

Brittle stars (Echinodermata: Ophiuroidea) from La Réunion and the systematic position of *Ophiocanops* Koehler, 1922

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Received 30 May 2007; accepted for publication 20 August 2007

The ophiuroid fauna of La Réunion, Indian Ocean, is still incompletely known. We report 13 different species from coral reefs, including five new records and a probably undescribed species of *Amphioplus*, which increases the number of ophiuroids known from La Réunion to 25. The most important find consists of three individuals of a previously unknown representative of the genus *Ophiocanops*. Originally placed in Ophiomyxidae, its systematic position has long been debated, with some authors advocating a placement with the otherwise extinct Palaeozoic Oegophiurida, based on the absence of several skeletal characters. The new species, *O. multispina* sp. nov., shows intermediate characters between its previously only known congener, *O. fugiens*, and the ophiomyxid *Renetheo felli*. The three species appear to represent a line of taxa with progressively reduced skeleton instead of an ancient condition. We propose to transfer *Ophiocanops* back to the Ophiomyxidae, to synonymize *Renetheo* with *Ophiocanops*, and to invalidate the Ophiocanopidae, for which there is no autapomorphy-based support. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 153, 545–560.

ADDITIONAL KEYWORDS: Indian Ocean – Oegophiurida – Ophiocanopidae – *Ophiocanops multispina* – *Ophiocoma* – Ophiocomidae – reef – *Renetheo felli* – systematics.

INTRODUCTION

La Réunion, situated in the Indian Ocean, about 800 km east of Madagascar, is one of three islands belonging to the Mascarenes, which also include Mauritius and Rodrigues. Echinoderm records from this area are few. Clark & Rowe (1971) counted 155 species of echinoderms for the Mascarenes. Guille & Ribes (1981) reported 28 species from a shallow (up to 40 m) reef at La Réunion, among them 21 ophiuroids. Vadon & Guille (1984) reported 20 species of ophiuroid from depths of 20–4000 m at La Réunion. Rowe & Richmond (1997) presented 38 ophiuroid species for the Western Indian Ocean and recently (Rowe &

Richmond, 2004) recorded 74 species of echinoderms, including 17 ophiuroid species, for the small island of Rodrigues.

Despite these studies, the ophiuroid fauna of La Réunion is still incompletely known and holds some surprises. We report ophiuroids from several recent collections at La Réunion. We also include some samples collected by Ribes, which appear accidentally not to have been included in the original study (Guille & Ribes, 1981). The most remarkable find is a previously undescribed species of the enigmatic genus *Ophiocanops* Koehler, 1922. The hitherto only known species *Ophiocanops fugiens* Koehler, 1922 has been suggested to be a 'living fossil', a member of the extinct order Oegophiurida Matsumoto, 1915, because it lacks bursae, and gonads and intestine extend for a considerable length into the arms (Fell, 1962).

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Hotchkiss (1977, 1995) refuted that view and argued instead that *Ophiocanops* belongs within the Phrynophiurida, close to the Ophiomyxidae, as earlier authors already suspected (Koehler, 1922; Mortensen, 1933). The new species shows characters that shed more light on the phylogenetic relationships of the genus. We will propose some changes to ophiuroid systematics based on the new data.

Abbreviations: dd, disc diameter; MNHN, Muséum national d'Histoire naturelle, Paris; NIWA, New Zealand Institute of Water and Atmospheric Research, Wellington; SMNH, Swedish Museum of Natural History, Stockholm; spms, specimens; USNM, United States National Museum (Smithsonian Institution), Washington, DC.

MATERIAL AND METHODS

The material was collected between 2002 and 2007 for several studies (Table 1; Fig. 1): Etang Salé reef study by E. Boissin, employing the quadrat method (15 × 15-cm squares) in coralline algae at Cap Carangue and searching under rocks, in crevices and coral debris at Four à Chaux; sampling along a depth gradient using a Van Veen grab (0.1 m²) to study soft bottom macrobenthic communities from outside the reef zone by L. Bigot, who collected the specimen of *Amphioplus* sp. (Bigot, 2006; Bigot *et al.*, 2006); sampling macrofauna from the reefal soft bottoms from Saint Gilles reef using an air lift system (five replicates of 0.1 m²) by D. Taddei (2006). C. Conand contributed material from routine reef monitoring (Conand, 2002), from sampling three reef stations using the quadrat method (each quadrat of 20 m²) (Conand & Mangion, 2002) and from St. Pierre; and M. Gallas collected the specimens of *Ophiocanops* during a dive. The samples collected by S. Ribes were rediscovered in the storage at the Endoume Marine Station in Marseille by H. Zibrowius. All samples are stored in ethanol, but were initially preserved in different media (some in formalin, some in ethanol).

The holotype of *Ophiocanops multispina* sp. nov. was lightly bleached in household bleach (NaOCl) diluted with water 1 : 1. Skeletal elements of a small part of the proximal arm were prepared by submerging the arm piece in concentrated bleach until the tissues had been removed. The holotype and the skeletal parts were washed in water, air-dried, mounted on aluminium stubs with spray-glue, gold-coated and examined with a Hitachi FE-SEM 4300 scanning electron microscope. The holotype was first examined from the dorsal side, then the glue was removed with

butyl acetate, and the specimen was remounted, ventral side up.

The systematics follows Smith, Paterson & Lafay (1995), with the exception of *Ophiocanops*. All material has been deposited at the Muséum national d'Histoire naturelle in Paris, except where otherwise noted.

RESULTS

We found a total of at least 13 species, including an unidentified juvenile *Ophiothrix* and four juvenile *Ophiocoma* (Table 1). The latter measure 1–1.5 mm dd, show a vivid black and white colour pattern, and may belong to one or several of the identified species of *Ophiocoma* found and are therefore not counted as separate species. The most abundant species are *Ophiactis savignyi* (Müller & Troschel, 1842) and *Ophioconis cupida* Koehler, 1905, although the latter was found at only a single locality, and *Ophiocoma erinaceus* Müller & Troschel, 1842 (Table 1). *Ophioplocus imbricatus* (Müller & Troschel, 1842) was collected only at St Pierre, but observed on several reefs in abundances similar to that for *O. erinaceus*. The most species-rich family is the Ophiocomidae with six species. All other families were represented by only a single species each (Table 1). The three specimens of *Ophiocanops* proved to be an undescribed species, differing considerably from *O. fugiens*, and are described in detail below. We also record a possibly undescribed *Amphioplus*. An unidentified basket star has been observed on the reefs, but none has been collected thus far.

CLASS OPHIUROIDEA GRAY, 1840
 ORDER OPHIURIDA MÜLLER & TROSCHEL, 1840
 FAMILY OPHIOMYXIDAE LJUNGMAN, 1867
 GENUS *OPHIOCANOPS* KOEHLER, 1922
***OPHIOCANOPS MULTISPINA* SP. NOV.**
 (FIGS 2A–N, 5A, B)

Holotype: 1.5 mm dd, on SEM stub, gold coated, La Réunion, Roche merveilleuse, 50 m, collector M. Gallas, on antipatharian coral; skeletal elements on two SEM stubs; MNHN EcOS 23818, 23819, 23820.

Paratypes: Two spms, in ethanol, locality same as for holotype; MNHN EcOH 8000, SMNH-Type-259.

Other material examined: *Ophiocanops fugiens*, holotype, USNM 41080, R/V *Albatross* Philippine Expedition, North Pacific Ocean, Philippines, Sulu Archipelago, Jolo Island, Candea Point, 6°03'45"N,

Table 1. Ophiuroid species, sampling sites off La Réunion and numbers of specimens collected

Species	Sampling sites and dates	No. of individuals
OPHIOMYXIDAE		
<i>Ophiocanops multispina</i>	Roche merveilleuse, on antipatharian coral, 50 m depth, east of Boucan Canot, 25.vi.2001, collector M. Gallas	3
OPHIURIDAE		
<i>Ophioplocus imbricatus</i>	Saint Pierre, 08.v.2007, collector C. Conand	6
AMPHIURIDAE		
<i>Amphipholis squamata</i>	Etang Salé reef, Cap Carangue, iii.2006, collector E. Boissin	3
	La Saline reef, Planch'Alizé, 27.ii.2001, collector D. Taddei	1
	Collector S. Ribes, no locality	1
<i>Amphioplus</i> sp.	Bois rouge, 160 m, iii.2003, collector L. Bigot	1
OPHIOTHRICIDAE		
Juv. <i>Ophiothrix</i> sp.	La Saline reef, outer slope, 30 m, 22.iv.1977, collector S. Ribes	1
OPHIACTIDAE		
<i>Ophiactis savignyi</i>	Etang Salé, Cap Carangue, iii.2006, collector E. Boissin	30
	La Saline reef, Trou d'Eau BR, D1, 06.iii.2002, collector D. Taddei	3
	La Saline reef, Trou d'Eau BR, B, iii.–iv.2002, collector D. Taddei	1
	La Saline reef, Trou d'Eau BR, C, 17.iii.2002, collector D. Taddei,	2
	La Saline reef, Trou d'Eau BR, B2, 17.iii.2002, collector D. Taddei,	1
	La Saline reef, Trou d'Eau BR, A, 23.iv.2002, collector D. Taddei	1
	La Saline reef, Trou d'Eau BR D, 31.iii.2002, collector D. Taddei	1
	La Saline reef, Trou d'Eau BR, 01.iv.2005, in a sponge	1
	Saint Pierre reef, ii.2006	2
	La Saline reef, 25.ix.1977, collector S. Ribes	1
OPHIONEREIDIDAE		
<i>Ophionereis porrecta</i>	La Saline reef, Trou d'Eau BR, vi.iii.2002, collector D. Taddei	1
	La Saline reef, outer slope, with <i>Montipora</i> , 30 m, 07.x.1977, collector S. Ribes	1
OPHIOCOMIDAE		
<i>Ophiocoma</i>	Etang Salé reef, Four à Chaux, iii.2006	6
<i>brevipes/doederleini</i>	Saint Pierre, 08.v.2007, collector C. Conand	6
<i>Ophiocoma erinaceus</i>	Etang Salé, Four à Chaux, iii.2006, collector E. Boissin	12
	La Saline reef, Trois Chameaux IRF, 26.i.1993	3
	La Saline reef, Trou d'Eau BR, 20.iii.2002	2
	La Saline reef, Planch'Alizé BR, 20.iii.2002	4
	Cap Homard, south of Boucan Canot, ORF, 05.ii.1993	5
	Saint Pierre, 08.v.2007	8
	La Saline reef, outer slope, 10 m, with <i>Galaxea</i> , 08.viii.1977, collector S. Ribes	1
<i>Ophiocoma scolopendrina</i>	La Saline reef, Planch'Alizé BR, 21.iii.2002, collector D. Taddei	1
Juv. <i>Ophiocoma</i> sp.	Etang Salé, Cap Carangue, iii.2006, collector E. Boissin	3
	Hermitage reef, BR, 12.v.2005, in a sponge, collector A. Barrere	1
<i>Ophiocomella sexradia</i>	La Saline reef, with <i>Acropora</i> , 30.vii.1977, collector S. Ribes	1
<i>Ophiopsila pantherina</i>	Collector S. Ribes, no locality	3
OPHIODERMATIDAE		
<i>Ophioconis cupida</i>	Collector S. Ribes, no locality	37

BR, back reef; IRF, inner reef flat; ORF, outer reef flat.

120°57'00"E, 36 m, 05.iii.1908. *Renetheo felli* Mc-Knight (2003), holotype, NIWA H-819, station Z9044, N of New Zealand, 32°11'42"S, 180°54'30"E, 122–307 m, 16.ix.1998; also a specimen (probably a

paratype) mounted on a SEM stub ventral side up, together with a short arm piece, mounted dorsal side up presumably from the type locality; and a single vertebra on a SEM stub.



Figure 1. Map of La Réunion with sampling localities of reef ophiuroids.

Etymology: The specific name refers to the high number of arm spines found in this species compared with its congener *O. fugiens*.

Diagnosis: Species of ophiuroid with extremely small disc and long arms, lacking bursae, radial shields, and ventral arm plates (except the first one). Gonads and intestine extend into the arm dorsally for 9–40 joints inside a gonadal chamber covered with strong connective tissue. Dorsal arm plates present distal to the gonadal chamber. Few rod-like disc spines and 8–9 arm spines for several segments beyond the gonadal chamber, fewer proximally and distally.

Description of holotype: Disc diameter 1.5 mm, arms broken at tips, strongly curling, at least 10 cm long (Figs 2A, 4A, B). Thick connective tissue covers disc and arms. There are few round scales in the integument of the dorsal disc, some of them bearing long spines, which flare slightly towards the distal end, with several thorns at the blunt tip; radial shields absent (Fig. 2B, D). Dorsal arm plates are absent for 9–16 joints on different arms, instead thick integument covers the vertebrae beneath which the gonads extend into the arm. Beyond this proximal part dorsal plates are present along the arm, rounded pentagonal, about as long as wide, with slanting lateral edges, their distal edge narrower than their proximal edge; plates on adjacent joints are widely separated (Fig. 2C). The dorsal plates and disc scales are thin, translucent and glassy, embedded in the thick skin.

The lateral arm plates are large and bulging, bearing up to eight erect spines (Fig. 2E). The number of arm spines increases distalwards, reaching its maximum number just beyond the gonad-bearing part. On some arms the number of spines alternates for several joints between seven and eight on every other joint, again decreasing in number distalwards. The dorsalmost spines are the longest, about as long as an arm joint, their stereom formed of three longitudinal rods, with perforated meshy areas between them, few small thorns along their edge and at the tip (Fig. 2E). The integument forms bulging lumps near the tip of the dorsalmost spines (Fig. 2F). Spine size decreases ventralwards; after three to four long dorsal spines, about four short spines follow, the ventralmost spines with close rows of thorns along their edges, slightly hook-shaped, half as long as an arm joint (Fig. 2G). The spine articulations on the lateral plates consist of two parallel ridges, open distally, connected by a groove proximally, a large hole between the ridges for the spine nerve and a small one at their proximal end for the muscle (Fig. 2H). The spine base is slightly inflated, with minute thorns on the meshy stereom. There is a large nerve opening in the centre of the spine and a narrow u-shaped projection to one side which fits into the groove uniting the ridges on the lateral plate (Fig. 2I).

The oral papillae are pointed conical, consisting of a single apical papilla or tooth and two lateral papillae to each side (Fig. 2J, K). Large, curved adoral shields are present, and a drop-shaped madreporite

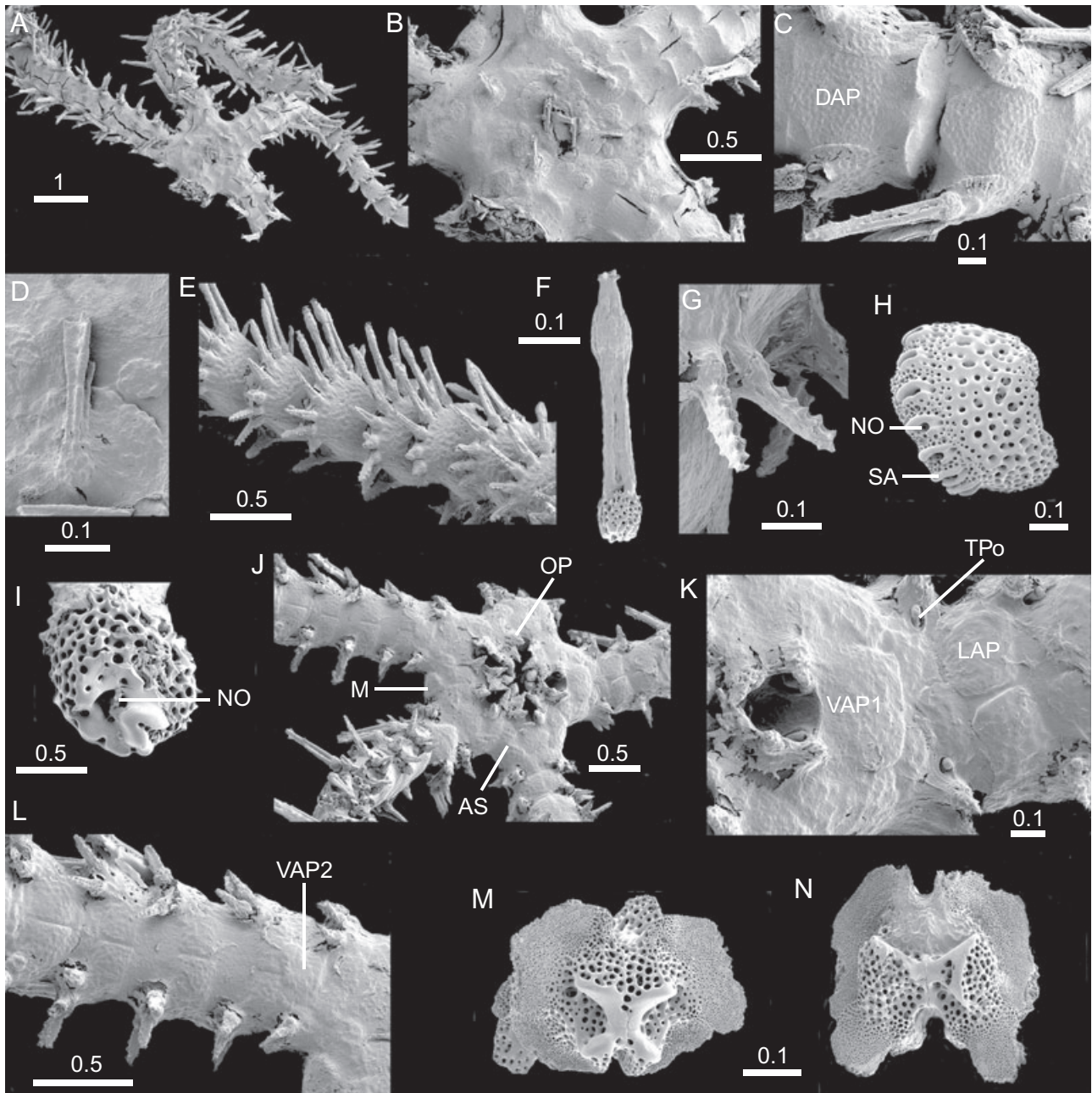


Figure 2. SEM images of *Ophiocanops multispina* sp. nov. holotype (MNHN EcOs 23818–23820). A, dorsal view; B, dorsal disc; C, dorsal arm plates beyond gonadal chamber; D, disc spine; E, arm laterally; F, dorsal arm spine; G, ventral arm spines; H, lateral arm plate; I, base of dorsal arm spine; J, ventral overview; K, first ventral arm plate; L, arm ventrally; M, proximal face of vertebra; N, distal face of vertebra. Abbreviations: AS, adoral shield; DAP, dorsal arm plate; LAP, lateral arm plate; M, madreporite; NO, nerve opening; OP, oral papillae; SA, spine articulation; VAP, ventral arm plate. Scale bars in millimetres.

at the disc edge (Fig. 2J, 4B), all other oral shields are tiny and hard to discern, positioned dorsolaterally at the disc edge; there are no bursal slits, and no ventral disc scales. Ventral arm plates are also absent, except for the large first plate and on two arms a smaller second ventral plate (Fig. 2K, L), but a dense strip of

tissue covers the midline of the ventral arm. The tentacle pores are inconspicuous, situated next to the ventralmost spine, present for the full length of the arm, lacking tentacle scales except for the small ventralmost arm spine (Fig. 2L). The arm vertebrae have wide aboral muscle flanges, and the articula-

tions are more streptospondylous than zygospondylous (Fig. 2M, N), but similar to Litvinova's (1994) aberrant type.

Colour in alcohol medium brown.

Paratype variations: Both paratype specimens are of similar size as the holotype, one medium brown in colour, the other dark chocolate brown. The dark specimen has the dorsal disc torn off, gonads along arms for up to 40 joints and up to nine spines for a short distance beyond the gonad-bearing part; further distally there are eight spines, fewer proximally. The dark specimen, in particular, shows many spines with thickened tissue lumps, and scattered low granules are visible on the surface of the tissue covering the proximal arm.

Remarks: *Ophiocanops multispina* differs from *O. fugiens* in several characters. It has up to nine arm spines (*O. fugiens* up to five) and the dorsal ones are longer and not hook-shaped, while the ventral spines are similar to those in *O. fugiens*. However, the latter has a dorsal spine completely enveloped by the integument over the gonads, supporting it like a chamber (Mortensen, 1933). In *O. multispina*, the skin is not supported by a spine. *Ophiocanops multispina* has disc scales and spines, while *O. fugiens* has no true disc spines, but low protruding ossicles in the dorsal disc integument (Pearse *et al.*, 1998), and lacks scales. In contrast to *O. fugiens*, *O. multispina* has dorsal arm plates distal to the gonadal chamber. The two species seem to differ in colour, although our preserved specimens may have lost some of their coloration. Koehler (1922) reports a dark purple colour, while the images in Pearse *et al.* (1998) show a banded and spotted pattern, also still visible in the holotype, which is absent in *O. multispina*. With regard to the lateral position of the oral shields, the position of the gonads along part of the arms, the absence of ventral arm plates, the thickened connective tissue and the shape of the vertebral articulation, *O. multispina* agrees with *O. fugiens* and the two species must be closely related. Koehler (1922) described the disc size as smaller than 3 mm, and the dried holotype has a dd of about 2.2 mm, which is somewhat larger than *O. multispina*. Both species have been found only on antipatharian coral and appear to be geographically restricted to the Indian Ocean and the Indonesian–Philippine region of the Pacific.

The vertebral articulations of *O. multispina* bear a striking resemblance to those of some ophiacanthids, such as *Ophiurothamnus clausa* (Lyman, 1878), or hemieuryalids, such as *Ophiomoeris obstricta* (Lyman, 1878), as shown by O'Hara & Stöhr (2006). These similarities are, however, most probably attrib-

utable to a similar (epizoic) life-style and are evidence of homoplasy. Arm spine articulations with parallel ridges can be found in several groups, such as Amphiruridae, Ophiactidae and part of the Ophiacanthidae (S. Stöhr, unpubl. observ.), but their taxonomic value has not yet been shown.

The closest affinities of *Ophiocanops* appear to be with *Renetheo* McKnight, 2003, which has a disc of similar size and extremely long arms, a thick skin and small lateral oral shields (Fig. 3A). Similar to *O. multispina*, the dorsal arms of *Renetheo felli* are covered with skin for about 30 joints, and the joints beyond the skin-clad part bear thin dorsal plates. According to McKnight (2003), the species has minute genital slits. SEM examination of the paratype of *R. felli* did not reveal these slits and their existence is doubtful (Fig. 3B). Like the darker paratype of *O. multispina*, the holotype of *R. felli* shows granules on the skin along the proximal arm (Fig. 3C). In contrast to both species of *Ophiocanops*, *Renetheo* has ventral arm plates for up to ten joints. Its arm spines are appressed; the dorsalmost spine bears many strong thorns all over and lies across the arm. *Renetheo felli* also bears numerous dorsal disc spines, which have a multifid crown and bear thorns along their length. The oral shields of *R. felli* are more ventral and slightly larger than in both species of *Ophiocanops*, and the adoral shields take up less space on the ventral disc. The vertebrae of all three species are similar (Figs 2M, N, 3D–F). A comparison of the species of *Ophiocanops* and *Renetheo* is given in Table 2.

FAMILY AMPHIURIDAE LJUNGMAN, 1867

GENUS AMPHIOPUS VERRILL, 1899

AMPHIOPUS SP.

(FIG. 4A–C)

Material: 1 spm (dd = 3 mm); Saint André, Bois Rouge, 160 m, collector L. Bigot.

Comparative material: Thirty-one spms of *Amphioplus* sp. from Rodrigues.

Description: This is a pentamerous species. All arms are broken off close to the oral frame, except one, which is still barely attached and broken off after 13 joints. The disc is irregularly round and inflated, dorsally covered by numerous small, round, imbricating scales, among which the primaries are not distinct. The radial shields are about one-quarter as long as the disc diameter, with convex outer and straight inner edge, pairs contiguous for their full length. The dorsal arm plates are wider than long, oval, with convex edges; adjacent plates are contiguous. There are three arm spines along the arm, except distally, the middle one longest, as long as an arm joint, about

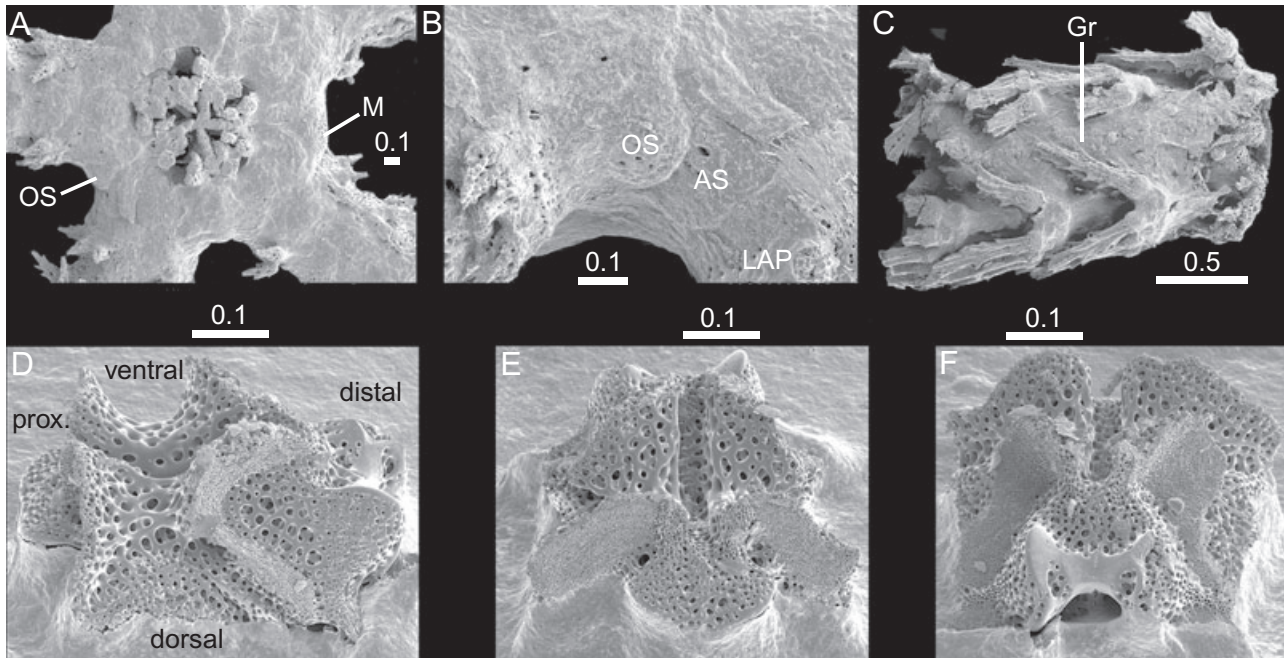


Figure 3. *Renetheo felli*. SEM images of a paratype and an isolated vertebra. A, ventral aspect, note the position of the oral shields, including the madreporite; B, ventro-lateral view of an interradius, note the absence of genital slits; C, arm piece, dorsal view, note the line of granules and the crossed dorsal spines; D, vertebra, lateral view; E, vertebra, proximal aspect, partly obscured by glue; F, vertebra, distal aspect. Abbreviations: AS, adoral shield; Gr, granules; LAP, lateral arm plate; M, madreporite; OS, oral shield. Scale bars in millimetres.

Table 2. Comparison of characters between *Renetheo felli* McKnight, 2003, *Ophiocanops multispina* sp. nov. and *O. fugiens* Koehler, 1922

	<i>R. felli</i>	<i>O. multispina</i>	<i>O. fugiens</i>
Disc diameter	1.8 mm	1.5 mm	2.2 mm
Arm length	> 25 mm	> 100 mm	> 30 mm
Radial shields	Absent	Absent	Absent
Disk spines	Multifid, many	Flat, trifid, few	Absent
Dorsal arm plates	Distally	Distally	Absent
Ventral arm plates	Up to 10	1–2	1
Arm spines	Thorny, appressed	Erect, rod-like, few thorns	Appressed, short, hook-like with teeth
No. of arm spines	6–8	6–9	4
Gonads in arms	Yes	Yes	Yes
Thick skin	Yes	Yes	Yes
Genital slits	Absent	Absent	Absent
Oral shields	Ventro-lateral, small	Lateral, minute	Lateral, minute
Madreporite	Present	Present	Present
Ambulacral groove skin-covered	Distally	Full length	Full length
On antipatharian coral	Yes	Yes	Yes

Disc diameters were measured on the holotypes of each species from an arm base across the dorsal disc to an interradius edge.

twice as wide as the dorsal spine, flat, all spines slightly tapering towards their tip, smooth. The ventral disc is covered with similar small scales as the dorsal side. The five oral papillae consist of the

paired infradentals, the buccal scale higher on the oral plate, a scale-like lateral papilla on the oral plate, another, wider papilla partly on the oral plate and partly on the adoral shield and a smaller papilla

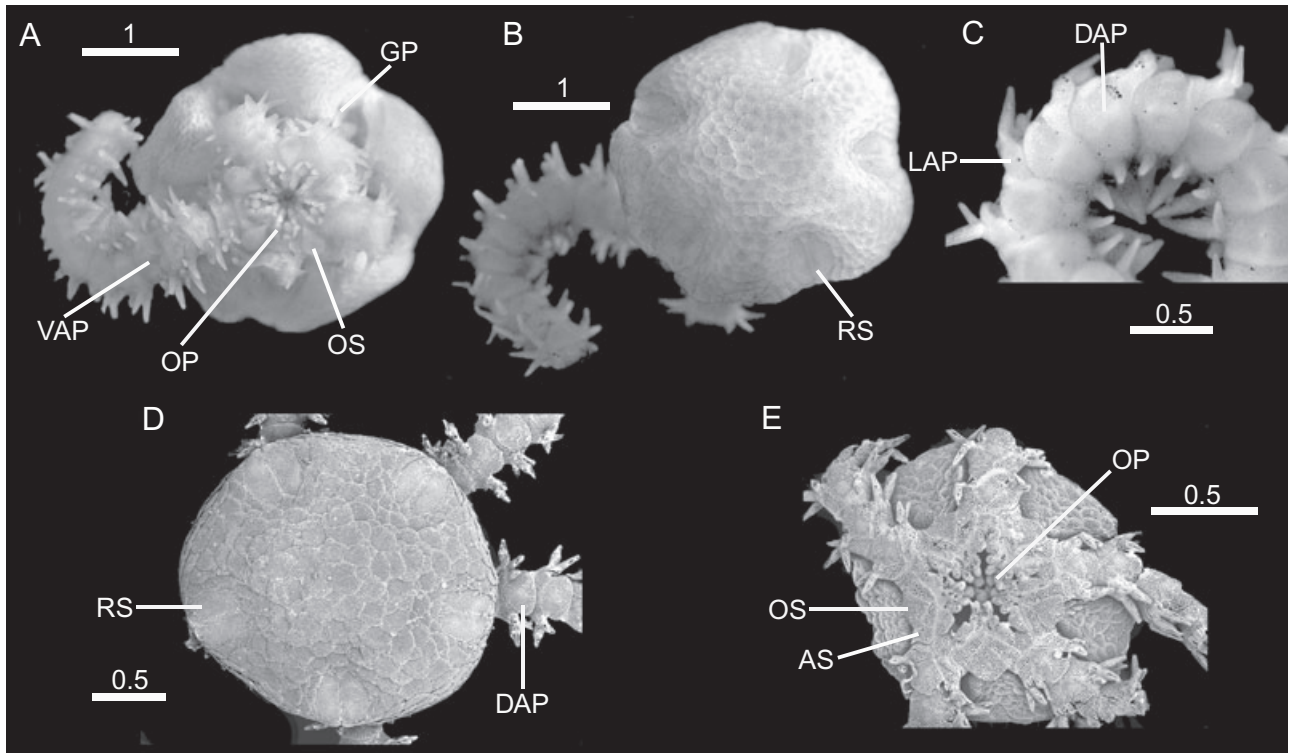


Figure 4. Digital images of *Amphipholis* sp.; A, ventral view; B, dorsal view; C, arm in dorsal view; SEM images of *Amphipholis squamata*; D, dorsal view; E, ventral view. Abbreviations: AS, adoral shield; DAP, dorsal arm plate; GP, genital plates; LAP, lateral arm plate; OP, oral papillae; OS, oral shield; RS, radial shield; VAP, ventral arm plate. Scale bars in millimetres.

on the adoral shield and first ventral arm plate. The oral shields are drop-shaped, with straight lateral and strongly convex distal edges; one of them is larger, presumably the madreporite. The adoral shields are wing-like, narrow proximally, flaring distally, abutting the lateral edges of the oral shield. The ventral arm plates are pentamerous, with straight edges, slightly convex distal edge, the first plate smaller, in contact with the second, all other ventral arm plates separated from each other by the lateral plates. Each tentacle pore is bordered by two low scales, a smaller one on the lateral plate and a wider one on the ventral plate.

Comments: Clark (1970) proposed four subgenera of *Amphipholis*, i.e. *Unioplus*, *Amphichilus*, *Lymanella* and *Amphipholis s.s.*, on the basis mainly of the number and position of the oral papillae. According to her view, the present species falls into *Amphipholis* (*Amphipholis*). The well-developed skeletal characters suggest that this specimen is fully grown, which makes it one of the smallest in the genus. It has some affinities with *A.* (*Amphipholis*) *titubantius* Cherbonnier & Guille, 1978, which reaches a size of 10 mm dd and has longer oral papillae. The present species differs from another unidentified small congener,

reported from Rodrigues (Rowe & Richmond, 2004), and may be undescribed. However, further analysis and preferably additional specimens are needed before a name can be assigned.

GENUS *AMPHIPHOLIS* LJUNGMAN, 1866

AMPHIPHOLIS *SQUAMATA* (DELLE CHIAJE, 1828)

(FIG. 4D, E)

Material: Five spms (dd = 1.2–2.1 mm); Etang Salé reef, Cap Carangue, iii.2006, by E. Boissin; a sample La Saline reef, Planch'Alizé, ii.2001 by D. Taddei; and a sample by S. Ribes from La Réunion, lacking locality data.

Comments: The specimens concur well with the diagnosis of the species. They have a pale beige colour on the arms and a beige or brown disc, which corresponds to one of the 11 colour varieties known for the species (Deheyn, Mallefet & Jangoux, 2000). *Amphipholis squamata* is in fact a species complex comprising several very divergent mitochondrial lineages (Sponer, 2002). Mitochondrial DNA sequencing reveals that these specimens belong to the most common lineage of the tropics (E. Boissin, unpubl. data). The specimens were found amongst coralline algae with *O. savignyi*.

Distribution: Worldwide except in polar waters, depth range from the intertidal to 1300 m (Gage *et al.*, 1983) according to the current species delimitation.

FAMILY OPHIACTIDAE MATSUMOTO, 1915

GENUS *OPHIACTIS* LÜTKEN, 1856

OPHIACTIS SAVIGNYI MÜLLER & TROSCHER, 1842

Material: Seventy-eight spms (0.90 < dd < 2.62 mm, mean dd = 1.47 mm); Etang Salé reef, Cap Carangue, iii.2006 by E. Boissin; Several specimens from La Saline reef, Trou d'Eau back reef iii.–iv.2002 by D. Taddei.

Comments: This six-armed species shows clear signs of fission. Of the 78 specimens only nine did not show some trace of regeneration of disc and arms; all the remaining have either only half a disc and three arms or show different stages of regeneration of the missing half. The specimens have a green and white pattern and concur well with the general diagnosis of the species. The specimens from Etang Salé reef were found among coralline red algae, while several specimens collected in La Saline reef were found in *Spheciospongia vagabunda* (Ridley, 1884), a common sponge (Clionidae).

Distribution: Circumtropical, to over 100 m depth (Schoppe, 2000); La Réunion (Guille & Ribes, 1981) and Rodrigues (Rowe & Richmond, 2004).

FAMILY OPHIURIDAE

GENUS *OPHIOPLOCUS* LYMAN, 1862

OPHIOPLOCUS IMBRICATUS (MÜLLER & TROSCHER, 1842)

(FIG. 5J, K)

Material: Six spms (dd = 20 mm); Saint Pierre, 08.v.2007, by C. Conand.

Comments: The specimens concur well with the species description. They have a dull, mottled brown colour. At St Pierre it is one of the most abundant ophiuroid species. It has also been observed on several reefs at La Saline.

Distribution: The species has a wide Indo-Pacific distribution, including La Réunion (Guille & Ribes, 1981) and Rodrigues (Rowe & Richmond, 2004).

FAMILY OPHIONEREIDIDAE LJUNGMAN, 1867

GENUS *OPHIONEREIS* LÜTKEN, 1859

OPHIONEREIS PORRECTA LYMAN, 1860

(FIG. 5C, D)

Material: Two spms (dd = 5 and 12 mm); La Saline reef, Trou d'Eau, back reef, by D. Taddei iii.2002; La Saline reef, outer slope, with *Montipora* spp., 30 m, by S. Ribes, 07.x.1977.

Comments: The specimens have a mottled brown colour; the larger specimen, in particular, shows the dark markings described by Cherbonnier & Guille (1978). This colour form has also been reported from Rodrigues (Rowe & Richmond, 2004). Otherwise they accord with the diagnosis of the species.

Distribution: Tropical Indo-west Pacific, Australia and Tasman Sea (Rowe & Gates, 1995); La Réunion (Guille & Ribes, 1981) and Rodrigues (Rowe & Richmond, 2004).

FAMILY OPHIOCOMIDAE

GENUS *OPHIOCOMA* L. AGASSIZ, 1835

Comments: The genus *Ophiocoma* contains many similar species, which are difficult to distinguish and probably include unknown species (T. O'Hara, pers. comm.). In particular, young specimens may be difficult to identify, because key characters include the number of arm spines, which increases during growth and overlaps between different stages of different species (Devaney, 1970). Likewise, the dorsal arm plate is usually longer and narrower in juveniles than in adult ophiuroids (Sumida *et al.*, 1998; Stöhr, 2005).

OPHIOCOMA BREVIPES PETERS, 1851

(FIG. 5E, F)

Material: Twelve spms (dd = 7–18 mm); Etang Salé reef, Four à Chauv, iii.2006, by E. Boissin.

Comments: The smaller specimens (dd = 7–8 mm) possess five spines on the fifth and sixth arm joints, four spines on several following joints, then three. They have a variegated dark brown and white colour pattern on the disc, mostly brown arms and annulated spines.

The larger specimens bear four long spines at their proximal arm joints, which are variegated or somewhat annulated. A short distance from the disc the number of spines decreases to three.

Some of these individuals may belong to *O. doederleini* De Loriol, 1899, although that species is described as having a grey colour with dark spots or a reticulated pattern. The final number of arm spines is most likely not yet present in the smallest specimens, but the already relatively high number on their proximal joints suggests that they may be a different species from the larger specimens. The coloration perhaps changes during development. This species is also closely related to *O. dentata* Müller & Troschel, 1842, from which it differs in having five instead of four spines on the sixth arm joint, a greater number of spines for a longer distance along the arm, and in having annulated spines (Devaney, 1970). These

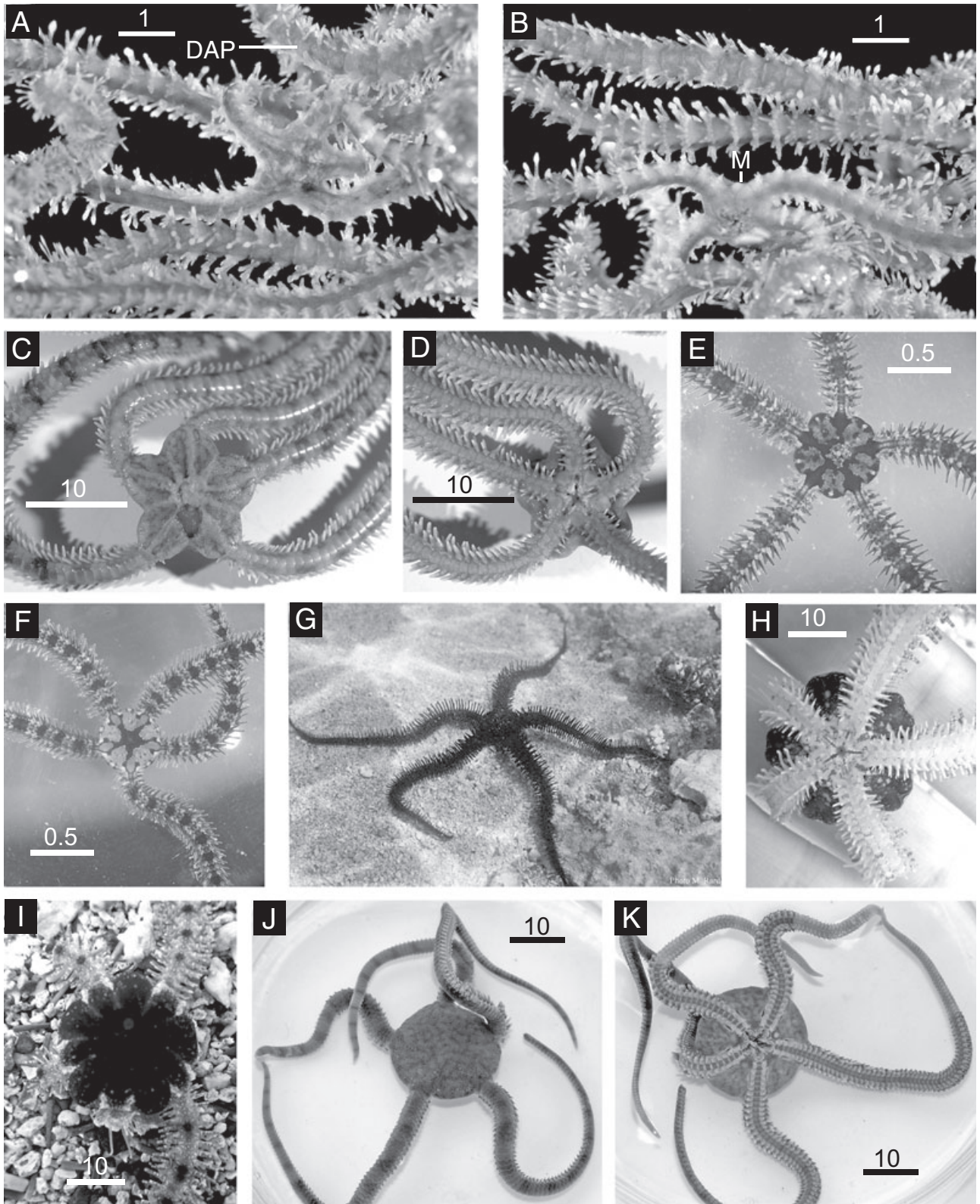


Figure 5. Digital images of common reef ophiuroids at La Réunion. A, *Ophiocanops multispina*, holotype, dorsal view, in alcohol, before preparation for SEM, note the tiny disc and long curling arms; B, same specimen, ventral view, note the lateral madreporite; C, *Ophionereis porrecta* (photos by A. Cerou), dorsal view; D, same specimen, ventral view; E, F, *Ophiocoma brevipes/doederleini*, live specimens, dorsal view; G, *Ophiocoma erinaceus*, *in situ* (photo by M. Rard); H, I, *Ophiocoma scolopendrina*; H, live specimen, ventral view; I, *in situ*, dorsal view (photos by T. B. Hoareau); J, *Ophioplocus imbricatus*, dorsal view; K, same specimen, ventral view. Abbreviations: DAP, dorsal arm plate; M, madreporite. Scale bars in millimetres.

brown species are very difficult to distinguish in the field, although they are very common, with densities of 2 per 10 m² at La Saline, Trou d'Eau BR and Planch'Alizé BR, and 0.3 per 10 m² at Tobogan BR (C.C., pers. observ., not collected). It is also possible that some of these specimens represent an unknown species, which cannot be resolved without a revision of the genus.

Distribution: Tropical Indo-Pacific, north-eastern Australia, Tasman Sea (Rowe & Gates, 1995); La Réunion (Guille & Ribes, 1981) and Rodrigues (Rowe & Richmond, 2004).

OPHIOCOMA ERINACEUS MÜLLER & TROSCHEL, 1842 (FIG. 5G)

Material: Twelve spms (dd = 3–28 mm); Etang Salé reef, Four à Chaux, among *Millepora* spp., iii.2006, by E. Boissin; La Saline reef, Trois Chameaux IRF, i.1993, Trou d'Eau BR iii.2002, Planch Alizé BR iii.2002, and Cap Homard reef flat ii.1993, by C. Conand; La Saline reef, outer slope, 10 m, with *Galaxea*, by S. Ribes, 08.viii.1977.

Comments: This species is always black. The specimens concur well with the diagnosis of the species. The number of arm spines alternates between three and four on consecutive joints on some specimens more regularly than on others. The dorsal arm spine is longer than the other spines in the largest specimens, shorter in small specimens. On some individuals several proximal arm joints bear five spines. This species is both very common in rubbles, on many reefs in La Reunion and very abundant, with densities of 0.5 per 10 m² at Trou d'Eau and 1 per 10 m² at Planch Alizé (C.C., pers. observ.).

The smallest specimen (3 mm dd), collected by S. Ribes, lacks disc granules and the dorsal arm spines are distinctly thickened. According to Devaney (1970), each species in the *scolopendrina*-group, to which *O. erinaceus* belongs, develops disc granules at a specific size, which in this species would be 7.5 mm dd. The closely related *O. scolopendrina* develops disc granules at 2.5 mm dd, which confirms the identity of the small specimen. In addition, the colour pattern

and the shape of the oral shield are more similar to the other specimens of *O. erinaceus* than to *O. scolopendrina*.

Distribution: Common in the shallow coral reef zone of the tropical Indo-West-Pacific, except the Gulf of Persia, Pakistan and the west coast of India (Schoppe, 2000); La Réunion (Guille & Ribes, 1981) and Rodrigues (Rowe & Richmond, 2004).

OPHIOCOMA SCOLOPENDRINA (LAMARCK, 1816)
(FIG. 5H, I)

Material: One spm (dd = 25 mm); La Saline reef, Planch' Alizé BR iii.2002 by D. Taddei.

Comments: Live specimens show a dark brown disc and yellow arms, while the arms in preserved specimens turn brownish. There is a dense dark brown reticulating pattern on the dorsal arm plates, distal on the arms with a more spotted pattern. The arm spines are banded to reticulated, alternating in number between three and four on neighbouring joints, but the same number on both sides of a joint. The dorsal spine is thicker than the others. The oral shield and the ventral arm plates also have a reticulated brown pattern, while the lateral arm plates have fine dark bands and small spots.

Distribution: Common in tropical shallow reef zones and intertidal; Red Sea, Indo-Pacific (Schoppe, 2000); new record for La Réunion and Mascarenes.

GENUS *OPHIOCOMELLA* A.H. CLARK, 1939
OPHIOCOMELLA SEXRADIA (DUNCAN, 1887)

Material: One spm (dd = 3 mm); La Saline reef, with *Acropora*, S. Ribes, 30.vii.1977.

Comments: This specimen has six arms of equal size, without signs of regeneration, although the species is known to be fissiparous (Wilkie, Emson & Mladenov, 1984). It accords well with the specimen of similar size described by Clark (Clark & Rowe, 1971). The dorsal disc is sparsely covered with short, blunt, slightly rugose spinelets; the arm spines are of equal size and finely serrated. According to Clark (Clark &

Rowe, 1971), the disc spinelets are reduced to granules in larger specimens. The key in Clark & Rowe (1971) distinguishes this species from *Ophiomastix sexradiata* A.H. Clark, 1952, but which is now regarded as a synonym (Devaney, 1970).

Distribution: Littoral to 15 m, tropical Indo-Pacific, Australia, Tasman Sea (Rowe & Gates, 1995); La Réunion (Guille & Ribes, 1981) and Rodrigues (Rowe & Richmond, 2004).

GENUS *OPHIOPSILA* FORBES, 1843

OPHIOPSILA PANTHERINA KOEHLER, 1898

Material: Three spms (dd = 3–5 mm); La Réunion, S. Ribes, no locality data.

Comments: This species can be distinguished from the other Indo-Pacific species *O. paucispina* Koehler, 1907 by its greater number of arm spines (Clark & Rowe, 1971). The specimens at hand have five to six, on few joints seven, spines, while *O. paucispina* has only four. The coloration in alcohol has faded, but a mottled red pattern is still visible on two of the specimens.

Distribution: Type locality is Burma, Andaman Sea; after synonymization with *O. gilletti* Kingston, 1980, also Great Barrier and Swain Reefs (Rowe & Gates, 1995), Australia; new record for La Réunion and Mascarenes.

FAMILY OPHIODERMATIDAE LJUNGMAN, 1867

GENUS *OPHIOCONIS* LÜTKEN, 1869

OPHIOCONIS CUPIDA KOEHLER, 1905

Material: Thirty-seven spms (dd = 3–4 mm); collected by S. Ribes, but no locality data on the label.

Comments: Clark & Rowe (1971) suggested that *O. cupida* may be a synonym of *O. cincta* Brock, 1888, along with *O. permixta* Koehler, 1905. The main difference between these three species is in the disc armament, which consists of a dense coat of granules in *O. cupida*, marginal rod-like spines in addition to granules in *O. cincta*, and scattered spines all over the disc with granules in *O. permixta* (Clark & Rowe, 1971). Later, Rowe, in Rowe & Gates (1995), repeated that suggestion, but no formal revision has yet been published. In the same volume, an unfortunate misspelling (F. W. E. Rowe, pers. comm.) of the genus as *Ophioconus* occurred, which has led to some confusion in later publications. The valid name is *Ophioconis* and any other spelling is discouraged.

The specimens from La Réunion all have only granules, no spines, which matches the current diagnosis

of *O. cupida*. The largest specimens measure about 4 mm dd, which is the same size as the type of that species (Koehler, 1905). Both *O. permixta* and *O. cincta* grow to a larger size (Koehler, 1905). However, the maximum size of these species is not known and the diagnostic value of size differences between them has not been shown.

Distribution: West Indian Ocean, west-central Pacific, north-eastern Australia (Rowe & Gates, 1995); new record for La Réunion and Mascarenes.

DISCUSSION

FAUNAL COMPARISONS

Guille & Ribes (1981) reported 20 species of ophiuroid and an unidentified *Ophiactis* from La Réunion. Among these the Ophiocomidae were represented by five species and the Ophiothricidae by four. The latter are absent in the present study, except for a small juvenile, which may perhaps be due to differences in collecting mode. New records for La Réunion include *Ophiocanops multispina* sp. nov., *Ophiocoma scolopendrina*, *Ophiopsila pantherina*, *Ophioconis cupida* and *Amphioplus* sp. We collected a single species of Ophiuridae, which were represented by three species in the report by Guille & Ribes (1981). The total number of reef ophiuroids known from La Réunion thus increases to 25. No basket stars have yet been documented from La Réunion, although they have been observed (R. Troadec, pers. comm.). Thus, the number of species will probably increase with further sampling. Not surprisingly, there is no overlap between this shallow-water fauna and the deep-water fauna on the slopes of the island, where another 20 species, all belonging to the families Ophiuridae and Ophiolepididae, have been recorded (Vadon & Guille, 1984). The deepest species recorded among our samples is *Amphioplus* sp. from 160 m outside the reef zone, not previously reported from the area and possibly undescribed.

Compared with the neighbouring island of Rodrigues, from which 17 species of ophiuroid are known (Rowe & Richmond, 2004), La Réunion has a more diverse fauna. However, both islands share only nine species, which is probably due to the still limited collecting effort, and future studies may find additional species at both islands.

The discovery of *O. multispina* emphasizes the importance of black coral as hosts for other species. Several brittle stars are now known to be associated with antipatharians, both species of *Ophiocanops* and *R. felli*, several species of *Astrogymnotes* H.L. Clark, 1914 from Australia, New Zealand and Japan (Baker, Clark & McKnight, 2001), and *Astrobrachion constrict-*

tum (Farquhar, 1900) from New Zealand (Grange, 1991). Anthipatharians are deep-water coral, usually difficult to access and threatened by overexploitation. The coral population that hosts *O. multispina* is, at a depth of 50 m, just within scuba diving range, which may allow future studies of the ecological relationships between the brittle star and its coral host.

Ophiocoma continues to be a problematic taxon with poorly delimited species and most probably species-complexes. A thorough revision including molecular characters is highly desired.

SYSTEMATIC POSITION OF *OPHIOCANOPS*

The phylogenetic relationships of *Ophiocanops* have been the subject of recurring discussions during the over 80 years since the discovery of the first species. Based on the thickened integument, the reduction of the skeleton and an interpretation of the vertebral articulation as zygospondylous, Koehler (1922) placed his new genus within Ophiomyxidae. Mortensen (1933) erected a separate family Ophiocanopidae to accommodate the unique features of gonads and stomach extending into the arms. He also interpreted the vertebral articulation as streptospondylous and saw *Ophiocanops* as a highly specialized and modified form. Fell (1962) argued instead that *Ophiocanops* is an archaic form, a member of the otherwise extinct Oegophiurida, based on the extension of gonads and stomach into the arms and on the absence of oral shields, and dorsal and ventral arm plates. However, as Hotchkiss (1977) pointed out, the non-madreporic oral shields are present in the holotype of *O. fugiens*, albeit tiny and in a lateral, almost dorsal position. The same is true for *O. multispina*. Ontogenetically, the oral shields and madreporite appear in a dorso-lateral position in many extant ophiuroids (Sumida *et al.*, 1998; Stöhr, 2005), which contradicts Fell's (1963) opinion that only Oegophiurida have lateral madreporites. However, as Hotchkiss (1977) suggested, the lateral position of the oral shields in *Ophiocanops* is most probably caused by the lack of space on the minute ventral interradial disc, which is occupied by the large adoral shields. Similarly, the positions of the gonads and stomach extensions in the arms are most likely a consequence of the diminutive size of the disc.

Ophiocanops multispina has a more complete skeleton than *O. fugiens*, including disc scales and dorsal arm plates, which suggests that for ophiuroids the absence of some typical skeletal elements is a consequence of reduction rather than an archaic condition. Radial shields are lacking in some other genera, such as the ophiacanthid *Ophiomyces* Lyman, 1869 and the ophiomyxid *Ophioscolex glacialis* Müller & Troschel, 1842, which may be why in both taxa the arms are

often found to stand erect above the disc, at least in preserved material. The stabilizing function of the radial shields is probably not needed when the disc is extremely small as in *Ophiocanops*, which may have led to their reduction and complete loss. The loss of dorsal plates on the proximal arm is common among Ophiomyxidae, and their replacement with strong connective tissue in *Ophiocanops* allows for a flexible chamber, which can accommodate the increasing size of maturing gonads. This gonadal chamber is best developed in *O. fugiens*, in which it is supported by the dorsal arm spine. In *O. multispina*, the dorsal arm plates are thin and glassy, but not yet completely reduced, while *O. fugiens* has lost them completely, again suggesting that the latter is more specialized and derived than the former.

Smith *et al.* (1995) noted that the articulation facets of ophiuroid vertebrae (usually divided in streptospondylous and zygospondylous types) are a difficult character for phylogenetic considerations. Both articulation types may occur within the same family and streptospondylous articulations are often found in epizoid forms, suggesting that their evolution may be driven by ecological adaptation. As the shape of the vertebral articulation found in *Ophiocanops* is present in several other taxa, we consider this a character of low significance for the systematic placement of the genus. The shape of the long arm spines of *O. multispina*, with its composition of several rods, resembles the spines of *Ophioscolex glacialis* and thus may suggest ophiomyxid affinities. However, the arm spine articulation is quite different between these taxa (A. Martynov, pers. comm.), although the taxonomic value of this character has not yet been shown. The tiny disc of *Ophiocanops* may perhaps have evolved as an adaptation for reducing predation pressure. Upon examination of our specimens we found that the disc is difficult to detect, as it is hardly more than a junction of the extremely long arms (Fig. 4A, B). A predator may have the same difficulties; and as long as the disc is protected, the ophiuroid can easily replace lost arms.

The description of *Renetheo felli* appears to have been based on more than one specimen without clearly separating the holotype. The pictures, which are labelled as showing the holotype, in fact show at least two different specimens. The holotype is the specimen shown dried, while the SEM image shows what may be a paratype, although it is unclear to which lot it belongs. Whether the vertebra originates from the holotype or a different specimen cannot be deduced from the material. According to McKnight (2003), the gonads of *R. felli* are restricted to the disc. However, in the dried holotype, globules are visible beneath the collapsed translucent skin on the proximal dorsal arm, which are probably gonads. It seems

unlikely that gonads would fit entirely inside the tiny disc of the species and the existence of a dorsal arm chamber suggests that the gonads indeed extend into the arms. Its strong and thorny dorsal arm spine lies across the arm, similar to *O. fugiens*, providing protection, but without supporting the skin. The number and shape of the arm spines of *R. felli* are more similar to *O. multispina* than to *O. fugiens*. McKnight (2003) described the vertebral articulation of *R. felli* as similar to *Astrogymnotes*, but the photograph shows a much longer vertebra than those of that genus (S. Stöhr, unpubl. data). *Astrogymnotes* has a modified zygospondylous vertebral articulation type (Mortensen, 1933), different from *Ophiocanops*. Examination of the single vertebra of *R. felli* prepared by McKnight showed that it is similar to those of *Ophiocanops* but not to *Astrogymnotes*. Both species of *Ophiocanops* and *R. felli* are associated with antipatharian corals and have never been found on another host or substrate. The three species are clearly closely related and appear to represent an evolutionary line with progressive reduction of the skeleton, in which *R. felli* has the most complete skeleton and *O. fugiens* the most reduced (Table 2).

McKnight (2003) placed his new genus in the family Ophiomyxidae, noting only a superficial resemblance to *Ophiocanops*, and based his decision on the fact that *Renetheo* has a more complete skeleton, as well as his erroneous interpretation of the presence of genital slits and lack of gonads and intestine in the arms. According to current understanding, Ophiomyxidae are characterized by a thick skin, covering dorsal and ventral disc surfaces, as well as arms and arm spines, while disc scales, radial shields and dorsal and ventral arm plates are often reduced (Ljungman, 1967; Paterson, 1985). Apart from the absence of genital slits and the extension of gonads and intestine into the arms (a character which is not part of the current family definition), *Ophiocanops* falls well within this definition. As the position of the gonads is probably caused by the small size of the disc, which is possibly an ecological adaptation, we regard this character as valuable on generic level, but not on familial level. The discovery of *O. multispina* appears to close the gap between *Renetheo* and *Ophiocanops* and we conclude that *Ophiocanops* is a highly specialized member of the Ophiomyxidae. Moreover, as the absence of gonads (and possibly intestine) from the arms of *Renetheo* as well as the presence of genital slits can no longer be maintained and the skeletal differences are minor, we propose to regard it as a junior synonym of *Ophiocanops*. However, the Ophiomyxidae are most likely a paraphyletic group (Smith *et al.*, 1995), e.g. poorly delimited from the ophiacanthid subfamily Ophiotominae (Paterson, 1985), and in need of revision, which may also shed

more light on the phylogenetic relationships of *Ophiocanops*. Unfortunately, our attempts to obtain molecular data from the specimens of *O. multispina* were unsuccessful, probably due to their initial preservation. Molecular data suggest that *Ophiocanops fugiens* may be a sister taxon to *Ophiomyxa* and both have been placed well within the Ophiuroidea (Littlewood *et al.*, 1997), which supports the inclusion of *Ophiocanops* in Ophiomyxidae and questions the current basal position of the family. A close relative of *Ophiocanops* may be the ophiomyxid *Astrogymnotes*, which has a small disc, but not as tiny as in the other two genera, and lacks dorsal arm plates (Mortensen, 1933). All known species of that genus are associated with antipatharians (Baker *et al.*, 2001) and at least one of them, *A. catasticta* H.L. Clark, 1914, has been found in sympatry with *O. fugiens* (Mortensen, 1933).

Fell's (1963) interpretation of *O. fugiens* as an archaic form was based on the absence of characters rather than the presence of unique apomorphies. The missing dorsal and ventral arm plates were interpreted as homologous to the oegophiurid state. In our view, this condition is instead due to homoplasy. Furthermore, Fell (1963) modified the definition of Oegophiurida based on the conditions found in *O. fugiens*. Prior to the discovery of *O. fugiens* and following Matsumoto's (1915) original definition, Oegophiurida were characterized by having an open ambulacral groove in addition to lacking many skeletal elements. Given that in *O. fugiens* the ambulacral groove is closed over by connective tissue and Fell (1962, 1963) interpreted the species as an oegophiurid, he concluded that the fossil forms also must have had the same feature and amended the definition of the group accordingly. Now that the open ambulacral groove is no longer a requirement, *O. fugiens* fits nicely in Oegophiurida. Although we cannot rule out that fossil forms did indeed have an ambulacrum closed over by tissue, we feel that the resulting circular argument is unsatisfactory. Hotchkiss (1977) laid out the arguments expertly and concluded that *Ophiocanops* is not an oegophiurid, but maintained the Ophiocanopidae and placed them in the order Phrynophiurida, suborder Ophiomyxina. Taking into account the additional morphological data from *O. multispina* and *Ophiocanops felli* comb. nov., we see no further reason to maintain the Ophiocanopidae as sister taxon to all modern ophiuroids as proposed by Smith *et al.* (1995), and the Oegophiurida are again an entirely Palaeozoic, extinct group. However, further study is needed to resolve the systematic position of the Ophiomyxidae.

It would be highly desirable to study the reproduction and ontogeny of *Ophiocanops* to find additional clues to its phylogenetic relationships, but thus far no juveniles of any of these species have been found and

it is not known if the development is through a planktotrophic or lecithotrophic larva. The best studied brittle star species associated with black coral (*Antipathes* spp.) is *A. constrictum* from New Zealand. Recruitment appears to be low in that species, as is typical for deep-sea brittle stars (Stewart & Mladenov, 1997). The same may be true for *Ophiocanops* and long-term monitoring at close intervals of an accessible population may be necessary to find juvenile specimens and to identify the reproductive season.

ACKNOWLEDGEMENTS

We are grateful to collectors D. Taddei, L. Bigot and M. Gallas for submitting their material to this study, to T. B. Hoareau for help in sampling at Etang Salé reef, and to H. Zibrowius for bringing the misplaced samples of *S. Ribes* to our attention. Photographs were taken in the field by M. Rard and T. B. Hoareau, and from preserved samples by A. Cerou. Many thanks to C. Ahearn and D. Pawson, Smithsonian Institution, Washington, DC, for the loan of the holotype of *O. fugiens*, to K. Schnabel at NIWA, Wellington, for the loan of the types of *R. felli*, to A. Cabrinovic at the Natural History Museum, London, for lending out the material of *Amphioplus* sp. from Rodrigues, and to F. Rowe, who submitted that material to London. S.S. thanks F. Hotchkiss, A. Martynov and F. Rowe for insightful discussions. The SEM imaging was financially supported by Riksmusei Väner, Stockholm.

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