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Uncovering hidden coral diversity: A new cryptic lobophylliid scleractinian from the Indian Ocean

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Abstract

Extant biodiversity can easily be underestimated by the presence of cryptic taxa, even among commonly observed species. Scleractinian corals are challenging to identify because of ~~their ecophenotypic variation~~ plasticity and morphological ~~plasticity variation determined by genotype~~. In addition, molecular ~~analyses~~ data have revealed the occurrence of cryptic speciation. Here, we described a new cryptic lobophylliid genus and species *Paraechinophyllia variabilis* gen. nov., sp. nov., which is morphologically ~~indistinguishable similar to from~~ *Echinophyllia aspera* and *E. orpheensis*. The new taxon occurs in Mayotte Island, Madagascar, the Gulf of Aden, and the Red Sea. Six molecular markers (COI, 12S, ATP6-NAD4, NAD3-NAD5, histone H3, and ITS) and 46 morphological characters at three different levels (macromorphology, micromorphology, and microstructure) were examined. The resulting molecular phylogeny reconstruction showed that *Paraechinophyllia* gen. nov. represents a distinct group ~~within the~~ Lobophylliidae that diverged from the lineage leading to *Echinophyllia* and *Oxypora* in the Early Miocene, approximately 21.5 million years ago. The morphological phylogeny reconstruction clustered *Paraechinophyllia* gen. nov., *Echinophyllia*, and *Oxypora* together in a single clade, ~~and~~ ~~A~~ sole morphological character, calice relief, discriminated *Paraechinophyllia* gen. nov. from the latter two genera, suggesting that limited morphological variation has occurred over a long period. These results highlight the importance of cryptic taxa in reef corals, with implications for population genetics, ecological studies, and conservation.

Introduction

Cryptic species are ~~considered-defined~~ as two or more ~~genetically~~ distinct species that are erroneously classified and hidden under one species name due to their morphological similarity (Bickford et al., 2007; Fišer et al., 2018). They are ~~a common and evenly distributed phenomena~~, ~~evenly distributed~~ throughout major metazoan taxa and biogeographical regions (Knowlton, 1993; Pfenninger and Schwenk, 2007), and ~~they do~~ certainly affect ~~correct~~ estimates of Earth's animal diversity (Mora et al., 2011; ~~Appeltans et al., 2012~~; Scheffers et al., 2012). Cryptic diversity represents a major concern in many biological fields and the accurate identification of these taxa is crucial for biodiversity conservation, management, disease monitoring, and understanding evolutionary processes that drive speciation (Chadè et al., 2008; Baird et al., 2011; Andrews et al., 2014). In the last two decades, molecular genetic techniques have facilitated the detection of genetically divergent but morphologically similar cryptic lineages (~~Fukami et al., 2004a~~; Leasi et al., 2013; Egea et al., 2016; Coleman et al., 2016). The number of these discoveries continues to increase exponentially (Pfenninger and Schwenk, 2007) and, despite the lack of morphological characters to distinguish cryptic species, ~~advances~~ in DNA taxonomy tools have ~~enabled~~ formal taxonomic descriptions based on diagnostic molecular characters (Sarkar et al., 2008; Cook et al., 2010; Jörger and Schrödl, 2013).

Species identification in scleractinian corals has been based on morphology ~~for centuries~~ (Veron, 2000) and represents a notoriously challenging task for ~~both~~ ecologists and taxonomists (Kitahara et al., 2016). Extremely ~~high~~ levels of intraspecific morphological variation, ~~common in several coral species~~, ~~have contributed to~~ complicate the definition of species boundaries ~~in corals and constitute a common feature of several coral species~~ (Veron and Pichon, 1976). Environment-induced phenotypic plasticity (Todd, 2008) and intraspecific morphological variation caused by genotype (Carlon and Budd, 2002) are typical attributes of these animals and ~~greatly further~~ contribute to the confusion of coral identification. In the last decade, genetic data have ~~discovered-revealed~~ molecular lineages that do not correspond to taxa defined by traditional taxonomy, suggesting that evolutionary convergence of morphological structures (~~Fukami et al., 2004b~~; ~~Gittenberger et al., 2011~~; Budd et al., 2012a; ~~Arrigoni et al., 2014c~~), morphological stasis over long periods (Flot et al., 2011; Arrigoni et al., 2016a), and genetic exchange through introgression (Combosh and Vollmer, 2015; Suzuki et al., 2016) occur in corals. Moreover, large geographic samplings across the Indo-Pacific have demonstrated the occurrence of genetic ~~structuring~~, demographic isolation, and cryptic lineages within taxa that were traditionally considered to be widespread and common in the Indo-Pacific. For example, several instances of cryptic taxa have been ~~demonstrated-discovered~~ in *Acropora* (Ladner and Palumbi, 2012; Richards et al., 2016), *Stylophora* (~~Flot et al., 2011~~; Stefani et al., 2011; ~~Flot et al., 2011~~), *Pocillopora* (Souter, 2010; Pinzón et al., 2013; Schmidt-Roach et al., 2013a; Gélín et al., 2017a), and *Seriatopora* (Bongaerts et al., 2010; Warner et al., 2015).

Lobophylliidae Dai & Horng, 2009 is an Indo-Pacific family of common and ecologically important reef corals (Veron and Pichon, 1980; Veron, 2000). Its taxonomy and systematics have been intensively investigated using a combination of molecular and morphological data ~~during the last in recent~~ years (Arrigoni et al., 2014a, b, 2015, 2016b). ~~The family and it~~ currently ~~comprises-is comprised of~~ 11 genera and 54 extant species (~~Arrigoni et al., 2016c~~; Huang et al., 2016; ~~Arrigoni et al., 2016e~~). ~~A-The~~ first comprehensive molecular phylogenetic ~~reconstruction~~ of the family based on two markers (COI and ITS) showed that most genera (as described by

traditional morphology) were not monophyletic (Arrigoni et al., 2014a). Subsequent studies addressed the phylogenetic position and taxonomy of several genera, such as *Australomussa* Veron, 1985 (now accepted as *Lobophyllia* de Blainville, 1830) and *Parascolymia* Wells, 1964 (now accepted as *Lobophyllia* de Blainville, 1830) (Arrigoni et al., 2014b), *Sclerophyllia* Klunzinger, 1879 (Arrigoni et al., 2015), *Micromussa* Veron, 2000, *Homophyllia* Brüggemann, 1877, and *Australophyllia* Benzoni & Arrigoni, 2016 (Arrigoni et al., 2016b). Finally, a monograph by Huang et al. (2016) formally revised the entire family at the genus level using three molecular markers (COI, ITS, and histone H3) and 46 corallite and subcorallite morphological characters. Molecular and morphological phylogenies yielded concordant results and the sole uncertainty was represented by *Oxypora* Saville-Kent, 1871 and *Echinophyllia* Klunzinger, 1879 (Huang et al., 2016). These two genera were genetically distinct but morphological characters were invariable amongst the analysed species and the authors did not redefine *Echinophyllia* and *Oxypora* because of insufficient data as “the majority of presumed members were not sampled” (Huang et al., 2016). Subsequently, Arrigoni et al. (2016c) described two new species of *Echinophyllia* from the Indian Ocean, using both genetics and morphology.

In this study, we discovered and described a new and cryptic genus and species ascribed to Lobophylliidae. Material was collected from the southern and western Indian Ocean, the ~~NW~~-northwestern Gulf of Aden, and the Red Sea and was initially identified as different species ascribed to *Echinophyllia*. Six molecular markers and a total of 46 morphological characters were examined to build separated molecular and morphological phylogenies of Lobophylliidae ~~in order~~ to evaluate the phylogenetic position and divergence time of this new lineage. Furthermore, *Echinophyllia* and *Oxypora* were redefined based on the obtained morpho-molecular results.

Materials and methods

Sampling and identification

A total of 58 scleractinian corals ascribed to Lobophylliidae were collected while SCUBA diving at Indo-Pacific different localities (Table 1). Sampling covered all ten molecular lineages that are currently ~~known to be~~ ascribed to the family (Arrigoni et al., 2014a; Huang et al., 2016) and included 45 species, ~~each of which~~ represented by a sole specimen. Four of the examined species, namely *Echinophyllia patula* (Hodgson & Ross, 1982), *Oxypora crassispinosa* Nemenzo, 1979, *Lobophyllia hataii* Yabe & Sugiyama, 1936, and *Lobophyllia hassi* Pillai & Scheer, 1976, were phylogenetically analysed for the first time using both molecular and morphological data in this study. A total of 13 specimens identified in the field as *Echinophyllia* spp. were collected from ~~n~~North~~ern~~ Madagascar (n = 4), Mayotte Island (n = 2), the Gulf of Aden (n = 2), and the Red Sea (n = 5).

Each coral specimen was photographed underwater (Fig. 1), collected, ~~and~~ tagged, ~~and a~~ Approximately 2 cm² of ~~the each~~ collected colony was sampled and fixed in 95% ethanol. The remaining material was immersed in sodium hypochlorite for 48 hours to remove all tissues, rinsed in freshwater, and air-dried for identification and microscope observations of the cleaned corallum (Figs. 2 and 3). Species-level identification was based ~~when possible~~ on original descriptions and type material analysis ~~when possible~~. Voucher samples were deposited at ~~the~~ Australian Museum (AM, Sydney, Australia), ~~the~~ Muséum ~~N~~ational d'Histoire ~~N~~aturelle (MNHN, Paris, France), ~~the~~ Institute de Recherche pour le Développement (IRD, Noumea, New Caledonia), King Abdullah University of

Science and Technology (KAUST, Thuwal, Saudi Arabia), Naturalis Biodiversity Center (RMNH, Leiden, the Netherlands), [the](#) Seto Marine Biological Laboratory at ~~the~~ Kyoto University (SMBL, Kyoto, Japan), University of Milano-Bicocca (UNIMIB, Milano, Italy), and [the](#) Western Australia Museum (WAM, Perth, Australia) (Table 1). Thin sections and SEM stubs with specimens used for microstructural observations were housed [at](#) the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland (ZPAL).

DNA extraction and amplification

DNA extractions were carried out with the DNeasy Blood and Tissue kit (Qiagen Inc., Hilden, Germany). Six genomic regions were amplified and used as molecular markers to infer phylogeny of Lobophylliidae: [1\)](#) the barcoding portion of the cytochrome oxidase subunit I gene (COI); ~~2)~~ [2\)](#) a portion of the small subunit rRNA gene (12S); ~~3)~~ [3\)](#) the 3' end of the ATP synthase subunit 6 and the 5' end of the NADH dehydrogenase subunit 4 gene (ATP6–NAD4); ~~4)~~ [4\)](#) the 3' end of the NADH dehydrogenase subunit 3 gene and the 5' end of the NADH dehydrogenase subunit 5 gene (NAD3–NAD5); ~~5)~~ [5\)](#) the histone H3 gene (histone H3); ~~and 6)~~ [and 6\)](#) the 3' end of the 18S rRNA; ~~7)~~ the complete ITS1, 5.8S ~~gene~~, and ITS2 ~~genes~~; ~~8)~~ and the 5' end of the 28S rRNA gene (ITS). Table 2 includes the list of primers used for amplifications. COI, histone H3, and ITS have been already used to infer phylogenetic relationships among representatives of Lobophylliidae (Arrigoni et al. 2014a, b, 2015, 2016b) ~~and~~ [and](#) ATP6–NAD4 has been used to define species boundaries between *Echinophyllia* and *Oxypora* species (Arrigoni et al., 2016c), ~~while but the~~ 12S and NAD3–NAD5 were sequenced ~~to infer phylogenetic relationships among for~~ lobophylliids for the first time in this work. All PCR products were purified with Illustra ExoStar (GE Healthcare, Buckinghamshire, UK) and directly sequenced in forward and reverse directions using an ABI 3130xl Genetic Analyzer (Applied Biosystems, Carlsbad, CA, USA). We did not find double peaks or ambiguous base calls in electropherograms of ITS and histone H3 sequences, avoiding the need to clone these loci. Chromatograms of the forward and reverse DNA strands were assembled and edited using Sequencher 5.3 (Gene Codes Corp., Ann Arbor, MI, USA). In total, 207 sequences (15 of COI, 54 of 12S, 54 of ATP6–NAD4, 54 of NAD3–NAD5, 15 of histone H3, and 15 of ITS) were generated and combined with 123 published sequences. Sequences obtained in this study were deposited in EMBL, and accession numbers [for all sequences](#) are listed in Table 1.

Morphological observations and characters

Skeletons of *Echinophyllia aspera* (UNIMIB BA001), *Oxypora lacera* (IRD HS3172), and of the specimens identified as *Echinophyllia* spp. (MNHN IK-2014-250 and MNHN IK-2014-252) were examined at three scales, *i.e.* [macromorphology](#), micromorphology, and microstructure, for a total of 46 characters (Appendices 1 and 2). These 46 characters (20 of macromorphology, 13 of micromorphology, and of 13 microstructure) were identical to those used by Huang et al. (2016; see especially their [Table 1](#) and Appendix S2) in their revision of ~~the~~ Lobophylliidae, Budd et al. (2012a; see especially their Appendix S3) in their monograph of the Mussidae, and Huang et al. (2014a) in their ~~revision~~ [treatise](#) of the Merulinidae. For the remaining lobophylliid species included in the phylogenetic analyses, we used the morphological character states scored by Huang et al. (2016).

Observations at [the](#) macromorphological level were made using a Leica M80 microscope equipped with a Leica IC80HD camera. For analysis at micromorphological and microstructural scales, specimens were observed intact, as broken and etched samples, or as thin sections (*ca.* 30 μ m thick). Transverse broken sections of septa were exposed for *ca.* 20 s of etching in 0.1% formic acid solution, rinsed with distilled water, and air-dried following the procedure described by Stolarski (2003). Once dried, the samples were mounted on stubs and sputter-coated with [a](#) conductive platinum film. Thin sections were observed and photographed with a Nikon Eclipse 80i (Tokyo, Japan) transmitted light microscope, whereas intact and broken/etched skeleton samples were observed with a Philips XL 20 (Amsterdam, the Netherlands) scanning electron microscope (SEM). Thin sections and skeletal fragments attached to microscope stubs are housed at ~~the Institute of Paleobiology (ZPAL, Warsaw).~~

Phylogenetic analyses

For both molecular and morphological phylogenetic analyses, *Orbicella annularis* (Ellis & Solander, 1786) was selected as [an](#) outgroup due to its divergence from Lobophylliidae (Huang et al., 2014; 2016). Sequences were aligned [with using](#) MAFFT v. 7.130b (Katoh and Standley, 2013) and the iterative refinement method E-INS-i. The obtained alignments were later ~~run through~~ [processed using](#) GBLOCKS v. 0.91b (Castresana, 2000; http://molevol.cmima.csic.es/castresana/Gblocks_server.html) to remove ambiguously aligned regions using the default [“less stringent”](#) settings (Data S1). General statistics concerning the obtained sequences and the variability of the six employed markers were calculated with DnaSP v. 5.10.1 (Librado and Rozas, 2009) (Table 2). Intra- and intergeneric genetic distances were calculated as *p*-distance based on both the combined matrix (Table 3) and the individual gene datasets (Table S1) using DnaSP v. 5.10.1, and variance was estimated with 1,000 bootstrap replicates.

We performed separated phylogenetic analyses for each DNA locus under three criteria, namely maximum parsimony (MP) using TNT v.1.1 (Goloboff et al., 2008), Bayesian inference (BI) using MrBayes v. 3.2.1 (Ronquist et al., 2012), and maximum likelihood (ML) using Garli v. 2.01 (Zwickl, 2006) (Fig. S1). MP analysis was performed with 10,000 random addition sequence replicates, each employing 100 cycles of sectorial searches, ratcheting, drifting, and tree fusing. Gaps were treated as missing data. Clade stability was determined through 1,000 bootstrap replications. Prior to BI and ML, we determined the best partition scheme and nucleotide substitution models using PartitionFinder v. 1.1.1 (Lanfear et al., 2012). We used unlinked branch lengths, the greedy search algorithm for nucleotide sequence, and considered 18 potential partitions: 12S, ITS region, histone H3, and the three codon positions in each of the five protein-coding genes (COI, ATP6, NAD4, NAD3, and NAD5). Partitioning scheme comparison was performed using the corrected Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC), testing the influence on the tree topology (Data S2). Four Markov Chain Monte Carlo (MCMC) chains were run for each BI analysis, saving a tree every 1,000 generations. The tree searches were stopped when the deviation of split frequencies was less than 0.01 and all parameters reached the stationarity for effective sampling size and unimodal posterior distribution using Tracer v. 1.6 (Rambaut et al., 2014). The first 25% trees sampled were discarded as burn-in following indications by Tracer. ML topology was obtained under runs repeated three times from random starting trees to check for dependency of the results upon starting conditions.

Runs were continued until no improvement in $\ln\text{Likelihood} > 0.01$ was observed for 50,000 generations. The robustness of the final ML tree was assessed by performing 1,000 nonparametric bootstrap replicates. A 50% majority rule consensus tree was generated from the 1,000 replicates.

To determine if the ~~six~~ individual ~~six~~ DNA loci had conflicting phylogenetic signals, the incongruence length difference test (ILD) (Farris et al., 1995), implemented in PAUP* v. 4.0b10 (Swofford, 2003) as the partition homogeneity test, was conducted. The analysis was run with heuristic searches and 1,000 bootstrap replicates with ten stepwise random additions, saving one tree at each step, followed by tree bisection reconnection (TBR) swapping. No conflicting signals were detected between the six molecular markers ($P = 0.78$). Therefore, the six DNA regions were concatenated (3965 bp) to infer a ~~fossiltime~~-calibrated phylogenetic hypothesis of Lobophylliidae. One calibration point was used as constraint for the phylogeny reconstruction. Following Simpson et al. (2011) and the Paleobiology Database (<https://paleobiodb.org/>), the stratigraphically oldest fossil occurrences of *Lobophyllia* (~~including and~~ *Symphyllia* Milne Edwards & Haime, 1848 ~~that is~~ (now accepted as junior synonym of *Lobophyllia*, following Huang et al. (2016)) ~~wasere~~ used as minimum bound, and the maximum bound was derived from 95% confidence intervals on this first appearance datum (Strauss and Sadler, 1989), resulting in a time range of 31.3–19 Ma. The phylogenetic relationships and timing of diversification among lobophylliid taxa were estimated by Bayesian Markov ~~Cehain~~ Monte Carlo (MCMC) analysis implemented in BEAST v. 1.8.2 (Drummond et al., 2012). We partitioned the dataset by gene under the evolutionary models presented in Table 2, with unlinked evolutionary models, and an uncorrelated (lognormal) clock model. The analysis was run for 300 million generations, with a sampling frequency of 30,000, using four parallel chains. Log files were imported into Tracer v. 1.6 to assess convergence and to ensure adequate ESS values (> 200 for each parameter), and then were combined in a single file using LogCombiner v. 1.8.2. We summarised output trees using TreeAnnotator v. 1.8.2 (Drummond et al., 2012), discarding the first 25% as burn-in, and visualised the maximum clade credibility tree in FigTree v. 1.4.3 (Rambaut, 2012).

Since the new taxon described in this paper could not be distinguished based on a matrix of a distinctive set of morphological characters, the CAOS (Characteristic Attribute Organization System) workbench was used to identify molecular diagnostic character states (Sarkar et al., 2008; <http://boli.uvm.edu/caos-workbench/caos.php>). Following the method by Jörger and Schrödl (2013), we restricted our search of diagnostic characters to simple pure character attributes (sPu) that exist across all members of a clade but never in any other clade.

For the morphological phylogenetic analysis, we performed a MP analysis on the 46-characters data matrix in TNT (Data S3). We used the same settings used for the MP analyses on the individual gene datasets. The morphological dataset was composed of 16 binary and 30 multistate characters. Among the latter ~~ones~~, 23 traits were treated as ordered, the remaining seven as unordered (Appendix 1). Bremer support values were calculated for each node using TreeRot v.3 (Sorenson and Franzosa, 2007).

To test hypotheses regarding character evolution of the new taxon described hereafter, we performed an ancestral character state reconstruction, mapping each character onto the molecular phylogenetic tree using Mesquite v. 3.02 (Maddison and Maddison, 2015).

Results

Molecular data

The six-loci concatenated alignment (COI, 12S, ATP6-NAD4, NAD3-NAD5, histone H3, and ITS) was composed by a total of 3965 characters, including 638 variable sites (SV), of which 143 were singletons, and 495 were parsimony informative (SPI) (Table 2). Alignment lengths varied from a minimum value of 317 bp (histone H3) to a maximum of 844 nucleotides (NAD3-NAD5). The two nuclear markers (histone H3 and ITS) showed the highest proportion of both SV and SPI (higher than 20%) among the six sequenced loci.

The six single-locus phylogenies were broadly concordant and showed no major evidence of conflicting support and phylogenetic signal among the analysed taxa (Fig. S1). Indeed, most phylogenies recovered the ten known molecular clades (A-J) of Lobophylliidae (Arrigoni et al., 2014b; Huang et al., 2016), with the addition of a novel clade (K). Although the relationships between clades varied between the six molecular markers, each of the analysed species belonged to the same molecular clade in all trees and phylogeny reconstruction criteria. Interestingly, the thirteen samples preliminarily identified as *Echinophyllia* spp. rather than being were not recovered within the expected clade E. Instead, they formed a single and separated lineage (clade K) within Lobophylliidae in all analyses, with high node support values (Fig. S1). Hereafter, we formally describe the new taxon *Paraechinophyllia* gen. nov. corresponding to clade K.

The identification of the sister taxon of *Paraechinophyllia* gen. nov. was less clear because, for example, it was represented by *Moseleya* Quelch, 1884 in both ITS and histone H3 trees and by a group composed of several genera such as *Micromussa*, *Homophyllia*, and *Australophyllia*. *Homophyllia*, and *Micromussa* in both COI and NAD3-NAD5 phylogenies. The pairwise comparisons of intergeneric genetic distances confirmed the evolutionary distinctiveness of *Paraechinophyllia* gen. nov. within Lobophylliidae. Indeed, the intergeneric values between *Paraechinophyllia* gen. nov. and the other nine genera within Lobophylliidae varied from $2.35 \pm 0.2\%$ (*Moseleya*) to $4.63 \pm 0.29\%$ (*Homophyllia*). These distances totally overlapped with the pairwise intergeneric distances for the other genera (Table 3).

The fossiltime-calibrated phylogeny of Lobophylliidae inferred from the six sequenced loci is shown in Fig. 4a. The family was subdivided in eleven well-supported molecular clades (A-K) whose posterior probabilities (pp) were all 1. As already shown by the six single-locus phylogenies, all samples of *Paraechinophyllia* gen. nov. clustered in a well-supported lineage (pp = 1). Within this clade, the two samples from Mayotte were basal and sister to the remaining samples from the Gulf of Aden, the Red Sea, and Madagascar. Notably, *Paraechinophyllia* gen. nov. received high support (pp=1) as sister to the lineage leading to *Echinophyllia* and *Oxypora*. The lineage including these three genera was sister to the monophyletic group containing *Sclerophyllia* and *Moseleya* (pp=1). Divergence time estimates for some main nodes and genera are listed in Table 4. Based on our results, extant *P. variabilis* sp. nov. originated during the Pliocene (3.2 Ma, 95% HPD: 1.2-6.4) and diverged from the ancestor of *Echinophyllia* and *Oxypora* in the Early Miocene (21.5 Ma, 95% HPD: 11.6-33.7). The split between *Echinophyllia* and *Oxypora* occurred in the Middle Miocene (13.7 Ma, 95% HPD: 6.3-22.9). The estimated establishment of *Paraechinophyllia* gen. nov. was comparable to that of *Oxypora* (3.1 Ma, 95% HPD: 1.6-5.3) and *Homophyllia* (4.7

Ma, 95% HPD: 1.9-9.7). The youngest genus was *Sclerophyllia* (0.7 Ma, 95% HPD: 0.1-2.1) and the oldest one was *Lobophyllia* (8.4 Ma, 95% HPD 5.8-13.4).

Morphological data

The strict consensus tree of the morphological phylogenetic analysis based on 46 characters is shown in Fig. 4b. The morphological phylogeny reconstruction is broadly consistent with the molecular one although ~~the presence of there are~~ some differences. Seven of the 11 molecular clades (A-D, H-J) were recovered in the morphological tree, of which three clades (~~–~~*Micromussa* (A), *Homophyllia* (B), and *Lobophyllia* (I)) ~~with had~~ at least moderate support. In contrast with the molecular tree, the representatives of *Paraechinophyllia* gen. nov. (K), *Echinophyllia* (F), and *Oxypora* (G) were grouped together in a monophyletic lineage with high support (MP bootstrap = 92, Bremer decay index = 4). Moreover, *Acanthastrea pachysepta* (Chevalier, 1975) was sister to the lineage leading to *Acanthastrea* Milne Edwards & Haime, 1848 (E) and *Paraechinophyllia* gen. nov. + *Echinophyllia* (F) + *Oxypora* (G), similarly to Huang et al. (2016). Therefore, the latter three genera are morphologically indistinguishable.

The ancestral character state reconstruction revealed that four characters represented unambiguous synapomorphies of the lineage leading to *Paraechinophyllia* gen. nov., *Echinophyllia*, and *Oxypora*: organically united corallites, extensive coenosteum, columellae $\geq 1/4$ of calice width, and loss of epitheca (Fig. S2). A total of 43 of the 46 analysed characters were invariable among the three genera. Notably, calice relief ~~was~~ medium (3–6 mm) in *Paraechinophyllia* gen. nov. and small (< 3 mm) in *Echinophyllia* and *Oxypora*. Trabecular and compact (1–3 threads) columella structure and ~~the~~ absence of development of paliform lobes ~~we are~~ ~~characters~~ found only in *Oxypora*. Conversely, *Paraechinophyllia* gen. nov. and *Echinophyllia* showed ~~esd~~ trabecular and spongy (> 3 threads) columella structure and weak or moderate development of paliform lobes.

The examined specimens of *Paraechinophyllia* gen. nov. consistently showed microtextural and microstructural features that previously were recognised in other lobophylliids (Huang et al., 2016); see ~~Figs-Figs~~ 5–7. These included distinct microtuberculate texture on surfaces of skeletal structures. Tips of these microtubercles corresponded to slender bundles of fibres that form thickening deposits (TD's). Consistent with symbiotic (zooxanthellate) status of *Paraechinophyllia* gen. nov., its thickening deposits showed regular growth banding (~~Figs~~ ~~Figs~~ 6j, 7h; see Frankowiak et al., 2016). The organization of Rapid Accretion Deposits (RAD's) in *Paraechinophyllia* gen. nov. showed the same overall pattern and variable arrangement as occurs in the closely related taxa *Echinophyllia* (Fig. 5j-m, see also Fig. S3) and *Oxypora* (Fig. 5g-i): RAD's of sectioned lower order septa of more robust morphotypes form clusters with projections extending toward the septal faces (these structures typically represent various stages of septal tooth development). In contrast, RAD's in higher order septa or septa of less robust morphotypes formed straight or wavy mid-septal zone (~~Figs-Figs~~ 5e, 6b).

Taxonomic account

Scleractinia Bourne, 1900

Lobophylliidae Dai and Horng, 2009

***Paraechinophyllia* Arrigoni, Benzoni & Stolarski gen. nov.**

Figs. 1-3, 5I-N, 7

Type species. Paraechinophyllia variabilis Arrigoni, Benzoni & Stolarski sp. nov.

Etymology. *Paraechinophyllia* alludes to its morphological similarities with *Echinophyllia*, but it is distinguished from the latter based on genetics.

Included species. Paraechinophyllia variabilis Arrigoni, Benzoni & Stolarski sp. nov.

Diagnosis (character different from both *Echinophyllia* and *Oxypora* in italics). Colonial and laminar. Budding intracalicular; peripheral budding may be present. Corallites may be polymorphic; organically united. Monticules absent. Coenosteum spinose; extensive amount of coenosteum ($\geq$ corallite diameter). Calice width medium to large (≥ 4 mm), with medium relief (3 mm). Costosepta mostly confluent. Septa in ≤ 3 cycles (≤ 16 septa). Free septa irregular. Septa spaced ≤ 4 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), $\geq 1/4$ of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Columellae centres clustered. Paliform lobes weakly or moderately developed. Development of septal lobes absent. Epitheca absent. Endotheca low–moderate (tabular). Tooth base at midcalice elliptical-parallel. Tooth tip outline irregular, forming multiaxial bulb. Tooth height medium (0.3–0.6 mm). Tooth spacing medium (0.3–1.0 mm), with ≤ 6 teeth per septum. Tooth size equal between wall and septum. Granules scattered on septal face; weak (rounded). Interarea smooth. Walls formed by dominant paratheca and partial septotheca. Thickening deposits with extensive stereome. Costa centre clusters weak; > 0.6 mm between clusters; medial lines strong. Septum centre clusters weak; 0.3–0.5 mm between clusters; medial lines weak.

Genetics. This genus ~~is a monophyletic clade within Lobophylliidae and~~ is sister to the lineage leading to *Echinophyllia* and *Oxypora* based on our multi-locus phylogeny reconstruction (COI, 12S, ATP6-NAD4, NAD3-NAD5, histone H3, and ITS) (Fig. 4a). The split between these two lineages occurred in the Early Miocene (21.5 Ma, 95% HPD: 11.6–33.7). A total of 21 diagnostic nucleotide characters (with position in alignment): COI: T (587); 12S: G (492), C (678); ATP6-NAD4: C (149), C (211), C (394), T (543); NAD3-NAD5: C (57), T (150), A (183), C (235); histone H3: G (7); ITS: G (108), G (109), G (114), G (140), C (232), C (245), C (261), C (282), G (482), G (553).

Distribution. Red Sea (Saudi Arabia), northern and western Gulf of Aden (Yemen), ~~and~~ southern and western Indian Ocean (Madagascar and Mayotte Island).

Remarks. This genus is monotypic, including only *Paraechinophyllia variabilis* sp. nov. It is morphologically indistinguishable from *Echinophyllia* and *Oxypora* as shown in the morphological phylogeny (Fig. 4b) and the establishment of this genus is based on genetic data. The ~~fossiltime~~-calibrated molecular phylogeny proposed in Fig. 4a demonstrated that this genus is a distinct and monophyletic clade of Lobophylliidae that is deeply divergent from the lineage leading to *Echinophyllia* and *Oxypora*. Each of the six single-locus phylogenies confirmed that this genus is not related to any other lobophylliid genus. It has been recorded from the Red Sea, the northern and western Gulf of Aden, and southern and western Indian Ocean but was not collected in Maldives and in several other localities of the Pacific Ocean (e.g. Papua New Guinea, New Caledonia, Australia) where a similar sampling effort on lobophylliid diversity has been carried out. Unfortunately, no other localities of the southern and

western Indian Ocean have been surveyed in this study and, therefore, the possible presence of this species in this region cannot be excluded.

***Paraechinophyllia variabilis* Arrigoni, Benzoni & Stolarski sp. nov.**

Figs. 1-3, 5I-N, 7

Etymology. *Variabilis* means “variable” in Latin and refers to the notable morphological variability of the species.

Type material. Holotype: MNHN-IK-2014-250, Tara Oceans Expedition, Mayotte Island (12°41.193'S; 44°59.039'E), 14/06/2010, collector Benzoni F, collection code UNIMIB MY236. Paratypes: MNHN-IK-2014-251, Tara Oceans Expedition, Mayotte Island (12°40.429'S; 45°3.690'E), 31/05/2010, collector Benzoni F, collection code UNIMIB MY050; MNHN-IK-2014-247, Al Mukallah, Yemen (14° 29.967'N; 49°10.328'E), 19/03/2007, collector Benzoni F, collection code UNIMIB MU132; MNHN-IK-2014-252, Al Mukallah, Yemen, (14° 30.793'N; 49°10.339'E), 20/03/2007, collector Benzoni F, collection code UNIMIB MU165.

Other material examined. Saudi Arabia, Red Sea, KAUST Biodiversity cruise, collector Benzoni F: KAUST SA0021, Al Lith, Shi'b Ammar (19°34.242'N; 40°00.527'E), 03/03/2013; KAUST SA0794, Jaz'air Silah (27°38.302'N; 35°18.369'E), 27/09/2013; KAUST SA0922, Magna Coast Guard (28°24.232'N; 34°44.440'E), 29/09/2013; KAUST SA0944, Magna Coast Guard (28°24.232'N; 34°44.440'E), 29/09/2013; KAUST SA1023, Gulf of Aqaba, Magna Coast Guard (28°24.232'N; 34°44.440'E), 30/09/2013; Madagascar, MAD cruise, collector Benzoni F: IRD MD239, Nosy Kalakajoro (13°19.028'S; 48°8.832'E), 28/10/2016; IRD MD240, Nosy Kalakajoro, (13°19.028'S; 48°8.832'E), 28/10/2016; MD241, Nosy Kalakajoro, (13°19.028'S; 48°8.832'E), 28/10/2016; MD265, Nosy Sakatia (13°55.749'S; 47°45.346'E), 30/10/2016.

Description. The holotype (MNHN-IK-2014-250) corallum is irregularly dome-shaped and circular in outline at the base with the largest diameter measuring 12 cm (Figs Figs. 1a, 3a). It was attached at the substrate at the centre of the colony and has free margins. Corallites are crowded and irregularly oriented at the centre of the specimen and tend to space out towards the margins. Corallite shape and size are variable, the largest has an elliptical shape and measures 18 mm in largest diameter and the smallest 10 mm (Fig 2a). Calices have medium relief. Columellae are trabecular and spongy seated deep in the fossa (Fig 2a) where moderately developed paliform lobes are found. Costosepta are equal, going from 12 to 24 in number. Septal teeth have irregular tip outline forming multiaxial bulbs visible to the naked eye. Paratype MNHN-IK-2014-251 is a dome-shape corallum similar in shape to the holotype but larger than it, measuring 16 cm in largest diameter (Figs Figs. 1b, 3b). Its corallites are more regularly arranged and exsert (Figs Figs. 2b, 3b). The specimen closely resembles the holotype in terms of size and shape of the corallites, and all the other aforementioned features. However, paratype MNHN-IK-2014-251 has particularly thick and high septal teeth, the most developed in the type series described here, which give the costosepta an even rougher appearance (Fig. 2b). Paratype, MNHN-IK-2014-252 (Fig. 3c) is the peripheral fragment of a larger colony. It measures 16 x 8cm and shows several visible differences with the two previously examined specimens in the type series. In particular, although the corallite size in this specimen remains within the medium to large (≥ 4 mm) range, it is smaller on average, with most corallites barely reaching 10 mm in diameter

(Fig. 2e). Moreover, radial elements are overall thinner and more distanced, with septal teeth similarly reduced in thickness when compared to the holotype. Because corallites are more scattered on the colony surface and radial elements are overall thinner, alveoli are easily visible in this paratype. Similarly to the previous specimen, paratype MNHN-IK-2014-247 (Figs Figs. 1e, 3d) is a peripheral portion of a predominantly foliose colony. It measures 11 x 7.5 cm and it most resembles MNHN-IK-2014-252 among the examined specimens having a similar corallite size, smaller than that of the holotype and paratype MNHN-IK-2014-251, and costosepta and septal teeth morphology, especially in terms of their reduced thickness (Fig. 2e).

Other specimens examined in this study and included in the genetic analyses fall within the corallum and corallite morphological variability range encompassed by the type specimens described above (Figs Figs. 1c, g-h, 2c-d, g-h) and mostly resembling either *Echinophyllia aspera* or *E. orpheensis*. Notably, some specimens may show particularly bulbous ornamentation on the primary septa typical of the recently described species *E. bulbosa* (Arrigoni et al. 2016c) (Figs Figs. 1f, 2f).

Genetics. Same as for the genus.

Distribution. Same as for the genus.

Remarks. This species is morphologically similar to both *Echinophyllia aspera* and *E. orpheensis* but the genetic data revealed its deep divergence from these two *Echinophyllia* species. ~~More in~~ particular, while the holotype and paratype MNHN-IK-2014-251 show strong resemblance with *Echinophyllia orpheensis*, paratypes MNHN-IK-2014-247 and MNHN-IK-2014-252 were initially identified as *E. aspera*. This species occurs in sympatry with *E. aspera* and *E. orpheensis*, sharing the same reef habitat where specimens of these three species were collected for this study.

Echinophyllia Klunzinger, 1879

Type species. Echinophyllia aspera (Ellis & Solander, 1786)

Revised diagnosis. Colonial and laminar. Budding intracalicular; peripheral budding may be present. Corallites may be polymorphic; organically united. Monticules absent. Coenosteum spinose; extensive amount ($\geq$ corallite diameter). Calice width medium to large (≥ 4 mm), with small relief (≤ 3 mm). Costosepta mostly confluent. Septa in ≤ 3 cycles (≤ 36 septa). Free septa irregular. Septa spaced ≤ 11 septa per 5 mm. Costosepta unequal in relative thickness. Columellae trabecular and spongy (> 3 threads), $\geq 1/4$ of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. Columellae centres clustered. Paliform lobes weakly or moderately developed. Septal lobes absent. Epithecium absent. Endotheca low–moderate (tabular). Tooth base at midcalice elliptical-parallel. Tooth tip outline irregular, forming multiaxial bulb. Tooth height medium (0.3–0.6 mm). Tooth spacing medium (0.3–1.0 mm), with ≤ 6 teeth per septum. Tooth size equal between wall and septum. Granules scattered on septal face; weak (rounded). Interarea smooth. Walls formed by dominant paratheca and partial septotheca. Thickening deposits extensively developed. Costa centre clusters weak; > 0.6 mm between clusters; medial lines strong. Septum centre clusters weak; 0.3–0.5 mm between clusters; medial lines weak.

Genetics. This genus is sister to *Oxypora* based on our multi-locus phylogeny reconstruction (COI, 12S, ATP6-NAD4, NAD3-NAD5, histone H3, and ITS) (Fig. 4a). The estimated split between the two genera occurred in

the Middle Miocene (13.7 Ma, 95% HPD: 6.3–22.9). A total of 22 diagnostic nucleotide characters (with position in alignment): COI: C (24), G (44), G (83), G (207), C (362); 12S: G (17), C (385), C (403), G (533), G (600), G (601); ATP6-NAD4: G (260), T (299), C (507), C (510), A (564), A (660); NAD3-NAD5: G (459); ITS: C (190), G (191), G (585), A (586).

Included species. *Echinophyllia aspera* (Ellis & Solander, 1786); *Echinophyllia bulbosa* Arrigoni, Benzoni & Berumen, 2016; *Echinophyllia costata* Fenner & Veron, 2000; *Echinophyllia echinoporoides* Veron & Pichon, 1980; *Echinophyllia gallii* Benzoni & Arrigoni, 2016; *Echinophyllia glabra* (Nemanzo, 1959); *Echinophyllia orpheensis* Veron & Pichon, 1980; *Echinophyllia patula* (Hodgson & Ross, 1982); *Echinophyllia pectinata* Veron, 2000; *Echinophyllia tarae* Benzoni, 2013.

Taxonomic remarks. Despite the absence of diagnosable morphological differences between *Echinophyllia* and *Oxypora*, the two genera are genetically distinct and represent two monophyletic lineages that deeply diverged in the past. Our molecular analysis showed that *Oxypora glabra* Nemanzo, 1959 is more closely related to *Echinophyllia* (F) than to *Oxypora* species (G). Therefore, *O. lacera* is transferred to *Echinophyllia* based on molecular evidence presented here and in previously works (Arrigoni et al., 2014a, 2016c; Huang et al., 2016). Notably, Chevalier (1975) placed *O. glabra* under *Echinophyllia* based on a specimen from New Caledonia.

***Oxypora* Saville-Kent, 1871**

Type species. ***Oxypora lacera* (Verrill, 1864)**

Revised diagnosis (characters different from both *Paraechinophyllia* and *Echinophyllia* in italics). Colonial and laminar. Budding intracalicular; peripheral budding may be present. Corallites may be polymorphic; organically united. Monticules absent. Coenosteum spinose; extensive amount of coenosteum ($\geq$ corallite diameter). Calice width medium (4–15 mm), with small relief ($\leq$ 3 mm). Costosepta mostly confluent. Septa in $\leq$ 3 cycles ($\leq$ 24 septa). Free septa irregular. Septa spaced $\leq$ 6 septa per 5 mm. Costosepta unequal in relative thickness. *Columellae trabecular and compact* (1–3 threads), $\geq$ 1/4 of calice width, and discontinuous amongst adjacent corallites with lamellar linkage. *Columellae centres clustered. Paliform lobes absent.* Septal lobes absent. Epitheca absent. Endotheca low–moderate (tabular). Tooth base at midcalice elliptical-parallel. *Tooth tip outline irregular, forming multiaxial bulb.* Tooth height medium (0.3–0.6 mm). Tooth spacing medium (0.3–1.0 mm), with $\leq$ 6 teeth per septum. Tooth size equal between wall and septum. Granules scattered on septal face; weak (rounded). Interarea smooth. Walls formed by dominant paratheca and partial septotheca. Thickening deposits extensively developed. Costa centre clusters weak; $>$ 0.6 mm between clusters; medial lines strong. Septum centre clusters weak; $\geq$ 0.6 mm between clusters; medial lines weak.

Genetics. This genus is sister to *Echinophyllia* based on our multi-locus phylogeny reconstruction (COI, 12S, ATP6-NAD4, NAD3-NAD5, histone H3, and ITS) (Fig. 4a). A total of 44 diagnostic nucleotide characters (with position in alignment): ATP6-NAD4: G (364), G (435), G (501), C (783); NAD3-NAD5: A (209); histone H3: A (10), C (22), T (40), C (55), C (58), G (88), T (91), T (94), T (109), C (115), T (118), C (124), C (136), G (142), G (145), C (163), C (184), T (187), C (202), T (211), C (214), G (217), C (223), A (230), G (232), T (238), T (247), T (256), C (259), C (269), A (277), C (280), T (287), C (295), G (307), C (310); ITS: T (196), G (479), C (629).

Included species. *Oxypora lacera* (Verrill, 1864); *Oxypora convoluta* Veron, 2000; *Oxypora crassispinosa* Nemenzo, 1979; *Oxypora echinata* (Saville-Kent, 1871) comb. nov.; *Oxypora egyptensis* Veron, 2000.

Taxonomic remarks. Given the deep molecular divergences between *Echinophyllia* (F) and *Oxypora* (G) and with the aim to maintain the two as monophyletic entities~~two genera monophyletic~~, *Echinophyllia echinata* (Saville-Kent, 1871) is transferred to *Oxypora* based on genetics. Therefore, the new combination *Oxypora echinata* is here established for the first time.

Discussion

As a result of the morphological and molecular analyses presented in this study, *Paraechinophyllia variabilis* was described as a new cryptic genus and species ascribed to ~~the~~ Lobophylliidae. The genus is genetically distinct from the other lobophylliids based on six molecular loci and diverged from the most closely related *Echinophyllia* and *Oxypora* approximately 21.5 Ma. Nevertheless, the ~~presented~~ morphological phylogeny reconstruction did not separate the new genus from *Echinophyllia* and *Oxypora* and only a one (medium calice relief, 3–6 mm) out of 46 morphological characters distinguished *Paraechinophyllia* from the latter two genera. Colony growth form and corallite features of *P. variabilis* closely resemble those of *E. aspera* and *E. orpheensis* and, moreover, the species is characterised by a notable intraspecific morphological variation.

Central ~~tenants~~ topics of cladistics are the concepts of monophyly and synapomorphy. A monophyletic taxon originates with speciation and it is defined as one that includes the ancestor and all ~~(-and only-)~~ its descendants (Wiley, 1981). Synapomorphy is the empirical trait used to discover and describe a monophyletic taxon (Hennig, 1957). The establishment of *P. variabilis* based on genetic data strictly followed the Hennigian principle of monophyly (Hennig 1950, 1966). The analysed samples of the new taxon consistently grouped in a well-supported monophyletic lineage in the phylogenetic tree of each individual gene; ~~phylogenetic tree and~~ retaining this taxon in *Echinophyllia* would have created a paraphyletic group given the non-sister relationship between *Paraechinophyllia* and *Echinophyllia* (Fig. S1). By analysing six independent DNA loci, CAOS discovered 21 diagnostic nucleotide characters for the new taxon. Although the detection of homologies and apomorphic conditions of a nucleotide is demanding because of the high chance of convergent multiple transformations generating homoplasy, we confidently assumed these characters as synapomorphies for *Paraechinophyllia* based on the following considerations: the CAOS search was restricted to sPu that exist across all members of *Paraechinophyllia* but never in any other lobophylliid clade; the high taxon coverage of the family by the inclusion into the phylogenetic analyses of all extant genera and of 46 out of the 54 (85%) valid species ascribed to Lobophylliidae; and the deep divergence time between *Paraechinophyllia* and the lineage leading to *Echinophyllia* and *Oxypora* increased the chance that the discovered sPu referred to unique mutations accumulated due to ~~selection~~the absence of gene exchange.

What is a cryptic taxon?

Speciation is not always accompanied by morphological change and the identification of cryptic taxa has challenged taxonomists and naturalists since the 18th century (Winker, 2005). Hidden diversity implicates mechanisms of morphologically static cladogenesis and suggests the occurrence of selection on ecological,

behavioural, and/or reproductive characters which do not correspond to phenotypic differences (Bickford et al., 2007; Fišer et al., 2018). Stabilising selection on morphology is often hypothesised in several models of cryptic speciation, especially in the presence of extreme environmental conditions (Schönrogge et al., 2002). Some studies highlighted that patterns of cryptic genetic divergence are strongly associated with ecological niche differentiation (Rissler and Apodaca, 2007). In addition, prezygotic and/or postzygotic barriers play an important role in speciation mechanisms despite morphological stability (Knowlton, 1993; Palumbi, 1994). In our case, *P. variabilis* occurs in sympatry with *E. aspera* and *E. oprheensis*, ~~even~~ sharing ~~also~~ the same reef habitat. Moreover, we did not find any depth partitioning or light and water condition preferences. Therefore, it seems that these three species have similar ecological characteristics. ~~Sexual~~ The sexual system and reproductive ~~veen~~ mode are known for three *Echinophyllia* species (*E. aspera*, *E. orpheensis*, and *E. glabra*) and two *Oxypora* species (*O. lacera* and *O. crassispinosa*) (Baird et al., 2009; Bouwmeester et al., 2015). All these species are gonochoric broadcast spawners. Since a difference in spawning timing may represent an important prezygotic barrier, further studies on spawning behaviour and reproductive mode of *P. variabilis* should be undertaken to investigate in detail the role of reproductive barriers among these taxa.

Some researchers advocated ~~d~~ that cryptic species ~~should beare often~~ included in the category of pseudo-cryptic species once the establishment of diagnosable morphological and non-morphological traits for their identification (Sáez and Lozano, 2005; Fišer et al., 2018). Indeed, in several cases further examinations of morphology, physiology, and behaviour resolved and identified pseudo-cryptic species (Knowlton, 1993; Sáez et al., 2003) and suggested the need of a critical investigation of the entire morphological space to test the real cryptic nature of a taxon. In this study, following the most updated works on coral cladistics (Budd and Stolarski, 2009; Budd et al., 2012a; Huang et al., 2016), a rigorous phylogenetic analysis of 46 morphological characters has been coupled with genetics to a taxon-rich dataset of Lobophylliidae. Nevertheless, we acknowledge that the analysed morphological traits refer exclusively to the coral skeleton and we do not exclude that key differences could be found by investigating other features, such as those related to the coral polyps or to embryogenesis. Histological characters remain under-explored in scleractinian phylogenetics ~~despiteeven though~~ they are routinely used in other cnidarian groups (Fautin, 2009). Recent works demonstrated that soft-tissue traits are taxonomically valid and increased phylogenetic resolution, although some caveats should be made (Martinez-Baraldés et al., 2014; Cordie et al., 2016). Embryogenetic morphological characters distinguished ~~ed~~ “complex” from “robust” corals, suggesting that patterns of early development and gastrulation are phylogenetically informative rather than being correlated with habitat or reproductive ~~veen~~ mode (Okubo et al., 2013; Okubo, 2016). Interestingly, Okubo (2016) stated that “gastrulation mode such as delamination, invagination, ingression etc. could be used for grouping at the family or genus level, because the gastrulation mode is different at least among genera”. Other non-morphological lines of evidence have been used to differentiate ~~found to be different in~~ some cryptic corals. For example, differences in spawning times and reproduction strategies were found in hidden lineages of *Acropora* (Rosser, 2015) and *Pocillopora* (Pinzón et al., 2013; Schmidt-Roach et al., 2013a). In addition, partitioning of *Symbiodinium* associated to distinct cryptic species ~~were was~~ detected in *Seriatopora* (Bongaerts et al., 2010; Warner et al., 2015) and *Pocillopora* (Schmidt-Roach et al., 2013a), thus suggesting the possible importance of symbionts in the host cryptic

diversity. In all these cases, it may be hypothesised that different ecological niches are associated with cryptic species (Rissler and Apodaca, 2007). In other instances, the lack of any known phenotypic and ecological differences suggests that cryptic species could occupy highly overlapping ecological niches, suggesting that their long-term coexistence could be unstable and that neutral mechanisms and ecological drift might be especially important in their community dynamics (McPeck and Gomulkiewicz, 2005).

With the aim to understand and discover cryptic species, researchers need to look for the conditions in which sibling taxa will thrive, ~~pursuing their causes whilst decrypting their nature~~. We need to apply systematic and quantitative comparisons across taxa, biogeographic areas, and habitats. Surveying poorly-studied groups and regions and understanding the biology of a taxon are two fundamental aspects to enhance the chances for discovering cryptic species and determining their origin. Under this premise, coral reefs and hard corals are promising candidates to explore the occurrence of sibling taxa (Knowlton, 1993). Coral reefs are heterogeneous environments, characterised by a plethora of different habitats, environmental parameters, and specialised interspecific interactions, enhancing the occurrence of severe selection and speciation (Bickford et al., 2007). Hard corals are relatively simple marine invertebrates (Veron, 2000), with few taxonomically informative characters, and thus with a high potential of hidden speciation (Knowlton, 1993). Therefore, it is not surprising that during the last years an increasing number of cryptic species has been ~~unravelling~~ revealed using various genetic approaches, suggesting that cryptic speciation occurs in several coral genera (Kitahara et al., 2016).

Origin of Paraechinophyllia

Several recent molecular studies discovered multiple instances of evolutionary differentiation between the Indian and Pacific coral fauna, including unique Indian lineages and unexpected evolutionary breaks between Indian and Pacific coral populations (Flot et al., 2011; Stefani et al., 2011; [Arrigoni et al., 2012, 2016a, 2016b, 2016c](#); Benzoni et al., 2012a; [Arrigoni et al., 2012, 2016a, 2016b, 2016c](#); Huang et al., 2014b; Kitano et al., 2014; Richards et al., 2016; Glin et al., 2017b). The description of *Paraechinophyllia* increases the number of coral genera endemic to the northern and/or western Indian Ocean, including *Anomastrea*, *Coscinaraea*, *Craterastrea*, *Ctenella*, *Gyrosmlia*, *Horastrea*, and *Sclerophyllia* (Veron, 2000; Benzoni et al., 2012a; Arrigoni et al., 2015). This result confirms the evolutionary distinctiveness of corals living in this region (Obura 2012) and strengthens the hypothesis of a second biodiversity hotspot for scleractinian corals ~~besides~~ after the Coral Triangle and the adjacent South China Sea (Hoeksema, 2007; Huang et al., [2015](#), 2017). In particular, two distinct centres of diversity are supposed to occur in the Indian Ocean, the northern Mozambique Channel and the Red Sea (Obura, 2012; Veron et al., 2015). ~~Notably, *Paraechinophyllia* occurs in both the northern Mozambique Channel and the Red Sea. Notably, the timetree showed that Mayotte samples of *P. variabilis* are basal while the Red Sea representatives are the most derived and recent (Fig. 4a). This result suggests an origin of *Paraechinophyllia* in the northern Mozambique Channel, followed by a recent dispersal towards the northern Indian Ocean.~~

It is now accepted that the distribution of extant scleractinian corals does not necessarily coincide with breaks in contemporary environmental conditions and habitats, but it is conversely influenced by geological features, such as tectonic plates and mantle plume tracks (Keith et al., 2013; Leprieur et al., 2016). The ~~fossiltime~~

calibrated phylogenetic tree indicated an Early Miocene timing (~21.5 Ma) for the beginning of the radiation of extant lineages of *Paraechinophyllia*, *Echinophyllia*, and *Oxypora* (Fig. 4a). Evidence from distribution patterns, phylogenetic studies, paleontology, and geology suggest that multiple centres of origin have occurred in the Indian Ocean from the Paleogene onwards as results of geological events (Obura, 2016). Important tectonic changes in what is now the northern and central Indian Ocean occurred in the Eocene, resulting in a narrowing of the Tethys Sea (Schettino and Turco, 2011). Europe became isolated from the Indian Ocean and the circumtropical Tethys Sea started a process of fragmentation that implicated the isolation of the western and northern Indian Ocean from the eastern Indian Ocean and the Central Indo-Pacific (Meulenkamp and Sissingh, 2003). Following the collision of India with Asia, the remnants of the Tethys Sea closed during the Miocene (25-15 Ma) and the emergent Mascarene Ridge islands constituted an intermittent north-south barrier that would have further isolated the western Indian Ocean (Obura, 2016). Therefore, the origin of the lineage leading to *P. variabilis* may have been driven by geological processes related to the fragmentation of the Tethys Sea and the transition of the biodiversity hotspot from the West Tethys Sea to the East Africa/Arabian plate (Obura, 2016).

The six-loci ~~timetree-chronogram~~ indicates~~s~~ an Oligocene/Miocene radiation of most extant lobophylliid genera (Fig. 4a) and this is concordant with fossil occurrences of the majority of these taxa (see the Paleobiology Database, <https://paleobiodb.org/> Fossil). Evidence suggests~~s~~ that tectonic events in the Late Oligocene and early Miocene promoted a general increase of shallow-water areas and the creation and diversification of a mosaic of distinct habitats (Wilson and Rosen, 1998; Zanchos et al., 2001; Crame and Rosen, 2002). ~~As outcome~~Because of these tectonic dynamics and habitat changes, this period is characterised by an exceptional documented diversification of zooxanthellate corals and reef-associated~~s~~ organisms (Bellwood et al., 2004; Cowman et al., 2011). Multiple and independent instances of increased rates of diversification in the Oligocene and Miocene have been described for reef fish (Alfaro et al., 2007; Bellwood et al., 2004; Cowman et al., 2011; Litsios et al., 2014), octocorals (Herrera et al., 2012; Dueñas et al., 2016), gastropods (Williams and Duda, 2008), crustaceans (Shank et al., 1999; Klaus et al., 2010), and molluscs (Strugnell et al., 2008).

Morphological considerations on Paraechinophyllia variabilis

Due to its cryptic nature and remarkable similarity with *Echinophyllia* and *Oxypora*, *Paraechinophyllia* has been overlooked so far. Considering the sister relationship between *Paraechinophyllia* and the molecular lineage leading to former two genera (Fig. 4a), it is likely that the morphological similarity is determined by the conservation of morphological traits from the~~ir~~ common ancestor over a very long period. ~~It seems that these three genera will occupy a similar morphospace (McGhee, 2006) and a~~ detailed re-examination of their fossil record may elucidate the possible occurrence of morphological stasis (Eldredge et al., 2005). Notably, a recent study showed that extant *Acropora* species conserved morphological microstructures and biomineralisation patterns identical to those of fossil *Acropora* from the Eocene, Oligocene, and Miocene, spanning a period of 48 Ma (Stolarski et al., 2016). Nevertheless, extant *Acropora* species are highly diversified and morphological different from ~~extinct ones~~the fossil species (Wallace, 1999; Wallace and Rosen, 2006; [Santodomingo et al., 2015](#)). In

contrast to our study case, *Acropora* species occupy distinct regions of morphospace (McGhee, 2006) and represent an example of morphology conservation from the ancestor.

Another interesting aspect is that *P. variabilis* is macromorphologically indistinguishable from *E. aspera* and its closely related species *E. orpheensis*, whereas it can be easily distinguished from all the other *Echinophyllia* and *Oxypora* species. Although *E. aspera* and *E. orpheensis* likely represent different morphs of a single species (Arrigoni et al., 2016a; see also discussion below), they are clearly separated from *P. variabilis* based on genetics. It seems therefore that the new taxon and the lineage including *E. aspera* and *E. orpheensis* have independently evolved similar macromorphologies. A similar example has recently been revealed among mushroom corals (Fungiidae), in which the new genus *Sinuorata* was discerned as a result of molecular analyses (Oku et al., 2017). A similar case has been recently described in mushroom corals. Oku et al. (2017) described *Sinuorata* as a result of molecular analyses. This monotypic genus is morphologically difficult to separate from free-living *Cycloseris* species (*sensu* Benzoni et al. 2012b) but it represents a distinct molecular lineage.

The large intraspecific morphological variability of *P. variabilis* may be due to either phenotypic plasticity, geographic variation, or morphological polymorphism. Different morphologies were collected in similar habitats and environmental conditions, suggesting that phenotypic plasticity is not the solely responsible for the observed morphological variation. Genetic segregation was detected among three of the four localities where we found *P. variabilis*: Mayotte Island, the Gulf of Aden, and the Red Sea. Despite the sample size is admittedly small for each locality, colonies from Mayotte Island and Madagascar were exclusively *E. orpheensis*-like (Figs Figs. 1a-b) whereas the ones from the Gulf Aden were *E. aspera*-like (Fig. 1e). This pattern may partly suggest the occurrence of geographic variation among the analysed colonies, but morphologies of the Red Sea population exhibited both morphs and were intermediate between those from Mayotte and the Gulf Aden (Figs Figs. 1c-d, f-h). These considerations suggest that genetic factors, perhaps related for example to calcification or development, are at least partially responsible of the encountered pattern of morphological polymorphism.

Paraechinophyllia variabilis exhibits a remarkable morphological variation at the colony and corallite level. Analogous cases of extreme intraspecific morphological variation were previously discussed in other genera of corals, including, for example, *Cycloseris* (Gittenberger and Hoeksema, 2006), *Stylophora* (Veron and Pichon, 1976; Flot et al., 2011), *Pocillopora* (Veron and Pichon, 1976; Pinzón et al., 2013), *Montastraea* (Budd et al., 2012b), and *Favia* (Carlson and Budd, 2002). On the one hand, colonies of *P. variabilis* can be encrusting, massive, and seldom foliaceous (Fig. 1). Nevertheless, colony shape and growth form can be plastic features affected by homoplasy and influenced by habitat, and therefore they are now recognised as uninformative characters in defining coral species (Flot et al., 2011; Hoeksema and Waheed, 2014; Huang et al., 2014b; Arrigoni et al., 2016a; Addamo et al., 2016). On the other hand, corallite dimension and protrusion considerable varied considerably among the analysed specimens: some colonies showed large and protruding corallites (Figs Figs. 2A-B and 3A-B) similar to *E. orpheensis*, while other specimens (Figs Figs. 2G-H and 3C-D) displayed smaller and less exsert corallites like *E. aspera*. The variability of these two corallite features in *E. aspera* and *E. orpheensis* was described and illustrated by Arrigoni et al. (2016c). The two morphological characters were greatly variable at both inter- and intracolony levels and a continuum morphological range of morphological variation was detected between the two species. Moreover,

E. aspera and *E. orpheensis* were genetically indistinguishable and the authors suggested that the two species should be considered as a single entity. Therefore, the large intraspecific morphological variation of *P. variabilis* is not surprising *per se* and it is indeed similar to what [was](#) already found in *E. aspera* and *E. orpheensis* (Arrigoni et al., 2016c).

Paraechinophyllia variabilis shows the same overall microstructural pattern as ~~found in~~ *Echinophyllia* and *Oxypora*: RAD's in lower order septa or in more robust morphotypes are arranged perpendicularly to the septal plane, whereas RAD's in higher order septa or septa of less robust morphotypes form ~~of a~~ straight or wavy mid-septal zone (Figs. 5-7). The surface of skeletal elements (especially newly growing septa) shows microtuberculate texture that corresponds to slender bundles of fibres that form thickening deposits (TD's). The latter skeletal character seems to be distinct to lobophylliids, similarly ~~to other family-specific characters, for example, as e.g.,~~ shingled TD's ~~are~~ typical of acroporids, or irregular meshwork of fiber bundles ~~is~~ typical of micrabaciids (Janiszewska et al. 2011; Stolarski et al. 2011, 2016;). A lack of microstructural characters that would separate *Paraechinophyllia* from closely related taxa suggests that the fine-scale biomineralisation activity was not affected by the processes that lead to molecular divergence.

Conclusions

~~Some~~ species are cryptic or hidden ~~to from~~ human perception largely due to the lack of conspicuous differences in outward appearance. The uptake of DNA sequencing techniques has resulted in the discovery of novel cryptic taxa that constitute an important fraction of contemporary biodiversity (Mora et al., 2011; Scheffers et al., 2012). However, the practice of describ~~ing~~ novel taxa based on DNA sequence information is still poorly adopted and various criticisms ~~are invoked~~ [have arisen](#) (DeSalle et al., 2005; Vogler and Monaghan, 2007). We strongly believe that the absence of diagnostic morphological characters should not preclude the formal description of a new taxon when molecular data are robust and summarised in reproducible protocols (Fišer et al., 2018), such as in the case of *PC. variabilis*. This is noteworthy in a time of ~~global biodiversity crisis~~ [and frequent high number of](#) extinction episodes (Barnosky et al., 2011). Moreover, in several cases further and detailed morphological and ecological analyses with the inclusion of additional or novel characters have recovered diagnostic traits for the identification of cryptic taxa (Sáez and Lozano, 2005). Finally, the establish~~ment~~ [ing](#) of standard protocols to retrieve molecular diagnostic nucleotides from DNA sequences, such as the ~~employed~~ [CAOS software employed here](#) (Sarkar et al., 2008; Jörgen and Schrödl, 2014), have introduced reliable and consistent procedures for species descriptions (Cook et al., 2010; Jörgen and Schrödl, 2013).

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Tables and Figures

Table 1 List of species, voucher, molecular clade to which they belong, collection locality, and accession numbers of the COI, 12S, ATP6-NAD4, NAD3-NAD5, histone H3, and ITS included in the molecular phylogeny. Newly-obtained sequences are in bold

Table 2 Statistics for each locus used in the analysis. Number of sites (S), Number of variable sites (%) (SV), Number of parsimony-informative sites (%) (SPI), Haplotype diversity (HD), Nucleotide diversity (ND), GC-content (GC)

Table 3 Pairwise comparisons of genetic distance values (p-distance) within and between genera of Lobophylliidae based on the combined dataset (COI, 12S, ATP6-NAD4, NAD3-NAD5, histone H3, ITS). Intergeneric pairwise comparisons of genetic distance are in bold, intrageneric genetic distances are indicated along the diagonal, and standard deviations are reported either in brackets or on the upper right hand portions for each set of comparisons. n.c. = not calculable

Table 4 Estimated divergence times (Ma) with 95% highest posterior density (HPD) distribution for genera of Lobophylliidae and the main nodes of the molecular phylogeny shown in Fig. 4. The posterior probabilities (pp) $\geq$ 0.70 obtained in BEAST are reported

Fig. 1. *Paraechinophyllia variabilis* gen. et sp. nov. *in situ*. (a) Holotype, MNHN-IK-2014-250, at Mayotte Island. (b) Paratype, MNHN-IK-2014-251, at Mayotte Island. (c) KAUST SA0922, at Magna, Saudi Arabia. (d) KAUST SA0021, at Al Lith, Saudi Arabia. (e) Paratype, MNHN-IK-2014-247, at Al Mukallah (same as in 2d), Yemen. (f) KAUST SA0794, at Jaz'air Silah, Saudi Arabia. (g) KAUST SA0944, at Magna, Saudi Arabia. (h) KAUST SA1023, at Magna, Saudi Arabia.

Fig. 2. *Paraechinophyllia variabilis* gen. et sp. nov. corallite macromorphology. (a) Holotype, MNHN-IK-2014-250 (same as in 1a). (b) Paratype, MNHN-IK-2014-251 (same as in 1b). (c) KAUST SA0922 (same as in 1c). (d) KAUST SA0021 (same as in 1d). (e) Paratype, MNHN-IK-2014-247 (same as in 1e). (f) KAUST SA0794 (same as in 1f). (g) KAUST SA0944 (same as in 1g). (h) KAUST SA1023 (same as in 1h).

Fig. 3. Type material *Paraechinophyllia variabilis* gen. et sp. nov. (a) Holotype, MNHN-IK-2014-250 (same as in 1a and 2a). (b) Paratype, MNHN-IK-2014-251 (same as in 1b and 2b). (c) Paratype, MNHN-IK-2014-252. (d) Paratype, MNHN-IK-2014-247 (same as in 1e and 2e).

Fig. 4. Phylogeny reconstruction of the family Lobophylliidae, showing the position of *Paraechinophyllia variabilis* gen. et sp. nov. (clade K). (a) Multi-locus ~~fossiltime~~-calibrated phylogeny reconstruction inferred from the

concatenated dataset (COI, 12S, ATP6-NAD4, NAD3-NAD5, histone H3, and ITS, 3965 bp), analysed using BEAST. The violet circle I marks the node that was time-constrained with fossil (the stratigraphically oldest fossil occurrence of *Lobophyllia*, 19-31.3 Mya) as described in the text. Node values are posterior probabilities (≥ 0.7) and violet bars display the 95% highest posterior density (HPD) interval of node ages. (b) Strict consensus of 19 maximum parsimony trees based on 46 morphological characters, analysed using TNT. Values above nodes are Bremer decay index (≥ 2) and below nodes are maximum parsimony bootstrap (≥ 50). Clades from A to J are labelled and coloured according to Arrigoni et al. (2014a) and Huang et al. (2016).

Fig. 5. Microstructural characteristics of *Paraechinophyllia variabilis* gen. et sp. nov. robust morphotype MNHN IK-2014-250 (a-c) and less robust MNHN IK-2014-252 (d-f) in direct comparison to *Oxypora* (*O. lacera*, g-i) and *Echinophyllia* (*E. aspera*, j-m); optical transmitted light microscopy (insets in right-upper corners of a,d,g,j show low magnification images of sections). In more robust coralla of MNHN IK-2014-250 lower order septa show clusters of Rapid Accretion Deposits (RAD's) with projections extending toward the septal faces (red outlined white arrows in b). Such lateral projections of RAD's can also be observed in lower order septa of less robust *O. lacera* and *E. aspera* (h, k). Septa of less robust MNHN IK-2014-252 and higher order septa of *O. lacera* and *E. aspera* have RAD's frequently in a form of straight or wavy mid-septal zone (red arrows, see e, h, j, l). Sectioned septal teeth show elliptical clusters of RAD's (dashed red outline in k). Thickening deposits (TD's) consists of well delineated, slender (typically longer than 100 μm) bundles of fibers, ca. 10 μm in diameter (c, i, m, polarized light). Thickness of fibre boundless is consistent with diameter of microtuberculate texture on septal faces (compare Fig. 6i, 7g).

Fig. 6. Microstructural characteristics of robust morphotype of *Paraechinophyllia variabilis* gen. et sp. nov. (MNHN IK-2014-250) in SEM: natural surfaces (a, d, f, i) and polished and delicately etched sections (b, c, e, g, h, j). Distinct tooth show several RAD's regions (d, f, white arrows). Septal faces (especially in distal region) are covered with microtuberculate texture ca. 10 μm in diameter (i). Rapid Accretion Deposits (RAD's) in more robust septa (also within well differentiated septal teeth) form projections extending toward the septal faces (red outlined arrows in e), however between such regions RAD's typically form continuous mid-septal line (red arrow in b). TD's show regular growth banding (red arrows in j). Mid-septal zone in longitudinal section of septum (c, h).

Fig. 7. Microstructural characteristics of less robust morphotype of *Paraechinophyllia variabilis* gen. et sp. nov. (MNHN IK-2014-252) in SEM: natural surfaces (a, c, e, g) and polished and delicately etched sections (b, d, f, h). Distinct tooth on lower cycle septa show several RAD's regions (d, white arrows). Septal faces are covered with microtuberculate texture ca. 10 μm in diameter (e, g). Rapid Accretion Deposits (RAD's) in less robust septa form continuous mid-septal line (red arrows in e, f), whereas in slightly more robust ones they form clusters with projections extending toward the septal faces as in robust morphotypes of *P. variabilis* (red outlined arrows in d). TD's show regular growth banding (red arrows in h).

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Nexus data file containing the aligned molecular data matrix (COI, 12S, ATP6-NAD3, NAD4-NAD5, histone H3, and ITS) used in this study.

Data S2. Output file of PartitonFinder to identify the best partition scheme and nucleotide substitution models.

Data S3. Nexus data file containing the aligned morphological data matrix (46 characters) used in this study.

Figure S1. Bayesian phylogeny reconstruction of the family Lobophylliidae for each individual gene dataset (COI, 12S, ATP6-NAD3, NAD4-NAD5, histone H3, and ITS). Numbers above branches indicate nodal support by means of Bayesian posterior probabilities (> 0.8), Maximum Likelihood bootstrap support (> 0.7), and Maximum Parsimony bootstrap support (> 50).

Figure S2. Phylogenetic character mapping of the 46 analysed morphological characters on the molecular phylogeny reconstruction of Lobophylliidae. Ancestral states have been reconstructed using maximum parsimony and calculated using MESQUITE. Character states are according to Huang et al. (2016), see Appendices 1 and 2.

Figure S3. Microstructural characteristics of robust morphotype of *Echinophyllia orpheensis* (morphologically very similar to *E. aspera*) in optical transmitted light microscopy and SEM images. Lower order septa in regions of teeth development show larger clusters of Rapid Accretion Deposits (RAD's) with projections extending toward the septal faces (red outlined white arrows in b); SEM images of these clusters on etched sections in e, f. Higher order septa show RAD's locally arranged as continuous mid-septal zone. Thickening deposits (TD's) consists of well delineated, slender (typically longer than 100 μm) bundles of fibers, ca. 10 μm in diameter (d, polarized light).

Table S1. Pairwise comparisons of genetic distance values (p-distance) within and between genera of Lobophylliidae based on the individual gene datasets (COI, 12S, ATP6-NAD4, NAD3-NAD5, histone H3, ITS). Intergeneric pairwise comparisons of genetic distance are in bold, intrageneric genetic distances are indicated along the diagonal, and standard deviations are reported either in brackets or on the upper right hand portions for each set of comparisons. n.c. = not calculable

Appendix 1. List of morphological characters, character states, and parsimony model used for the morphological phylogenetic analysis.

Appendix 2a. Morphological character-state matrix based on characters presented in Appendix 1 (characters 1-23). * new data provided in this study; ? missing data; - not applicable.

Appendix 2b. Morphological character-state matrix based on characters presented in Appendix 1 (characters 24-46). ? missing data; - not applicable.

Table 1
List of species, voucher, molecular clade to which they belong, collection locality, and accession numbers of the COI, 12S, ATP6-NAD4, NAD3-NAD5, Histone H3, and ITS included in the molecular phylogeny. Newly-obtained sequences are in bold

Voucher	Other	Genus	Species	Molecular clade	Locality	COI	12S	ATP6-NAD4	NAD3-NAD5	Histone H3	ITS
MNH N-IK-2014-247	M U1 32	Cryptophyllia Paraechinia ophyllia	variabilis	K	Gulf of Aden, Yemen	MF426 191XX XX	MF42 6177X XX	MF42 6037X XX	MF53 9828X XX	MF426 114XX X	MF426 095XX X
MNH N-IK-2014-252	M U1 65	Paraechino phyllia Cryptophyllia	variabilis	K	Gulf of Aden, Yemen	MF426 192XX X	MF42 6178X XX	MF42 6038X XX	MF53 9829X XX	MF426 115XX X	MF426 096XX X
MNH N-IK-2014-251	M Y0 50	Paraechino phyllia Cryptophyllia	variabilis	K	Mayotte Island	MF426 193XX X	MF42 6179X XX	MF42 6039X XX	MF53 9830X XX	MF426 116XX X	MF426 097XX X
MNH N-IK-2014-250	M Y2 36	Paraechino phyllia Cryptophyllia	variabilis	K	Mayotte Island	MF426 194XX X	MF42 6180X XX	MF42 6040X XX	MF53 9831X XX	MF426 117XX X	MF426 098XX X
KAU ST SA0021		Paraechino phyllia Cryptophyllia	variabilis	K	Red Sea, Saudi Arabia	MF426 195XX X	MF42 6181X XX	MF42 6041X XX	MF53 9832X XX	MF426 118XX X	MF426 099XX X
KAU ST SA1023		Paraechino phyllia Cryptophyllia	variabilis	K	Red Sea, Saudi Arabia	MF426 199XX X	MF42 6185X XX	MF42 6045X XX	MF53 9836X XX	MF426 122XX X	MF426 103XX X
KAU ST SA0794		Paraechino phyllia Cryptophyllia	variabilis	K	Red Sea, Saudi Arabia	MF426 196XX X	MF42 6182X XX	MF42 6042X XX	MF53 9833X XX	MF426 119XX X	MF426 100XX X
KAU ST SA0922		Paraechino phyllia Cryptophyllia	variabilis	K	Red Sea, Saudi Arabia	MF426 197XX X	MF42 6183X XX	MF42 6043X XX	MF53 9834X XX	MF426 120XX X	MF426 101XX X
KAU ST SA0944		Paraechino phyllia Cryptophyllia	variabilis	K	Red Sea, Saudi Arabia	MF426 198XX X	MF42 6184X XX	MF42 6044X XX	MF53 9835X XX	MF426 121XX X	MF426 102XX X
MD2 39		Paraechino phyllia Cryptophyllia	variabilis	K	Madagascar	MF426 200XX X	MF42 6186X XX	MF42 6046X XX	MF53 9837X XX	MF426 123XX X	MF426 104XX X
MD2 40		Paraechino phyllia Cryptophyllia	variabilis	K	Madagascar	MF426 201XX X	MF42 6187X XX	MF42 6047X XX	MF53 9838X XX	MF426 124XX X	MF426 105XX X
MD2 41		Paraechino phyllia Cryptophyllia	variabilis	K	Madagascar	MF426 202XX X	MF42 6188X XX	MF42 6048X XX	MF53 9839X XX	MF426 125XX X	MF426 106XX X
MD2 65		Paraechino phyllia Cryptophyllia	variabilis	K	Madagascar	MF426 203XX X	MF42 6189X XX	MF42 6049X XX	MF53 9840X XX	MF426 126XX X	MF426 107XX X
AM MH0		<i>Micromussa</i>	<i>lordhowensis</i>	A	Australia	LN875 913	MF42 6152X	MF42 6080X	MF53 9870X	LN875 992	LN876 069

42							XX	XX	XX		
UNI											
MIB					French		MF42	MF42	MF53		
GA15					Polyne	LN875	6151X	6079X	9869X	LN875	LN876
0	<i>Micromussa</i>	<i>pacifica</i>	A	sia	888		XX	XX	XX	966	044
				Gulf							
				of							
MNH				Aden,			MF42	MF42	MF53		
N IK-				Yeme	LN875		6153X	6081X	9871X	LN875	LN876
2012-	<i>Micromussa</i>	<i>indiana</i>	A	n	886		XX	XX	XX	963	042
16046											
SMB											
L							MF42	MF42	MF53		
Cni-		<i>amakusen</i>			LN875		6150X	6078X	9868X	LN875	LN876
11060	<i>Micromussa</i>	<i>sis</i>	A	Japan	880		XX	XX	XX	956	036
RMN							MF42	MF42	MF53		
H		<i>multipunct</i>		Malay	LN875		6149X	6077X	9867X	LN875	LN876
40077	<i>Micromussa</i>	<i>ata</i>	A	sia	898		XX	XX	XX	976	054
							MF42	MF42	MF53		
AM	<i>Homophylli</i>	<i>bowerban</i>		Austra	LN875		6147X	6062X	9853X	LN875	LN876
4629	<i>a</i>	<i>ki</i>	B	lia	865		XX	XX	XX	940	021
							MF42	MF42	MF53		
AM	<i>Homophylli</i>			Austra	LN875		6148X	6063X	9854X	LN875	LN876
4631	<i>a</i>	<i>australis</i>	B	lia	854		XX	XX	XX	929	010
				Gulf							
UNI				of			MF42	MF42	MF53		
MIB				Aden,			6157X	6085X	9875X	LK022	HE648
MU1	<i>Sclerophylli</i>	<i>maxima</i>	C	Yeme	HE654		XX	XX	XX	407	543
61	<i>a</i>			n	627						
KAU				Red			MF42	MF42	MF53		
ST				Sea,			6158X	6086X	9876X	LM993	LM993
SA08	<i>Sclerophylli</i>	<i>margaritic</i>		Saudi	LM993		XX	XX	XX	310	347
80	<i>a</i>	<i>ola</i>	C	Arabia	330						
KAU							MF426	MF42	MF42	MF53	MF426
ST							204XX	6175X	6092X	9882X	127XX
TAU	<i>Moseleya</i>	<i>latistellata</i>	D	lia			X	XX	XX	X	108XX
263											
UNI							MF42	MF42	MF53		
MIB							6133X	6050X	9841X	LK022	HF954
DJ28	<i>Acanthastre</i>	<i>echinata</i>	E	Djibou	HF954		XX	XX	XX	408	301
8	<i>a</i>			ti	214						
IRD				New			MF42	MF42	MF53		
HS30	<i>Acanthastre</i>	<i>hemprichi</i>		Caled	HF954		6134X	6051X	9842X	LK022	HF954
65	<i>a</i>	<i>i</i>	E	onia	221		XX	XX	XX	411	309
IRD				New			MF42	MF42	MF53		
HS31	<i>Acanthastre</i>	<i>rotundoflo</i>		Caled	HF954		6135X	6052X	9843X	LN999	HF954
66	<i>a</i>	<i>ra</i>	E	onia	216		XX	XX	XX	917	303
IRD				New			MF42	MF42	MF53		
HS32	<i>Acanthastre</i>	<i>subechina</i>		Caled	HF954		6136X	6053X	9844X	LK022	HF954
28	<i>a</i>	<i>ta</i>	E	onia	219		XX	XX	XX	409	304
IRD				New			MF42	MF42	MF53		
HS32	<i>Acanthastre</i>	<i>pachysept</i>		Caled	LN999		6137X	6054X	9845X	LN999	LN999
54	<i>a</i>	<i>a</i>	E	onia	910		XX	XX	XX	916	928
							MF42	MF42	MF53		
AM	<i>Echinophyll</i>	<i>orpheensi</i>		Austra	LN999		6140X	6057X	9848X	LN999	LN999
6813	<i>ia</i>	<i>s</i>	F	lia	911		XX	XX	XX	918	930
UNI											
MIB							MF42	MF42	MF53		
GA07	<i>Echinophyll</i>			French	HF954		6142X	6059X	9850X	LN999	HF954
1	<i>ia</i>	<i>tarae</i>	F	Polyne	229		XX	XX	XX	919	317
UNI				Gulf			MF42		MF53		
MIB	<i>Echinophyll</i>			of	HE654		6141X	MF42	9849X	LK022	HE648
BA00	<i>ia</i>	<i>aspera</i>	F	Aden,	648		XX	6058	XX	412	564

Cladistics

HS33	<i>nsis</i>		Caledonia	207XX	6174X	6091X	9881X	130XX	111XX
58			Papua	X	XX	XX	XX	X	X
UNI			New Guinea		MF42	MF42	MF53		
PFB0	<i>Lobophyllia</i>	<i>vitiensis</i>	a	LK022 355	6164X	6069X	9859X	LK022 394.	LK022 373
52			Papua		XX	XX	XX		
UNI			New Guinea	HF954 248	MF42	MF42	MF53	LN999 923	HF954 335
PFB1	<i>Lobophyllia</i>	<i>flabelliformis</i>	a		6165X	6070X	9860X		
03			Papua		XX	XX	XX		
UNI			New Guinea	HF954 263	MF42	MF42	MF53	LK022 424	HF954 350
PFB1	<i>Lobophyllia</i>	<i>agaricia</i>	a		6166X	6071X	9861X		
04			Papua		XX	XX	XX		
UNI			New Guinea	HF954 250	MF42	MF42	MF53	LK022 423	HF954 337
PFB1	<i>Lobophyllia</i>	<i>robusta</i>	a		6167X	6072X	9862X		
83			Papua		XX	XX	XX		
UNI			New Guinea		MF426	MF42	MF42	MF53	MF426
PFB7	<i>Lobophyllia</i>	<i>hassii</i>	a		208XX	6172X	6089X	9879X	131XX
83			Papua		X	XX	XX	X	X
UNI			New Guinea		MF426	MF42	MF42	MF53	MF426
PFB7	<i>Lobophyllia</i>	<i>hataii</i>	a		209XX	6173X	6090X	9880X	132XX
97			Papua		X	XX	XX	X	X
KAU			Red Sea,						
ST			Saudi Arabia	LN999 913	MF42	MF42	MF53	LN999 922	LN999 932
SA03	<i>Lobophyllia</i>	<i>erythraea</i>			6168X	6073X	9863X		
65			Red Sea,		XX	XX	XX		
KAU			Saudi Arabia	LN999 912	MF42	MF42	MF53	LN999 920	LN999 931
ST	<i>Lobophyllia</i>	<i>corymbosa</i>			6169X	6074X	9864X		
SA03			Red Sea,		XX	XX	XX		
77			Saudi Arabia	LN999 914	MF42	MF42	MF53	LN999 924	LN999 933
KAU	<i>Lobophyllia</i>	<i>hemprichii</i>			6170X	6075X	9865X		
ST			Red Sea,		XX	XX	XX		
SA04			Saudi Arabia	LN999 915	MF42	MF42	MF53	LN999 924	LN999 933
51	<i>Lobophyllia</i>	<i>i</i>			6170X	6075X	9865X		
AM			Red Sea,		XX	XX	XX		
WIL0	<i>Australophyllia</i>	<i>wilsoni</i>	Australia	LN875 915	6138X	6055X	9846X	LN875 994	LN876 071
2				AP008	XX	XX	XX	HQ203	HQ203
	<i>Orbicella</i>	<i>annularis</i>	outgroup	974	974	974	974	600	367

Table 2
Primer information and gene statistics for each locus used in the analysis. Number of sites (S), Number of variable sites (%) (SV), Number of parsimony-informative sites (%) (SPI), Haplotype diversity (HD), Nucleotide diversity (ND), GC-content (GC), ~~best fit model of molecular evolution (M)~~

Locus	Primers	Reference	S	SV	SPI	HD	ND	GC
COI	MCOIF- MCOIR	Fukami et al. (2004)	628	65 (10.3%)	40 (6.3%)	0.95 ± 0.02	0.02 ± 0.01	37.1
12S	ANTMT12SF- ANTMT12SR	Chen and Yu (2000)	694	55 (7.9%)	37 (5.3%)	0.94 ± 0.01	0.02 ± 0.01	34.1
ATP6- NAD4	RSF6-RSR6	Lin et al. (2011)	825	131 (15.8%)	104 (12.6%)	0.94 ± 0.01	0.02 ± 0.01	33.7
NAD3- NAD5	RSF13-RSR13	Lin et al. (2011)	844	57 (6.7%)	35 (4.1%)	0.93 ± 0.01	0.01 ± 0.01	31.3
Histone H3	H3F-H3R	Colgan et al. (1998)	317	75 (23.6%)	70 (22.1%)	0.89 ± 0.03	0.05 ± 0.02	52.5
ITS	A18S-ITS4	White et al. (1990), Takabayashi et al. (1998)	652	255 (39.7%)	209 (32.2%)	0.99 ± 0.01	0.09 ± 0.03	56.2

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Table 3

Pairwise comparisons of genetic distance values (p-distance) within and between genera of Lobophylliidae based on the combined dataset (COI, 12S, ATP6-NAD4, NAD3-NAD5, Histone H3, ITS). Intergeneric pairwise comparisons of genetic distance are in bold, intrageneric genetic distances are indicated along the diagonal, and standard deviations are reported either in brackets or on the upper right hand portions for each set of comparisons. n.c. = not calculable

	<i>Micromu ssa</i>	<i>Homo phyllia</i>	<i>Sclero phyllia</i>	<i>Mos eleya</i>	<i>Acanth astrea</i>	<i>Echino phyllia</i>	<i>Oxyppo ra</i>	<i>Cynarin a</i>	<i>Loboph yllia</i> <i>Australophyllia</i>	<i>Austral ophyllia</i>	<i>Paraec hinophy llia</i> <i>Cryptophyllia</i>
<i>Micromu ssa</i>	0.57 (0.08)	0.25	0.28	0.30	0.25	0.30	0.37	0.28	0.30	0.21	0.28
<i>Homoph yllia</i>	2.14	0.71 (0.14)	0.29	0.31	0.28	0.27	0.36	0.28	0.29	0.22	0.29
<i>Scleroph yllia</i>	4.59	4.63	0.03 (0.03)	0.24	0.25	0.25	0.31	0.22	0.21	0.29	0.24
<i>Moseley a</i>	4.54	4.54	2.72	n.c.	0.28	0.24	0.27	0.25	0.25	0.33	0.20
<i>Acanthas trea</i>	4.41	4.42	3.46	3.10	0.37 (0.07)	0.27	0.28	0.26	0.25	0.29	0.25
<i>Echinop hyllia</i>	5.28	5.27	3.41	2.51	3.53	0.41 (0.06)	0.26	0.26	0.23	0.30	0.24
<i>Oxyppora</i>	6.13	6.25	4.43	3.26	4.02	2.89	0.27 (0.05)	0.31	0.25	0.39	0.31
<i>Cynarina</i>	4.66	4.69	2.26	2.44	3.05	3.12	4.03	n.c.	0.21	0.31	0.19
<i>Lobophy llia</i>	4.87	4.90	2.93	2.58	3.01	2.66	3.63	2.41	0.58 (0.07)	0.31	0.22
<i>Australo phyllia</i>	2.01	2.10	4.40	4.42	4.44	5.11	6.06	4.54	4.75	n.c.	0.29
<i>Paraechi nophylli a</i> <i>Cryptophyllia</i>	4.42	4.63	2.71	2.35	3.27	2.68	3.45	2.77	2.63	4.44	0.10 (0.03)

Table 4
Estimated divergence times (Ma) with 95% highest posterior density (HPD) distribution for genera of
Lobophylliidae and for some main nodes of the molecular phylogeny shown in Fig. 4. The posterior probabilities
(pp) ≥ 0.70 obtained in BEAST are reported

Taxon (Clade)	Node	Age in Ma (95% HPD)	pp
Paraechinophyllia Cryptophyllia (K)	II	3.29-2 (1.2-6.45-3-16.4)	1
Echinophyllia (F)	III	5.315-1 (2.3-9.58-3-23.5)	1
Oxypora (G)	IV	3.18-8 (1.6-5.34-9-15.2)	1
Echinophyllia/Oxypora (F vs. G)	V	13.731-4 (6.3-22.912-7-50.3)	1
Paraechinophyllia Cryptophyllia vs.	VI	21.545-4 (11.6-33.725-71.1)	1
Echinophyllia/Oxypora (K vs. F-G)			
Micromussa (A)	VII	8.221-1 (3.4-14.810-7-32.5)	1
Homophyllia (B)	VIII	4.712-8 (1.9-9.76-5-24.4)	1
Australophyllia vs.	IX	20.345-2 (11.2-33.626-4-66.8)	1
Micromussa/Homophyllia (J vs. A-B)			
Acanthastrea (E)	X	412-4 (1.5-8.16-5-26.1)	1
Sclerophyllia (C)	XI	0.72-1 (0.1-2.10-2-5.4)	1
Sclerophyllia vs. Moseleya (C vs. D)	XII	21.242-8 (12.4-32.118-9-72.5)	1
Lobophyllia vs. Cynarina (I vs. H)	XIII	8.446-4 (5.8-13.426-9-67.1)	1

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Fig. 5. Microstructural characteristics of *Paraechinophyllia variabilis* gen. et sp. nov. robust morphotype MNHN IK-2014-250 (a-c) and less robust MNHN IK-2014-252 (d-f) in direct comparison to *Oxyrpora* (*O. lacera*, g-i) and *Echinophyllia* (*E. aspera*, j-m); optical transmitted light microscopy (insets in right-upper corners of a,d,g,j show low magnification images of sections). In more robust coralla of MNHN IK-2014-250 lower order septa show clusters of Rapid Accretion Deposits (RAD's) with projections extending toward the septal faces (red outlined white arrows in b). Such lateral projections of RAD's can also be observed in lower order septa of less robust *O. lacera* and *E. aspera* (h, k). Septa of less robust MNHN IK-2014-252 and higher order septa of *O. lacera* and *E. aspera* have RAD's frequently in a form of straight or wavy mid-septal zone (red arrows, see e, h, j, l). Sectioned septal teeth show elliptical clusters of RAD's (dashed red outline in k). Thickening deposits (TD's) consists of well delineated, slender (typically longer than 100 μm) bundles of fibers, ca. 10 μm in diameter (c, i, m, polarized light). Thickness of fibre bundles is consistent with diameter of microtuberculate texture on septal faces (compare Fig. 6i, 7g).

292x280mm (300 x 300 DPI)

Fig. 6. Microstructural characteristics of robust morphotype of *Paraechinophyllia variabilis* gen. et sp. nov. (MNHN IK-2014-250) in SEM: natural surfaces (a, d, f, i) and polished and delicately etched sections (b, c, e, g, h, j). Distinct tooth show several RAD's regions (d, f, white arrows). Septal faces (especially in distal region) are covered with microtuberculate texture ca. 10 μm in diameter (i). Rapid Accretion Deposits (RAD's) in more robust septa (also within well differentiated septal teeth) form projections extending toward the septal faces (red outlined arrows in e), however between such regions RAD's typically form continuous mid-septal line (red arrow in b). TD's show regular growth banding (red arrows in j). Mid-septal zone in longitudinal section of septum (c, h).

290x260mm (300 x 300 DPI)

Fig. 7. Microstructural characteristics of less robust morphotype of *Paraechinophyllia variabilis* gen. et sp. nov. (MNHN IK-2014-252) in SEM: natural surfaces (a, c, e, g) and polished and delicately etched sections (b, d, f, h). Distinct tooth on lower cycle septa show several RAD's regions (d, white arrows). Septal faces are covered with microtuberculate texture ca. 10 μ m in diameter (e, g). Rapid Accretion Deposits (RAD's) in less robust septa form continuous mid-septal line (red arrows in e, f), whereas in slightly more robust ones they form clusters with projections extending toward the septal faces as in robust morphotypes of *P. variabilis* (red outlined arrows in d). TD's show regular growth banding (red arrows in h).

193x260mm (300 x 300 DPI)