



Shallow-water reef ophiuroids (Echinodermata: Ophiuroidea) of Réunion (Mascarene Islands), with biogeographic considerations

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Abstract

Despite their importance in marine biodiversity, invertebrates are far less studied than vertebrates. Given the current global biodiversity crisis and insufficient taxonomic resources, sustained efforts need to be undertaken to assess species diversity, especially in the highly threatened 'biodiversity hotspots'. Réunion is a young volcanic island lying in the Mascarene Islands (south-western Indian Ocean, SWIO), a marine biodiversity hotspot. A substantial sampling effort was conducted around Réunion Island to document shallow water reef-associated ophiuroid (brittle-stars) diversity, a class recognised as the most diverse among echinoderms. A total of 33 species were documented, increasing the known species richness of the island by 56%. Findings include 15 new records for Réunion, 11 for the Mascarene Islands and 8 for the Indian Ocean. The most diverse family was Ophiocomidae, a family of large, abundant and conspicuous tropical species. Even in this well studied family, a new species was revealed by this survey. Morphological variants together with DNA sequence variations within several species revealed cryptic species. We compared our results with the known fauna of other Mascarene Islands and discuss biogeographic implications for the region.

Key words: brittle-stars, biodiversity, morphotype, cryptic species, dispersal ability, coral reefs

Résumé

Malgré leur importance dans la biodiversité marine, les taxons d'invertébrés sont beaucoup moins étudiés que les vertébrés. Dans le contexte actuel de crise de la biodiversité, un effort taxonomique sur tous les taxons doit être entrepris dans le but d'estimer correctement et rapidement le nombre d'espèces, et ce particulièrement dans les régions fortement menacées, tels que les points chauds de biodiversité. L'île de La Réunion appartient à l'archipel des Mascareignes, point chaud de biodiversité. La classe des Ophiuroidea est reconnue comme la plus diversifiée parmi les échinodermes et représente une composante essentielle des écosystèmes coralliens. Un effort d'échantillonnage particulier a été fait autour de La Réunion afin de documenter la diversité des ophiures associées aux écosystèmes coralliens. Un total de 33 espèces a été trouvé, élevant le nombre d'espèces connues pour La Réunion de 56%. Ces résultats incluent 15 nouvelles observations pour la Réunion, 11 pour l'archipel des Mascareignes et 8 pour l'océan Indien. La famille la plus communément rencontrée dans les eaux Réunionnaises est celle des Ophiocomidae. Celle-ci est diversifiée, commune et remarquable parmi les espèces tropicales. Pourtant même chez cette famille relativement bien connue, ce travail a révélé une nouvelle espèce. De plus, des variations morphologiques ainsi que des variations dans les séquences ADN de certaines espèces ont révélé des complexes d'espèces. Enfin, la structure de la communauté des ophiures de La Réunion a été comparée à celles publiées pour d'autres îles des Mascareignes et les implications biogéographiques pour la région sont discutées.

Mot-clé: ophiure, biodiversité, capacités de dispersion, complexe d'espèces, morphotype, récifs coralliens

Introduction

Rapid global change and loss of species make taxonomic inventories more important now than ever for monitoring biodiversity (Wheeler 1995; Gaston & Blackburn 2000; Corona *et al.* 2011). Coral reefs are among the most threatened habitats, because of both local human impacts (Roberts *et al.* 2002; Hixon 2011) and vulnerability to global climate change and acidification (Hoegh-Guldberg *et al.* 2007). Reef diversity remains poorly understood, and in great need of taxonomic attention. Ophiuroids (or brittle-stars) are a case in point, they are large, abundant, conspicuous, and ecologically important members of coral reef ecosystems, but remain little studied and are poorly known at most localities.

Réunion together with Mauritius and Rodrigues, forms the Mascarene Islands in the south-western Indian Ocean (SWIO), one of the 10 identified marine biodiversity hotspots (Roberts *et al.* 2002). The SWIO was recently proposed as an evosspot (i.e. evolutionary hotspot), a region able to generate and maintain marine biodiversity (Hoareau *et al.* 2013), highlighting the importance of documenting the biodiversity of the region. Ophiuroids from Réunion have been studied on few occasions. First, Guille & Ribes (1981) reported 21 species associated with scleractinian corals from a single locality on the west coast (La Saline). Soon after this first survey, 20 species collected from deep water around Réunion by the 'Marion Dufresne' cruise in 1982 were reported by Vadon & Guille (1984). The only species in common between these two studies was *Ophiolepis irregularis* Brock, 1888. More recently, non-focal sampling and the description of *Ophiocanops multispina* Stöhr, Conand & Boissin, 2008 raised the known fauna to 45 species, 26 of which were recorded from shallow waters (Stöhr *et al.* 2008). De Lorient (1893a) recorded 29 shallow water ophiuroid species from neighbouring Mauritius, while Rowe & Richmond (2004) documented 17 species from Rodrigues. Numerous species recorded from Mauritius or Rodrigues have not yet been documented from Réunion, suggesting that the regional fauna remains poorly known.

The aim of the present study is to better document the species diversity of ophiuroids from Réunion Island. An extensive sampling effort in the coral reef-associated coastal zone (<20m) was undertaken at 12 localities around the island. Below, we discuss each species encountered, compare species composition between Réunion and neighbouring areas, and discuss the biogeographic implications of our findings.

Material and methods

Sampling. Brittle-stars were collected by snorkelling or diving to a depth of ~20m. Numerous habitats for reef-associated ophiuroids were sampled (Table I) and algae and sponges were also collected to search for cryptic ophiuroids. No sampling was conducted along the east coast of Réunion, an area dominated by volcanic sandy beaches. Night-time collections were also undertaken on St-Leu reef flats. A total of 12 locations were explored in the North, West and South coasts of the island (Fig. 1) during July-August 2007 and February-March 2009. All but four locations (Banc des Lataniers, Cap La Houssaye, Vincendo & St-Philippe) are fringing reefs (Fig. 1; Table I). The abundance of each species is given as 1=rare, 2=common (few specimens from several sites), 3=abundant (numerous specimens from several sites). Specimens were relaxed with magnesium chloride, photographed, arm tips subsampled for ongoing genetic studies, and the remaining specimen fixed in 95% ethanol.

Taxonomic determination. Initial taxonomic determination was made with the aid of the Clark & Rowe (1971) and Cherbonnier & Guille (1978) monographs. Determinations were confirmed using available revisions: Devaney (1970) for *Ophiocoma*, Hoggett (1990, 1991, 2006) for *Macrophiothrix*, Clark (1953) for *Ophionereis*, Vail & Rowe (1989) for *Ophiopeza*, Thomas (1975) for *Ophioplocus*. Species records from the SWIO region were taken from de Lorient (1893a) for Mauritius, Rowe & Richmond (2004) for Rodrigues, Sloan *et al.* (1979) for Aldabra (Seychelles), Balinsky (1957) for Inhaca Island (Mozambique), as well as from Devaney (1974) for southern Polynesia. We also consulted monographs from the *Sindbad*, *Siboga*, *Snellius*, *Albatross*, and MUSORSTOM expeditions (Price & Rowe 1996, Koehler 1905; Guille & Wolf 1984; Koehler 1922; Guille 1981). Systematic treatment follows O'Hara *et al.* (2014) and Stöhr *et al.* (2016). Specimens from Réunion were compared to specimens from other localities across the Indo-west Pacific (IWP) region as available in the collection of the Florida Museum of Natural History, University of Florida (UF). Specimens used in the present study were deposited in the Florida Museum of Natural History (UF-number) or in the collection at Université de La Réunion (REU-number). For each species one voucher is indicated.



Data Sources: Habitats_Littoraux_EcoDDen. Spatial Reference System : WGS 84 (EPSG:4326). 2016

FIGURE 1. Map of the sampling locations around Réunion Island.

Genetic results available from concurrent studies (Hoareau *et al.* 2013, Boissin *et al.* in revision) are noted under the respective species and in Table II, GenBank accession numbers for COI sequences are indicated under the species name when available. Distributional ranges presented are based on past morpho-species concept, and do not include finer geographic divisions emerging from new genetic and morphological studies.

Abbreviations: spm(s)—specimen(s), DD—disc diameter, St.—station, SWIO—south-western Indian Ocean, UF—Florida Museum of Natural History, University of Florida, NW—North-West, IWP—Indo-west Pacific.

Results

Among the 12 localities sampled, only Vincendo (St. 11; Fig. 1) did not yield any ophiuroid. A total of 33 ophiuroid species belonging to nine families and 13 genera are reported here (Table II). The 15 new records increase the Réunion fauna to 61 species, with 42 recorded from shallow-waters. The number of species known from the Mascarene Islands is also increased by 11 species, while 8 appear to be new records for the Indian Ocean. Fourteen species are known to be shared between Réunion and Mauritius and 11 between Réunion and Rodrigues (Table II), but only four are known from all three islands: *Ophiocoma erinaceus* Müller & Troschel, 1842; *Ophiocoma brevipes* Peters, 1851; *Ophiarachnella gorgonia* (Müller & Troschel, 1842) and *Macrophiothrix longipeda* (Lamarck, 1816). Also noteworthy are several common genera (*Ophiarachna*, *Ophiarthrum* and *Ophiomastix*), that have not yet been recorded from Réunion, but are abundant elsewhere in the SWIO, including the other Mascarene Islands.

The Ophiocomidae was the most diverse family with 10 species collected. The most abundant species encountered was a new species revealed by our survey and recently described *Ophiocoma krohi* Stöhr *et al.* 2013. Other common species in shallow water habitats were the ophiolepidid *Ophioplocus imbricatus* (Müller & Troschel, 1842) and the amphiuroid *Amphipholis squamata* (Delle Chiaje, 1828).

Besides *Ophiocoma krohi*, several species appear to be new to science (*Ophiolepis cincta* complex sp. 2, *Ophiarachnella cf gorgonia*, *Ophionereis porrecta* complex sp. 2).

Systematic section

Family Gorgonocephalidae Ljungman, 1867

Genus *Astroboa* Döderlein, 1911

Astroboa nuda (LYMAN, 1874)

(UF-6431, Fig. 2a, KU594357)

Material. 1 spm, St. 7 (night-time snorkelling)

Remarks. *Astroboa* currently includes nine species, three of which occur in shallow-water in the IWP (Clark & Rowe 1971): *A. tuberculosa*, *A. nuda* and *A. clavata*. The specimen concurs well with characteristics of the species: the disc granules are smooth and the granulation is even, unlike *A. tuberculosa* that presents enlarged tubercles among the granules. The double belt of hooked granules on the branching arms is conspicuous and distinguishes this from *A. clavata* where the hooked granules are rendered inconspicuous because of the presence of flattened platelets. Abundance: 1.

Distribution. Reported from East Africa and Madagascar, Red Sea, Persian Gulf, East Indies, Philippines, China and South Japan (Clark & Rowe 1971) and Australia (Baker 1980). This is a first record for Réunion Island and Mascarene Islands.

Family Ophiomyxidae Ljungman, 1867

Genus *Neoplax* Bell, 1884

Neoplax ophiodes Bell, 1884 complex

(UF 6535, Fig. 2b,c, KU594358)

Material. 1 spm, St 7.

Remarks. The genus *Neoplax* has elongated ventral arm spines, spiniform oral papillae, and short spines on the disk. It does not have the glassy, denticulate oral papillae of *Ophiomyxa*.

The genus includes two species, this one described from the Seychelles and *N. crassipes* Koehler, 1922. The latter can be distinguished by the much larger ventralmost spines on the arm. The colour pattern of the specimen from Réunion is distinctive, differs from the unpatterned disk reported by Bell (1884), but is shared by a second

specimen collected from Lizard Island, Queensland, Australia (UF 8517). The two specimens are also very similar in structural characters, but are differentiated at ~10% in their COI sequences (Tim O'Hara, unpublished), suggesting that they may be part of a species complex. Both specimens were collected among coral rubble at 13–16 m depth on fore reefs. Abundance: 1.

Distribution. Recorded from the Seychelles (Bell, 1884), Mauritius (Bell, 1909) and Reunion (Guille & Ribes, 1981), and now Queensland, Australia.



FIGURE 2. Pictures of species encountered in Réunion Island waters. Pictures were taken of freshly collected specimens except when indicated. Photo credit: BIOTAS.

a) *Astroboa nuda* in situ; b) *Neoplax ophiodes*; c) *Neoplax ophiodes* oral side; photo of preserved specimen d) *Ophiactis savignyi*; e) *Ophiactis quadrispina*; f) *Ophiactis modesta*; g) *Ophiothrix (Ophiothrix) trilineata*; h) *Ophiothrix (Ophiothrix) trilineata*; i) *Macrophiolithrix longipeda*

Family Amphiuroidae Ljungman, 1867

Genus *Amphipholis* Ljungman, 1866

Amphipholis squamata (DELLE CHIAJE, 1828) complex (UF-6449, KU594365)

Material. 1 spm, St. 5; 27 spms, St. 8; 20 spms, St. 9 & 7 spms, St. 10

Remarks. *Amphipholis* is currently composed of 26 recognized species. *A. squamata* is a tiny organism (DD < 5mm) and the only one in the genus with a worldwide. Distribution. The specimens collected at Réunion concur well with the diagnosis showing joint radial shields of about one third of disc radius, scale-like distal oral papillae and 3 to 4 arm spines on each segment. *A. squamata* was revealed to be a species complex comprising numerous cryptic lineages (Sponer 2002; Boissin *et al.* 2008a). Specimens from Réunion are cream coloured, sometimes with a pale brown disc, and belong to the tropical lineage E (Boissin 2008). They were collected from under rocks and

among coral rubble, commonly along the arms of *Ophiocoma* species. This association has also been noticed at Mer Island (Torres Strait), Hawaii and French Polynesia (Devaney 1974). Abundance: 3.

Distribution. A cosmopolitan species complex known from all oceans except polar ones, from shore to 1300 m (Gage *et al.* 1983). The species was already recorded from Rodrigues (Rowe & Richmond 2004) and Réunion (Stöhr *et al.* 2008).

Family Ophiactidae Matsumoto, 1915

Genus *Ophiactis* Lütken, 1856

The genus includes 51 recognized species. Clark and Rowe (1971) report 18 species from the shallow IWP, but currently only 11 of these are recognized (Stöhr *et al.* 2016). They can be divided into two groups: (i) species with two distal oral papillae on each side of a jaw and six or more arm spines (4 species), and (ii) species with a single distal oral papilla and up to five arm spines per side (7 species).

Ophiactis savignyi MÜLLER & TROSCHER, 1842

(UF-6463, Fig. 2d, GU480578)

Material. 2 spms, St. 2; 4 spms, St. 5

Remarks. max DD in Reunion Island: 2.62 mm (Stöhr *et al.* 2008). The specimens have six arms, two distal oral papillae and the dorsal arm plates are elliptical with a small median distal lobe. Radial shields are large and their length is about half the radius. There are five to six spines on the proximal segments then four spines along the rest of the arm. The colouration is variegated green and white. *O. savignyi* is common among algae, in coral crevices, and sponges. Specimens from St. 2 were found on the coral *Stylocoeniella guentheri*, while those from St. 5 were found in the sponge *Sphaciospongia*. All specimens show evidence of fissiparity, a common mode of asexual reproduction for this species. *Ophiactis savignyi* shows limited genetic differentiation in mtDNA within the Indo-Pacific and is best considered a single species (Roy & Sponer 2002).

Abundance: 3.

Distribution. Known from the Atlantic and the Indo-Pacific; previously recorded from Réunion (Guille & Ribes 1981; Stöhr *et al.* 2008) and Rodrigues (Rowe & Richmond 2004).

Ophiactis picteti (DE LORIO, 1893)

(REU-3733)

Material. 1 spm, St. 7

Remarks. A five-armed species, much bigger (DD: 8 mm) than *O. savignyi* (max DD in Reunion island: 2.62 mm, Stöhr *et al.* 2008), with two distal oral papillae and six arm spines along the length of the arm. The overall colouration is pale brown. Among the 11 shallow IWP *Ophiactis* species, only four have two oral papillae. The colouration, size of the adoral shields and length of the arms (~ 6DD), of our specimen are consistent with *O. picteti*. The specimen was found in a crevice of the fire coral *Millepora platyphylla*. Abundance: 1.

Distribution. Described from the Amboina (Moluccas, de Loriol 1893b), it has also been recorded from Mozambique (Balinsky 1957); Aldabra (Sloan *et al.* 1979) and Madagascar (Cherbonnier & Guille 1978). This is a first record for Réunion and the Mascarene Islands.

Ophiactis quadrispina HL CLARK 1915

(REU-0220-1, Fig. 2e, GU480579)

Material. 2 spms, St. 5

Remarks. This species is similar to *O. savignyi* in size and in having six arms, but differs in having only one, distal oral papilla. Dorsal arm plates are elliptical and broadly in contact, the length of the radial shields is about half the disc radius, the dorsal arm plates are wider than long, the adoral shields meet radially and separate the first and the second ventral arm plates. The colouration is not green such as *O. savignyi*, but yellowish-brown. Cherbonnier & Guille (1978) synonymized this species with *O. savignyi*. However, later, Guille (1981) recognized that the species was different from *O. savignyi* and Price & Rowe (1996) also did not recognize the synonymy. The morphotypes are clearly different and our recent DNA barcoding survey confirmed their status as distinct species (Hoareau & Boissin 2010). Abundance: 1.

Distribution. This is a first record for the Indian Ocean, the Mascarenes and Réunion. This species was previously only known from the Philippines (Clark & Rowe 1971).

***Ophiactis modesta* BROCK, 1888**

(UF-6323, Fig. 2f, GU480580)

Material. 3 spms, St. 5

Remarks. Another species of about the same size and overall aspect as *O. savignyi*, fissiparous with six arms, but displaying blue instead of green colouration. Like *O. quadrispina* it has only one distal oral papilla but is differentiated in having 5 arm spines, with the 2nd longer than the segment length. Commonly found in sympatry with *O. savignyi* (Clark & Rowe 1971), with which it can be confused. Similarly to *O. quadrispina*, Cherbonnier & Guille (1978) synonymized this species with *O. savignyi*; but the morphotypes are clearly different and our recent DNA barcoding survey confirmed that they are distinct species (Hoareau & Boissin 2010). Guille (1981) and Price & Rowe (1996) also did not recognize the synonymy. Abundance: 1.

Distribution. Widespread in the IWP from Mozambique (Balinsky 1957), Lakshadweep Islands, India and Sri Lanka (Price & Rowe 1996), to the South Pacific islands & Hawaii (Clark & Rowe 1971). This is the first record for Réunion and the Mascarene Islands.

Family Ophiotrichidae Ljungman, 1867

Genus *Ophiotrix* (*Ophiotrix*) H.L. Clark, 1938

***Ophiotrix trilineata* LÜTKEN, 1869 complex**

(REU-0888, Fig. 2g, h, GU 480577)

Material. 1 spm, St. 2; 4 spms, St. 3; 1 spm, St. 5; 2 spms, St. 7

Remarks. The specimens concur well with the species diagnosis in possessing three light lines along the length of each arm: a yellow line and two blue lines separated by four black lines. The disc bears long and thin spines, with shorter spines along the edges. Two colour varieties are encountered at Réunion: a red and a yellow/brownish one. Similarly, Cherbonnier & Guille (1978) recorded two main colour types in Madagascar: most of the specimens were blue, but several were pink to red. While this species is considered to have an Indo-Pacific-wide distribution, COI sequence data indicates that SWIO populations are deeply divergent from populations in the W Pacific (Boissin *et al.* in revision). With the type locality in the W Pacific (Samoa), Indian Ocean specimens are here assigned to the *O. trilineata* complex. Further research is required to elucidate species boundaries in this complex. Abundance: 1.

Distribution. Considered to be widespread in the IWP (Clark & Rowe, 1971), previously recorded from Réunion (Guille & Ribes, 1981) and Mauritius (de Loriol, 1893a).

Genus *Macrophiotrix* H.L. Clark, 1938

This common tropical genus is of rather large size and has characteristically very long arms (10-15 x DD). Australian species were thoroughly documented by Hoggett (1990, 1991). Species fall into two groups: those

bearing trapeziform dorsal arm plates and those with hexagonal, elliptical or fan-shaped arm plates (Hoggett 1990, 1991, 2006). *Ophiothrix* (*Keystonea*) was synonymized with *Macrophiothrix* (Hoggett 1990), and the genus currently includes 46 recognized species (Stöhr *et al.* 2016).

***Macrophiothrix longipeda* (LAMARCK, 1816)**

(UF-6441, Fig. 2i, GU 480574)

Material. 5 spms, St. 1; 1 spm, St. 2; 4 spms, St. 3; 5 spms, St. 5; 2 spms, St. 7

Remarks. A large ophiuroid with a yellow overall colouration and conspicuous black dots on the dorsal side of the disc and dorsal arm plates. The dorsal side of the disc bears short multifid granules (2-3 x as high as wide) some of them blunt; the radial shields are covered with rugose granules. Arm plates are trapeziform and 2-3 x broader than long. Seven arm spines are present on each side per segment. No spinelets are present on oral shields. Hoggett (2006) described a new species, *M. caenosa*, very similar to *M. longipeda* from which it can be distinguished by Scanning Electronic Microscopy (SEM) of the dental plates. Dental plates of *M. longipeda* are shorter and broader and without an obvious central constriction. We did not perform SEM analyses; however, our barcoding survey confirmed that our specimens belong to *M. longipeda* and not *M. caenosa* (Hoareau & Boissin 2010). COI sequence data indicates that SWIO populations are deeply divergent from populations in W Australia and the Pacific (Boissin *et al.* in revision). While additional research is required to define species in this complex, the specimens from Réunion are likely to be the nominal form, as the species was described from neighbouring Mauritius. Abundance: 2.

Distribution. *M. longipeda* is widely distributed in the IWP (Clark & Rowe 1971), and was previously recorded from Rodrigues (Rowe & Richmond 2004), Mauritius (type locality, de Lorient 1893a), and Réunion (Ribes & Guille 1981).

***Macrophiothrix cf. belli* (DÖDERLEIN, 1896)**

(REU-1503)

Material. 1 spm, St. 12

Remarks. The specimen has trapeziform dorsal arm plates, a character shared by only seven species of *Macrophiothrix* (Hoggett 2006). The disc granules are tall and multifid, the radial shields are mostly bare; characters that match most closely with *M. belli* (Hoggett 1991; Hoggett 2006). Abundance: 1.

Distribution. This species has previously been recorded only from the Great Barrier Reef; comparison with the type or topotypical material is needed to verify this range extension. This is a new *Macrophiothrix* species record for Réunion and the Mascarene Islands.

***Macrophiothrix cf. paucispina* HOGGETT, 1991**

(REU-3722, Fig. 3a)

Material. 1 spm, St. 7

Remarks. Another species with trapeziform arm plates, but unlike in *M. belli* the disc granules are mostly trifid rather than multifid and the radial shields display low granules at similar density to the disc stumps, characteristics that match the description of *M. paucispina* (Hoggett 1991). Abundance: 1.

Distribution. *M. paucispina* has been recorded only from Australian waters (Hoggett 1991); comparison with the type or topotypical material is needed to verify this range extension. This is a new *Macrophiothrix* species record for Réunion and the Mascarene Islands.



FIGURE 3. Pictures of species encountered in Réunion Island waters. Pictures were taken of freshly collected specimens except when indicated. Photo credit: BIOTAS.

a) *Macrophiothrix paucispina* (after ethanol preservation); b) *Macrophiothrix propinqua*; c) *Macrophiothrix cf. robillardi*; d) *Ophiocoma brevipes*; e) *Ophiocoma doederleini* morphotype 1; f) *Ophiocoma doederleini* morphotype 2; g) *Ophiocoma doederleini* morphotype 3; h) *Ophiocoma dentata*; i) *Ophiocoma krohi*

***Macrophiothrix propinqua* (Lyman, 1861)**

(UF-6556, Fig. 3b, KU594366)

Material. 1 spm, St. 2; 3 spms, St. 4; 1 spm, St. 7

Remarks. Radial shields about three fifths as long as disc radius, bare. Both disc and arms bright reddish/orange. Scales on the disc bear small flat white tubercles. There are 8-10 strips of interradial scales and one strip of scales that separates the radial shields. This species fits the former subgenus *Keystonea*, now synonymized with *Macrophiothrix*. Abundance: 1.

Distribution. A widespread IWP species (Clark & Rowe, 1971; Stöhr *et al.* 2016).

***Macrophiothrix robillardi* (DE LORIO, 1893)**

(REU-3614, Fig. 3c)

Material. 2 spms, St. 8

Remarks. These two specimens, contrary to those from the three previous species, do not present trapeziform dorsal arm plates. The disc bears elongate granules dorsally and the radial shields are bare. Some elongated granules are present at the distal edge of the radial shields and form a kind of crown, as also visible in the holotype of *M. rugosa* (synonymised with *M. robillardi*) (Hoggett 1991). The dorsal arm plates have a characteristic rugose

aspect when not wet. The arm spines are not conspicuously thorny as in other *Macrophiothrix* species. The oral shields do not bear spinelets. The colour is variegated; the disc and the radial shields are blue/grey, with beige/pale yellow granules. The dorsal arm plates are darker (red/brown) every three to four segments. A yellow median line runs along the arms in living animals; Hoggett (1991) reported a white line in preserved specimens. Disc granules are denser in one of the two specimens at hand; a character that often distinguishes species in this genus (Hoggett 1991). Abundance: 1.

Distribution. Known from Mauritius (type locality; de Loriol, 1893a), Rodrigues (Rowe & Richmond 2004), Guam (Starmer 2003), Australia, China and Cook Islands (reviewed in Hoggett 1991). This is the first record for Réunion.

Family Ophiocomidae Ljungman, 1867

Genus *Ophiocoma* L. Agassiz, 1835

Ophiocoma is perhaps the most conspicuous and abundant genus of large ophiuroids on coral reefs. It can be subdivided into four groups (Devaney 1970): (1) SCOLOPENDRINA GROUP: easily recognisable by arm-spines alternating sequentially between three and four; (2) Subgenus *Breviturma* Stöhr *et al.* 2013 (i.e. former BREVIPES GROUP): upper arm plates with broadly rounded margins, disc granules closely packed up to the oral shields; (3) PICA GROUP with angular arm plates; (4) PUMILA GROUP with elongated granules on disc and one tentacle scale on all but the first five proximal segments. Currently 23 *Ophiocoma* species are recognized (Stöhr *et al.* 2016).

Subgenus *Breviturma* Stöhr, Boissin & Hoareau, 2013

Ophiocoma (Breviturma) brevipes PETERS, 1851

(UF-6451, Fig. 3d, KC759765)

Material. 4 spms, St. 3; 5 spms, St. 5; 2 spms, St. 7; 1 spm, St. 8

Remarks. Distinguishable from the three other species of *Ophiocoma (Breviturma)* by its light colour: white or pale beige, with darker lines on the disc and oral surface of arms; mouth plates are nearly white to light cream. Unlike in *O. dentata* and *O. doederleini* the longest arm spine of *O. brevipes* is less than the breadth of the arm plates (Devaney 1970). COI sequence data indicates that SWIO populations are deeply divergent from W Pacific populations (Hoareau *et al.* 2013; Boissin *et al.* in revision). As the type locality of the species is in the SWIO (Mozambique), the specimens from Réunion represent the nominal form. Abundance: 2.

Distribution. Widespread in the IWP to Hawaii (Clark & Rowe 1971); including Réunion (Guille & Ribes 1981), Mauritius (de Loriol 1893a) and Rodrigues (Rowe & Richmond 2004).

Ophiocoma (Breviturma) doederleini DE LORIOL, 1899

(UF-6512, Fig. 3e,f,g, KF662924)

Material. 4 spms, St. 3; 1 spm, St. 7

Remarks. A species of the *Breviturma* subgenus easily recognizable by its finely annulated arm spines. At Réunion three morphotypes are distinguishable: (1) with a reticulated pattern on the disc (Fig. 2-13), (2) with small white flecks on the disc (Fig. 2-14), and (3) with a brown disc that bears dark spots encircled by a white line (Fig. 2-12). COI sequence data did not show any differentiation between these morphotypes, however SWIO populations are deeply divergent from W Pacific populations (Boissin *et al.* in revision). Réunion specimens pertain to the nominal form, as the species was described from Mauritius. Abundance: 1.

Distribution. Widespread across the IWP (Devaney 1970); new record for Réunion.

***Ophiocoma (Breviturma) dentata* MÜLLER & TROSCHEL, 1842 complex**
(UF-6460, Fig. 3h, KU594360)

Material. 2 spms, St. 1; 7 spms, St. 5; 1 spm, St. 7; 5 spms, St. 8

Remarks. This species displays several distinct disc colour patterns across its range: the three patterns noted above for *O. doederleini* as well as a fourth one that is uniformly dark. However, all specimens encountered on Reunion had a uniformly dark brown/reddish disc. COI sequence data did not show any differentiation between these morphotypes, however SWIO populations are deeply divergent from populations in W Australia and the Pacific (Boissin *et al.* in revision). As the type locality is likely Sulawesi (Olbers & Samyn, 2012), we recognize this diversity by assigning these specimens to a species complex. Abundance: 2.

Distribution. Widespread across the IWP to Hawaii (Clark & Rowe 1971). This is a first record for Réunion Island, but the species was already known from the Mascarenes, from Rodrigues (Rowe & Richmond 2004).

***Ophiocoma (Breviturma) krohi* Stöhr, Boissin & Hoareau, 2013.**
(UF-6454, Fig. 3i, KC759802)

Material. 2 spms, St. 1; 3 spms, St. 2; 15 spms, St. 3; 5 spms, St. 5; 19 spms, St. 8

Remarks. A species of *Ophiocoma* that was previously confused with *O. dentata* was recently described based on material from this survey (Stöhr *et al.*, 2013). It can be distinguished from *O. dentata* by the number of arm spines: five (instead of four) spines on the 5th and 6th segments, followed by four (instead of three) and finally three spines on more distal segments. The two species also differ in the density of disc granulation. Specimens are usually smaller than other *Ophiocoma (Breviturma)*, with a mean DD of about 8 mm; but do not correspond to juveniles of these three species, also observed during this survey. Although the colour pattern is highly variable, four forms can be roughly delineated: (1) mottled olive/brown disc and arms, (2) yellow/beige and brown, with darker lines outlining each arm plate, (3) uniformly black, and (4) black, with sparse white on disc and arms. These colour forms are not differentiated in mtDNA sequences and appear to be intraspecific variations rather than cryptic species. COI sequence data shows little genetic differentiation across the range of this species (Hoareau *et al.* 2013 as *Ophiocoma* sp. nov.). Abundance: 3.

Distribution. Described from Réunion, Stöhr *et al.* (2013) noted that the species is widespread in the IWP, but did not provide specific localities. The UF collections hold material of *O. krohi* from the Mariana Islands, Wake Island, Society Islands, Samoa, Niue, Palau, Hawaii and Okinawa.

Scolopendrina Group

***Ophiocoma cynthiae* BENAVIDES-SERRATO & O'HARA, 2008**
(UF-6335, Fig. 4a, KC759867)

Material. 2 spms, St. 1; 9 spms, St. 3; 7 spms, St. 5; 5 spms, St. 8

Remarks. This species is the latest described from the '*O. erinaceus*' complex (O'Hara *et al.* 2004). This complex was shown to include at least three forms: *Ophiocoma erinaceus* Müller and Troschel, 1842, *Ophiocoma schoenleinii* Müller and Troschel, 1842 and *O. cynthiae*. *Ophiocoma erinaceus* is readily distinguishable from the other two by its bright red tube feet (white in alcohol), compared with the dark podia of *O. cynthiae* and *O. schoenleinii*. The latter two species can be distinguished by the lack of granules on the ventral disc surface (except for a few near the genital plates) and by the presence of two tentacle scales along the arm beyond the first couple of segments for *O. cynthiae*. In *O. schoenleinii*, the granules persist as a wedge near the ventral margin and only one wide tentacle scale is present beyond the first couple of segments (Benavides-Serrato & O'Hara 2008). COI sequence data show little genetic differentiation across the range of this species (Hoareau *et al.* 2013). Abundance: 3.

Distribution. This new record from the Mascarenes extends the range of this species, previously recorded from the Great Barrier Reef to Tonga (Benavides-Serrato & O'Hara 2008). It is much more abundant than *O. erinaceus* at Réunion. Previous studies in the Mascarenes likely misidentified this species as *O. erinaceus*.



FIGURE 4. Pictures of species encountered in Réunion Island waters. Pictures were taken of freshly collected specimens except when indicated. Photo credit: BIOTAS.

a) *Ophiocoma cynthiae*; b) *Ophiocoma erinaceus*; c) *Ophiocoma erinaceus* oral side; d) *Ophiocoma scolopendrina*; e) *Ophiocoma pica*; f) *Ophiocoma pusilla*; g) *Ophiocomella sexradia*; h) *Ophionereis porrecta* complex sp. 1; i) *Ophionereis porrecta* complex sp. 2

***Ophiocoma erinaceus* MÜLLER & TROSCHER, 1842**

(UF-6525, Fig. 4b,c, KU594361)

Material. 2 spms, St. 3; 1 spm, St. 7.

Remarks. The specimens concur well with the diagnosis of this species. The colour is black on both sides, while the tube feet are red in life, turning whitish in ethanol. The dorsal arm spines are longer than other spines in large specimens and sometimes club-shaped. Juveniles lack granules on the disc and have cream lines on the radial shields; these were described as *O. similanensis* Bussarawit and Rowe, 1985; but later recognized as juveniles and synonymized (Price and Rowe 1996). Granules appear gradually with growth, and the cream lines disappear when $DD > 11\text{mm}$. COI sequence data indicates that SWIO populations are moderately divergent from populations in W Australia and the Pacific (Boissin *et al.* in revision). The type locality of the species is the Red Sea & Indian Ocean (Olbers & Samyn 2012), thus Réunion specimens are attributable to the nominal form. Abundance: 1.

Distribution. Found in shallow waters across the IWP to the Hawaiian Islands (Clark & Rowe 1971); previously recorded from Réunion (Guille & Ribes 1981; Stöhr *et al.* 2008), Mauritius (de Loriol 1893a) and Rodrigues (Rowe & Richmond 2004). However old records are unreliable because of past confusion with the sibling species *O. schoenleinii* and *O. cynthiae*.

***Ophiocoma scolopendrina* (LAMARCK, 1816)**

(REU-3652, Fig. 4d, KC759913)

Material. 1 spm, St. 5; 7 spms, St. 8

Remarks. This species is strictly intertidal (Fontaine 1965) and has longer arms than other members of the ‘SCOLOPENDRINA GROUP’. An abundant species on reef flats at Etang Salé, where they are found hidden under rocks. Only the arms are visible as they sweep the air-water interface using an unusual feeding mode: surface-film feeding at low tide (Oak & Scheibling 2006). This species is distinguishable from others of the ‘SCOLOPENDRINA GROUP’ by its colouration: brown and variegated with a yellowish ventral side, whereas other species display a black/dark ventral side. COI sequence data shows little genetic differentiation across the range of this species (Hoareau *et al.* 2013). Abundance: 2.

Distribution. Common across the IWP (Clark & Rowe 1971); recently reported from Réunion (Stöhr *et al.* 2008) and already known from Mauritius (de Loriol 1893a).

Pica Group

***Ophiocoma pica* MÜLLER ET TROSCHEL, 1842 complex**

(UF-6627, Fig. 4e, KU594362)

Material. 1 spm, St. 3; 1 spm, St. 5; 2 spms, St. 7

Remarks. This species is easily recognized with its black overall colouration, punctuated by gold dots and lines. COI sequence data indicates that SWIO populations are deeply divergent from populations in W Australia and the Pacific (Boissin *et al.* in revision). As the type locality is unknown (Olbers & Samyn 2012), we attribute specimens to the species complex. Abundance: 1.

Distribution. Widespread across the IWP to the Hawaiian Islands (Clark & Rowe 1971); previously reported from Réunion (Guille & Ribes 1981) and Mauritius (de Loriol 1893a).

***Ophiocoma pusilla* (BROCK, 1888) complex**

(UF-6596, Fig. 4f, KU594364)

Material. 1 spm, St. 2; 1 spm, St. 5

Remarks. This small species (DD < 1cm) is easily distinguished from other *Ophiocoma* by its angular dorsal arm plates and its thinner, hollow arm spines. COI sequence data indicates that SWIO populations are deeply divergent from populations in W Australia and the Pacific (Boissin *et al.* in revision). The type locality lies in the W Pacific (Ambon, Olbers & Samyn 2012), thus we attribute these specimens to the species complex. Abundance: 1.

Distribution. An uncommon species that is nevertheless widespread from the Red Sea to the Pitcairn Islands across the IWP (Clark & Rowe 1971, Devaney 1970); previously reported from Réunion (Guille & Ribes 1981).

Genus *Ophiocomella* A.H. Clark, 1939

Ophiocomella encompasses four recognised species, but only *O. sexradia* occurs in the IWP, the others live in the East Pacific and West Atlantic.

***Ophiocomella sexradia* (DUNCAN, 1887)**

(UF-6491, Fig. 4g, KU594363)

Material. 1 spm, St. 5; 1 spm, St. 8

Remarks. This small (DD = 2 mm) species is the only known ophiocomid with six arms. Specimens have small elongate granules on the dorsal surface of the disc, three to four arm spines, and are mottled green and whitish. Abundance: 1.

Distribution. Widespread across the IWP (Clark & Rowe 1971), previously recorded from Réunion (Guille & Ribes 1981; Stöhr *et al.* 2008) and Rodrigues (Rowe & Richmond 2004).

Family Ophionereididae Ljungman, 1867

Genus *Ophionereis* Lütken, 1859

This genus currently encompasses 29 species (Stöhr *et al.* 2016), including 11 from the IWP (Clark & Rowe 1971). They can be divided into 2 groups: species with vs. without papillae bordering the genital slits.

Ophionereis porrecta LYMAN, 1860 complex sp. 1 (UF-6437, Fig. 4h, KC760063)

Material. 1 spm, St. 3; 9 spms, St. 5; 2 spms, St. 7

Remarks. Two colour forms of *O. porrecta* occur on Réunion and they are genetically deeply divergent indicating that they represent two species. They are treated as sp. 1 and sp. 2 in the *O. porrecta* complex here. Species 1 shows little differentiation in COI sequence across the Indian Ocean from Madagascar to W Australia, but is deeply divergent from sister populations in the Pacific (Boissin *et al.* in revision). Specimens concur well with the description of the species: they have small radial shields, enlarged disc scales on the periphery, one supplementary arm plate on each side of the dorsal arm plates, genital papillae. *O. porrecta* can be differentiated from *O. degeneri* by its longer arm spines, the presence of larger marginal disc plates and smaller supplementary dorsal arm plates (Stöhr 2011). The mottled brown colour of sp. 1 matches Lyman's description well. The type locality of *O. porrecta* is unknown (Lyman 1860). Abundance: 2.

Distribution. A widespread IWP species previously recorded from Réunion (Guille & Ribes 1981; Stöhr *et al.* 2008) and Rodrigues (Rowe & Richmond 2004).

Ophionereis porrecta LYMAN, 1860 complex sp. 2 (UF 6436, Fig. 4i, KC760073)

Material. 1 spm, St. 4; 1 spm, St. 5

Remarks. A distinct colour morph is structurally very similar to *O. porrecta* but confirmed to be genetically distinct (Hoareau *et al.* 2013). The orange-brown reticulate pattern differs from the typical colour form for *O. porrecta* sp. 1.

Distribution. A new record for Reunion, the Mascarene Islands and the Indian Ocean.

Family Ophi Dermatidae Ljungman, 1867

Genus *Ophiopeza* Peters, 1851

Four species and two additional subspecies of *Ophiopeza* are presently recognized: *O. exilis* Koehler, 1905; *O. kingi* Devaney, 1974 and *O. spinosa* (Ljungman, 1867), *O. fallax fallax* Peters, 1851, *O. fallax arabica* A.M. Clark, 1968, and the temperate *O. cylindrica* (Hutton, 1872) (Stöhr *et al.* 2016).

***Ophiopeza fallax* PETERS, 1851 complex**
(UF-6521, Fig. 5a, KC760045)

Material. 2 spms, St. 3; 2 spms, St. 7

Remarks. The granules covering the disc and the radial shields indicate the specimens match the nominal subspecies, *O. fallax fallax* morphologically, rather than *O. fallax arabica*, which has some bare disc plates and bare radial shields. The disc is brownish-beige, with some pink or red patches and black dots. The third dorsal arm plate on each arm is dark red, as was noticed on specimens from Mauritius by de Loriol (1893a). *O. fallax* can easily be distinguished from *O. exilis* by the shape of the dorsal arm plates (broad and rectangular in *O. exilis* and fan-shaped in *O. fallax*) and the number of spines (5 in *O. exilis*, up to 12 in *O. fallax*). *O. kingi* also has fewer arm spines (up to 8-9) and longer arms (>5x DD) (Devaney, 1974), compared with arms 3-4x DD in *O. fallax*. COI sequence data shows deep genetic differentiation between two lineages that are both attributable to *O. f. fallax* morphologically. Both occur in the SWIO, but only one has been encountered at Réunion (Hoareau *et al.* 2013). *Ophiopeza fallax* clearly needs an overview with genetic data; for the present we recognize *O. fallax* as a potential species complex. Abundance: 1.

Distribution. Widespread across the IWP from East Africa & Madagascar, Mascarene Islands, Persian Gulf, East Indies to the Philippines. The species was already reported from Mauritius (de Loriol 1893a) and Réunion (Guille & Ribes 1981).



FIGURE 5. Pictures of species encountered in Réunion Island waters. Pictures were taken of freshly collected specimens except when indicated. Photo credit: BIOTAS.

a) *Ophiopeza fallax*; b) *Ophiopeza spinosa*; c) *Ophiarachnella gorgonia*; d) *Ophiarachnella gorgonia* oral side; e) *Ophiarachnella septemspinosa*; f) *Ophioplocus imbricatus*; g) *Ophiolepis cincta* complex sp. 1; h) *Ophiolepis cincta* complex sp. 2; i) *Ophiolepis superba*.

***Ophiopeza spinosa* (LJUNGMAN, 1867)**

(REU-0158, Fig. 5b)

Material. 1 spm, St. 3

Remarks. The specimen presents a pale brown/beige overall colouration and the characteristic dorsal pattern resulting from enlarged marginal disc scales. The radial shields are concealed by granules. The disc granules are slightly depressed in their centres. The arm spines are much longer than in *O. fallax* and the dorsal arm plates are fan-shaped but narrower than in *O. fallax*. Abundance: 1.

Distribution. Widespread across the IWP (Clark & Rowe 1971), previously reported from Réunion (Guille & Ribes 1981).

Genus *Ophiarachnella* Ljungman, 1872

Of the 23 recognized species of *Ophiarachnella*, 12 are recorded from shallow IWP waters (Clark & Rowe, 1971; Stöhr *et al.* 2016). Three of these IWP species are peculiar in showing a number of naked dorsal plates in addition to the naked radial shields: *O. sphenisci* (Bell, 1894), *O. infernalis* (MÜLLER ET TROSCHER, 1842) and *O. similis* (Koehler, 1905). The remaining can be divided into two distinct groups: *O. gorgonia* (MÜLLER ET TROSCHER, 1842), *O. parvispina* HL Clark, 1925, *O. ramsayi* (Bell, 1888), and *O. elegans* (Bell, 1894) have eight to 12 oral papillae and lowest arm spines are hardly longer than other spines; while *O. macracantha* HL Clark, 1909, *O. paucigranulata* H.L. Clark, 1938, *O. septemspinosa* (MÜLLER ET TROSCHER, 1842), *O. stabilis* (Koehler, 1905) and *O. snelli* AH Clark, 1964 present only five to seven leaf-like oral papillae, have small circular radial shields and the lowest arm spines are distinctly longer than the rest, exceeding the length of the segment.

***Ophiarachnella gorgonia* (MÜLLER ET TROSCHER, 1842) complex**

(UF-6578, Fig. 5c,d, KC760012)

Material. 2 spms, St. 2; 1 spm, St. 3; 2 spms, St. 7

Remarks. Specimens have eight to nine oral papillae, elongate radial shields, and large supplementary oral shields. These characters identify them as *O. gorgonia*. Several colour morphs co-occur on Réunion: the two specimens from Cap La Houssaye (St. 2) are dark grey, while those from Pointe des Aigrettes (St. 3) and St-Leu (St. 7) are banded with three or four white segments alternating with three or four dark grey segments. One specimen from St-Leu also displays some pink/red on the disc. These colour patterns differ from the well known green and white colour pattern exhibited by this species elsewhere, including Madagascar (personal observation), Mayotte (Comoros; personal observation), Rodrigues (Rowe & Richmond, 2004), Mauritius (de Lorient 1893a) and throughout the IWP region (Clark & Rowe 1971). However, there is no other obvious differentiation compared to other *O. gorgonia* specimens. The dorsal and ventral disc and arm plates have the same size, shape or arrangement in both dark and green specimens. These Réunion morphotypes were, however, recently confirmed to represent a cryptic species, genetically closely related to the more general green morphotype found elsewhere (Hoareau *et al.* 2013). The type locality of *O. gorgonia* is unknown. Abundance: 2.

Distribution. *Ophiarachnella gorgonia* as presently understood is widespread across the IWP from East Africa to the West Pacific, but is absent from southeastern Polynesia (Devaney 1974). Hoareau *et al.* (2013) found substantial genetic differentiation across this range. Previously recorded from the Mascarenes at Rodrigues (Rowe & Richmond 2004), this is the first record for Réunion.

***Ophiarachnella septemspinosa* (MÜLLER ET TROSCHER, 1842)**

(UF-6636, Fig. 5e)

Material. 1 spm, St. 7

Remarks. The specimen shows the characteristic five to six leaf-like oral papillae. The radial shields are small

and circular, distinctly darker than the rest of the disc. The arm spines are distinctly shorter than the segment, unlike in *O. macracantha* that displays longer middle and upper arm spines. The specimen is uniformly chocolate brown all over the body. In contrast some Pacific specimens (e.g. from Okinawa) display lighter segments on the arms that create a banding pattern. Abundance: 1.

Distribution. This species ranges from the SWIO to the Philippines and China/Japan (Clark & Rowe 1971). The species was previously recorded from Mauritius (de Loriol 1893a); this is the first record for Réunion.

Family Ophiopodidae Ljungman, 1867

Genus *Ophioplocus* Lyman, 1862

Four of the seven species of *Ophioplocus* are recorded from the IWP: the widespread *O. imbricatus* (MÜLLER & TROSCHER, 1842), *O. declinans* (Koehler, 1904) known from the Philippines, *O. japonicus* HL Clark, 1911 from Japan, and *O. giganteus* Irimura & Yoshino, 1999 from Okinawa; only the first species is known from the Indian Ocean.

Ophioplocus imbricatus (MÜLLER & TROSCHER, 1842) complex (UF-6489, Fig. 5f, KC759944)

Material. 2 spms, St. 1; 1 spm, St. 3; 2 spms, St. 4; 3 spms, St. 5; 3 spms, St. 8

Remarks. The specimens are easily recognizable by the fragmented dorsal arm plates arranged in a symmetrical pattern. The radial shields are very small and elongate. They are grey/brown with darker lines. Little morphological variation was evident in specimens we studied across the distribution of this species. The only noticeable variation was in the dark lines on the disc that sometimes form a circle and give an impression of a soccer ball, and in the ventral side that can be more or less dark coloured. This species is common under rocks. COI sequence data indicates that SWIO populations are deeply divergent from populations in W Australia and the Pacific (Boissin *et al.* in revision). The species was described from Mauritius and Timor. Abundance: 3.

Distribution. Widespread in the IWP from East Africa to Hawaii (Clark & Rowe 1971), previously reported from Réunion (Guille & Ribes 1981; Stöhr *et al.* 2008) and Rodrigues (Rowe & Richmond 2004).

Genus *Ophiopodis* MÜLLER & TROSCHER, 1842

The genus currently includes 24 species, eight in the Atlantic, six in the East Pacific and nine in the IWP.

Ophiopodis cincta MÜLLER & TROSCHER, 1842 complex sp. 1 (UF-6581, Fig. 5g, KC759971)

Material. 1 spm, St. 4; 1 spm, St. 7

Remarks. The specimens present a symmetrical arrangement of the disc scales (contrary to *O. irregularis* Brock, 1888). The disc scales are naked and do not present tubercles (contrary to *O. rugosa* Koehler, 1898 and *O. nodosa* Duncan, 1887). Disc scales are encircled by small scales; series of supplementary scales are also present on the distal edge of each arm segment (contrary to *O. unicolor* HL Clark, 1938 that lacks supplementary scales on the arm segments). The entire disc is smooth and lacks larger scales thickened at the edges [contrary to *O. cardioplax* (Murakami, 1943) whose disc has an irregular profile]. Finally, *O. cincta* is easily distinguishable from *O. superba* HL Clark, 1915 that has a peculiar colour pattern (see below). Ongoing work indicates that *O. cincta* is a species complex of at least 18 lineages (Pineda *et al.* in prep). Two species that differ in colour pattern and COI sequence are present on Réunion: *O. sp. 1.* with a reddish brown disc with some white patches, and banded arms, and *O. sp. 2* with a relatively even, tan or grey colour. As these two sympatric forms are reciprocally monophyletic in COI

sequences and have consistent colour differences, they are demonstrably biological species. Sloan *et al.* (1979) also noted these two forms in Aldabra and assigned them to *O. cincta cincta* and *O. cincta garretti*, respectively. Specimens from Madagascar and Mayotte (personal observation) and Aldabra (Sloan *et al.* 1979) that are related to *O. sp. 1* are a darker reddish brown with white patches, and are genetically differentiated (Hoareau *et al.* 2013). *Ophiolepis cincta* was described from the Red Sea. The Red Sea population is genetically divergent from both forms on Réunion (unpublished data), but is relatively close to, and forms an allopatric complex with, this species and the Madagascar-Mayotte lineage. Abundance: 1.

Distribution. The complex is widely recorded across the IWP from the Red Sea and East Africa to Polynesia (Clark & Rowe, 1971); however Hoareau *et al.* (2013) show substantial cryptic diversity across this range. This species complex is a new record for Réunion and the Mascarene Islands. Within this complex, *sp. 1* is currently only known from Réunion.

***Ophiolepis cincta* MÜLLER & TROSCHER, 1842 complex sp. 2**

(UF-6416, Fig. 5h, KC759973)

= *O. cincta garretti* SLOAN ET AL, 1987, NON LYMAN, 1865

Material. 2 spms, St. 1; 1 spm, St. 5; 5 spms, St. 8

Remarks. Differs from *O. cincta* complex sp. 1 mainly in its tan or grey colour. Aldabran specimens of this form were attributed to *O. cincta garretti* by Sloan *et al.* (1987), a taxon described from the Central Pacific Gilbert Islands (Tungaru, Kiribati). The animals from Réunion, however, are genetically deeply divergent from the Central Pacific form, as well as all other members of the complex. Abundance: 2.

Distribution. See under *O. cincta* sp. 1. This genetically deeply divergent taxon is currently only known from Réunion and likely (based on color pattern but no sequence data) from Aldabra..

***Ophiolepis superba* H.L CLARK, 1915**

(UF-6544, Fig. 5i, KU594359)

Material. 3 spms, St. 7

Remarks. A large harlequin-patterned *Ophiolepis* with alternating darker beige/pale brown with red/brown banding on the arms and dark star-like patch on the disc extending outwards in each interradius. This is a conspicuous and unmistakable species because of its colour pattern, much larger than *O. cincta* complex, with supplementary plates on disc and arms not arranged as neatly as in *O. cincta*, and with radial shields, larger and more conspicuous than the disc plates. COI sequence data indicates that SWIO populations are deeply divergent from populations in the Pacific (Boissin *et al.* in revision). The Indian Ocean population corresponds to the nominal species as the type locality is Ceylon. Abundance: 1.

Distribution. Widespread across the IWP (Clark & Rowe 1971); previously reported from Mauritius (de Loriol 1893a) and Réunion (Vadon & Guille 1984).

Discussion

New records, cryptic species and need for taxonomic revision. Fifteen of the species observed in Réunion during this survey were new records for the island (Table II) and represent a ~56% increase in recorded diversity. Eleven of these are also new records for the Mascarenes and six for the Indian Ocean. One of these, *Ophiocoma krohi*, was recently described based on these collections (Stöhr *et al.* 2013). Most ophiuroid genera are in need of taxonomic revision as they have either never been revised or were revised more than 50 years ago. Even within groups that have been revised, like *Ophiocoma* (Devaney 1970), recent surveys and molecular approaches are uncovering overlooked diversity (e.g., Benavides-Serrato & O'Hara 2008, Stöhr *et al.* 2013; Boissin *et al.* in revision). *Macrophiothrix* has been revised in Australia (Hoggett 1991), but needs global attention.

Several species (*Ophiarachnella gorgonia*, *Ophiolepis cincta*, *Ophiopeza fallax*, *Ophiothrix trilineata*, *Ophiocoma dentata*, *Ophiocoma doederleini*, *Ophiocoma krohi*) show distinct morphotypes on Réunion or in the SWIO. Such variants may represent intraspecific variability or cryptic species. The ophiocomids *O. doederleini*, *O. dentata* and *O. krohi*, all display several distinct disc colour patterns that are each widely distributed across the IWP (Devaney 1970; Starmer 2003) but that do not seem to represent distinct lineages based on genetic evidence (Hoareau *et al.* 2013; Boissin *et al.* in revision). *Ophiolepis cincta* also has several morphotypes, a uniform tan form [here identified as *O. sp.* 2 (Fig. 5h)] and a red with white patches form [*O. sp.* 1 (Fig. 5g)]; these have recently been identified as distinct species (Hoareau *et al.* 2013). No less than 18 distinct lineages are discernible among *O. cincta* studied across its range (Pineda *et al.* in prep) that likely represent distinct species (Hoareau *et al.* 2013). *Ophiarachnella gorgonia* has a distinct dark colouration on Réunion, contrasting with the typical green and white pattern it shows elsewhere. Interestingly, another (brown) colour morph was found in Okinawa (Japan) and an undescribed brown sister species has recently been collected in Moorea, French Polynesia (G. Paulay, personal observation). Réunion, Okinawa and Moorea may be instances of local differentiations of the widespread *O. gorgonia* into endemic species at remote, peripheral locations (see biogeographic section). Phylogenetic analyses confirmed that the Réunion morphotype of *O. gorgonia* is genetically distinct (Hoareau *et al.* 2013).

Widespread species are prone to cryptic differentiation, and are often a mosaic of distinct, allopatric lineages (Dawson 2005; Meyer *et al.* 2005; Murray 2007). In brittle-stars, a previous review suggested that cryptic speciation is also common (Boissin *et al.* 2011). Five species from the present survey (*Ophionereis porrecta*, *Ophiolepis cincta* 1 & 2, *Ophiarachnella gorgonia* and *Ophiopeza fallax*) were recently shown to include cryptic species within the SWIO (Hoareau *et al.* 2013). It is likely that future investigations will identify and differentiate additional species complexes.

Biogeographic considerations. Réunion Island, 800 km east of Madagascar and >5000 km west of the Indo-Australasian archipelago (IAA), is geographically isolated, and harbours a typical IWP fauna. Most species encountered on Réunion are widespread, IWP morpho-species, based on current ophiuroid taxonomy (Table II). Thirty-six (88%) have ranges that extend eastward at least to the western Pacific. Four of the six other species are unidentified and potentially undescribed, and their range outside Réunion unevaluated. *Ophiocanops multispina* was only recently described from Réunion, while the fifth, *Amphiura crispa*, is known from several locations in the Indian Ocean.

Genetic evidence indicates however that these widespread species are mostly complexes of allopatrically-differentiated, regional endemics. Populations of 79% of the widespread IWP species studied on Réunion (N=14) were reciprocally monophyletic to samples from the Pacific basin, with pairwise divergence of 3-15% (Boissin *et al.* in revision), indicating that they have been on an independent evolutionary trajectory for a long time. Samples were available for 8 of these species (*O. dentata*, *O. erinaceus*, *O. pica*, *O. pusilla*, *O. gorgonia*, *O. imbricatus*, *O. porrecta* and *M. longipeda*) from the eastern Indian Ocean (Western Australia), and in 7 of these (88%) western Australian populations were divergent, demonstrating genetic differentiation across the southern Indian Ocean basin. Furthermore, 3 species (*O. pusilla*, *O. superba*, *O. erinaceus*) were also recently sampled from another site in the eastern Indian Ocean (South Twin island, Myanmar), and 2 species show differentiated populations from the SWIO (*O. superba* and *O. erinaceus*). No eastern Indian Ocean samples were tested for the remaining species (Boissin *et al.* in revision, Table II). Some species also show differentiation within the SWIO, between populations on Réunion and neighbouring islands (Hoareau *et al.* 2013).

Most ophiuroids are broadcast spawners, and their larvae can be transported large distances by ocean currents. The South Equatorial Current (SEC), the main current affecting the SWIO region, runs from the IAA to the SWIO (Schott & McCreary 2001), and may explain the high proportion of IWP species in the region (Obura 2012). However, the majority of ophiuroids on Réunion are genetically differentiated from eastern Indian Ocean and Pacific populations, indicating that they have evolved into endemic forms (Hoareau & Boissin 2010; Hoareau *et al.* 2013; Boissin *et al.* in revision).

Two species studied have specialized reproductive modes: *Amphipholis squamata* broods to a crawl-away juvenile stage and shows high levels of self-reproduction (Boissin *et al.* 2008b) and *Ophiactis savignyi* reproduces extensively asexually by fissiparity. Interestingly, these species show the widest distributions; they are cosmopolitan and tropicopolitan, respectively. Brooders and fragmenters are especially well-adapted for founding new populations, and can disperse by rafting (Highsmith 1985; Thiel & Haye 2006) or through human-mediated transport (Carlton 1985). *Amphipholis squamata* has been collected from floating macro-algae (Highsmith 1985)

and *O. savignyi* was likely transported by humans to some areas (Roy & Sporer 2002). Given the stochastic nature of these processes, recurrent gene flow is unlikely and such dispersal events are prone to trigger founder speciation (Thiel & Haye 2006). Species with a short planktonic larval phase such as *O. gorgonia* [larvae settle only three days after fertilization (Cisternas & Byrne 2005)] are also prone to founder speciation and this may explain the distinct morphotypes at peripheral locations (Réunion, Okinawa and Moorea) in the complex.

Finally, only four species are currently known from all three Mascarene Islands, and several common regional species were not encountered on Réunion Island (Table III). While uneven sampling among islands may be partly responsible for these differences, the apparent absence of several common regional species (e.g. *Ophiomastix venosa*, *Ophiarthrum elegans*) on Réunion is noteworthy. A recent survey of echinoderms collected on underwater lava flows of the east side of Réunion also did not reveal additional species, except for a couple of as yet unidentified *Macrophiothrix* species (Bollard *et al.* 2013). The three Mascarene Islands differ markedly in their nearshore environments. While Rodrigues and Mauritius are eroded high islands with well-developed reefs and lagoons, Réunion is a young and high (3,069 m elevation) volcanic island, with no lagoons or barrier reefs, limited reef development, volcanic rocky and sandy shores, and near-shore habitats are exposed to substantial terrigenous runoff. These environmental characters exert a marked influence on near-shore communities, and may account for the absence of some otherwise common IWP species and genera, as well as the presence/abundance of more continental species (e.g. the bull shark *Carcharhinus leucas*).

Synthesis and perspectives. This study revealed several unreported species from the shallow waters around Réunion, raising the number of known reef-associated species to over 40. Although this number will certainly be augmented by additional sampling, especially at night or in soft bottom habitats (which dominate along the east coast of the island), we believe that the present sampling effort provides a good overview of the reef-associated ophiuroids of Réunion. Taxonomic surveys are quintessential to improving our knowledge of the natural environment and furthering ecological and/or genetic studies. The discovery of cryptic species is particularly interesting as they represent promising models to unravel speciation dynamics, to understand the origin of biodiversity and the assemblage of communities (Boissin *et al.* 2011; Boissin *et al.* 2015). Similar studies of ophiuroid and other invertebrate communities from other islands in the SWIO should help better understand regional biogeography and diversification patterns.

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TABLE I. Habitat, microhabitat, depth and sampling period of the localities analysed in the study. St. = Station; Period 1 = July/August 2007 and Period 2 = February/March 2009.

| St. | Locality | Habitat | Microhabitat | Depth | Period |
|-----|--------------------|--|---|-------|--------|
| 1 | Banc des Lataniers | shore front exposed coral banks basalt shore front with coral | under rocks/coral rubbles | 0–3m | 1 & 2 |
| 2 | Cap La Houssaye | colonies | various | 0–11m | 1 |
| 3 | Cap Homard | fore reef | under rocks or in coral matrices | 6–22m | 1 |
| 3 | Cap Homard | exposed reef flat | under rocks | 0–1m | 2 |
| 4 | L'Ermitage | reef flat | under rocks | 0–2m | 1 |
| 5 | Trou d'eau | reef flat | under rocks | 0–2m | 1 |
| 6 | Souris Chaude | fore reef | under rocks and cryptofauna in <i>Acropora</i> | 8–12m | 1 |
| 7 | St-Leu | rocky slope / basalt blocks / fore reef | under rocks | 0–19m | 1 & 2 |
| 8 | Etang Salé | reef flat | under rocks or associated with <i>Millepora</i> | 0–2m | 2 |
| 9 | St-Pierre | reef flat | under rocks or in coral boulders | 0–2m | 2 |
| 10 | Grand'Anse | small reef flat | under rocks or in coral boulders | 0–2m | 2 |
| 11 | Vincendo | basaltic tide pools | under rocks | 0–1m | 1 |
| 12 | St-Philippe | exposed rocky shore pool | under rocks | 0–2m | 1 & 2 |

TABLE II. Brittle star species from Réunion Island and the Mascarene Islands. X: present record, 1: Guille & Ribes (1981), 2: Stöhr *et al.* (2008), 3: Vadon & Guille (1984), 4 : Stöhr *et al.* (2013). Abbreviations: REU: Réunion; MAU: Mauritius; ROD: Rodrigues; IWP: Indo-West Pacific; SWIO: South-western Indian Ocean; IO: Indian Ocean; PO: Pacific Ocean; WA: Western Australia; WP: West Pacific; COS: cosmopolitan; TROP: tropicopolitan; pan-IWP: little genetic differentiation between Indian and Pacific populations sampled; Mas: Mascarenes; N. rec.: New record; NA: Not Applicable. Cryptic differentiation: pan-IWP: Réunion and Pacific populations not reciprocally monophyletic; vs: genetic differentiation between SWIO and other area noted.

| Family | Genus | Species | REU | MAU | ROD | Distribution | Cryptic differentiation | N. rec. Reu | N. rec. Mas | N. rec. IO |
|---------------------|-------------------------|----------------------|-------------------|-----|-----|----------------|-------------------------|-------------|-------------|------------|
| Gorgonocephalidae | <i>Astroboa</i> | <i>nuda</i> | X | | | IWP | untested | X | X | |
| Ophiomyxidae | <i>Neoplax</i> | <i>ophiodes</i> | 1,X | | | IWP | SWIO vs WP | | | |
| | <i>Ophiocanops</i> | <i>multispina</i> | 2 | | | REU | NA | | | |
| Ophiocomidae | <i>Ophiocoma</i> | <i>cynthiae</i> | X | | | IWP | pan-IWP | X | X | X |
| | | <i>erinaceus</i> | 1, X | X | X | IWP | SWIO vs WA/WP | | | |
| | | <i>scolopendrina</i> | 2, X | X | | IWP | pan-IWP | | | |
| | | <i>brevipes</i> | 1, 2, X | X | X | IWP | SWIO vs WP | | | |
| | | <i>dentata</i> | X | | X | IWP | SWIO vs WA/WP | X | | |
| | | <i>krohi</i> | 4, X | | | IWP | pan-IWP | X | X | X |
| | | <i>doederleini</i> | X | | | IWP | SWIO vs WP | X | X | |
| | | <i>pica</i> | 1, X | X | | IWP | SWIO vs WA/WP | | | |
| | | <i>pusilla</i> | 1, X | | | IWP | SWIO vs WA/WP | | | |
| | | <i>Ophiopsila</i> | <i>pantherina</i> | 2 | | | IWP | untested | | |
| <i>Ophiocomella</i> | <i>sexradia</i> | 1, X | | X | IWP | untested | | | | |
| Ophiidermatidae | <i>Ophiarachnella</i> | <i>gorgonia</i> | X | X | X | IWP | SWIO vs WA/WP | X | | |
| | | <i>septemspinosa</i> | X | X | | IWP | untested | X | | |
| | <i>Ophiopeza</i> | <i>spinosa</i> | 1, X | X | | IWP | untested | | | |
| | | <i>fallax</i> | 1, X | X | | IWP | untested beyond SWIO | | | |
| <i>Ophioconis</i> | <i>cupida</i> | 2 | | | IWP | untested | | | | |
| Ophiolepididae | <i>Ophiolepis</i> | <i>superba</i> | 3, X | X | | IWP | IO vs WP | | | |
| | | <i>cincta 1</i> | 1, X | X | | IWP | complex | | | |
| | | <i>cincta 2</i> | X | | | SWIO | untested | X | X | X |
| | | <i>irregularis</i> | 1 | | | IWP | untested | | | |
| <i>Ophioplocus</i> | <i>imbricatus</i> | 1, 2, X | | X | IWP | SWIO vs WA /WP | | | | |
| Ophionereididae | <i>Ophionereis</i> | <i>porrecta 1</i> | 1, 2, X | | X | IWP | IO vs PO | | | |
| | | <i>porrecta 2</i> | X | | | REU | NA | X | X | X |
| Ophiotrichidae | <i>Macrophiolithrix</i> | <i>longipeda</i> | 1, X | X | X | IWP | SWIO vs WA /WP | | | |
| | | <i>cf belli</i> | X | | | IWP | untested | X | X | X |
| | | <i>robillardi</i> | X | X | X | IWP | untested | X | | |
| | | <i>cf paucispina</i> | X | | | IWP | untested | X | X | X |
| | | <i>propinqua</i> | 1,X | X | | IWP | untested | | | |
| | <i>Ophiolithrix</i> | <i>foveolata</i> | 1 | | | IWP | untested | | | |
| <i>trilineata</i> | 1, X | X | | | IWP | SWIO vs WP | | | | |
| Ophiactidae | <i>Ophiactis</i> | sp. | 1 | | | REU | NA | | | |
| | | <i>savignyi</i> | 1, X | | X | TROP | complex | | | |
| | | <i>lymani</i> | 1 | | | IWP | untested | | | |
| | | <i>quadrispina</i> | X | | | IWP | untested | X | X | X |
| | | <i>modesta</i> | X | | | IWP | untested | X | X | |
| | | <i>picteti</i> | X | | | IWP | untested | X | X | X |
| Amphiuridae | <i>Amphipholis</i> | <i>squamata</i> | 1, X | | X | COS | complex | | | |
| | <i>Amphiura</i> | <i>crispa</i> | 1 | | | IO | untested | | | |
| | <i>Amphioplus</i> | sp. | 2 | | | REU | NA | | | |

TABLE III. Other species found in the Mascarene Islands (de Lorient (1893a); Rowe & Richmond (2004)) but not reported from Réunion, with their known geographic distribution. Abbreviations as in Table II.

| Family | Genus | Species | MAU | ROD | Distribution |
|-------------------|-------------------------------------|---------------------|-----|-----|--------------|
| Ophiomyxidae | <i>Ophiomyxa</i> | <i>australis</i> | X | X | IWP |
| Gorgonocephalidae | <i>Astroboa</i> | <i>clavata</i> | X | | IWP |
| | <i>Astrocladus</i> | <i>tonganus</i> | | X | TONGA, SWIO |
| Euryalidae | <i>Asteromorpha</i> | <i>rousseaui</i> | X | | SWIO |
| | <i>Ophiocoma</i> | <i>valenciae</i> | X | | SWIO |
| Ophiocomidae | <i>Ophiomastix</i> | <i>venosa</i> | | X | SWIO |
| | <i>Ophiarthrum</i> | <i>elegans</i> | | X | IWP |
| | | <i>lymani</i> | X | | MAU |
| Ophiodermatidae | <i>Ophiarachna</i> | <i>robillardi</i> | X | | MAU |
| | | <i>mauritiensis</i> | X | | MAU |
| Ophionereididae | <i>Ophionereis</i> | <i>dubia</i> | X | | IWP |
| | <i>Macrophiothrix</i> | <i>demessa</i> | X | | IWP |
| Ophiotrichidae | <i>Ophiotrix (Acanthophiothrix)</i> | <i>purpurea</i> | X | | IWP |
| | <i>Ophiothela</i> | <i>danae</i> | X | | IWP |
| Amphiuridae | <i>Amphiodia</i> | <i>dividua</i> | | X | SWIO |
| | <i>Amphioplus</i> | <i>sp nov</i> | | X | ROD |