0.02–0.04 mm long ($\bar{x}$ = 0.03 mm, s.d. = 0.01, n = 30) (Fig. 21*a*). Plates are made of calcite rods that spread radially. In the rest of the anthocodia, sclerites are arranged as points comprised by spindles with simple and sparse tubercles, occasionally curved, 0.53–1.79 mm long ($\bar{x}$ = 1.22 mm, s.d. = 0.39, n = 16) (Fig. 21*b*). The calyx comprises long spindles, occasionally bifurcated at one end and with simple and sparse tubercles, 0.82–2.76 mm long ($\bar{x}$ = 1.96 mm, s.d. = 0.56, n = 17) (Fig. 21*c*). Sclerites from the stolon are irregular spindles, with simple and sparse tubercles and often bifurcated on both ends, mostly in the shape of a slingshot, 0.87–1.96 mm long ($\bar{x}$ = 1.48 mm, s.d. = 0.28, n = 20) (Fig. 21*d*).

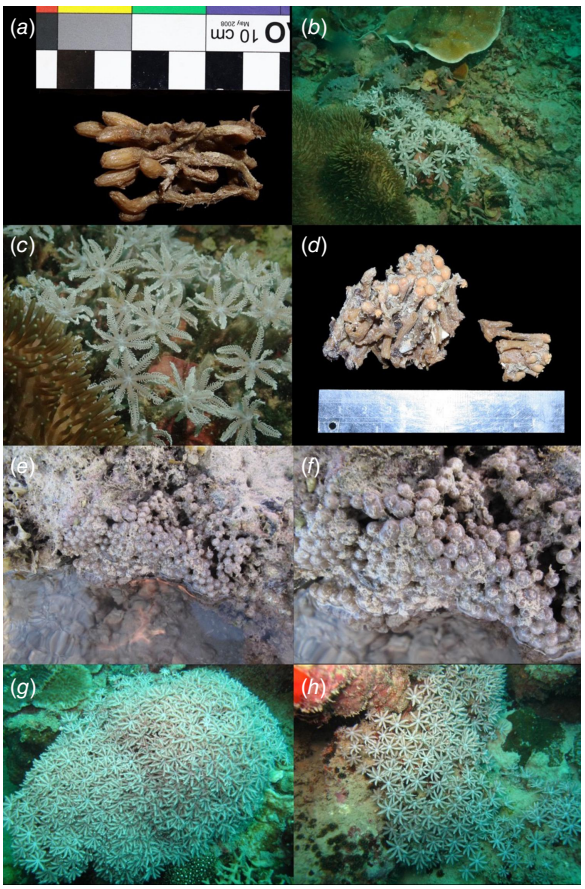

Fig. 20. (*a*) Holotype of *Hicksonia tohrui* **sp. nov.** (QMT G84405) with field images (*b*, *c*). (*d*) Paratype of *Hicksonia tohrui* **sp. nov.** (QM G334154) with field images (*e*, *f*). *In situ* images of *Hicksonia tohrui* **sp. nov.**; (*g*) QM G334101 and (*h*) QM G334058.

Etymology

The species name *tohrui* is given after Dr Tohru Naruse, of the Tropical Biosphere Research Center at the University of the Ryukyus, Japan. We dedicate the species name to Dr Tohru Naruse in acknowledgement of his frequent assistance with fieldwork carried out by Prof. Andrew Baird (the collector) and colleagues on Iriomote Is., and later by the

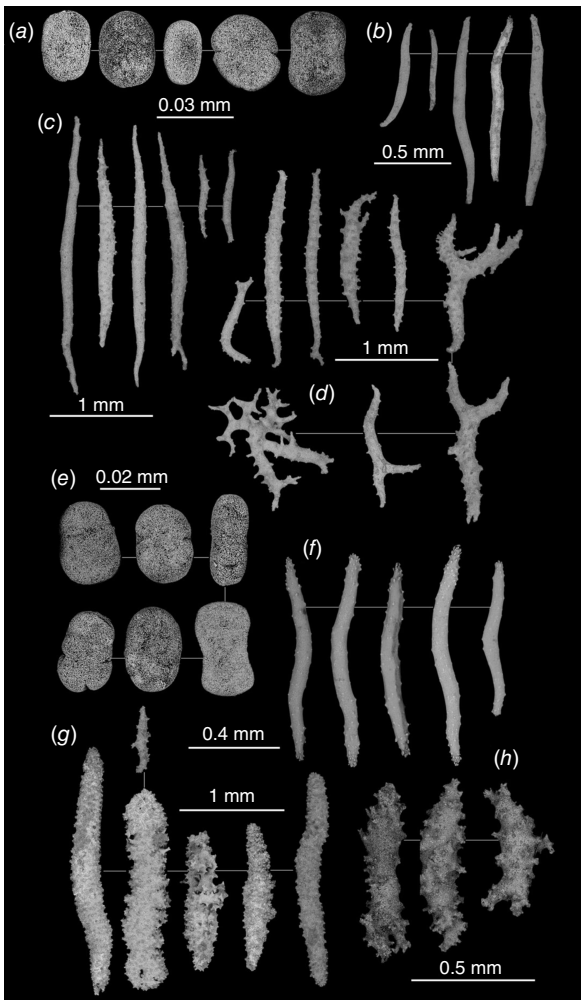

Fig. 21. Scanning electron micrographs of sclerites of *Hicksonia tohrui* **sp. nov.**; holotype (QMT G84405). Sclerites from (*a*) pinnules, (*b*) the anthocodia, (*c*) the calyx and (*d*) the stolon; paratype (QM G334154). Sclerites from (*e*) pinnules, (*f*) the anthocodia, (*g*) calyx and (*h*) the stolon.

first author during an internship at the University of the Ryukyus, Okinawa, Japan, and also for being a wonderful host.

Living features

The holotype is characterised by white polyps with long and pointed tentacles and short pinnules arranged in a single row across the entire tentacle length (Fig. 20*b*, *c*). The calyces are connected on multiple levels by an intricate architecture of stolonic bridges, which are even visible *in situ*. Western Australian colonies are characterised by numerous polyps densely aggregated. *In situ* photographs show colonies in intertidal zones, fully exposed during low tide, and with the polyps completely retracted into a bulbous-looking calyx (Fig. 20*e*, *f*). There are no photographs of the extended polyps of the paratype.

Comparison with the paratype

The paratype QM G334154 examined from Western Australia consists of two fragments of the same colony: one small fragment of less than 10 polyps, 2.65 cm in length, and a larger fragment, 5.94 cm in length, with polyps set close together (Fig. 20*d*). Tentacles fully retractile inside the calyx. Preserved polyps are 1.45–2.46 cm long ($\bar{x}$ = 1.87 cm, s.d. = 0.31, n = 8) and slightly clavate, 0.37–0.51 cm in diameter in the upper section ($\bar{x}$ = 0.43 cm, s.d. = 0.05, n = 8) and 0.27–0.43 cm in the lower section ($\bar{x}$ = 0.32, s.d. = 0.06, n = 6).

Sclerites are abundant across all sections. Sclerites in the pinnules are small plates similar in shape and size to those from the holotype. Sclerites can be both oval or with medial constrictions, 0.02–0.03 mm ($\bar{x}$ = 0.03 mm, s.d. = 0.01, n = 20) (Fig. 21*e*), with fibrils arranged to form triangular structures similar to calthrops (Fig. 19*h*). In the tentacles, similar to the holotype, sclerites are long rods with simple and sparse tubercles, 0.68–0.98 mm long ($\bar{x}$ = 0.87, s.d. = 0.12, n = 5) (Fig. 21*f*). Sclerites from the calyx and stolon are a similar length to the holotype but are thicker and more heavily tuberculated (Fig. 21*g*, *h*). These spindles are arranged longitudinally across the calyx section, 0.66–2.36 cm long ($\bar{x}$ = 1.65, s.d. = 0.61, n = 6) (Fig. 21*g*). Smaller highly tuberculated and occasionally bifurcated spindles are in the stolon, 0.56–0.74 mm long ($\bar{x}$ = 0.67, s.d. = 0.09, n = 3). Similar to the holotype, sclerites in the stolon are never fused (Fig. 21*h*).

The paratype QM G334154 was collected during low tide on an intertidal reef, which has a tidal range of up to 11 m, and was partially out of the water. Therefore, we lack an image of the living extended polyps. Upon morphological examination, specimens QM G334058 and QM G334101 are considered to be the same species. *In situ* images of these specimens show the appearance of the polyps when not retracted (Fig. 20*g*, *h*): long and slender tentacles, with short pinnules organised in a single row. The specimens from WA differ from the holotype in having stout spindles in the calyx (Fig. 21*g*). In addition, some of the spindles in the tentacles appear to have clear longitudinal ridges, which make the sclerites appear square rather than cylindrical in cross-section.

Comparison with the Brazilian specimen

The specimen examined from Brazil consists of one fragment, which comprises 21 polyps (Fig. 2*e*–*g*). Polyps range in length from 4.39 to 6.15 cm ($\bar{x}$ = 5.56 cm, s.d. = 5.67, n = 5). The polyps are clavate. The diameter of the top portion of the calyx measures between 5.98 and 7.70 mm ($\bar{x}$ = 6.70 mm, s.d. = 0.06, n = 8), whereas the diameter at the base is 3.30–4.10 mm ($\bar{x}$ = 3.90 mm, s.d. = 0.03, n = 7). In the preserved specimen, the stolon is a rigid ribbon-like structure that develops in one plane only

(Fig. 2*g*), 1.05–1.49 mm thick ($\bar{x}$ = 1.30 mm, s.d. = 0.16, n = 6). However, *in situ* photographs suggest the stolon can form bridges connecting polyps on multiple levels in the lower half of the calyx (see Mantelatto *et al.* 2018), as opposed to the morphology shown in Fig. 2*e–g*.

Sclerites are abundant in all regions of the colony. Small plates can be found in the tentacles, the majority of which have smooth edges, whereas others are more irregular (Fig. 19*h* and 22*a*). Plates range in size between 0.02 and 0.03 mm ($\bar{x}$ = 0.03 mm, s.d. = 0.01, n = 30). The anthocodia sclerites are long rods (Fig. 22*b*). Rods can be unornamented when small, but larger rods are often bent, 0.67 and 1.74 mm ($\bar{x}$ = 1.35 mm, s.d. = 0.35, n = 16), and with large tubercles. Sclerites from the calyx are highly tuberculated rods, 0.28–1.65 mm in length ($\bar{x}$ = 1.01 mm, s.d. = 0.51, n = 11) (Fig. 22*c*). Tubercles are very pronounced and often grow outwards, forming irregular shapes. The stolon is a rigid structure of highly tuberculated rods and irregular sclerites clumped together (Fig. 22*d–f*). These sclerites, however, are shorter than the ones from the calyx, 0.38–1.32 mm ($\bar{x}$ = 0.63 mm, s.d. = 0.29, n = 20).

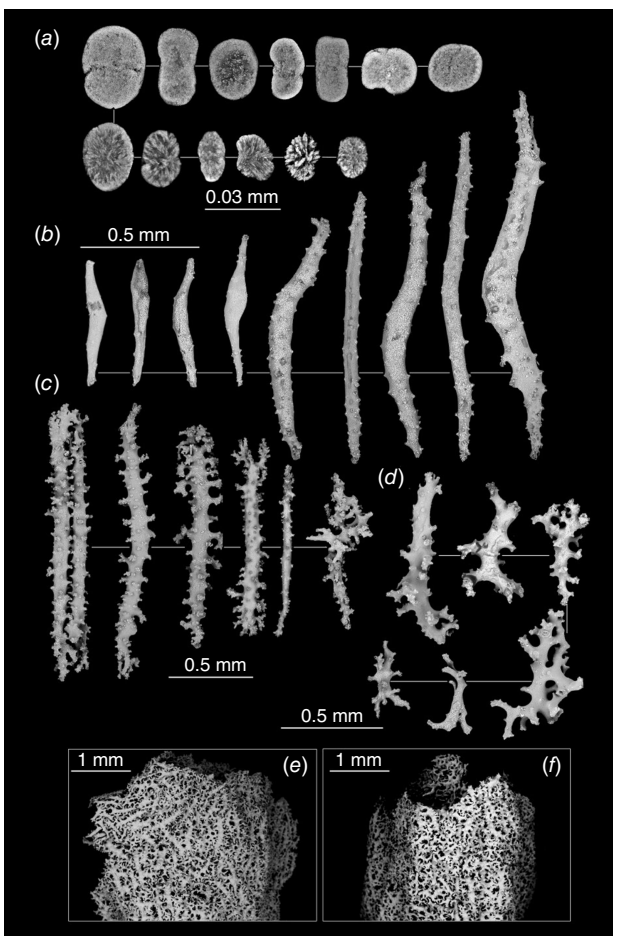

Fig. 22. Scanning electron micrographs of sclerites of *Hicksonia tohrui* **sp. nov.** from Brazil (SMNHTAU Co_38221). Sclerites from (*a*) pinnules and tentacles, (*b*) the anthocodia, (*c*) the calyx, and (*d*) the stolon. (*e*, *f*) Arrangement of sclerites across the ribbon-like stolon.

Remarks

Additional sampling was conducted in August 2024 across reefs in Iriomote Is. and Okinawa, but no additional specimens were observed or collected, suggesting the species is uncommon. *H. tohrui* from Japan has the longest sclerites in the calyx and the most prominent bridges connecting polyps on multiple levels across the calyx among all specimens here examined. The Japanese material differs from other specimens in having white pinnules rather than brown, and in the intricacy of the stolonic structure on which polyps sit (Fig. 20*a*). Indeed, material from both Brazil and WA have flatter stolons which connect polyps mostly in the lower section of their calyces, whereas over half of the colony height in the Japanese material is made of connecting stolons. Differences also occur in sclerites. Within the pinnules, the material from Brazil is the only one to have small crystalline plates with laminar rods radially arranged (Fig. 22*a*). The Brazilian material also shows tightly interlocked sclerites in the stolons (Fig. 22*e*, *f*).

Although we acknowledge the Japanese, Australian and Brazilian specimens could belong to different species, we consider the molecular and morphological differences to be insufficient to describe them as distinct. Indeed, the presence of longitudinal ridges in tentacle sclerites in the WA material is a unique feature not found in other specimens, but many tentacle rods lack that feature and are rather similar in size and shape to the rods found in the holotype. Pinnule sclerites are also similar in both shape and size.

Distribution

The species is only known from Iriomote Is., Japan, and from shallow reefs of NW Western Australia. The Brazilian specimen here examined was collected at Ilha Grande Bay, Rio de Janeiro State, Brazil, where the species is considered to be non-indigenous. It has now been eradicated from Brazil although it is still available in the aquarium trade there (CS McFadden, pers. comm.).

Targeted capture data

A total of 2876 loci were extracted in the incomplete matrix using the octocoral baitset from Erickson *et al.* (2021) across 58 samples. The number of contigs recovered per sample after the mapping and cleaning pipeline in *phyluce* varied from 179 to 1722 (see Supplementary Table S1). Total numbers of trimmed reads and length of assembled loci are provided in the Supplementary Table S4. A total of 839 loci were recovered in the 60% taxon matrix, compared to 1156 and 401 loci from the 50 and 75% matrices respectively. The lectotype (ZMA.COEL.2683) and paralectotype (ZMA.COEL.2694) of *C. koellikeri* are the oldest samples

included in our phylogeny, having been collected in 1899 (126 years old). After mapping and correction, we retrieved from them 510 and 503 UCE contigs respectively.

Phylogenomic results

The analysis recovered strong support for the division of the family Clavulariidae into four genera, namely *Clavularia*, *Knopia*, *Hanabira* and *Bairdium* gen. nov. *Bairdium* gen. nov. differs from *Clavularia* not only morphologically, but also genetically, as it is found sister to *Knopia* and *Hanabira* rather than *Clavularia* (Fig. 23).

Within the genus *Clavularia*, three different species-level clades are identified. The topotype of *C. viridis* from Vanuatu did not cluster with other *Clavularia* specimens, and the split between *C. viridis* and other *Clavularia* species is supported with high bootstrap value (100) and both sCF and gCF greater than 50 (Supplementary Fig. S3–S5). None of the samples from Japan or the GBR were supported to be part of the *C. viridis* group, suggesting its geographical range is likely confined to shallow reefs across Vanuatu and the Solomon Islands. In contrast, most samples from Japan and central and northern GBR are revealed to be part of the *C. koellikeri* clade. In our ML phylogeny, *C. koellikeri* is

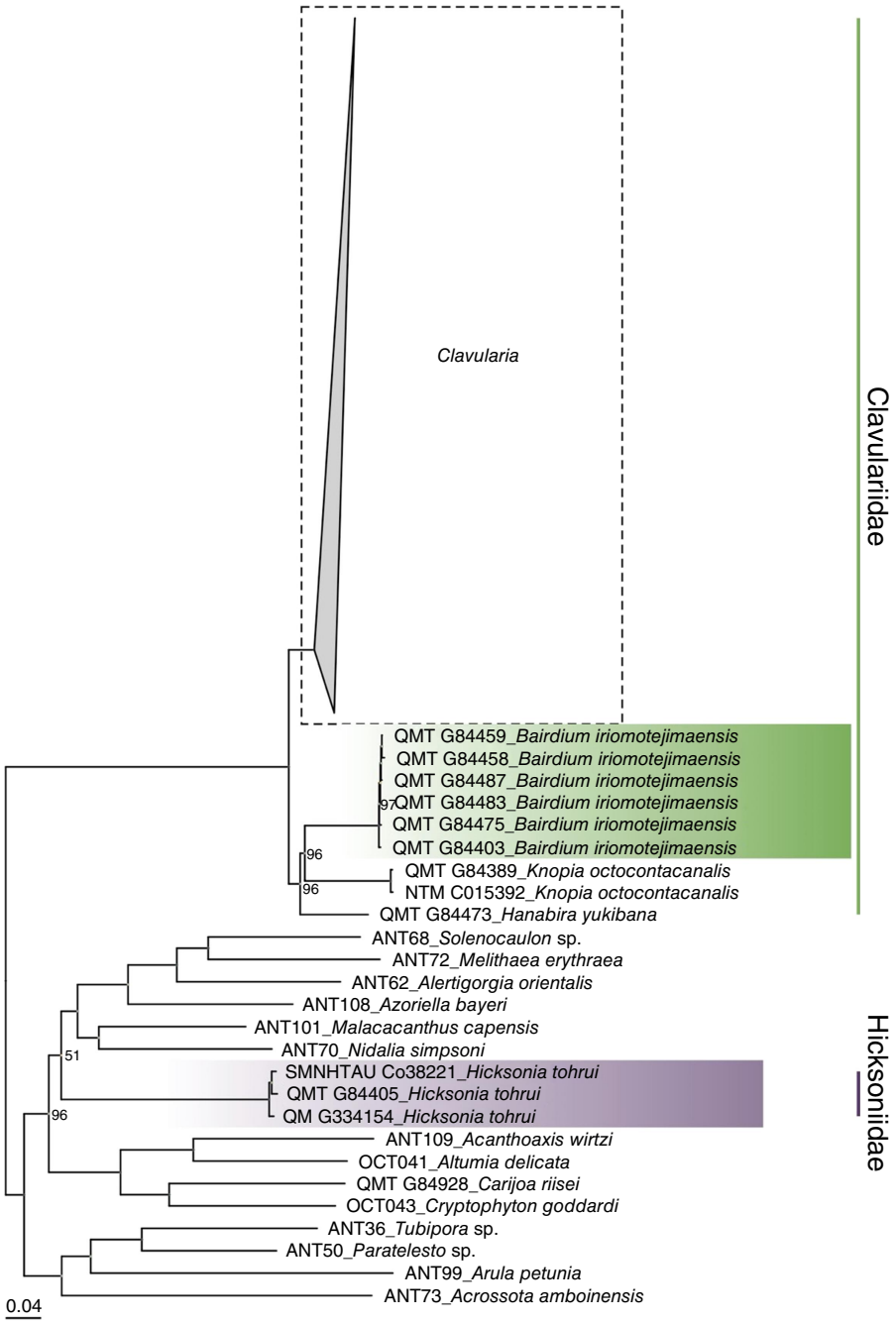

Fig. 23. Maximum likelihood (ML) phylogeny of soft corals of the order Malacalcyonacea (Octocorallia) inferred from the 60% complete internal-trimmed alignment matrix of 839 UCE and exon loci. Bootstrap values lower than 100 are shown at the nodes. The genus *Bairdium* gen. nov. within the family Clavulariidae and species of the family Hicksoniidae (status revised) are highlighted. The genus *Clavularia* is indicated in the dashed box, the phylogeny of which is shown in Fig. 24*a*.

monophyletic within *Clavularia*, but comprises two geographic clades, one including the GBR material, and a second one including Japanese samples. Our ML phylogeny also supports *C. brunafolia* sp. nov. as distinct from the other *Clavularia* species. The sample QMT G84672, which was previously identified as *C. inflata* (McFadden *et al.* 2022), does not match the lectotype of that species morphologically (Supplementary Fig. S1) and it falls within the *C. koellikeri* species complex.

Some of the samples identified in museum collections or previous publications as *C.* cf. *viridis* are here revealed to be a new species of the genus *Hicksonia* within Hicksoniidae (status revised) namely *Hicksonia tohrui* sp. nov. (QMT G84405 and QM G334154). Despite the morphological differences between *H. tohrui* specimens, a pairwise distance matrix on the alignments revealed a percentage of identical base pairs between the holotype and paratype of 92.0, 92.2% between the paratype and the material from Brazil, and 96.1% between the holotype and the Brazilian specimen, further suggesting only one species is represented in our phylogeny. The pairwise distance matrix is calculated in Geneious based on percentage of identical base pairs from aligned sequences (Supplementary Table S3). Our phylogenomic analysis confirms previous studies (McFadden *et al.* 2022) and places the family Hicksoniidae sister to a clade that includes a mix of stoloniferous genera (e.g. *Azoriella*), and the genera *Melithaea*, *Solenocaulon*, *Alertigorgia*, *Malacacanthus* and *Nidalia*. However, the position of Hicksoniidae within Octocorallia remains poorly supported.

Species delimitation

By morphologically comparing all voucher specimens within the *Clavularia* clade to the type material, we identify two nominal species, namely *C. viridis* and *C. koellikeri*. None of the voucher specimens matched the type specimen of *C. inflata*. One additional genetic clade could not be matched with the type material of any nominal species, and it represents a new species (*C. brunafolia* sp. nov.; see taxonomic account). The *C. koellikeri* species complex is monophyletic, and voucher specimens vary in both gross morphology and sclerites. Our phylogenomic analysis shows two geographic clades, one that includes all specimens from Japan, and a second group of specimens from the GBR, Palau and Indonesia (Fig. 24*a*, *c*, *d*).

For the *STRUCTURE*, PCA + PCA and t-SNE analyses, we obtained 1534 SNPs (14.13% missing data) using the UCE sample QMT G84408 as reference. The *STRUCTURE* analysis shows two distinct genetic clusters ($K = 2$; Fig. 24). Cluster 1 includes the lectotype and paralectotype of *C. koellikeri*, together with the *C. inflata* from Palau (McFadden *et al.* 2022), and all *Clavularia* specimens from Japan (Okinawa and Iriomote Island) and central and northern GBR. Cluster 2 contains three specimens registered and identified as *Clavularia* sp. and here described as a new species: *C. brunafolia* sp. nov. from the GBR. However, the PCA did not show clear clusters (Fig. 24*c*). The t-SNE analysis resolved the clusters better than the PCA (Fig. 24*d*), but both analyses showed the Japanese *C. koellikeri* as distinct from the GBR specimens.

We ran an additional *STRUCTURE* analysis on the monophyletic *C. koellikeri* clade (Supplementary Fig. S2) to see if the geographic clades separate. The analysis resulted in two distinct genetic clusters ($K = 2$). This time, the Japanese specimens were clustered with the Palau specimen, and both the lectotype and paralectotype of *C. koellikeri*, whereas the GBR samples were mostly shown as a second cluster. However, we consider this second *STRUCTURE* unreliable for a few reasons: the two clusters do not correspond to the clades in the tree, since in our phylogeny the lectotype and paralectotype of *C. koellikeri* are grouped with the GBR specimens rather than the ones from Japan. Second, the *STRUCTURE* clusters appeared to separate the UCEs we obtained from genome skimming data from the targeted capture sequences, suggesting a potential batch effect.

Discussion

Our phylogeny reconstructed from UCE loci represents the first attempt to resolve the taxonomy and systematics of the Clavulariidae clade by including genetic data from key nominal species of *Clavularia*, including a topotype of the type species *C. viridis* and the lectotype and one of the paralectotypes of *C. koellikeri* (here designated), collected in 1899. Our study provides morphological re-descriptions of all three nominal species of shallow-water, zooxanthellate *Clavularia* (*C. viridis*, *C. koellikeri* and *C. inflata*), creating a taxonomic and genetic baseline for future studies of the group. Unfortunately, we were unable to obtain sufficient molecular data from the types of *C. viridis* and *C. inflata*. The recently collected specimens identified as *C. inflata* based on morphology were reconstructed in the molecular phylogeny as *C. koellikeri*. Additionally, our study also includes the first description of a *Clavularia* species from the GBR, demonstrating that the diversity of species within the genus *Clavularia* has been hidden by the historical assumption that all tropical *Clavularia* belong to one of the three nominal species here re-examined (*C. viridis*, *C. koellikeri* and *C. inflata*).

Our phylogeny is well supported, and congruent with previous studies (McFadden *et al.* 2022). However, by increasing the taxon sampling for the genus *Clavularia*, we describe one additional genus within Clavulariidae (*Bairdium* gen. nov.), and reinstate the family Hicksoniidae Delage & Hérouard, 1901. In doing so, our study shows that the distribution of nominal species of *Clavularia* needs to be reconsidered. Indeed, *C. viridis*, *C. koellikeri* and *C. inflata* have all historically been considered to be widespread across the West Pacific (Bastidas *et al.* 2002; Benayahu 2002; Benayahu *et al.* 2004). *Clavularia viridis* was even considered to

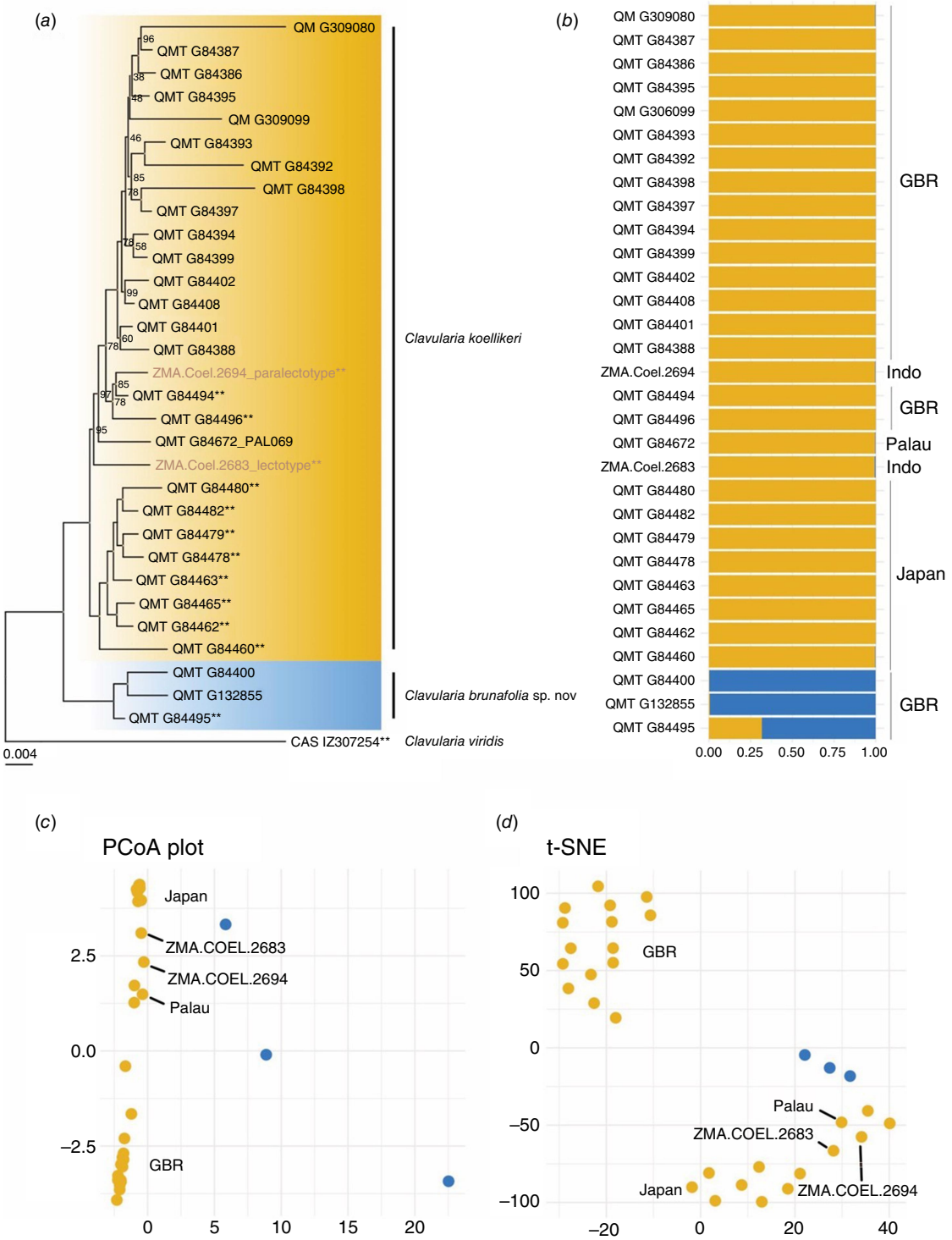

Fig. 24. (*Caption on next page*)

have been introduced to the southwest Atlantic coast of Brazil (Mantelatto *et al.* 2018). However, none of the newly collected specimens examined in this study matched the name-bearing specimens of *C. viridis* and *C. inflata* morphologically, suggesting these species may not occur on the GBR, or in Australia or Japan. A Brazilian specimen previously classified as *C.* cf. *viridis* (Mantelatto *et al.* 2018; McFadden *et al.* 2022) is here described as a new species within the resurrected genus *Hicksonia* (family Hicksoniidae), along with specimens from Western Australia and Japan. The clade with the lectotype of *C. koellikeri*, however, suggests that that species is widespread from the central GBR to Japan,

Fig. 24. Results from multiple species delimitation methods; (*a*) phylogeny of the genus *Clavularia* (Octocorallia) inferred from the 60% complete internal-trimmed alignment matrix (subsampled from Fig. 23). Bootstrap values are plotted at the nodes. Asterisks (**) indicate genome skimming data. SNP-based species delimitation for *C. brunafolia* **sp. nov.** and *C. koellikeri*; (*b*) *STRUCTURE* result for the *Clavularia* clade ($K = 2$). (*c*) Principal coordinates analysis (PCA) to explore the overall genetic diversity and (*d*) results from the unsupervised machine learning method t-SNE. Colour scheme reflects the clusters as per the *STRUCTURE* analysis (e.g. *C. koellikeri* in yellow and *C. brunafolia* sp. nov. in blue). The outgroup CAS IZ307254 is the topotype of *C. viridis*. The two geographic clades in *Clavularia koellikeri* are evident in both the PCA and t-SNE analyses. In those, the lectotype and paralectotype of *C. koellikeri* are highlighted.

including Palau. Interestingly, no members of the genera *Hicksonia* (family Hicksoniidae) and *Bairdium* (family Clavulariidae) have yet been found on the east coast of Australia, whereas the only Australian examples of *Hicksonia* came from Western Australia. Certainly, the inclusion of additional samples from other geographic regions is required to provide greater certainty regarding the range of the genus *Clavularia*.

Recent molecular studies (Subhan *et al.* 2022*b*) on Indonesian *Clavularia* based on the mitochondrial *mtMuts* implied that only one species of large-polyped *Clavularia* occurs across Indonesia, which was identified to be *C. inflata*. That study included specimens collected from close to the type localities of both *C. inflata* and *C. koellikeri*. Unfortunately, the study fails to compare the specimens with the respective type material. The figures included in the papers, however, suggest the specimens collected are a closer match to the lectotype of *C. koellikeri* rather than the lectotype of *C. inflata* (see Subhan *et al.* 2022*a*). Therefore, the current distribution of *C. inflata* remains unknown. Based on our morphological re-description of the type material, the lectotype of *C. inflata* is morphologically distinct from any specimen of *C. koellikeri* we examined, suggesting both species are valid. However, increasing taxon sampling and the collection of topotypes is necessary in future phylogenomic reconstructions. In this study, we did not obtain any molecular data for *C. inflata*, and therefore we cannot genetically confirm that it belongs to *Clavularia*. The smooth and peanut-shaped plate sclerites in the pinnules, however, suggest the species should remain within *Clavularia*. For the collection of a topotype of *C. inflata*, the smooth and branched rods in the stolon appear to be the most unique feature of the species, as no other sclerite shapes are found within the same section.

Within Clavulariidae, the *C. koellikeri* clade specimens showed great variability in habitat preference, gross morphology and sclerites. Bayer (1981) proposed calyx height as a subfamilial character potentially informative to genus level and consequently divided the Clavulariidae into two subfamilies: Clavulariinae for genera with tall calyces, and Sarcodictyiinae for genera with calyces that retract almost completely into the stolon. Based on Bayer's classification, McFadden and van Ofwegen (2012) noted that species of *Inconstantia* are characterised by both tall and tubular calyces, and short and bulbous calyces, showing how variable the calyx height can be among congeners. Our results further show how variable calyx height can be within a single species clade, as specimens of *C. koellikeri* included in this study have features of both subfamilies proposed by Bayer (1981).

This is not the first instance where morphological variations do not translate into distinct species in Octocorallia. For example, within the Clavulariidae clade, *Hanabira yukibana* Lau, Stokvis, Imahara & Reimer, 2019 shows considerable morphological variability in the field in both gross morphology and polyp colour, but mitochondrial and nuclear genes combined (*28S*, *COI* and mtMuts) did not support the distinction of multiple species (Lau *et al.* 2019). Similarly, within the genus *Ovabunda* Alderslade, 2001 only 4 out of 10 species described based on morphology were supported by molecular data (Halász *et al.* 2014; McFadden *et al.* 2017), further corroborating the importance of integrating morphology-based taxonomies with genetic data for species delimitation (Kessel *et al.* 2023).

Our findings highlight how our limited knowledge on the morphology of key Clavulariidae species historically obscured taxonomic, systematic and biogeographic patterns, which is a fundamental issue in Octocorallia (see McFadden *et al.* 2024), as well as in other marine taxa. For instance, Bridge *et al.* (2024) and Rassmussen *et al.* (2025) demonstrated that morphology-based taxonomies underestimated the taxonomic diversity in *Acropora* species, with incorrect assessments of geographical ranges and population sizes due to lumping of distinct species from different biogeographic regions of the Indo-Pacific. Moving forward, robust taxonomies combining morphological re-descriptions of type specimens with genetic data are necessary to identify species and correctly establish conservation needs and extinction risks in soft corals. Our study provides the valuable baseline data regarding the family Clavulariidae, pivotal for the comprehensive revision of the genus *Clavularia* and other genera currently considered to be *incertae sedis* (McFadden *et al.* 2022).

Supplementary material

Supplementary material is available online.

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Author affiliations

[A]College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia.

[B]Biodiversity and Geosciences Program, Queensland Museum Tropics, Townsville, QLD 4810, Australia.

[C]Molecular Invertebrate Systematics and Ecology Laboratory, Faculty of Science, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan.

[D]Department of Biology, Harvey Mudd College, Claremont, CA 91711, USA.

[E]Biodiversity and Geosciences Program, Queensland Museum, South Brisbane BC, QLD 4101, Australia.

[F]Tropical Biosphere Research Center, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan.

[G]Centre for Tropical Bioinformatics and Molecular Biology, James Cook University, Townsville, QLD 4811, Australia.