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Re-discovery of the type material of *Leptoseris fragilis* (Cnidaria, Anthozoa, Scleractinia) from the upper mesophotic in La Réunion, a taxonomic puzzle

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"*We feel that some of the references to* L. fragilis *in literature cannot be correct*" – Scheer & Pillai (1983)

Significant advances in the revision of the classification of scleractinian corals were made in the last years due to the use of an integrated systematics approach to resolve species boundaries and phylogenetic relationships (Kitahara *et al.* 2016). They are based on, yet not limited to, morphological and molecular analyses of specimens from multiple localities and the study of the type and historical specimens from museum collections (e.g. Benzoni *et al.* 2010, 2016). However, some coral lineages are still under study and remain unrevised taxonomically. The Agariciidae Gray, 1847 is one of those lineages. Including zooxanthellate and azooxanthellate taxa occurring from shallow to deep coral ecosystems worldwide (Veron 2000), Agariciidae are a typical component of shallow and Mesophotic Coral Ecosystems (MCEs) (Loya *et al.* 2019). In particular, agariciids of the genus *Leptoseris* Milne Edwards & Haime, 1849 are abundant, diverse and can dominate the benthic assemblages below 30 m depth in the Indo-Pacific, yet they are seldom identified to species level. In fact, their species boundaries are poorly understood and most observed morphologies *in situ* remain reported as *Leptoseris* spp. (e.g. Tamir *et al.* 2019, Hoarau *et al.* 2021). This uncertainty even remains when specimens are collected. It stems from a classification that is still largely based on morphological characters known to be uninformative and plagued by homoplasy (Kitahara *et al.* 2016).

The few molecular phylogenies of Agariciidae published to date indicate that two of the eight genera currently ascribed to the family, the polytypic *Pavona* Lamarck, 1801 and *Leptoseris*, are polyphyletic and in need of revision (Luck *et al.* 2013, Terraneo *et al.* 2017). In this situation, the type material of the genus type species is the fundamental reference to re-assess the systematics of these taxa and revise them. However, only skeletons were deposited as type material traditionally, and animal tissue for DNA extraction is usually unavailable for older taxa. Hence, molecular analyses are performed on newly collected material matching the type morphology and, ideally, from the type locality or region (e.g. Benzoni *et al.* 2016). In the case of a polyphyletic genus, the molecular lineage including the specimen(s) matching the genus type species morphology maintains the genus name, and the remainder is moved to available or new genera. A real impediment to this process arises if the genus type species morphology is unknown due to its holotype being missing. Such is the case for the holotype of *Leptoseris fragilis* Milne Edwards & Haime 1849, considered lost for over 60 years (Dinesen 1980, Scheer & Pillai 1983). This situation impairs formal revision of an already challenging genus of corals.

M. L. Rousseau collected the material that was later designated as the type of *L. fragilis* from the upper mesophotic in the bay of Saint Denis, north of La Réunion Island (Île Bourbon), SW Indian Ocean, at 46 m ("*25 brasses*") (Rousseau, 1854). The material was deposited at the Museum national d'Histoire naturelle (MNHN) in Paris, France. There, in their original description of the genus *Leptoseris*, Milne-Edwards & Haime (1849) studied and described this material without giving a registration number or an indication of the number of the type specimen(s). They referred to multiple specimens ("*les exemplaires*") in a later description (Milne-Edwards & Haime 1851:134). Subsequently, Rousseau (1854:Pl.29, Figs. 1, 1a-h) published a color illustration in which different specimens of variable size were referred to as *L. fragilis*, namely, a large block of substrate bearing three coralla (1 in Fig. 1a), and five smaller ones around it (1a–e in Fig. 1a). He stated that these five specimens are different life stages of the same species without mentioning a holotype (Rousseau, 1854). Allegedly, J.P. Chevalier (1961) was the last coral taxonomist to see the material. He referred to part of it as the *L. fragilis* "genotype" (Dinesen 1980, Scheer & Pillai 1983). When Dinesen (1980) revised *Leptoseris*, she could not examine what she thought was a holotype and thus did not address the species in her taxonomic treatment. While declaring the holotype lost, she added, "*the specimen in the Paris Museum which is supposed to be the holotype is a* Coscinaraea*, and does*

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not fit the description by Milne-Edwards and Haime" (Dinesen 1980:186). Scheer & Pillai (1983) also referred to four small specimens collected by Rousseau at the type locality as "paratypes", and agreed with Dinesen (1980) that these are *Coscinaraea*, rather than *Leptoseris*. However, a neotype was never designated for this species.

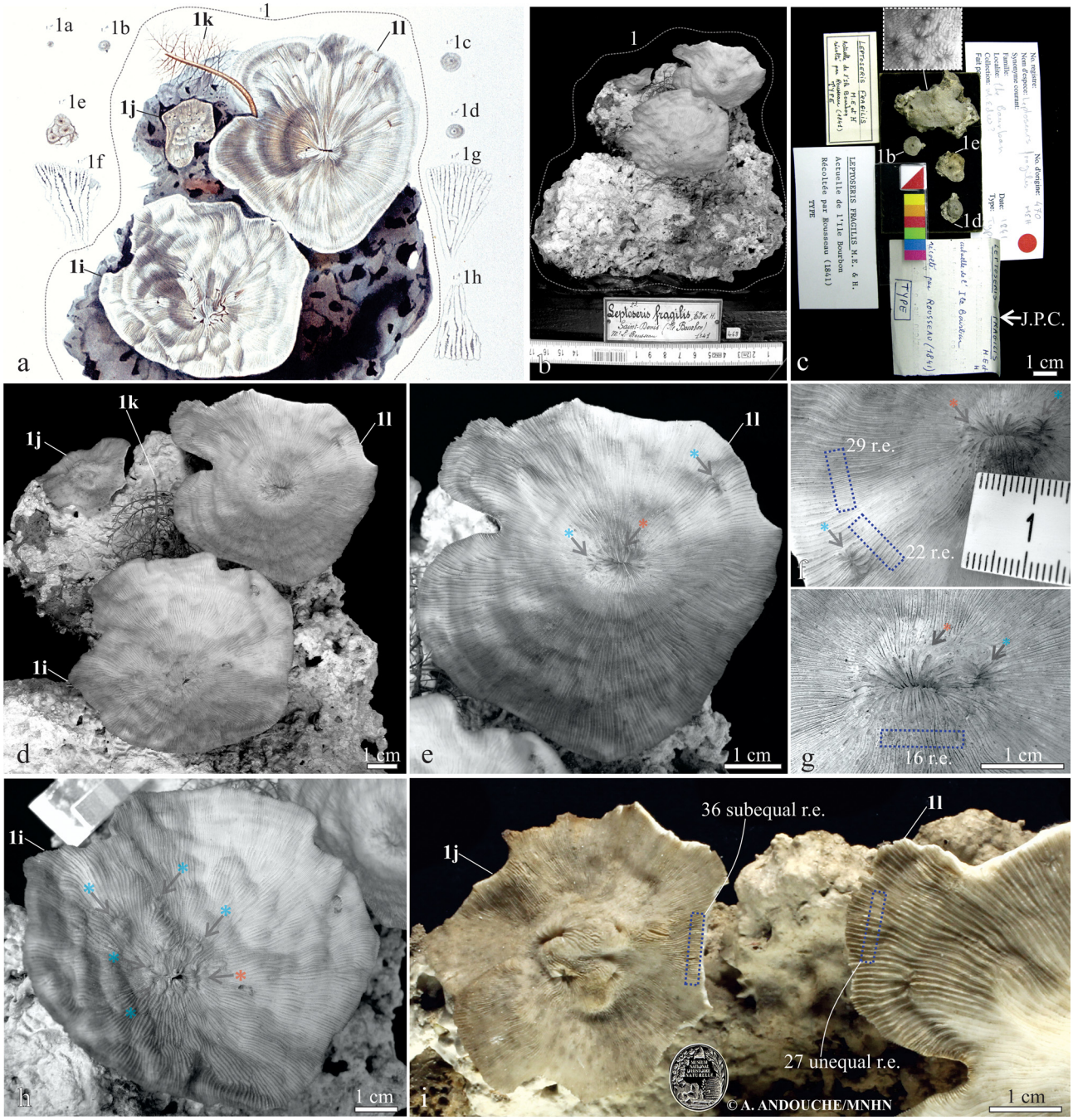

FIGURE 1. The *Leptoseris fragilis* type material puzzle; **a** Plate 29 (*partim*) by Rousseau (1854) in which the largest specimen was appended as 1 (dashed grey line), while drawings of smaller specimens and radial elements (r.e.) details by 1a-e and 1f-h, respectively. The original codes were re-drawn with larger font size for readability. Additionally, the multiple coralla on 1 (d-i) are here appended as 1i-l (in bold); **b** MNHN468 (later re-catalogued as MNHN-IK-2010-494), 1 in a; **c** MNHN470, four *Cycloseris wellsi* specimens bearing the tags of the *L. fragilis* holotype by multiple hands, including Chevalier's (J.P.C.). The smaller are juveniles and correspond to the 1b, 1d-e in a, the largest, absent from b, has the typical species morphology (inset, see Benzoni *et al.*, 2016: Fig. 6); **d** specimen 1 in a and b. The biogenic block is substrate for three *Leptoseris* (1i-j, l) and one antipatharian (1k); **e** specimen 1l; **f** detail of 1l; **g** detail of 1l; **h** specimen 1i; **i** specimens 1j (left) and 1l (right). Grey arrows point to central protocorallite (red *) and secondary corallites (turquoise *); dashed blue rectangles (larger side is 10mm) show the corallum surface where r.e. counts were performed. Pictures b-h, by F. Benzoni (2010), i, © A. Andouche/MNHN (2014).

On 28/09/2010, during a visit to the MNHN collections, I examined four specimens tagged MNHN470 and bearing the holotype label series of *L. fragilis*. They included at least one handwritten by J.P. Chevalier, of whom I have studied the collections and some *cahiers de terrain* and recognize the calligraphy (Fig. 1c). These specimens, housed in the type material compactus, were the ones mentioned by previous authors (Dinesen 1980, Scheer & Pillai 1983). They belong to the Fungiidae *Cycloseris wellsi*, once ascribed to *Coscinaraea* and revised in Benzoni *et al*. (2012). Three of them are juveniles around 1 cm in diameter or less and match the morphology of the smaller specimens figured in Rousseau (1854: Pl.29, Figs. 1b, d–e). In fact, these *C. wellsi* juveniles that disappointed Dinesen, Scheer and Pillai, were indeed part of the original material collected by Rousseau. The fourth is a polystomatous encrusting corallum of the same species apparently missing from the original illustration (Fig. 1c, inset), although similar in outline to specimen 1j in it (Fig. 1a). In the general collection, I unexpectedly found the larger specimen by Rousseau (1854: Pl.29, Fig. 1) bearing the MNHN code 468 on the side of the wooden pedestal on which it is mounted, and the date 1841 on the label, possibly the year of collection (Fig. 1b). The whole specimen comprises a block of biogenic substrate encrusted by the remains of crustose coralline algae and sponges and different corals, namely one antipatharian (1k, Fig. 1d) and three *Leptoseris* colonies (1i, 1j, 1l, Fig. 1d). Among the latter, 1j has different morphology from 1i and 1l. These two larger coralla have similar size, ranging from 8 to 9 cm in diameter, they are cup-shaped with a thick stalk and a larger central protocorallite and smaller scattered secondary corallites, all bearing composite columellae, strongly alternating radial elements (r.e.), the thicker ones being more coarsely ornamented on their upper margin (Figs. 1d–i). Finally, the number of r.e. in 1 cm is variable depending on the position, ranging from 16 close to the protocorallite where they are thicker to 29 away from the corallites where they are thinner (Figs. 1f–g). The third, smaller and disk-shaped *Leptoseris* corallum (Figs. 1d, i) has a protruding central part where the protocorallite and the secondary corallites are clustered. It has a small solid columella, and sub-equal r.e., which are thinner and have smaller and more homogeneous ornamentation than those in 1i and 1l. The number of r.e. in 1 cm is rather conserved when the r.e. are straight, and it is approximately 36 (Figs. 1i). The whole block was later re-coded as MNHN-IK-2010-494 and photographed by A. Andouche (MNHN) in 2014. What happened to it for almost 50 years after J.P. Chevalier last examined it and before its re-discovery in 2010 remains unclear. Likely, following several re-arrangements and re-housing of the MNHN collections in the years, the larger and heavier block might have been separated from the rest and lost track of. The crucial question, however, is which one(s) of these specimens did Milne Edwards & Haime (1849) describe when designating the type material of *L. fragilis* and can be designated as lectotype?

The original *Leptoseris* diagnosis ("*Polypier fixé, a plateau s'élevant en disque subcratériforme, dont le centre est occupé par un grand individu-souche. Gemmation rare. Rayons très-allongés. Calices très-peu circonscrits, mais bien radiés*», Milne Edwards & Haime 1849:72) refers to a crater-like corallum, a larger central protocorallite and rare secondary corallites. This description rules out the encrusting *C. wellsi* specimens and best fits specimens 1i and 1l. Specimen 1j, with a disk-shaped corallum the central part of which protrudes in a bulge where all corallites are clustered (Fig. 1i), is not a close match. Moreover, the same authors (Milne-Edwards & Haime 1851) later described a short and thick stalk and strongly alternating r.e., observed in 1i and 1l but not in 1j which has equal to sub-equal r.e. thinner than in the other two *Leptoseris*. Therefore, considering all these features and the statement "*les exemplaires que nous avons observés, sont larges des 8 centimètres*", I conclude that based on skeletal morphology and corallum size, only specimens 1i and 1l (Fig. 1) fit their description of *L. fragilis*. Henceforth, specimen 1l (Figs. 1a, d–g, i) is the lectotype of *L. fragilis* by present designation.

The actual *in situ* appearance of *L. fragilis* is unknown. However, recent exploration efforts in the MCEs of La Réunion by Hoarau *et al.* (2021) have led to a first description of some exquisite coral dominated benthic assemblages at 83–95 m depth. Based on the syntypes morphology described above and here illustrated, including the cup-shaped corallum in the center of their Fig. 1f, with its obvious protocorallite and the strongly alternating septa, the Hoarau *et al.* (2021) coral seems a good candidate to be the first *in situ* image of *L. fragilis* at type locality in the literature.

Overall, due to the aforementioned history, little is known about *L. fragilis*. For example, this species was not included in Veron's (2000) Corals of the World. However, a large body of scientific literature refers to a lower-mesophotic specialist coral species consistently identified as *L. fragilis* in the Gulf of Aqaba MCEs (e.g. Fricke & Schuhmacher 1983, Fricke 1996, Loya *et al.* 2019, Tamir *et al*. 2019). Scheer & Pillai (1983) disagreed with Dinesen's (1980) lack of treatment of *L. fragilis* due to the unavailability of type material. They thus used the species name to identify two lower mesophotic specimens from Eilat, from 110 and 128 m depth, based on what they could observe in Rousseau's (1854) illustration. The photographs in Fricke (1996: Fig. 14) and Fricke & Schuhmacher (1983: Fig. 15b) show specimens of the same species as in Scheer & Pillai (1983: Figs. 3–6). Several morphological features reported by Scheer & Pillai (1983:68) for the two Gulf of Aqaba specimens, however, are different from those of the *L. fragilis* syntypes. For example, they described the

corallum as a "*rounded thin plate*" rather than cup-shaped, and a central "*hillock*" where the corallites are clustered rather than a central larger protocorallite. Moreover, they defined the columella as "*a solid oval boss*" rather than composed of multiple processes. Finally, the r.e. in the species they examined were "*equal, mostly straight, sometimes flexuous, and between the corallites and over other raised areas very contorted*", and, most interestingly, "*about 35 in 10 mm*". Oddly, the Red Sea obligate mesophotic *Leptoseris* is more similar to the aforementioned unidentified specimen in Rousseau's material (1j in Figs. 1d, e) than to the *L. fragilis* syntypes. An integrated systematic approach is needed to ascertain the identity of this species.

While the actual distribution and phylogenetic relationships of *L. fragilis* remain unclear and unstudied, respectively, the re-discovery and morphological analysis of Rousseau's type material presented here allowed understanding which specimens did Milne-Edwards and Haime base their original description on. As such, the re-description of the *L. fragilis* type material and lectotype designation is a fundamental first step towards integrated systematics studies of shallow and MCEs *Leptoseris*. Moreover, it will hopefully support the revision of the genus allowing sampling material for genetic analyses that matches the actual type material morphology. Finally, the current geographic records of *L. fragilis* can now be verified based on type material morphology. In the future, any revision of *Leptoseris* will be possible only with a focused sampling effort in MCEs.

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