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New records and new species of Ophiuroidea (Echinodermata) from Lifou, Loyalty Islands, New Caledonia

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Abstract

New Caledonia is a species-rich region that has been the focus of biodiversity research for over 40 years. The expedition "Atelier Lifou 2000" collected benthic fauna at the island of Lifou, Loyalty Islands, New Caledonia, in November of 2000. This is a taxonomic account of the brittle stars found. 94 species were identified, 51 of them new for the region, and seven new to science, increasing the total number of species known from the New Caledonia region to 204. New species are described in the genera *Squamophis*, *Astroceras*, *Astrogymnotes*, *Ophiochondrus*, *Ophiomoeris*, *Ophiozonella* and *Amphipholis*. Three species and a subspecies are revised, one of them placed in a new genus. The taxonomic status of *Euryale* Lamarck, 1816, a junior homonym of *Euryale* Péron & Lesueur, 1810 (a medusa), is stabilized by formally establishing precedence over the senior name.

Key words: brittle stars, taxonomy, nomenclature, scanning electron microscopy, morphology

Introduction

New Caledonia is a particularly species rich area, a so-called "hotspot" of biodiversity. Since 1977, a concerted effort has been made to study the biochemistry, geology and biology of the sea around New Caledonia (Richer de Forge 1990). A recent study (Bouchet *et al.* 2002) found 2738 species of marine molluscs on a 295 km^2-site on the west coast of the main island, Grande Terre, the highest number ever recorded anywhere in the world. Brittle stars, with currently about 2200 described species worldwide (Stöhr & O'Hara 2007) are a comparatively small group and not considered a key indicator taxon for biodiversity assessments of tropical areas, but 146 species have so far been reported from New Caledonia (Ameziane 2007). Many of these have been found only once and/or in small numbers. The true richness of the ophiuroid fauna around New Caledonia is still unknown. This reflects the global situation, since in the past decade on average seven species a year have been described as new (Stöhr & O'Hara 2007), even from well-studied regions such as the North Atlantic Ocean.

Previous expeditions covered the continental slope of Grande Terre, the Loyalty Ridge and seamounts to the east, the Norfolk Ridge and the area around the Chesterfield Islands (Bouchet *et al.* 2008). Part of the ophiuroid fauna collected has been reviewed by O'Hara & Stöhr (2006). Two expeditions have previously collected benthic fauna at Lifou, the largest of the Loyalty islands, MUSORSTOM 6 off its northwest and east coasts (Richer de Forge 1990) and CALSUB in the Bay of Santal and off the north coast (Roux 1994). These expeditions collected mainly at greater depth, from several hundred to almost three thousand metres. In 2000, an expedition to Lifou was

carried out as part of the "Our Planet Reviewed... Taking a Closer Look at Biodiversity Hotspots" programme, organized and lead jointly by the Muséum national d'Histoire naturelle, Paris, and the Institut de Recherche pour le Développement (IRD), Noumea.

The Loyalty Islands are situated on the Loyalty Ridge, separated from New Caledonia by a 2000 m deep trench. Unlike Grande Terre, which is surrounded by a lagoon, Lifou is a raised atoll, lacking an extensive continental shelf zone, with steep coral reefs ascending from great depth. Due to this geomorphological difference it was suspected that the fauna at Lifou may contain more deep water species at shallower depths and fewer littoral ones. The expedition “Atelier Lifou 2000” targeted mainly shallower areas, focussing on a single site, the Bay of Santal, collecting benthic marine species, mainly invertebrates, during the month of November, 2000. This study is an account of the Ophiuroidea collected, with taxonomic remarks on problematic taxa and description of seven new species.

Material and methods

The main study site was the Bay of Santal at the northwest coast of the island of Lifou, with a few additional samples collected in the Bay of Chateaubriand at the east coast (Fig. 1). Brittle stars were collected with a suction pump handled by divers, by dredging at sites too deep for diving, and by hand collecting at low tide (Table 1). Most samples were preserved directly in 80% ethanol, some in 95% ethanol. The samples from stations DW1650 and DW1650C where initially fixed in a 4% formaldehyde-sea water solution and later transferred to 80% ethanol. After transport to the Swedish Museum of Natural History, the samples were sorted and the species identified using overviews and keys (Fell 1960; Devaney 1970; Clark & Rowe 1971; Devaney 1974a, 1978; Liao & Clark 1995) and a variety of original descriptions (Koehler 1897, 1905, 1911, 1922, 1930; Baker 1980; Baker *et al.* 2001; Hoggett 2006).

To document colour patterns, some animals were photographed with a digital camera, mounted on the ocular tube of a dissecting microscope. Small specimens and microstructures were examined with a scanning electron microscope (SEM) Hitachi FE-4300. For SEM examination, whole animals were bleached in a 1:1 solution of household bleach (NaOCl) diluted with tap water for about 10–20 seconds to remove the outer layers of the integument. Skeletal elements were isolated by dissolving all soft tissue in undiluted bleach. After bleaching, animals and skeletal parts were washed in tap water, remaining tissue was removed with a small artist brush and the specimens were mounted wet, or after air drying, on aluminum stubs with semi-permanent spray glue (Geiger *et al.* 2007). Holotypes and single specimens were mounted this way, examined and photographed by SEM, then the glue was dissolved with butyl acetate to free the animal, which was cleaned from glue residue and remounted with the opposite side exposed for further SEM examination. A specimen each of *Ophionereis degeneri* (A.H. Clark, 1949) and *Ophionereis porrecta* Lyman, 1860 were first examined externally from dorsal and ventral side and then dissected in bleach as described to prepare the internal skeleton. The holotype of *Ophiomoeris exuta* **sp. nov.** was submerged in 99% ethanol for an hour after bleaching, then in butyl acetate over night, to prevent the naked interradial disk from collapsing and contracting when the specimen dried. To preserve potentially valuable information, of colourful new species represented by single specimens only arm pieces were dissected and subjected to SEM treatment.

All holotypes have been deposited at the Muséum national d'Histoire naturelle in Paris; paratypes and all non-type material are kept at the Swedish Museum of Natural History in Stockholm, if not indicated otherwise below.

Abbreviations

dd—disk diameter
MNHN—Muséum national d'Histoire naturelle, Paris, France
MoV—Museum of Victoria, Melbourne, Australia
NSMT—National Science Museum, Tokyo, Japan
spm, spms—specimen(s)
SMNH—Swedish Museum of Natural History, Stockholm, Sweden
sta.—station
ZMA—Zooloogisch Museum Amsterdam, The Netherlands

TABLE 1. Collecting stations from the expedition "Atelier Lifou 2000", in New Caledonia, Loyalty Islands, Lifou Island, at which ophiuroids have been collected.

Station	Locality	Latitude	Longitude	Depth [m]	Bottom	Collecting method	Collecting date
1406	Baie du Santal, around dock	20° 46'S	167° 07'E	0-2	subtidal coral platform		2000-11-10 –18
1410	Baie du Santal, between Jua Wekutr and Jua Wajez	20° 56'S	167° 03'	2-4	edge of coral platform		2000-11-25
1411	Baie du Santal, off Kiki	20° 47'S	167° 10'E	4-8	sand		2000-11-24
1413	Naie du Santal, beach off Drueulu	20° 55'S	167° 05'E	3-10	loose bottom		2000-11-15/ 18/ 26/ 27
1415	Baie du Santal, off Chépénéhé	20° 47'S	167° 09'E	3-7			2000-11-25
1418	Baie de Santal, W of Pointe d'Easo, wharf	20° 46'S	167° 07'E	1-5	sand and plant matter		2000-11-11/ 21–25
1420	Baie du Santal, Pte de Chépénéhé	20° 47'S	167° 09'E	4-5	sediment-covered rocks	scuba	2000-11-19
1421	Baie du Santal, between Huca Hutghé and Cúte Islands	20° 52'S	167° 08'E	4	rocks and coral heads covered by sand	scuba	2000-11-26
1422	Baie du Santal, small bay east of Point Easo	20° 47'S	167° 07'E	4	sand on rocks and coral heads		2000-11-01
1423	Baie du Santal, off Peng	20° 54'S	167° 07'E	12	sandy passages between coral heads		2000-10-14
1429	Baie du Santal, east of Point Easo	20° 47'S	167° 07'E	8-18	coral heads		2000-11-01
1431	New Caledonia, Loyalty Islands, Baie du Santal, east of Pte d'Easo	20° 47'S	167° 07'E	18-35			2000-11-03–24
1432	Baie du Santal, SE of Pte d'Easo	20° 53'S	167° 02'E	12-32	sand and coral rubble		2000-11-01
1433	Pte d'Easo	20° 47'S	167° 07'E	12-17	below precipice; coral blocks and debris	scuba	2000-11-01
1440	Baie du Santal, Chépénéhé	20° 47'S	167° 08'E	15-35	coral heads and canyons	scuba	2000-11-14
1441	Baie du Santal, Cape Aimé Martin (=Acadro)	20° 46'S	167° 02'E	20	rocks		2000-10-13
1446	E of Baie du Santal, Mepinyö	20° 50'S	167° 09'E	36-40		suction	2000-11-16
1448	Baie du Santal, N of Cap Aimé Martin (=Acadro)	20° 45'S	167° 01'E	20	hard bottom	suction	2000-11-17
1449	Baie du Santal, N of Cape Aimé Martin (=Arcado)	20° 45'S	167° 01'E	17	rocks	rock-wash	2000-11-17
1450	N of Cap Aimé Martin (=Acadro)	20° 45'S	167° 01'E	27-31	rocks and coral	rock-wash	2000-11-17 / 21
1451	W of Pte dÉaso, second coral head	20° 47'S	167° 06'E	10-21		rock-wash	2000-11-19
1452	entrance Cap Lefévre and Cap Mandé	20° 54'S	167° 02'E	2-25			2000-11-20
1453	entrance Cap Mandé and Cap Lefévre	20° 54'S	167° 02'E	2-25		rock-	2000-11-01
1454	S of Pointe Lefèvre (=Nem)	20° 56'S	167° 02'	15-18	rocky precipice		2000-11-23

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TABLE 1. (continued)

Station	Locality	Latitude	Longitude	Depth [m]	Bottom	Collecting method	Collecting date
1455	Baie du Santal, between Cap Wekutr and Cap Wajez	20° 56'S	167° 02'E	15-20		Scuba	2000-11-25
1456	NE Baie du Santal, at level of Cila	20° 49'S	167° 10'E	25-30	precipices		2000-11-01
1457	Baie du Santal, off Ngoni beach	20° 46'S	167° 02'E	5-10	sand, rocks		2000-11-27
1459	Baie du Santal, off Ngoni beach	20° 47'S	167° 03'E	55-80		dredging	2000-11-05/13
1461	reef Shelter	20° 54'S	167° 02'E	100-120		dredging	2000-11-01
1462	SE of Aimé Martin, edge (aréte)	20° 47'S	167° 01'E	70-120		dredging	2000-11-21
1464	Baie du Santal, Peng	20° 54'S	167° 05'E	35-50	calcareous algae	dredging	2000-11-14
1465	Pte Easo	20° 47'S	167° 07'E	35-45	rocks and coral	dredging	2000-11-16
1466	Baie du Santal, Baie d'Huneti	20° 46'S	167° 06'E	25-45	coral boulders	dredging	2000-11-17
1467	off Hunetë	20° 46'S	167° 02'E	90		dredging	2000-11-20
1468	off Huneteë	20° 46'S	167° 05'E	30-80		dredging	2000-11-20
1469	off Cap Lefévre, bank	20° 54'S	167° 00'E	70-130		Warén dredge	2000-11-22
1472	Baie de Chateaubriand, Wé	20° 54'S	167° 16'E	0-1		manual	2000-11-24
1475	S of Bay de Chateaubriand, Traput	20° 55'S	167° 19'E	subtidal			2000-11-11
CP1646	off Cap des Pins	21° 02'S	167° 31'E	420-480			2000-11-24
DW1648	SE of reef Shelter	20° 54'S	167° 03'E	150-200		dredging	2000-11-01
DW1650	SW of reef Shelter	20° 54'S	167° 01'E	120-250	sand bottom	dredging + beam trawl	2000-11-18
DW1650C	SW of reef Shelter	20° 54'S	167° 01'E	200-260	sand bottom	dredging + beam trawl	2000-11-20
NC00-17	Baie de Chateaubriand, reef flat at Traput (SW of Wé)	20° 55'S	167° 18'E	1-1.5	small patches of sand on reef platform, fine to coarse sand	Sediment collected by hand	2000-11-20
NC00-2	Baie du Santal, Cape Aimé Martin	20° 46'S	167° 02'E	20	sand	sediment collected by scuba diver	2000-11-14
NC00-3	Baie du Santal, Easo Village	20° 47'S	167° 08'E	0.5	seagrass with coarse sand and some corals	sediment collected by hand	2000-11-14
NC00-35	W side of island, SE of Pointe Lefèvre (S of Baie du Santal), Between Jua Wekutr and Jua Wajez	20° 56'S	167° 02'E	20-22	medium sand	sediment collected by scuba diver	2000-11-25
NC00-38	Baie du Santal, S of Pointe de Chépénéhé	20° 49'S	167° 10'E	40	poorly sorted sand	Sediment collected by scuba diver	2000-11-26
NC00-44	Baie du Santal, E of Cape Aimé Martin	20° 46'S	167° 02'E	15-18	poorly sorted, largely medium sand	Sediment collected by scuba diver	2000-11-27
NC00-8	Baie du Santal, Mepingö	20° 50'S	167° 10'E	4-9	patches of coarse to medium sand in coral reef	Sediment collected by scuba diver	2000-11-16

Results

94 species could be identified (Table 2). This excludes some of the Ophiotrichidae, because the available keys proved insufficient for the task and even comparisons with original descriptions and comparative museum material were not always successful. Instead, this family has been selected for molecular analysis, which will be published separately. 51 species have been found for the first time in New Caledonia (Table 2) and seven species will be described below as new to science. Among the unidentified individuals are juveniles, specimens too damaged for certain identification, and possibly additional undescribed species. Some genera, such as *Ophiomusium*, are known to be in need of revision, without which a decision on the taxonomic status of putative new species should not be made. Such a revision is however outside the scope of this work. Three species will be transferred to different genera, one of them to a new genus that will be described below. Taxonomically problematic species are also discussed below.

Of the identified species, including the new species, 42 were found only once (Table 2), 32 represented by a single specimen. Of the 30 species represented by more than five specimens, 18 species had more than ten specimens, and ten species more than 20 individuals. The most common species were *Ophiocoma erinaceus* Müller & Troschel, 1842, *Ophiocoma pusilla* (Brock, 1888), *Ophiomastix variabilis* Koehler, 1905, and *Ophionereis porrecta* Lyman, 1860.

TABLE 2. Species of brittle star found at Lifou, New Caledonia. Among the unidentified specimens, recorded under their genus or family name, more than one species may be present, possibly also undescribed species, and many are juveniles. New records for New Caledonia are marked with an asterisk.

Family	Species name	Station (specimens)
Euryalidae	*Astroceras aurantiacum* **sp. nov.**	1461 (1)
	**Astroceras kermadecensis*	1462 (9)
	Euryale aspera	1433 (1), 1429 (1), 1461 (1)
Asteroschematidae	*Squamophis lifouensis* **sp. nov.**	1469 (2)
Ophiomyxidae	*Astrogymnotes oharai* **sp. nov.**	1461 (1)
	Ophiomyxa australis	1461 (1), 1466 (1), 1467 (1), DW1650C (1)
	**Ophiomyxa compacta*? (damaged)	CP1646 (4)
Ophiacanthidae	*Ophiacantha fuscina*	CP1646 (1)
	Ophiacantha serrata	CP1646 (2)
	Ophiocamax vitrea	DW1648 (1)
	Ophiochondrus variospinus **sp. nov.**	1469 (1)
	Ophiocopa spatula	CP1646 (4)
	Ophiomitra leucorhabdota	CP1646 (1)
	Ophiomitrella granulosa	CP1646 (5)
	Ophiomoeris exuta **sp. nov.**	CP1646 (5)
	Ophiomoeris obstricta	CP1646 (2)
	Ophiotreta stimulea	1461 (1), DW1650C (2)
	Ophiotreta valenciennesi	CP1646 (4)
Ophiuridae	**Amphiophiura confecta*	1461 (2), DW1650 (1), DW1650C (2)
	**Amphiophiura distincta*	1461 (2), DW1648 (8), DW1650 (15), DW1650C (10)
	**Amphiophiura insolita*	CP1646 (31), DW1648 (2), DW1650 (11)
	Ophiura micracantha	1467 (1), DW1648 (1), DW1650 (11), DW1650C (9)
	Ophiura sp.	1448 (1)
	**Ophioleuce seminudum*	DW1650C (2)
	**Ophiopallas paradoxa*	CP1646 (15)

continued next page

TABLE 2. (continued)

Family	Species name	Station (specimens)
	Ophiophycis johni	DW1650C (1)
Amphiuridae	**Amphiodia debita*	1451 (1)
	**Amphiodia (Amphispina) loripes*	1448 (1), NC00-35 (5), NC00-38 (1), NC00-44 (3)
	Amphiodia sp.	1418 (1), 1420 (3), 1432 (1), 1472 (4), NC00-8 (1), NC00-17 (1)
	**Amphioplus platyacanthus*	1418 (3)
	Amphioplus sp.	1423 (1), 1450 (2), 1451 (1), NC00-17 (6)
	**Amphipholis misera*?	1418 (2)
	**Amphipholis squamata*	1418 (8), 1449 (2), 1459 (20), 1475 (6), NC00-3 (2)
	Amphipholis tuberosa **sp. nov.**	1413 (1), 1415 (1), 1450 (2), NC00-35 (2)
	**Amphiura bidentata*	DW1650C (1)
	**Amphiura bountyia*	1461 (1)
	**Amphiura brachyactis*	1469 (1)
	**Amphiura dejectoidea*	1462 (3), 1467 (2)
	Amphiura luetkeni	1461 (9), DW1650C (1)
	**Amphiura microsoma*	1455 (1)
	Amphiura sp.	1418 (3), 1448 (1), 1450 (1), 1454 (3), 1475 (1), DW1648 (1), DW1650C (3)
	**Amphiura velox*	1449 (2), 1432 (1), 1450 (1), 1459 (1), 1462 (1)
	Ophiocentrus dilatatus	1429 (1), 1464 (2), 1467 (1), 1469 (1)
	**Ophiocentrus inaequalis*	1456 (1)
	Ophiocnida sp.	1462 (1)
	Amphiuridae	1418 (1), 1432 (1), NC00-2 (4), NC00-8 (1), CP1646 (1), DW1650C (1)
Ophiactidae	**Histampica duplicata/canescens*	uncertain, in seagrass (2)
	**Ophiactis brachyura*	1461 (3)
	**Ophiactis fuscolineata*	1461 (1)
	**Ophiactis hemiteles*	1450 (1), 1469 (2)
	**Ophiactis macrolepidota*	1429 (1), 1449 (5), 1457 (1), 1461 (1), 1469 (1)
	**Ophiactis savignyi*	1410 (1), 1420 (1), 1446 (2), 1449 (1), 1457 (1), 1469 (3)
	Ophiactis sp.	1432 (1), 1456 (1), 1469 (1)
Ophiotrichidae	**Macrophiothrix demessa*	1457 (1)
	Macrophiothrix longipeda	1456 (1)
	**Macrophiothrix lorioli*	1421 (1), 1429 (3)
	**Macrophiothrix paucispina*	1429 (1)
	Macrophiothrix propinqua	1410 (5), 1429 (3), 1449 (3), 1451 (1), 1453 (2), 1455 (9), 1457 (1), 1462 (1), 1464 (2), 1466 (1), 1467 (1)
	Macrophiothrix sp.	1410 (1)
	Ophiopteron elegans	1462 (2), 1468 (1)
	Ophiothela danae	1429 (17), 1431 (1), 1449 (11), 1452 (2), 1459 (2)
	**Ophiothrix exigua*	1466 (4)
	Ophiothrix sp.	1410 (3), 1418 (1), 1420 (4), 1421 (1), 1429 (4), 1432 (1), 1441 (1), 1449 (3), 1450 (14), 1455 (1), 1456 (7), 1457 (2), 1461 (2), 1462 (6), 1464 (7), 1466 (4), 1469 (2), DW1648 (1), DW1650C (1)

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TABLE 2. (continued)

Family	Species name	Station (specimens)
	Ophiothrix trilineata	1429 (2)
	Ophiothrix (Acanthophiothrix) purpurea	1441 (1), 1461 (2), 1462 (1), 1464 (2), 1465 (4), 1466 (1), 1468 (1), 1469 (2)
	Ophiothrix (Ophiothrix) savignyi	1466 (1)
Ophiocomidae	*Ophiocoma dentata*	1406 (3), 1456 (1)
	**Ophiocoma doederleini*	1410 (1)
	Ophiocoma erinaceus	1410 (1), 1420 (7), 1429 (1), 1441 (1), 1450 (1), 1451 (1), 1454 (1), 1455 (1), 1457 (1)
	**Ophiocoma macroplaca*	1420 (1), 1461 (1), 1469 (4), DW1648 (3)
	Ophiocoma pusilla	1410 (14), 1420 (8), 1429 (5), 1432 (5), 1440 (1), 1441 (1), 1446 (2), 1449 (4), 1450 (2), 1456 (3), 1457 (2), 1461 (1), 1464 (1), 1466 (1)
	**Ophiocoma schoenleinii*	1406 (2), 1420 (10)
	Ophiocoma scolopendrina	1406 (24), 1418 (4), 1472 (41), NC00-44 (1)
	**Ophiocomella sexradia*	1410 (1)
	Ophiomastix caryophyllata	1454 (1)
	**Ophiomastix ornata*	1461 (1), 1466 (1), DW1648 (1)
	Ophiomastix variabilis	1420 (2), 1421 (1), 1446 (1), 1449 (1), 1450 (2), 1452 (2), 1455 (1), 1456 (2), 1457 (2), 1464 (2), 1465 (1), 1466 (1)
Ophionereididae	**Ophionereis degeneri*	1450 (1), 1455 (1), 1456 (2), 1465 (3), 1467 (2)
	Ophionereis fusca	1455 (1), 1456 (1), DW1648 (1), DW1650C (3)
	Ophionereis porrecta	1411 (1), 1422 (5), 1429 (1), 1446 (2), 1450 (1), 1451 (1), 1453 (1), 1455 (1), 1456 (1), 1461 (5), 1462 (1), 1465 (6), 1466 (5), 1467 (4), 1468 (1), 1469 (1)
Ophiodermatidae	**Ophiarachna affinis*? (juveniles)	1462 (1), 1465 (1), 1466 (1)
	Ophiarachna incrassata	1432 (1)
	Ophiarachna sp. (juvenile)	1461 (1)
	Ophiarachnella gorgonia	DW1650C (2)
	**Ophiochaeta hirsuta*	1454 (1)
	Ophioclastus hataii	1429 (1), 1462 (2)
	**Ophioconis cincta*	1440 (1)
	Ophioconis cupida	1454 (1), 1461 (2), 1467 (3)
	**Ophioconis permixta*	1449 (1)
	**Ophiodyscrita acosmeta*	1456 (1)
	**Ophiopeza fallax*	1450 (1)
	**Ophiopeza kingi*	1461 (2), 1462 (2), 1466 (1)
	**Ophiopsammus yoldii*	1462 (1), 1468 (1)
Ophiolepididae	**Actinozonella texturata*	1468 (1), DW1650C (>50)
	**Ophiomusium luetkeni*	CP1646 (20), DW1650C (1)
	**Ophiomusium morio*	DW1650C (1)
	**Ophiomusium relictum*	DW1648 (5), DW1650C (4)
	**Ophiomusium scalare*	1461 (13), 1462 (1),1469 (1), CP1646 (3)
	Ophiomusium sp.	1449 (1), CP1646 (1), DW1648 (9)
	Ophiolepis sp. juv.	1454 (2)

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TABLE 2. (continued)

Family	Species name	Station (specimens)
	Ophiolepis cincta	1432 (1)
	**Ophiolepis nodosa*	1475 (3)
	Ophiolepis superba	1421 (1)
	Ophiozonella hexactis **sp. nov.**	1461 (1), 1467 (1)
	Ophiozonella sp.	1456 (1), 1440 (1)
	**Ophiozonella molesta/subtilis/insularia*	1456 (2), 1461 (4), 1462 (5), DW1648 (1)
	**Ophiozonella projecta*	1461 (2), DW1648 (1), DW1650C (7)

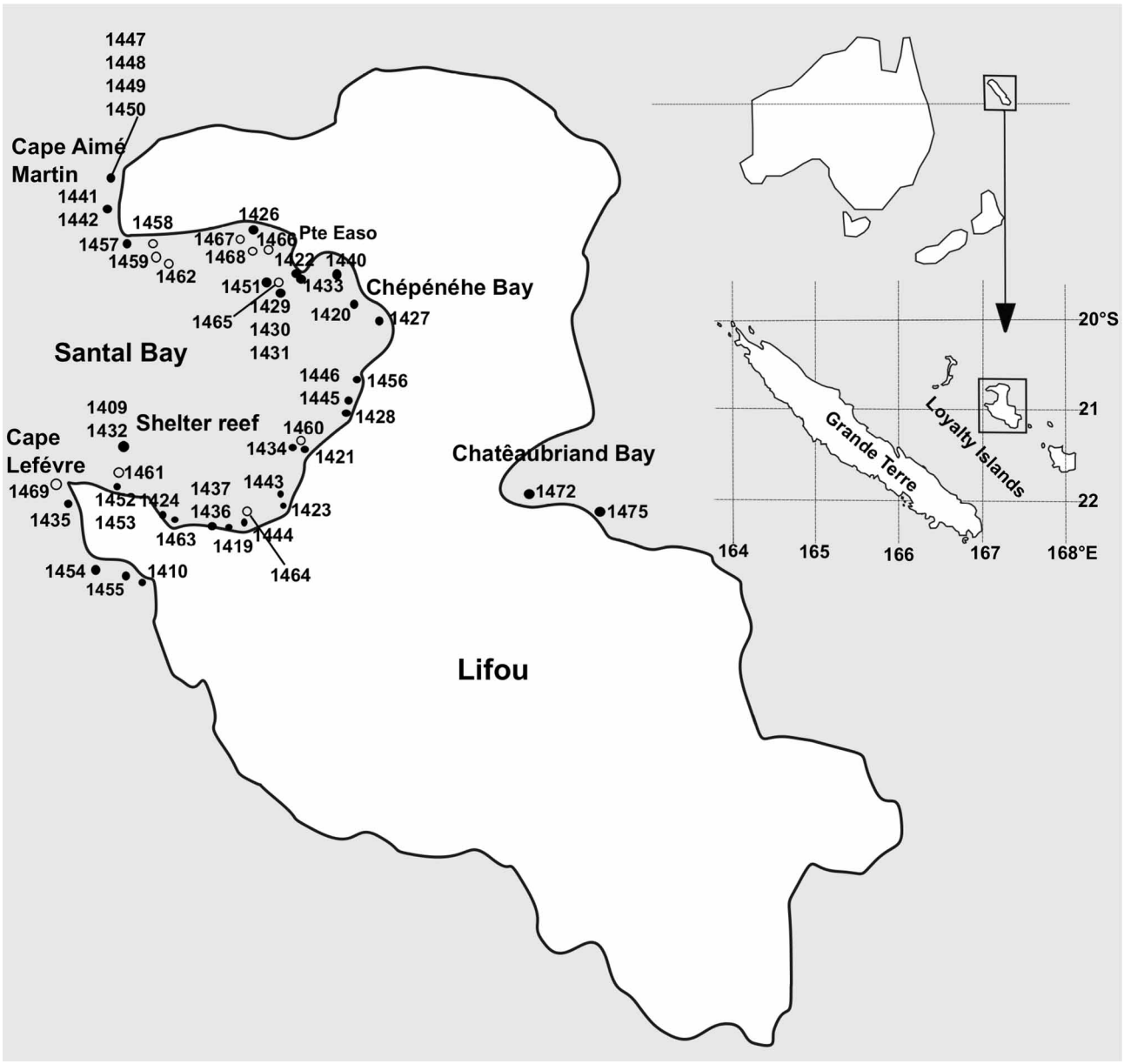

FIGURE 1. Collecting stations at Lifou, New Caledonia (NE of Australia), during the expedition "Atelier Lifou 2000". Open circles indicate dredging, closed circles diving. For details see Table 1.

Systematics

Order Euryalida Lamarck, 1816

Family Euryalidae Lamarck, 1816, sensu Okanishi *et al.* (2011a)

Subfamily Astrocharinae Okanishi *et al.*, 2011

Genus *Squamophis* Okanishi *et al.*, 2011

***Squamophis lifouensis* sp. nov.**
Figures 2–3

Type material. Holotype, in 80% ethanol, sta. 1469, off Cap Lefévre, bank, 20°54.2' S, 167°00.4' E, 70–130 m [MNHN IE-2009-9200]; skeletal elements on SEM stubs [MNHN IE-2009-9201]. Paratype from type locality, in 80% ethanol, [SMNH-Type-8076].

Etymology. The specific name alludes to the type locality.

Holotype description. Disk diameter 4.8 mm, five non-branching arms, strongly coiled. One arm broken off at disk (but preserved), one arm narrower and probably regenerating. Disk surface folded, centre sunken in. Dorsal disk and arms covered with large, flat, smooth, round to oval granules, embedded in thick skin, completely obscuring any scales or plates. Arms inflated proximally, although constricted at disk, elsewhere as wide as high, ventral side flat, tapering distalwards. Radial shield (exposed after bleaching) composed of single ossicle, with a long bar-like branch extending for about two thirds of the disk radius and a wider, short branch distally. Inflated part of arms supported by rib-like processes at lateral arm plates, forming a gonadal chamber.

Arms covered dorsally and laterally with similar granules as the disk, embedded in thick skin; double bands of granules, interspersed with bands of skin with small scales or granules. At the latero-ventral edge of the arms a dense covering of small round granules. A single thick, blunt, slightly club-shaped arm spine as long as an arm segment, along most of the arm, at the distal arm transformed into a hook with three teeth.

Ventral disk, oral frame and arms with thick skin and tiny flat, round granules (dermal ossicles) obscuring any plates. Ventral interradii vertical, bursal slits at arm bases as long as disk. Each jaw bears five pointed triangular teeth, larger low, round granules at tip of jaws and lateral edges, also higher up at jaw sides. Adoral shields large, rounded triangular. Oral shield minute at vertical edge. Second tube foot outside of mouth angle, no tentacle scales. Gonads extend into arms.

Vertebrae with streptospondylous articulation and open ventral furrow. Dorsal and ventral arm plates lacking. Lateral arm plates curved around the vertebrae, bearing a massive spine articulation, consisting of two upwards curved strong ribs, connected at their dorsal end, open ventralwards, with a deep wide furrow between them. There is a hole between the ribs (presumably the muscle opening) and another in front of them (presumably the nerve opening).

Colouration creamy white with narrow reddish brown bands on the disk, forming a reticulating pattern. On arms horizontal white bands largely correlated with the large granules, and narrow brown bands. Ventral side uniformly white.

Paratype variations. Disk diameter 3 mm, arms not swollen, disk without folds, otherwise similar to the holotype. This is clearly a juvenile specimen with immature gonads. It is attached to a piece of black coral, *Antipathes* sp.

Remarks. The open vertebrae of streptospondylous type and the absence of hook girdles on the arms place this species in the family Asteroschematidae. Among the asteroschematid genera, *Ophiocreas* has a thick, smooth, naked skin, while *Astrocharis* has small naked radial shields and very small arm spines (Okanishi & Fujita 2011). Mortensen (Mortensen & Stephensen 1918) concluded that the presence of inflated arm bases, previously used to differentiate *Astrocharis* from *Asteroschema* is not useful as a generic character, since *Astrocharis gracilis* Mortensen, 1933 lacked swollen arms. Okanishi *et al.* (2011b) also found that this character is not reliable. In addition, the arms may be swollen in some *Ophiocreas* species (personal observation), whereas they are not swollen in juveniles (see the paratype of the new species). Okanishi *et al.* (2011b) recognized morphological and molecular (Okanishi *et al.* 2011a) differences between the species until then included in *Asteroschema* and proposed a new

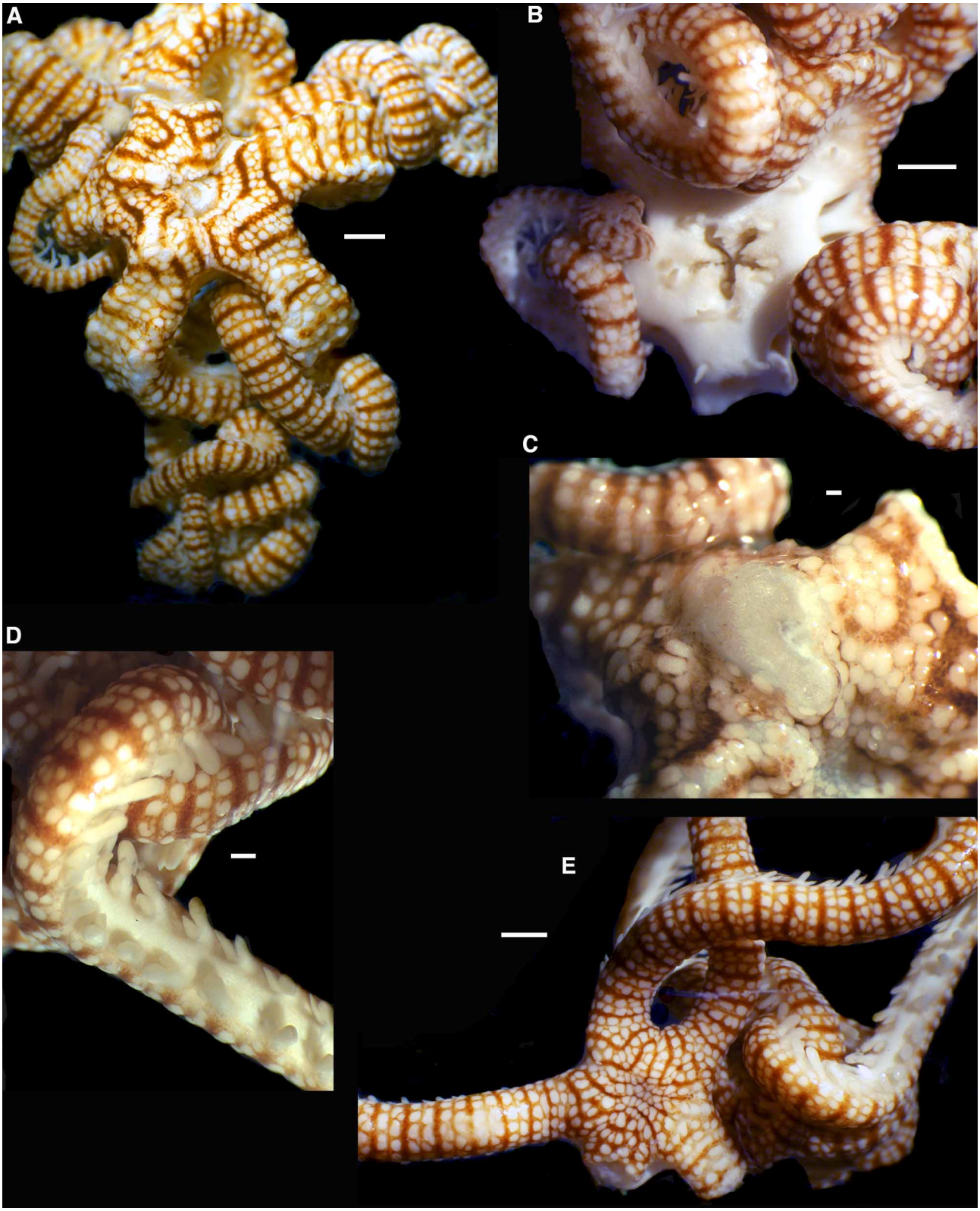

FIGURE 2. *Squamophis lifouensis* **sp. nov.**, A–C, holotype MNHN IE-2009-9200, D, E, paratype SMNH-Type-8076; A, dorsal aspect; B, ventral aspect; C, exposed radial shield; D, dorsal aspect; E, arm details, note the club-shaped single spines. Scale bars 1 mm.

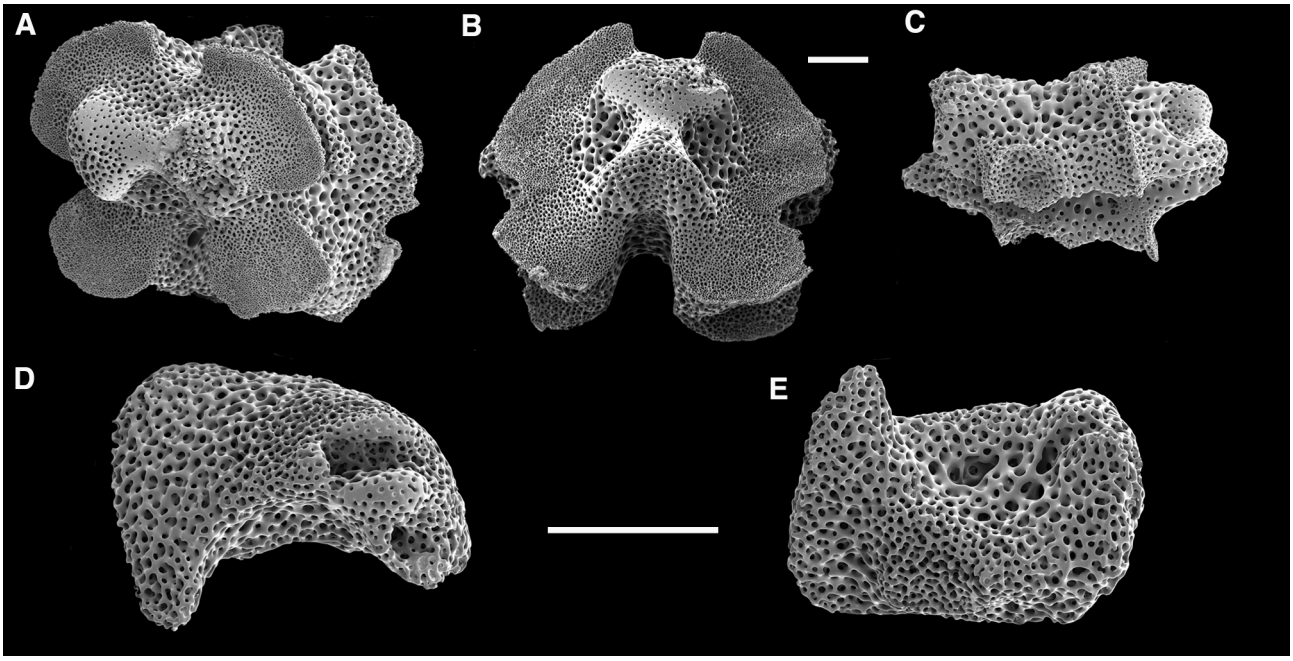

FIGURE 3. SEM images of skeletal elements of *Squamophis lifouensis* **sp. nov.** holotype MNHN IE-2009-9201. A, proximal vertebra distal face, streptospondylous articulation; B, proximal vertebra proximal face; proximal vertebra lateral aspect; D, lateral arm plate external, note the large spine articulation; E, lateral arm plate internal. Scale bars 0.1 mm.

genus, *Squamophis*, for those species that have flat dermal ossicles completely covering the disk and radial shields, single ossicle radial shields, and arm spines as long as an arm segment. The new species shares all of these characters and thus is best placed in *Squamophis*. A tissue sample of the holotype was sequenced for several genes by Okanishi and the data also placed the new species within *Squamophis* (Okanishi, personal communication). Also, the colour pattern is unusually conspicuous for *Asteroschema*, but not for *Squamophis*. Its closest affinities are with *A. igloo* Baker, 1980, a species suggested by Okanishi *et al.* (2011b) to belong in *Squamophis*, from which it differs in larger and flatter granules and the presence of only a single arm spine (two in *A. igloo*), and *S. amamiensis* (Okanishi & Fujita 2009), from which it differs in smooth arm spines, slightly larger, not as densely placed dermal ossicles, and in colour pattern. *Squamophis lifouensis* **sp. nov.** differs from *S. albozosteres* Okanishi *et al.*, 2011 in larger dermal ossicles, in the shape of the radial shield and in colour pattern. The massive spine articulation of the new species differs from the shape indicated for Gorgonocephalidae and Asteronychidae by Martynov (2010a) and from the large half-circle shaped opening with protruding lower lip found in *Asteroschema tubiferum* Matsumoto, 1915 and *Ophiocreas sibogae* Koehler, 1904 (unpublished personal observations), but does not concur with any shape found in Ophiurida either. This may be additional support for the genus *Squamophis*.

Distribution. Known only from the type locality.

Subfamily Euryalinae Lamarck, 1816, sensu Okanishi *et al.* (2011)

Genus *Astroceras* Lyman, 1879

Astroceras aurantiacum sp. nov.

Figures 4A–D, 5

Type material. Holotype, in 80% ethanol, sta. 1461, reef Shelter, 20°54.0'S, 167°02.1'E, 100–120 m, collected by dredging, [MNHN IE-2009-9202]; skeletal elements on SEM stubs [MNHN IE-2009-9203].

Etymology. The specific name is derived from the Latin word for orange, alluding to the colour pattern of this species.

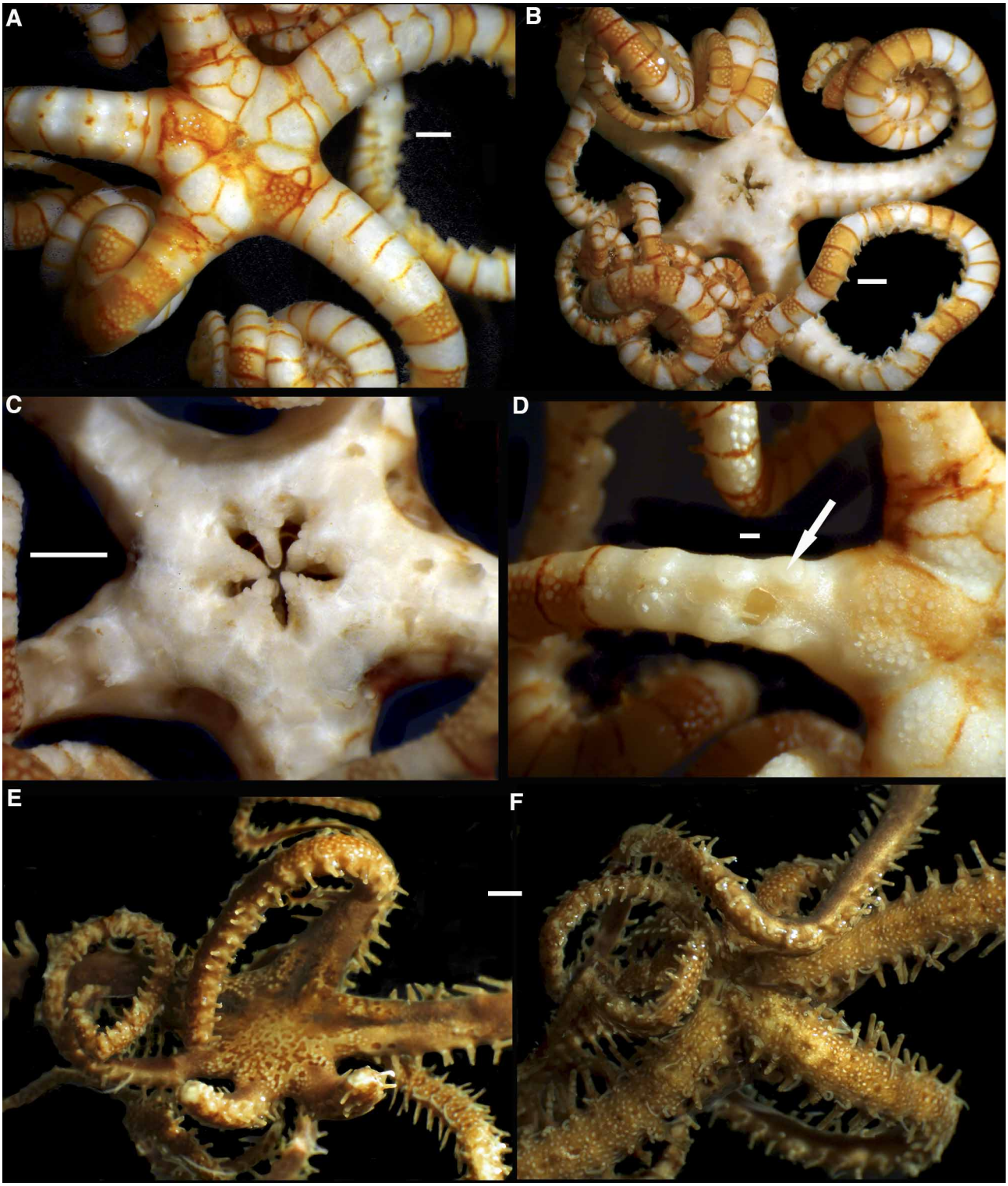

FIGURE 4. A–D, *Astroceras aurantiacum* **sp. nov.**, holotype MNHN IE-2009-9202. A, dorsal aspect showing colour pattern; B, ventral overview; C, ventral disk, lower two sectors lightly bleached to expose adoral plates; D, dorsal arm and disk section, bleached to reveal rib-like processes (arrow) of the lateral plates and radial shields. E, F, *Astrogymnotes oharai* **sp. nov.** holotype MNHN IE-2009-9204. E, dorsal aspect; F, ventral aspect. Scale bars 1 mm.

Holotype description. Disk diameter 4.5 mm, five non-branching arms, strongly coiled. Four arms proximally inflated, the fifth narrower, all tapering gradually beyond the inflated part, where they are as wide as high, ventral side flat. Arms almost touching, leaving only a narrow interradial space. Dorsal disk with smooth, round, low granules on the radial shields, embedded in thick skin, interradially naked, no scales visible. After bleaching of a radius,

large radial shields exposed, almost as long as the disk radius, pairs contiguous, forming most of the dorsal disk. Dorsal arms covered with similar granules, proximally as four longitudinal rows, distally as three. Lateral arms naked. Proximally arms dorsally slightly noded, after bleaching, rib-like processes on the lateral arm plates are exposed. These support the skin, forming a chamber for the gonads. Two short, stump-like arm spines at latero-ventral edge of arm, ventral spine longer than dorsal one. Spines on proximal arm thorny, distally turning into hooks with three, distalmost two, long thorns of about equal length, lamina indistinct. Granules on distal arm rugose (after bleaching).

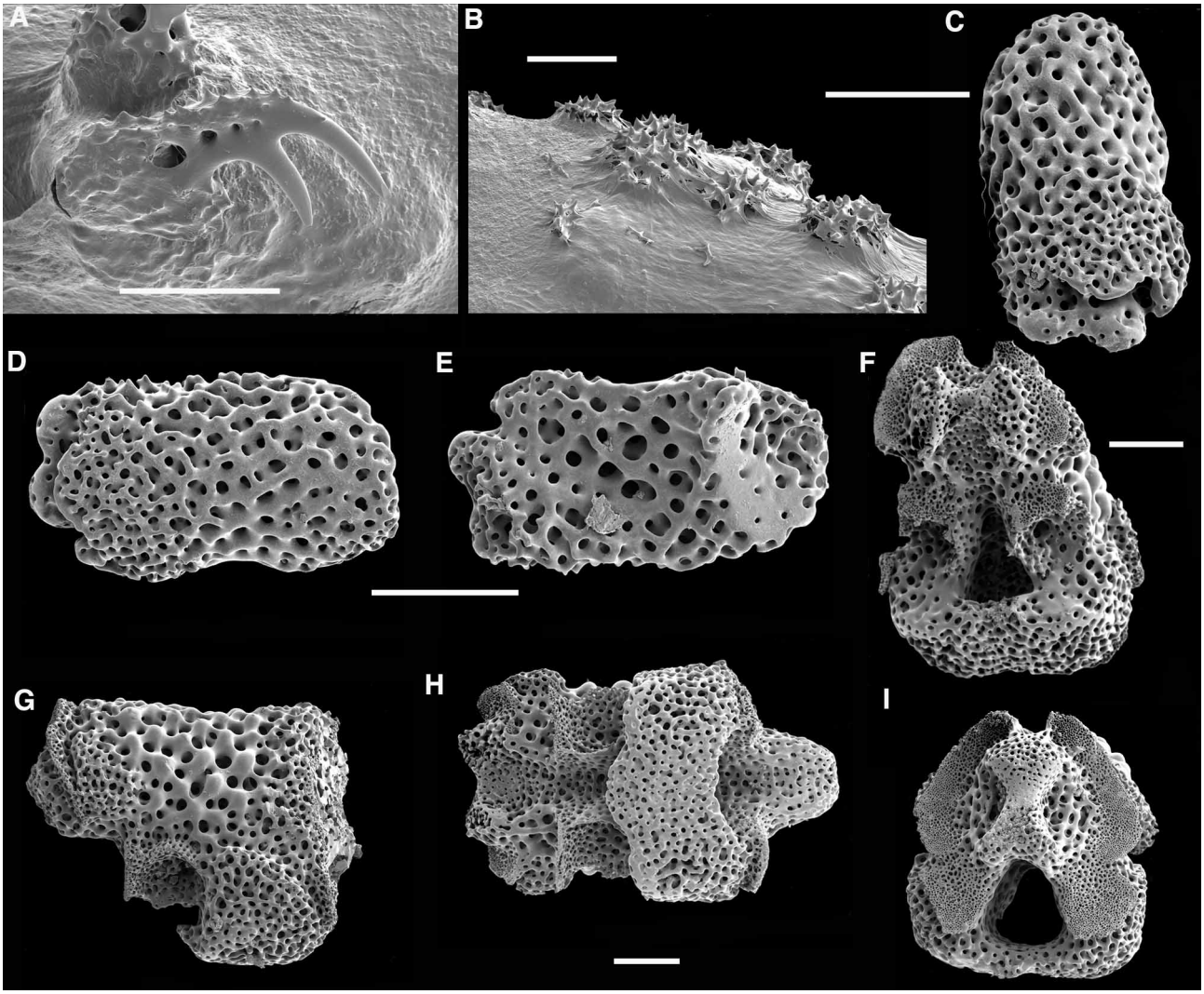

FIGURE 5. SEM images of skeletal details from distal part of arm of *Astroceras aurantiacum* **sp. nov.**, holotype, MNHN IE-2009-9203. A, hook spine; B, granules on dorsal arm; C, lateral arm plate distal aspect of spine articulation; D, lateral arm plate external, spine articulation to the left; E, lateral arm plate, internal, spine articulation to the left; F, distal vertebra, distal face; G, vertebra, lateral aspect,; H, vertebra, ventral aspect, note the roof-like bar covering the proximal part; I, vertebra, proximal face. note the closed ventral nerve canal. Scale bars 0.1 mm.

Ventral disk and arms covered by thick naked skin, obscuring all plates. Jaws with large triangular apical papilla and five rectangular, massive teeth. At the lateral jaw edge a cluster of up to seven granules or papillae, a larger one higher up at the jaw. Second tentacle pore inside mouth angle, without scale or spine. Third tentacle pore lacking spine, fourth and fifth with one spine each, two spines on following segments. In each ventral interradius, almost vertically, a deep depression with two short bursal slits. After bleaching of an interradius, the adoral shields are just visible, triangular, distally 2.5 times as wide as proximally, with straight lateral edges and slightly convex distal edge, filling the whole interradius. Oral shields not visible, possibly absent. Gonads extend into arms.

Vertebrae from the distal arm closed over their proximal ventral half by a bridge-like flat structure, firmly

fused to the sides of the vertebra and separating the lateral arm plates. Articulation streptospondylous. No sign of ventral arm plates anywhere along arm. Lateral arm plate from distal arm twice as long as high, curved in a wave-like shape at its distal edge to form the spine articulations, that consist of two round flat shapes projecting from the lower edge, with the upper edge roof-like above them. No regular dorsal arm plates, but ossicles embedded in the deeper layers of the skin on the middle to distal arm; none proximally in area of ribs.

Colouration dorsally white with narrow orange lines, dividing dorsal disk into sections, two of which are completely orange, the others white. Thin transverse orange lines at each arm segment junction, some wider bands of orange irregularly distributed along dorsal arms. Ventral disk and arms uniformly white.

Remarks. The closed vertebrae of streptospondylous type clearly place this species in the family Euryalidae. Its generic placement is more difficult. There are three euryalid genera with non-branching arms, *Astroceras*, *Asteromorpha* and *Asterostegus*. *Asterostegus* is characterized by dorso-lateral ridges on the arms, bearing prominent tubercles and by ventral disk plates distal to the adoral shields (Fell 1960). Neither of these characters is present in the new species. In *Asteromorpha* the arms are covered with a dense coat of granules dorsally and laterally (Fell 1960), while the new species has granules only on the dorsal arm. *Astroceras* has been diagnosed as having a naked skin with at most some tubercles or spines on the proximal arm (Mortensen 1933a), but in *Astroceras elegans* (Bell, 1917) the arms may bear a dense cover of granules (Baker 1980) and *A. kermadecensis* Baker, 1980 has a dense granulation all over the disk and arms, lacking any larger tubercles. The granulation is thus not a good character to differentiate these genera and Baker (1980) suggested that the structure of the lamina of the hook spines in *Astroceras* and *Asteromorpha* may be used to differentiate between both genera. *Asteromorpha* has a distinct smooth lamina, while *Astroceras* has an indistinct one, which concurs with the new species. The spine articulations of the new species are different from all previously presented ones (Martynov 2010a).

Distribution. Known only from the type locality.

Genus *Euryale* Lamarck, 1816

Material. *Euryale aspera* Lamarck, 1816. Stn. 1433: 1 spm, stn. 1429: 1 spm, stn. 1461: 1 spm.

Remarks. The nomenclatural status of this genus is currently unclear. According to the principle of priority, the ophiuroid *Euryale* Lamarck, 1816 is a junior homonym of a medusa *Euryale* Péron & Lesueur, 1810. Since *Euryale* Lamarck, 1816 is the type genus of Euryalidae and also the order Euryalida depends on the validity of the name, it is highly desirable to establish its precedence over the older homonym. In accordance with article 23.9.1. of the International Code of Zoological Nomenclature, prevailing usage of a name must be maintained when a) 'the senior homonym has not been used as a valid name after 1899' and b) 'the junior homonym has been used for a particular taxon, as its presumed valid name in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years'. This appears to be the case with *Euryale*, which has been (and still is) widely used for almost two centuries for an ophiuroid genus by a large number of publications from different fields, 25 of which (published 1966–2007) are listed in the appendix to fulfill the requirements of articles 23.9.1.2. and 23.9.2. To my knowledge, the name *Euryale* has not been used for a medusa after 1899.

Lamarck (1816) synonymized the cnidariantype species *E. antarctica* Péron & Lesueur, 1810 with *Ephyra*, while using *Euryale* for ophiuroids. This latter decision was not accepted by Fleming (1828), who proposed *Astrophyton* instead. *Astrophyton* is currently regarded as a gorgonocephalid genus and indeed, *Euryale*, *Astrophyton* and *Gorgonocephalus* were synonyms as originally published and used (Verrill 1899a), but split up and delimited from each other by Lyman (1882). Thus, since the requirements of article 23.9.1. are fulfilled, from hereon, the junior homonym is valid, protected (*nomen protectum*) and has precedence over the older name, which from hereon should be referred to as a *nomen oblitum* (see article 23.9.2.).

Fell (1960) argued that *Euryale* should be attributed to Oken, 1815 instead of Lamarck, 1816 on the grounds of priority, probably unaware that Oken (1815) had been rejected for nomenclatural purposes by the international commission in opinion 417 (International Commission on Zoological Nomenclature 1956). Subsequently, several genera and species from that work have been ruled valid in the interest of preventing confusion and establishing nomenclatural stability, but no such ruling exists for *Euryale*. Consequently, Lamarck (1816) must be considered as authority of the name. Since Oken like his peers used *Euryale* as a synonym of *Gorgonocephalus*, no stability on

the understanding of the generic concept can be achieved by a ruling in favour of his authority on the name. Furthermore, Oken (1915) used *Euryale* also for a medusa, which makes the name under his authority ambiguous. Lyman (1882), attributed *Euryale* to Lamarck, 1816, thus providing an unambiguous concept of the name that was in common use until Fell's (1960) decision to attribute it to Oken.

Cnidara and Ophiuroidea are widely separated taxa, and cnidarian workers may not easily become aware of this nomenclatural act that changes the precedence of the names. To avoid the risk that *Euryale* Péron & Lesueur, 1810 may be revived in the future, causing confusion again, a proposal to the commission will be prepared to formally suppress the older homonym. This act to establish precedence of the younger name is the required first step.

Order Ophiurida Müller & Troschel, 1840

Family Ophiomyxidae Ljungman, 1867

Genus *Astrogymnotes* H.L. Clark, 1914

Astrogymnotes oharai sp. nov.

Figures 4E, F, 6

Type material. Holotype, in 80% ethanol, sta. 1461, reef Shelter, 20°54.0'S, 167°02.1'E, 100–120 m, collected by dredging, [MNHN IE-2009-9204]; skeletal elements on SEM stubs [MNHN IE-2009-9205].

Comparative material. *Astrogymnotes irimurai* Baker *et al.*, 2001, holotype, Japan, Izu Archipelago, Nii-jima Island, 15 m, on Antipathes sp. B, scuba, collector I. Soyama, 25 June 1997, [NSMT E-3700]; 2 paratypes, Japan, Izu-Oshima Island, Akino-hama, 27 m, collector I. Soyama, 4 May 1997 [NSMT E-3702 and 3705]

Etymology. This species is named for Timothy D. O'Hara, eminent Australian ophiuroid expert, who once taught me the basics of ophiuroid taxonomy.

Holotype description. Disk diameter 5 mm, six arms, three larger and three smaller ones, indicating a fissiparous nature. Two arms broken off close to the disk, the others near their tip. Disk interradially deeply incised. Disk and arms covered with thick skin, in which scattered round, low granules are embedded, concentrated on the radial areas. Radial shields not visible, but indicated by granule-covered ridges. Scraping away the skin on one of these ridges proved the existence of bar-like long radial shields, widely separated from each other. No other scales or plates present.

Smaller granules form a dense cover on the dorsal side of the gradually tapering arms. Dorsal arm plates are obscured by skin. First arm segment under the disk spine-less, the following three bear a single spine each, which increases in length from a short stump to rod-like. From segment five there are two spines along the arm, of about equal length, longer than an arm segment, distally the ventral spine is shorter. Spines smooth, tapering towards a blunt tip.

Ventral disk covered by naked skin. Each of the fully developed jaws bears a pointed triangular apical tooth and three to four smaller, conical, lateral papillae at each edge. On the regenerating jaws the conical oral papillae form a cluster. All plates obscured by skin, including oral shields and madreporite, which are however visible when the skin is scraped off. Ventral arms likewise covered with thick skin, obscuring any plates, with small round to oval embedded granules. Ventral arm spines flat, wing-shaped on the proximal arm, rounded rectangular with indented distal edge on the distal arm. A single, semi-erect tentacle scale resembling a short arm spine or granule. Genital slits open, about 1.5 arm segments long; a strong abradial genital plate supports the outer edge.

Vertebral articulation zygospondylous with large proximal dorsal side flanges and smaller distal ones. Arm spine articulations on lateral arm plates vary in shape from round depressions with several larger holes to horseshoe shaped elevations with large hole towards the closed end. The corresponding articulation at the proximal end of the spine of curved shape with flat, denser surface and central hole. Isolated dorsal arm plate proximally wing-shaped, twice as wide as long, curving inwards at about mid-length to a narrower distal part, with convex proximal and distal edges. Ventral plate about as wide as long, lateral edges straight, proximal and distal edges with deep notches.

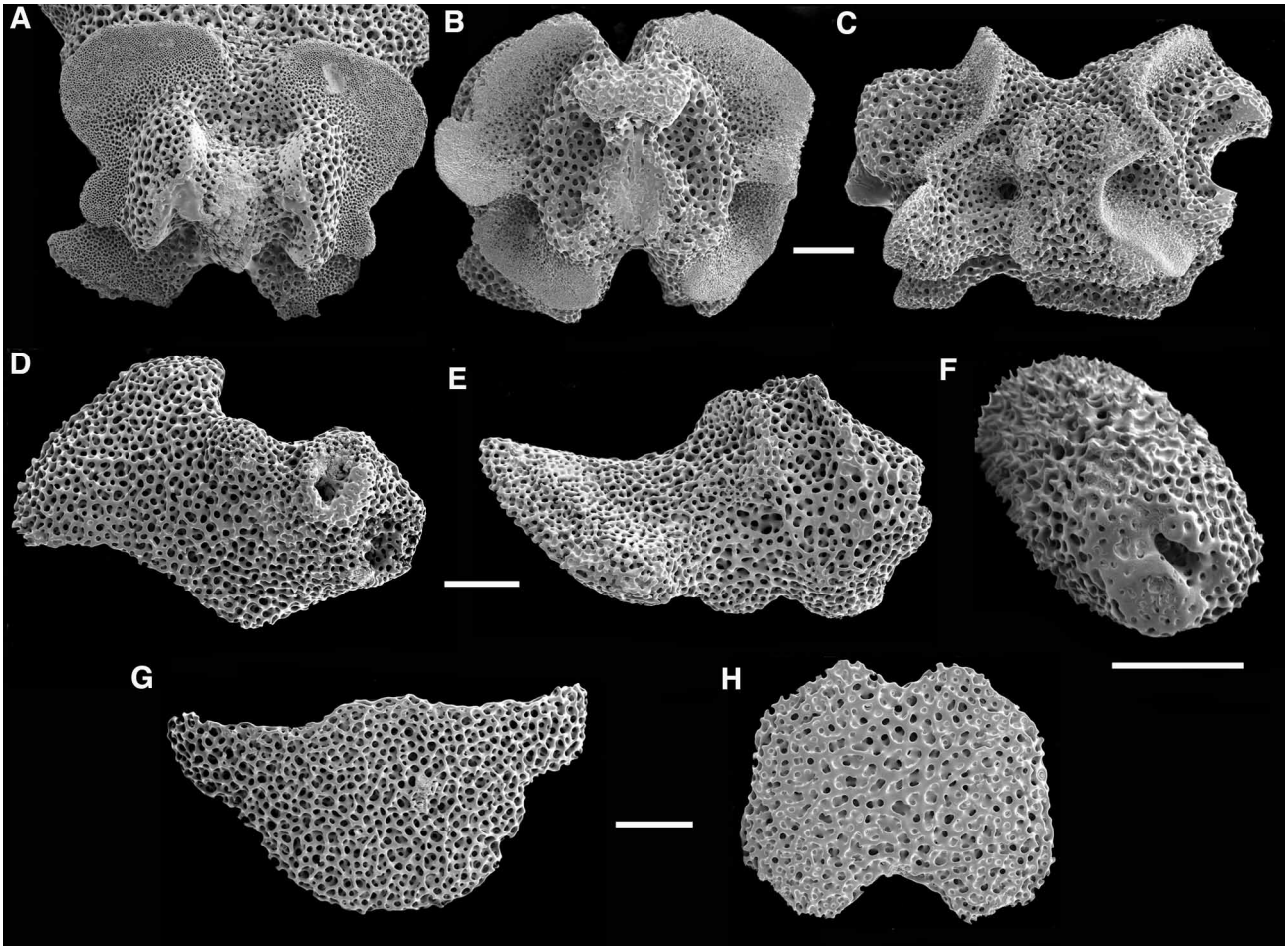

FIGURE 6. SEM images of skeletal details of the distal arm of *Astrogymnotes oharai* **sp. nov.**, holotype MNHN IE-2009-9205. A, vertebra, distal face; B, vertebra, proximal face; C, vertebra, lateral aspect; D, lateral arm plate, external, note the weakly developed spine articulations; E, lateral arm plate internal aspect; F, arm spine, articulation; G, dorsal arm plate; H, ventral arm plate. Scale bars 0.1 mm.

Colouration of dorsal disk golden brown with darker irregular patches, white granules. Arms uniformly darker brown, in some radii a broad dark median line continues onto the arms. Ventral disk with large dark spots, arms and jaws light golden brown with small white spots that correspond to the granules; an interrupted darker brown median line or series of spots along the arms.

This animal was collected without its host, but there is no reason to assume that it was not associated with black coral like all its conspecifics.

Remarks. The arm spine articulation of *Astrogmynotes* has not been shown yet and the articulations found on the new species differ from those of *Ophiomyxa* and *Ophiolycus* (Martynov 2010b) in being less pronounced and having a more porous stereom. It may still be a variation of the articulation typical for Ophiomyxidae, but further study is needed. The genus *Astrogymnotes* formerly included four species, the pentamerous *A. thomasinae* Baker *et al.*, 2001 and *A. hamishia* Baker *et al.*, 2001, and two hexamerous ones, *A. irimurai* Baker *et al.*, 2001 and the type species *A. catasticta* H. L. Clark, 1914 (Baker *et al.* 2001). The colour pattern of the new species resembles the holotype of *A. irimurai*, from which it differs by its smaller and more sparsely distributed granules, and the longer, thinner and smooth arm spines that don't turn into hooks. A paratype of *A. irimurai* showed a darker, almost black colour with larger white patches than the holotype and differed even more from *A. oharai*. In that specimen, the madreporites or oral shields were obscured, whereas they are obvious, covered only with thin skin and white in colour in the holotype. Another paratype had three small, obviously regenerating, arms and three large ones, an indication of the fissiparous nature of the species. *Astrogymnotes oharai* differs from *A. catasticta* in the colour pattern and length of arm spines. The intraspecific variation of *A. oharai* is not known since only a single specimen was found, but it is probably fissiparous and somewhat variable in colouration. The largest species is *A. catasticta*,

which reaches a disk diameter of 9 mm, but *A. thomasinae* with a holotype of 7 mm may possibly reach a similar size, while the remaining species have only been found at sizes of about 4–5 mm dd. Unusual among ophiuroids, the ventral side is often more brightly coloured in these species, and they orientate themselves with the ventral side outwards, dorsal side towards their coral host.

Distribution. The depth distribution of the species of *Astrogymnotes* is probably dependent upon that of their hosts, the black coral *Antipathes* spp., and varies greatly, with *A. irimurai* occurring at the shallowest depth at 15 m and *A. hamishia* at 1225 m at the greatest depth. The new species was found at medium depth of 100–120 m, similar to *A. catasticta*, which has been found at 55–205 m depth (Liao & Clark 1995). So far, the widest geographic distribution has been documented for *A. catasticta*, found off Western Australia (type locality), the Philippines and Southern China (Clark 1911; Liao & Clark 1995). *Astrogymnotes irimurai* has only been found in Japan. The remaining two species were described from Kermadec Islands; *A. hamishia* has also been found in New Caledonia (O'Hara & Stöhr, unpublished result).

Family Ophiacanthidae Perrier, 1891

Genus *Ophiochondrus* Lyman, 1869

Ophiochondrus variospinus sp. nov.

Figure 7

Type material. Holotype, on SEM stub, sta. 1469, off Cap Lefévre, bank, 20°54.2' S, 167°00.4' E, 70–130 m [MNHN IE-2009-9206].

Comparative material. *Ophiochondrus convolutus* Lyman, 1869, Blake expedition 1878–1879, Caribbean Sea, St. Vincent, 88 fms (160 m), determined by Lyman [SMNH-110799]. *Ophiochondrus falklandicus* Koehler, 1923 (junior synonym of *O. stelliger* Lyman, 1879), 5 syntypes, Swedish South Polar Expedition, S of Falkland Islands, 52°29' S, 60°36'W, 197 m, 11.09.1902 [SMNH-Type-1094].

Etymology. The specific name is derived from the Latin words for different and spine, alluding to the different sizes of arm spines in the new species.

Holotype description. Disk rounded pentagonal, slightly indented interradially, 2.2 mm dd. Dorsal disk densely covered by granules, embedded in a thick layer of integument concealing all plates except the distal ends of the radial shields. Radial shields bar-like, separated for their entire length, about 1/3 of dd long. Arms noded, curled under disk. Dorsal arm plates fan-shaped, twice as wide as long, with convex distal edge, consecutive plates widely separated by lateral plates. On the second free arm joint the dorsalmost spines greatly enlarged, thicker and most likely considerably longer. Only one of these spines is still attached, pointing across the disk, its tip broken, and the remains of the base of another on another arm, but the large spine articulations on all arms indicate that this spine is not an aberration and that similar ones must have been present on all arms. Six spines proximally, including the enlarged dorsal spine, fewer spines distalwards. All other spines about same size, shorter than an arm segment, conically tapered, ventralmost spines minutely thorny, others smooth, perforated by vertical columns of holes. Spine articulation consisting of two ribs, one of them longer and slightly curved at one end, with nerve and muscle opening between them.

Ventral disk covered by granules similar to dorsal disk, but not completely obscuring the small scales. A large abradial genital plate borders the distal end of each bursal slit. Jaws short, with large pointed apical papilla or tooth, 3–4 smaller, papilliform lateral oral papillae to either side. Oral shields fan-shaped, not quite twice as wide as long, with convex distal edge and straight lateral edges. Adoral shields rounded trapezoid, bordering the lateral edges of the oral shield, barely meeting proximally. First ventral arm plate oval, twice as long as wide, in mouth angle. Other ventral arm plates fan-shaped, twice as wide as long, distal edge convex, lateral edges straight, consecutive plates widely separated by lateral plates. Single round tentacle scale, completely covering the small pore. All plates with glass bead-like structure.

Remarks. *Ophiochondrus* resembles *Ophiolebes* in most characters and among the species currently included in *Ophiolebes*, some may rather belong in *Ophiochondrus*. The type species *Ophiolebes scorteus* Lyman, 1878 differs from *Ophiochondrus* in the thick skin that covers dorsal and ventral disk, arms and spines, obscuring all plates

(Lyman 1878). Later, species lacking a thick skin (e.g. *O. pachyphylax* H.L. Clark 1915, *O. comatulinae* McKnight, 2003) were included in *Ophiolebes*, resulting in two badly delimited genera. The thick skin may not be a diagnostic character on generic level and both genera may need to be combined. Pending a revision of both genera, the new species is placed in *Ophiochondrus*, because the thick skin is restricted to the dorsal disk. Among the species assigned to *Ophiolebes*, the new species is most similar to *O. sagamiensis* Irimura, 1982, which has elongated dorsal spines on the first two arm segments, but these are not enlarged in width. That species has spinelets on the skin-covered radial shields and a large madreporite, wheras *O. variospinus* **sp. nov.** has only granules and an indistinguishable madreporite.

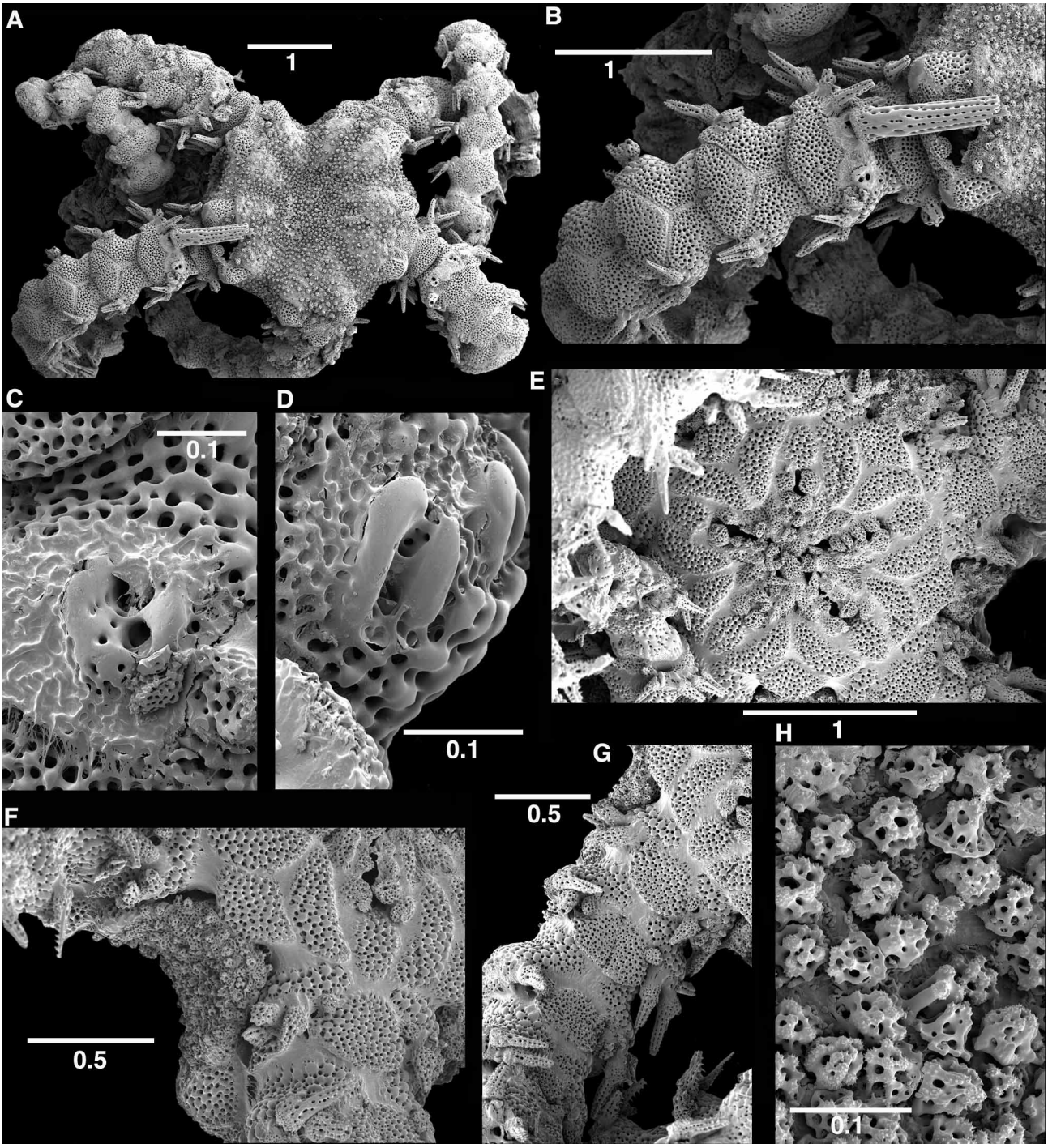

FIGURE 7. SEM images of *Ophiochondrus variospinus* holotype, MNHN IE-2009-9206. A, dorsal aspect; B, dorsal arm, note the large spine on the first joint; C, articulation of large spine on first joint; D, articulation of other spines; E, oral frame; F, ventral interradius with bursal slits; G, ventral arm; H, disk granules. Scale bars in millimetre.

The familial placement of *Ophiochondrus* has long been debated and Martynov (2010b) proposed to place it in Ophiacanthidae instead of Hemieuryalidae on the basis of similarities in the shape of the arm spine articulation. All other characters also suggest ophiacanthid relationships and the granulated disk, bar-like radial shields, exposed only distally, and the long dorsal spine all point to Paterson's (1985) subfamily Ophiacanthinae, although a subfamilial division may no longer be justifiable as Martynov (2010b) showed. *Ophiochondrus* is distinguished from *Ophiomoeris*, also previously included in Hemieuryalidae (see below), by its disk being covered with thick granulated skin, the shape of its radial shields and only weak interradial incisions (Fell 1960). In addition to *O. variospinus* **sp. nov.** the genus *Ophiochondrus* comprises six species (Stöhr & O'Hara 2007). The type species *O. convolutus* Lyman, 1869 has similar adoral and oral shields and mouth papillae, but it lacks a tentacle scale, although Lyman (1869) described a tooth-like scale that is actually one of the spines. Its up to seven arm spines (six in the original description) are half as long as an arm joint, about equal in length. Its disk is also covered by granulated skin and the arms are noded. In the syntypes of *O. falklandicus* the dorsalmost of the four spines on the second and sometimes first arm joint is twice as long as all other spines, but it is more lateral in position and not as large as in the new species. The arms are not as strongly noded in this species.

According to Fell (1960), *Ophiochondrus* lacks true tentacle scales, but that must be a misunderstanding since the syntypes of *O. falklandicus* all possess a single small, oval tentacle scale on all pores along the arms. This scale appears to have been missed by Koehler (1923), who described the small ventral arm spine as tentacle scale, giving the number of spines as only three. The oral papillae are squarish and larger in *O. falklandicus* (= *O. stelliger*) than in *O. variospinus* **sp. nov.**, but in all three examined species the number of oral papillae varies between three and four between different jaws in the same specimen. *Ophiochondrus armatus* (Koehler, 1907) has only few small, scattered granules on the dorsal disk, which do not obscure the disk scales; it has five arm spines of which the dorsalmost is elongated on proximal joints. Paterson (1985) questioned its placement in *Ophiochondrus* due to similarities with *Ophiolebes retecta* (Koehler, 1896), but the latter differs in the thick skin on jaws and ventral arms. *Ophiochondrus granulatus* Koehler, 1914 is with 7 mm dd a much larger species than *O. variospinus* **sp. nov.**, its disk bears large thorny granules in a thin skin that does not obscure the disk scales, and the up to five slender arm spines are longer than in the new species. Also in this species the dorsal spine is much longer than the other spines, but as in the above species with enlarged dorsal spines, previous authors missed the fact that the spine is elongated only on the most proximal joints. *Ophiochondrus crassispinus* Lyman, 1883 is distinguished by up to eight short arm spines, apparently none elongated, lack of a tentacle scale and exposed radial shields. *Ophiochondrus gracilis* Verrill, 1899 was described from a specimen that lacked the dorsal disk. It differs from the new species in the shape of its dorsal and ventral arm plates. Verrill (1899b) noted up to eight short stout arm spines along most of the arm and slightly longer dorsal spines near the base of the arm. However, Clark (1941) reported a small specimen with intact disk, which is strongly lobed, interradially deeply incised, with large triangular radial shields separated by narrow plates, each of which bears a large thorny granule. He compared the specimen to *Ophiocamax hystrix* Lyman, 1878 and his description differs so markedly from the characteristics of *Ophiochondrus*, particularly by the absence of granules, that its position in this genus is doubtful and should be investigated further.

O. variospinus **sp. nov.** differs from all other species by its extremely large dorsal arm spines on the second free arm joint. The tendency to enlarge the dorsalmost spine on a few proximal joints appears to be a common trait in most species of *Ophiochondrus* and may deserve further study. Enlarged dorsal spines on proximal segments are known also from other genera, for example in *Ophiacantha dallasii* Duncan, 1879.

Distribution. Four of the previously known species of *Ophiochondrus* are restricted to the Atlantic Ocean and one (*O. stelliger* Lyman, 1879) is found in the Southern Ocean. The type locality of *O. granulatus* is unknown and it appears not to have been reported since its description. The new species is thus the first record of the genus in the Pacific Ocean, but taking into account the confusion with *Ophiolebes*, this may not hold true.

Genus *Ophiotreta* Verrill,1899

Ophiotreta valenciennesi (Lyman, 1878)

Material. Sta. CP1646: 4 spms.

Remarks. Currently, two subspecies are recognized within *O. valenciennesi*, the nominate Indo-Pacific form

and the Atlanto-Mediterranean *O. valenciennesi rufescens* Koehler, 1896. The differences between these are more rugose disk granules and longer adoral shields in the nominate subspecies (Paterson 1985). Mortensen (1933b) observed a large variability in the oral shields of Atlantic specimens, which he referred to *rufescens*, because he found them different from typical *valenciennesi*. This distinction cannot be maintained though, since Pacific specimens fall within the variability of *rufescens* (O'Hara & Stöhr 2006, and Lifou material). Given the high variability of several characters it is possible that these forms represent a species complex, but a subspecies distinction cannot be maintained.

The delimitation of *Ophiotreta* from *Ophiacantha* rests mainly on the usually spatulate shape of the distal oral papilla in *Ophiotreta (Verrill 1899b)*. This character has however also been shown for *Ophiacantha bidentata* (Bruzelius, 1805), the type species of *Ophiacantha* (Martynov & Litvinova 2008). Another generic character, the flat and serrated arm spines, is shared by *Ophiopristis*, of which *Ophiotreta* originally was a subgenus (Verrill 1899), and by *Ophiocopa*, suggesting possible affinities between these genera, which were placed in three different subfamilies (Paterson 1985). This may be additional evidence supporting Martynov's (2010b) decision to drop the subfamilies.

Genus *Ophiomoeris* Koehler, 1904

Ophiomoeris exuta sp. nov.

Figure 8A, B, 9

Type material. Holotype, on SEM stub, sta. CP1646, off Cap des Pins, 21°02.6'S, 167°31.6'E, 420–480 m [MNHN IE-2009-9207]; 4 paratypes, in 80% ethanol, type locality [SMNH-Type-8077]

Etymology. The specific name is derived from the Latin word for bared, alluding to the naked interradial disk.

Holotype description. Disk lobed, interradially incised, dd 3.0 mm (prior to SEM preparation); five curled arms. Not attached to coral (although probably dislodged). Radial shields much longer than wide, narrow, with convex outer and straight inner edge; pairs contiguous over almost entire length, except at distal end, where a small fan-shaped dorsal arm plate separates them. Single round scales of variable size, bearing conical granules, lay on top of the radial shields, but do not separate them. Centre of disk with large round centrodorsal plate, larger round plates bearing small conical granules (presumably the radial primary plates), interspersed with smaller scales lacking granules. Dorsal interradial disk consists of naked skin. Arms noded, dorsal arm plates small, rounded triangular to fan-shaped, about 1.5 times as wide as long, widely separated by the lateral plates. Six conical arm spines on arm base, dorsalmost longest, longer than an arm segment, spines decreasing in size ventralwards. Spines on proximal arm smooth, distally with fine teeth at ventral edge and terminal tooth, slightly hook-shaped.

Ventral disk naked skin, jaws with pointed apical papilla similar to teeth, three spiniform lateral papillae. Large adoral shields with angled abradial edge, concave adradial edge, pairs meeting over half their abradial edges, not separating the oral shield from the arm. Oral shield smaller than an adoral shield, fan-shaped, wider than long, with proximal point, concave lateral and convex distal edges. First ventral arm plate integrated into oral frame, longer than wide, strongly convex lateral edges. Second ventral arm plate twice as wide as long, trapeziform with wider proximal edge, fragmented on two arms. Following ventral arm plates reduced to small, round, thin scales, embedded in a strand of thick skin running along the entire arm. A single oval tentacle scale at each pore. The stereom structure of all plates is glass bead-like.

Bursal slits half as long as interradial ventral disk, lined with long adradial genital plate and several scales on abradial edge.

Colouration in ethanol cream with brown longitudinal line on dorsal arms and midline of radial shield pairs.

Paratype variations. Disk diameters of four paratypes are 1.6 mm, 2.4 mm, 3.2 mm, and 3.5 mm. All are attached to various species of coral. Some lack granules on the dorsal disk, others have fewer than the holotype or just tumid scales. The size of the scales overlaying the radial shields varies between individuals, as does the number of central dorsal scales. Smaller specimens have fewer arm spines than the holotype, none has more than six.

Remarks. The arrangement of the oral frame, the glass bead-like structure of the stereom, the lobe-like shape of the disk all concur with *Ophiomoeris*, a genus that has until recently been placed in Hemieuryalidae. The arm spine articulations of the new species concur with that shown for *Ophiochondrus* by Martynov (2010a), interpreted

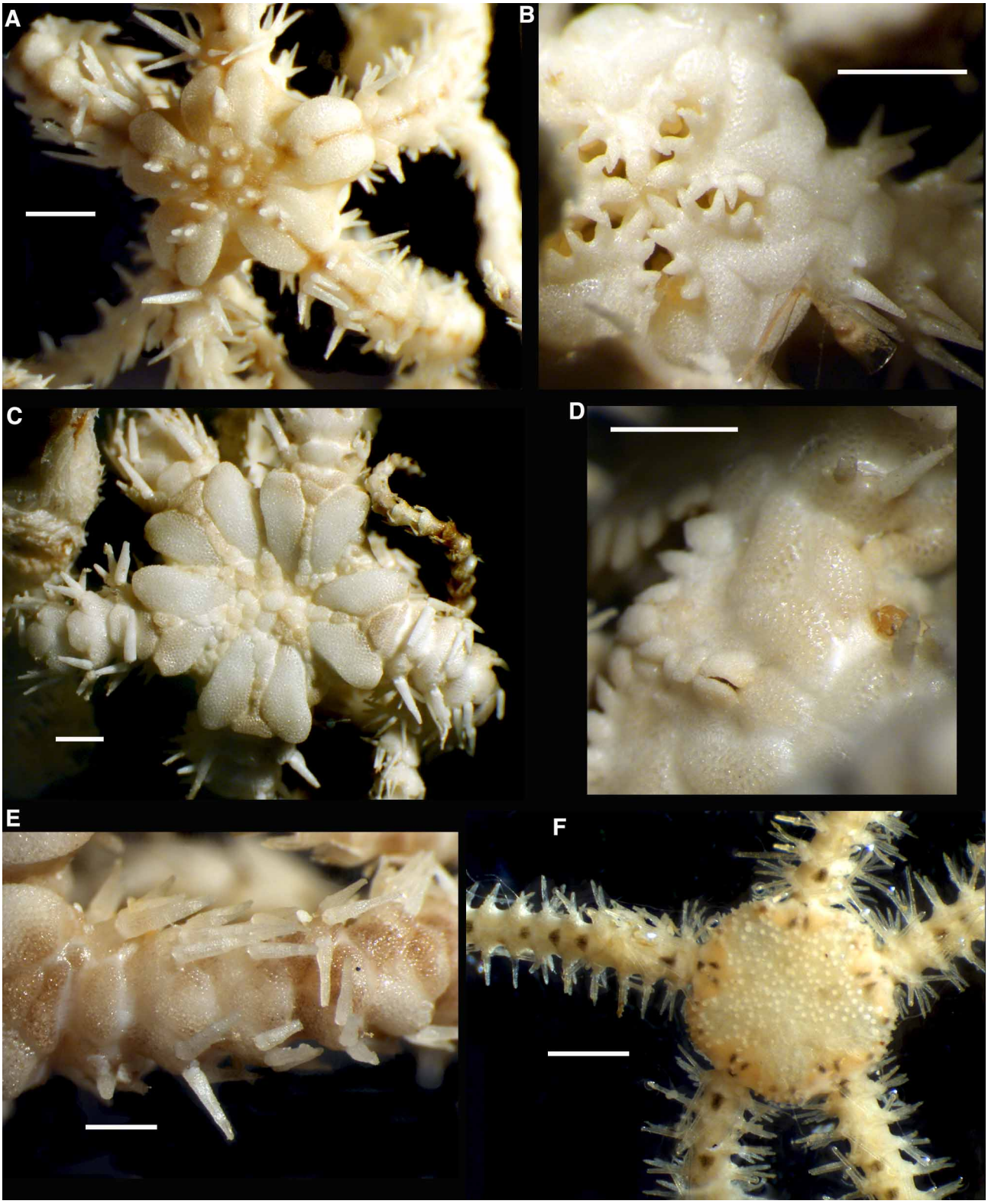

FIGURE 8. A, B, *Ophiomoeris exuta* **sp. nov.**, holotype MNHN IE-2009-9207, prior to SEM preparation; A, dorsal aspect; B, oral frame and ventral arm. C–E, *Ophiomoeris* cf. *obstricta*; C, dorsal aspect; D, jaw details; E, dorsal arm. F, *Ophiomitrella granulosa*, spotted form, dorsal aspect. Scale bars 1 mm.

as a variation of the for Ophiacanthidae typical comma-shape (Paterson 1985; Martynov 2010b). In combination with the spiniform oral papillae, the shape of adoral and oral shields, and the long arm spines that turn into hooks, a placement within Ophiacanthidae seems indeed more appropriate. The large naked radial shields and deeply incised disk are characters of Paterson's (1985) subfamily Ophioplinthacinae. There is some similarity in the radial

shields with *Ophiohamus*, but that genus has a round flat disk and specialized arm hooks. Previously, three species of *Ophiomoeris* were recognized (see below), but none of them has a naked disk. The naked disk interradii, both dorsally and ventrally, are an unusual feature among hemieuryalids as well as ophiacanthids, which separates the new species from all others. Also, the long, narrow and contiguous radial shields differ from all other species of *Ophiomoeris*.

Distribution. Known only from the type locality.

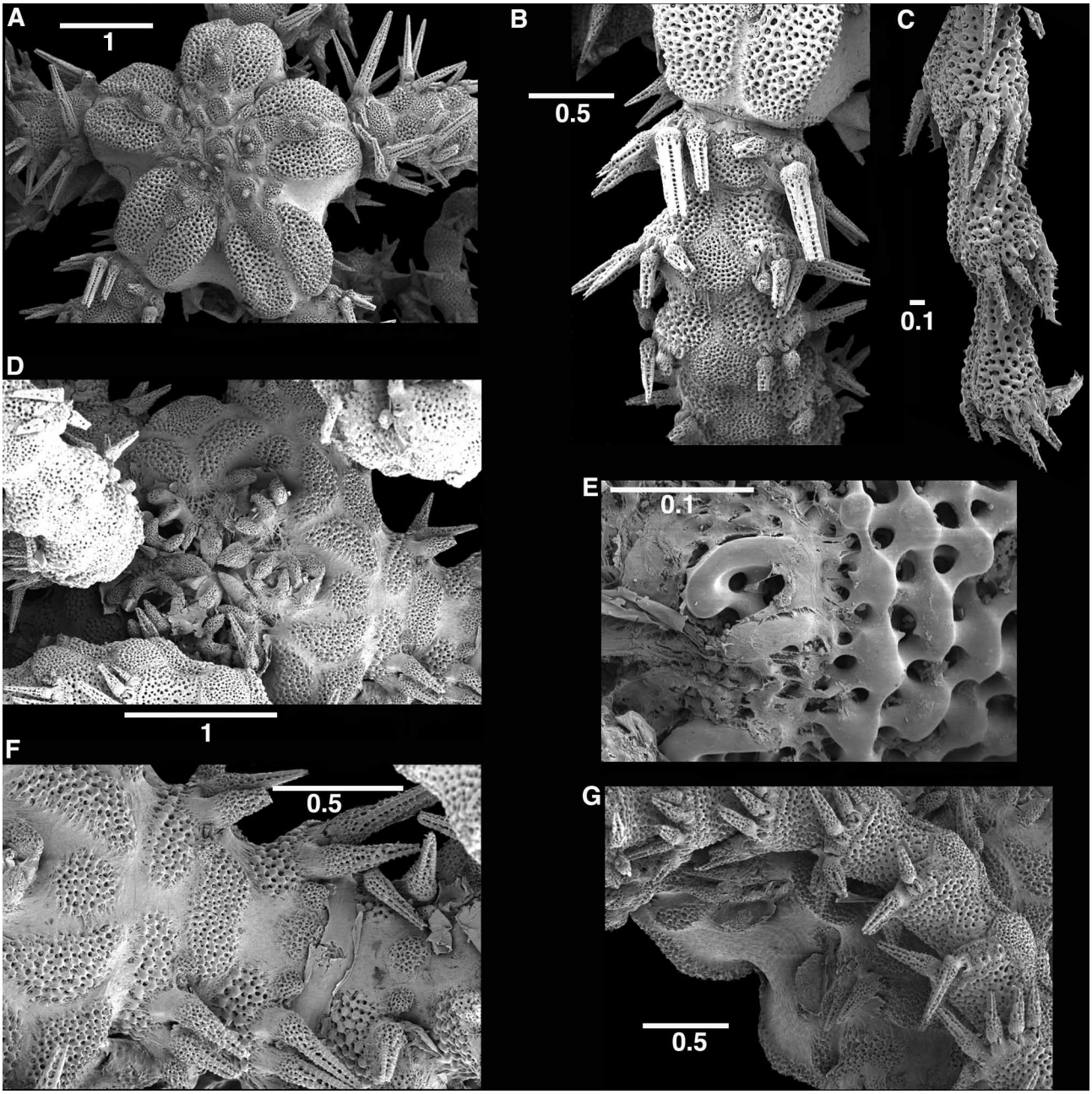

FIGURE 9. SEM images of *Ophiomoeris exuta* **sp. nov.** holotype MNHN IE-2009-9207. A, dorsal aspect, note the naked interradials; B, dorsal arm; C, distal arm laterally, note the hook-shaped spines; D, oral frame; E, arm spine articulation; F, ventral arm; G, ventral interradius, naked except for genital plates. Scale bars in millimetre.

Ophiomoeris cf. *obstricta* (Lyman, 1878)

Figure 8C–E

Material. Sta. CP1646: 2 spms, 5.3 and 3.3 mm dd.

Description. Radial shields almost oval, separated over their entire length by small, tumid scales in the larger

specimen, diverging distally and there separated by a triangular plate (dorsal arm plate) about twice as wide as long. Central dorsal disk plate knob-like, encircled by round, likewise knob-like, tumid scales of different sizes. No granules. In the smaller specimen all scales flat, suggesting ontogenetic differences. Interradially small flat scales embedded in skin. Larger specimen with six arm spines proximally, reducing in number distalwards. Dorsalmost spine longest, longer than an arm segment, and spines decrease in size ventralwards. Jaws with a large pointed apical papilla, two pointed lateral papillae proximally and a scale-like distal one. Adoral shields large, curved and not reaching around the small fan-shaped oral shield. Ventral arm plates short, at least twice as wide as long proximally. All plates have a glassy bead-like stereom.

Remarks. *Ophiomoeris* currently contains four species, *O. nodosa* (Koehler, 1905), *O. obstricta*, *O. exuta* **sp. nov.** and *O. tenera*, but the status of the last species is still unclear (O'Hara & Stöhr 2006). The Lifou specimens fall within the variability of *O. obstricta* documented by O'Hara & Stöhr (2006), but further study will have to show whether *O. obstricta* is a morphologically highly variable species with a wide geographic distribution or a complex of several genetic lineages.

Distribution. Widely distributed across the Indo-Pacific Ocean.

Genus *Ophiomitrella* Verrill, 1899

Ophiomitrella granulosa (Lyman, 1878)

Figure 8F

Material. Sta. CP1646: 5 spms 1.75–4.5 mm dd

Remarks. These specimens agree well with those previously found in New Caledonian waters (O'Hara & Stöhr 2006). Four of them show a longitudinal dark stripe along the arms, the fifth is spotted. All of them are juveniles, since the species is known to reach at least 9 mm dd.

Distribution. The species is found at its greatest depth in New Caledonia (383–500 m), in contrast to the type locality in the Philippines (152–189 m; Lyman 1878) and records from Japan (97–192 m).

Family Ophiuridae Müller & Troschel, 1840

Subfamily Ophiurinae Lyman, 1865

Genus *Amphiophiura* Matsumoto, 1915

Amphiophiura confecta (Koehler, 1930) new combination

Figure 10A–I

Stegophiura confecta Koehler, 1930: 234, pl. 19 figs 1, 2 ; Guille 1981: 449, pl. 8 fig. 46.
Amphiophiura taranui McKnight, 1968: 20–210, fig. 2. [new synonymy]

Material. Sta. 1461: 2 spms; sta. DW1650: 1 spm, sta. DW1650C: 2.

Description. In a specimen of 7.5 mm dd, disk high, dorsally covered by few large plates, among which the primary rosette is prominent, occupying most of the disk surface. Radial primary plates abut oval, contiguous radial shields. In each interradius a pentagonal proximal plate abutting two adjacent radial primaries, a smaller rectangular plate distally and a row of three smaller plates at the disk edge, the middle of them square, the left and right plate with convex sides. Radial shields slightly domed, robust, stereom with rough surface with large pores. Arm comb well developed, with spiniform papillae. Dorsal arm plates fan shaped, wider than long, contiguous, first plate overlapped by radial shields, microstructure finely porous. Lateral arm plates thick, protruding from arm, their microstructure similar to the radial shields. Arm spines three, two dorsal ones widely separated from each other, with wide base, abruptly constricted into an elongated point. Ventral spine conical, close to the single leaf-like tentacle scale, both at the edge of the pore. All spines half as long as an arm joint. Spine articulation a large round hole with smooth patch at one edge.

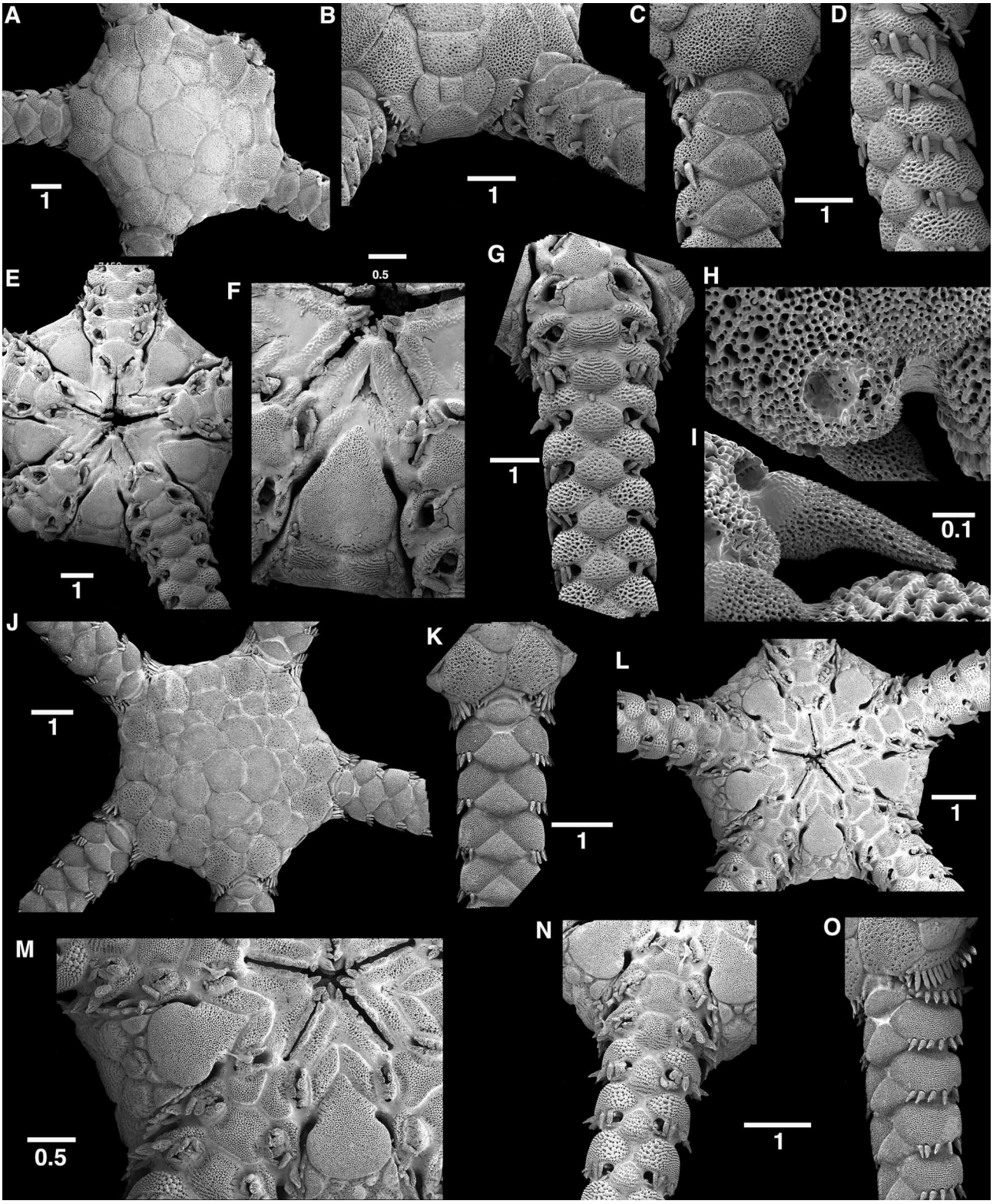

FIGURE 10. SEM images, A–I, *Amphiophiura confecta*. A, dorsal aspect; B, interadial disk dorsolateral aspect; C, dorsal arm; D, lateral arm; E, ventral aspect; F, oral details; G, ventral arm; H, arm spine articulation on lateral plate; I, dorsal arm spine. J–O, *Amphiophiura distincta*. J, dorsal aspect; K, dorsal arm, L, ventral aspect; M, oral details; N, ventral arm; O, arm lateral aspect. Scale bars in millimetre.

Jaws with single small pointed apical papilla, a small round infradental papilla to either side of the dental plate, three to four wider than high, scale-like lateral papillae at oral plate. Second tentacle pore superficial, encircled by low wide scales, two along adoral shield, two on first ventral plate. Oral shield elongated drop-shaped, occupying

two thirds of interradial space. Distal to it two smaller triangular plates and a large pentagonal plate, abutting the three interradial plates at the disk edge. These ventral interradial plates and distal edge of oral shield with transverse grooves. Bursal slits extend from adoral shields to disk edge, lined with large genital plate, bearing a row of spiniform papillae. Ventral arm plates tumid, wider than long, with proximal angle, distal edge convex, separated, on joint 3 and 4 with transverse grooves, farther out with holes.

Remarks. *Amphiophiura* is characterized by a high dorsal disk, covered with relatively few large scales among which the primary plates are clearly distinguishable, the presence of an arm comb, and stout, short arms. In these characters it is similar to *Stegophiura* and the boundaries between both genera are ill-defined. The difference between them is supposed to be in that the arms are widened at the base and tapering more rapidly in *Stegophiura* than in *Amphiophiura*. However, this character varies between the species placed in both genera (Koehler 1922) and already Matsumoto (1915) remarked on the possible overlap between certain species placed in either genus. A more useful distinction appears to be the presence of two types of arm spines in *Stegophiura*, where in addition to regular spines a fringe of numerous small spines can be found along the dorsal part of the lateral plate edge. Since these secondary spines are lacking in *A. confecta* I propose to transfer it to *Amphiophiura*. A revision of these genera is obviously needed.

According to the images of the holotype (McKnight 1968), *A. taranui* is conspecific with *A. confecta*. As McKnight (1968) commented, there is also some similarity with *A. urbana* (Koehler, 1904), but that species reaches twice the size of *A. confecta* and has more dorsal disk scales, which create a different pattern at the disk edge. *Amphiophiura laudata* Koehler, 1904 is of similar size to *A. confecta*, but has an additional circle of plates between primaries and radial shields and more plates on the ventral interradius.

Distribution. Type locality is Banda, Indonesia, at 100 m (Koehler 1930). At Lifou the species was found at 100–260 m and it is a new record for New Caledonia.

Amphiophiura distincta (Koehler, 1904)

Figure 10J–O

Ophioglypha distincta Koehler, 1904: 44, pl. 9 figs 7–9.
Amphiophiura distincta – Matsumoto 1915: 78; Koehler 1930: 224–5.

Material. Sta. 1461: 2 spms; sta. DW1648: 8 spms; sta. DW1650: 15 spms, sta. DW1650C: 10 spms.

Description. At 5.5 mm dd dorsal disk covered by a large primary rosette and two overlapping rounded plates interradially. Distal to radial primary plates two smaller half-circle shaped plates frame a wider wedge-shaped plate, separating the radial shields proximally. Radial shields round, slightly narrower at proximal ends, same size as primaries, stereom with larger holes. Dorsal arm plates wide triangular to fan-shaped with convex distal edge, slightly domed, separated. Lateral arm plates larger than dorsal plates, bearing up to seven short conical spines.

Ventral disk covered by large oral shields and a mosaic of smaller tumid plates. Oral shield constricted proximal to its mid-line, distally oval, proximally angular. Adoral shields narrow, abutting only proximal angle of oral shield. Jaws with pointed apical papilla, two similar pointed papillae to either side of dental plate, three wide, low lateral papillae along each side. First tentacle pore superficial, encircled by 7–8 low scales.

Bursal slits extend from adoral shields to disk edge. Abradial genital plate with spiniform papillae along entire length, distally spines elongated, forming an arm comb.

Ventral arm plates tumid, pentagonal, stereom with pores and transverse grooves, about as long as wide, on first joints rectangular, separated from fourth joint. Tentacle scales on lateral plates hardly distinguishable from arm spines, on proximal joints round, scale-like tentacle scales on ventral plate, further out only spiniform tentacle scales on lateral plate. Lateral plates on ventral side with holes.

Remarks. *Amphiophiura distincta* is superficially similar to *A. confecta*, but can be distinguished by a greater number of dorsal disk plates, more numerous and spiniform arm spines, and differences in the ventral disk scales. The oral shields approach the shape of *A. confecta* in some specimens.

Distribution. Type locality is Indonesia at 216 m and 794 m (Koehler 1904). It is a new record for New Caledonia.

***Amphiophiura insolita* (Koehler, 1904)**
Fig. 11A–C

Ophioglypha insolita Koehler, 1904: 47, pl. 7 figs 5–6, 8.
Amphiophiura insolita – Matsumoto 1915: 77; Koehler 1922: 362–363, Pl. 84 figs 8, 9; Koehler 1930: 225.

Material. Sta. CP1646: 31 spms; sta. DW1648: 2 spms; sta. DW1650: 11 spms.

Description. Dorsal disk centre covered by small, round, imbricating scales with a central primary plate; radially a large round plate (possibly a primary plate) separates each pair of round radial shields. Interradially, a large pentagonal plate abutts a wide thick marginal plate. Dorsal arm plates hexagonal, twice as wide as long, on first segment triangular, distally separating radial shields. A single large pentagonal oral shield in each interradius directly abutts the dorsal marginal plate. Ventral interradius formed by this single large, distally bulging shield that also creates the ventral disk margin. Adoral shields longer than wide, restricted to proximal angle of oral shield. 7 block-like lateral oral papillae at each jaw edge, proximalmost papilla longer, 2 distal papillae widened. Genital slits next to oral shield, abradial genital plates restricted to disk edge, forming arm comb. Ventral arm plates hexagonal, wider than long. Lateral plates of second arm segment (incorporated into disk) enlarged and bulging. Up to six pointed arm spines proximally (at 12 mm dd), increasing in length from dorsal to ventral, the ventralmost spine being shorter again. Longest spines about half a segment long. All plates with glass bead-like structure.

Remarks. This species may be conspecific with *A. monaria* (A.H. Clark, 1949), according to O'Hara (personal communication), but a more detailed study is needed to resolve their taxonomic status.

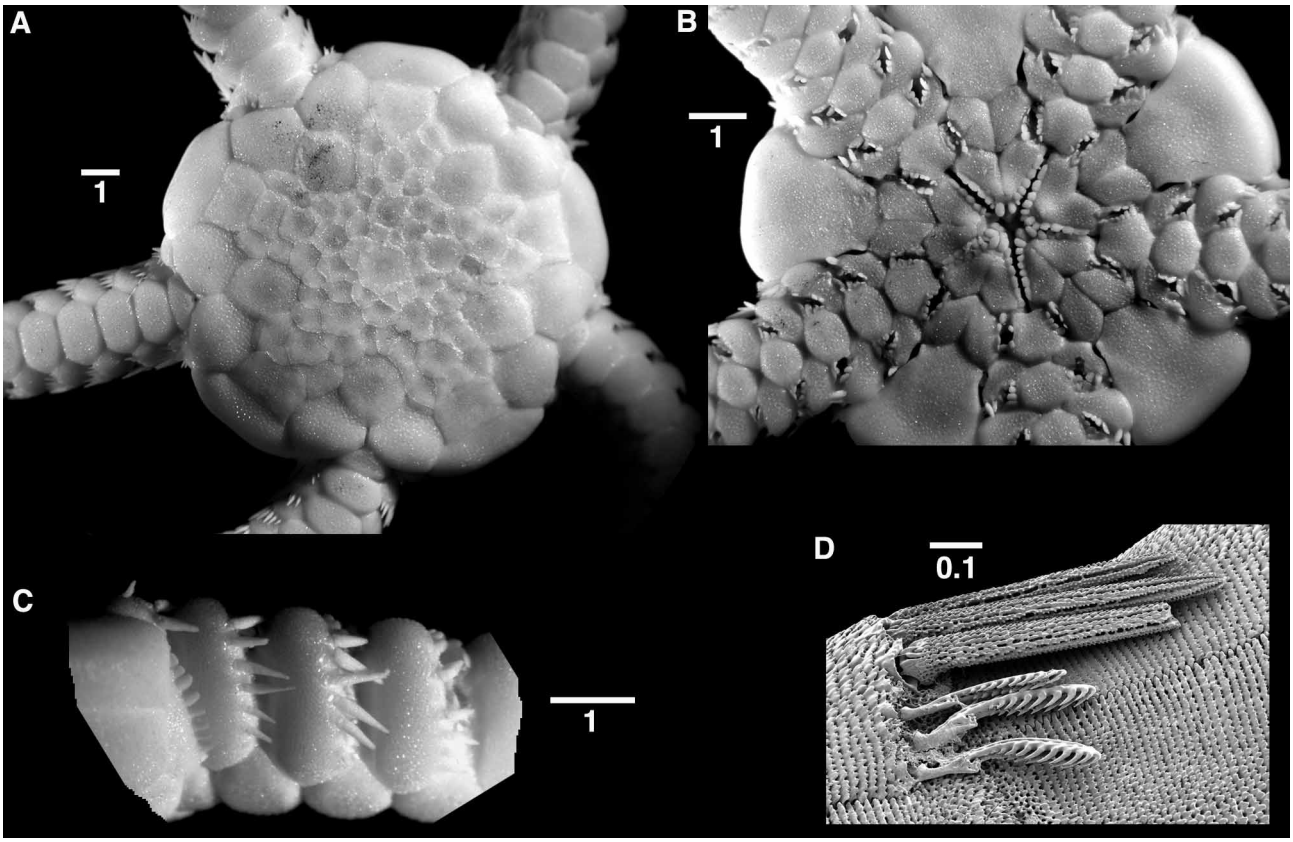

FIGURE 11. A–C, *Amphiophiura insolita*. A, dorsal aspect; B, ventral aspect; C, proximal lateral arm. D, *Ophiopallas paradoxa*, arm spines. Scale bars in millimetre.

Genus *Ophiophycis* Koehler, 1901

Ophiophycis johni McKnight, 2003

Ophiophycis aff. *guillei* – Vadon 1991: 339–341, figs 3, 4, 15–17.

Material. Sta. DW1650C: 1 spm.

Remarks. The specimen reported by Vadon (1991) is similar to *O. johni* according to the images and here proposed as conspecific. The species is separated from *O. guillei* Vadon, 1991 by a smaller disk size, fewer proximal arm joints incorporated into the disk, fewer tentacle pores, dorsal arm plates and enlarged lateral arm plates. Vadon (1991) considered that these characters may be caused by the small size of her specimens (2–4 mm dd) compared to the holotype of *O. guillei* (6 mm dd) and refrained from describing them as a separate species. McKnight's (2003) specimen was with 5.5 mm dd almost as large as *O. guillei*, which suggeststst that these characters are indeed species specific. The Lifou specimen is with 2.8 mm dd comparable to Vadon's specimens. It is clearly identified by its distinctely stellate (five-lobed) centrodorsal plate, the swollen disk plates and the glass bead-like structure of the plates.

Distribution. This new record extends the depth range to a shallow 200–260 m, whereas previous New Caledonian records were collected at 410–1640 m. In New Zealand waters the species was found at 985–1000 m.

Subfamily Ophioleucinae Matsumoto, 1915

Genus *Ophiopallas* Koehler, 1904

Ophiopallas paradoxa Koehler, 1904

Figure 11D

Material. CP1646: 15 spms.

Remarks. A character of the genus *Ophiopallas* is the presence of minute, comb-like accessory arm spines. These were described in detail by Madsen (1983). Accessory arm spines are also found in two other genera of Ophioleucinae. In *Ophiernus* they are bristle-like, but in *Ophiopyren* they look identical to those of *Ophiopallas* (Madsen 1983). *Ophiopyren* is currently a monospecific genus, since all other species previously placed in it have been transferred to other genera. Madsen (1983) maintained the genus as separated from *Ophiopallas* by its shorter genital slits that do not extend onto the dorsal disk and its longer arm spines. The length of genital slits has been shown to be a character of low taxonomic value in *Ophioplinthus* (Martynov & Litvinova 2008) and its value for generic delimitation in these species should be re-analysed. Instead, the accessory arm spines may suggest a close relationship between *Ophiopyren* and *Ophiopallas* or even congeneric status.

Family Amphiuridae Ljungman, 1867

Genus *Amphipholis* Ljungman, 1866

Amphipholis tuberosa sp. nov.

Figure 12

Type material. Holotype on SEM stub, sta. 1415, New Caledonia, Loyalty Islands, Lifou, Baie du Santal, off Chépénéhé, 20°47.1'S, 167°09.1'E, 3–7 m [MNHN IE-2009-9208]. Paratypes: Sta. 1413: 1 spm, in 95% ethanol [SMNH-Type-8078]; sta. 1450: 2 spms, in 80% ethanol [SMNH-Type-8079]; NC00-35: 2 spms, in 95% ethanol [SMNH-Type-8080].

Etymology. The specific name is derived from the Latin word for “full of lumps or protuberances” (Brown 1956), alluding to the structure of the disk scales and other plates.

Holotype description. Dorsal disk covered with a central plate, a circle of five large radial, irregularly lobed

plates, and columns of three overlapping plates of similar size interradially, all of which bear several small non-articulated protuberances, 30–70 µm wide, 10–30 µm high, irregularly round to oval; 1.9 mm dd. Radial shields half-circle shaped, contiguous for their entire length, with several lower and some higher protuberances. Disk edge well-defined. Arms all broken, at least twice as long as dd. Dorsal arm plates bell shaped, separated by lateral plates, distal edges slightly convex, surface with low protuberances. Four spines on proximal joints, ventralmost spine smallest. All spines flat, hollow, shorter than an arm joint, with pointed finger-like extension in middle of distal end.

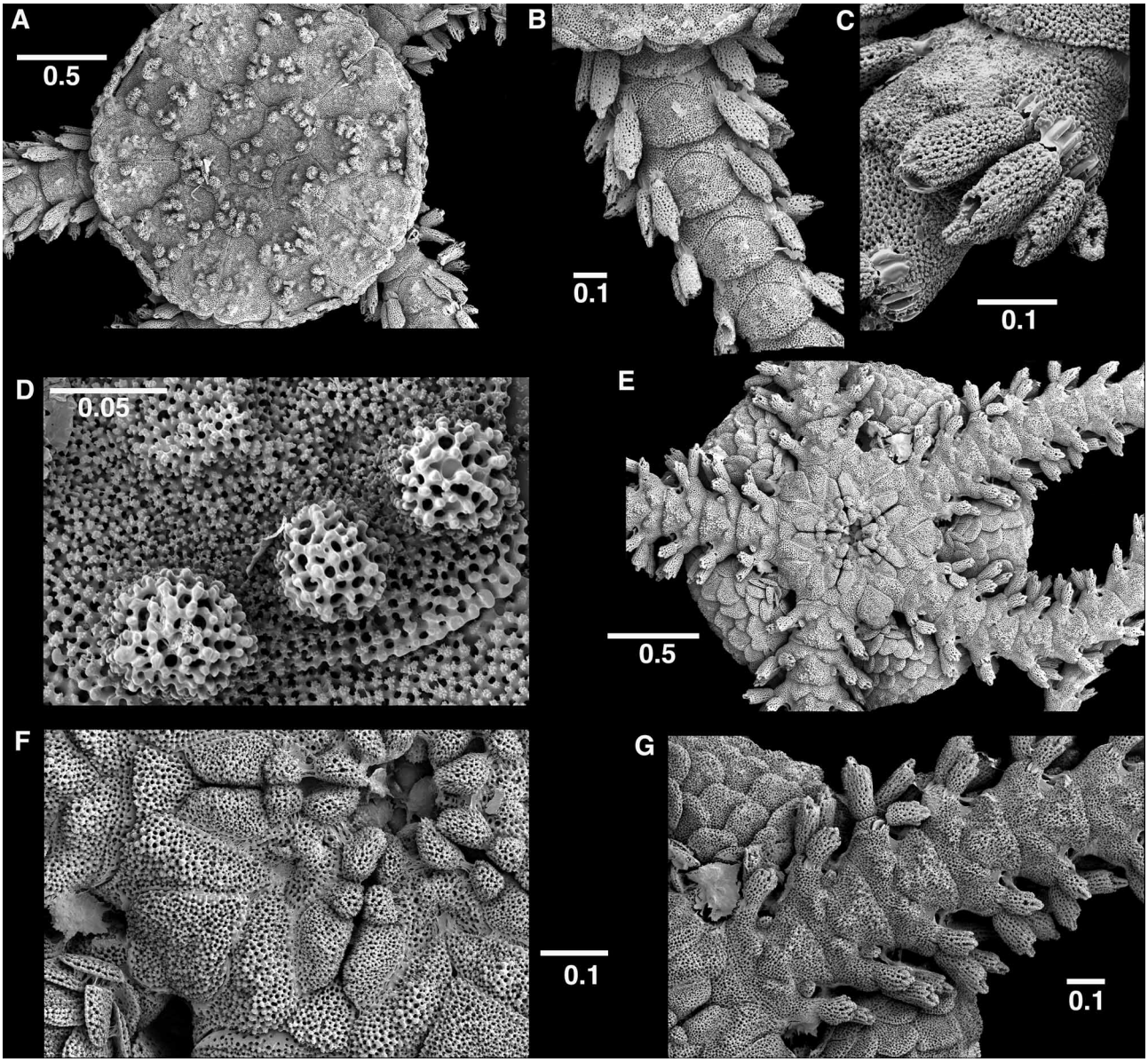

FIGURE 12. SEM images of *Amphipholis tuberosa* **sp. nov.** holotype MNHN IE-2009-9208. A, dorsal aspect, note the protuberances; B, dorsal arm, note the peculiar shape of the spines; C, arm lateral; D, disk protuberances; E, ventral aspect; F, oral details; G, ventral arm. Scale bars in millimetre.

Ventral disk covered by thick, round overlapping scales of uneven appearance. Jaws bear paired pointed infradental papillae on the dental plate, followed by a low round lateral papilla on the proximal end of the oral plate, and an operculiform, much enlarged distal lateral papilla, partly on the oral plate and partly on the adoral shield. Oral shields spearhead-shaped, one of them with two hydropores to either side of the distal lobe. Adoral shields wing-like, flaring, separating the oral shield from the arm. Adoral and oral shields as well as distal oral papilla microscopically tuberculous. First ventral arm plate between two jaws pentagonal, about as wide as long, rough. Following plates separated, pentagonal, twice as wide as long, distal edge slightly convex, lateral edges indented, surface

microscopically tuberculous. A single small round tentacle scale on the first two joints, non on following joints.

Paratype variations. The paratypes measured 0.8, 1.2, 1.6, 1.75 and 1.9 mm dd. In the smallest paratypes the plates are light microscopically smooth, lacking tubercles, but the characteristic shape of the arm spines is present. The larger ones are similar to the holotype.

Remarks. The pattern of the oral papillae and the relatively short arms clearly place this species in the genus *Amphipholis*, which currently includes 30 species (Stöhr & O'Hara 2007). *Amphipholis tuberosa* **sp. nov.** differs from all other species by its tuberculous plates and scales and the shape of the arm spines. Its closest affinities may be with *A. sigillata* Cherbonnier & Guille, 1978, described from Madagascar, which shares the large primary rosette, some sculpturing of the disk scales and the lack of tentacle scales on all but the most proximal joints.

Distribution. Known only from the type locality. Found at depths of 3–31 m at Lifou on rocky and sandy bottoms.

Genus *Amphiodia* Verrill, 1899

Subgenus *Amphispina* Nielsen, 1932

Amphiodia (*Amphispina*) *loripes* (Koehler, 1922) new combination

Figure 13

Amphipholis loripes Koehler, 1922: 164, pl. 68, figs 4,5; A.M. Clark 1970: 29, 76, fig. 6a; Cherbonnier & Guille 1978:100–101.

Material. Sta. NC00-38: 1 spm; sta. NC00-35: 5 spms; sta. NC00-44: 3 spms; sta. 1448: 1 spm (used for SEM).

Description. About 2 mm dd, disk round, high raised, ventral disk separated from proximal arms, but apparently without damage. Arms all broken, but longest more than 20 times dd. Dorsal disk covered by small, round, overlapping scales, which stand almost upright at the disk edge. Scale stereom a uniform meshwork of small holes and round bead-like structures. Radial shields bar-like, at least four times as long as wide, about 1/4 as long as dd, outer edges overlapped by disk scales; pairs separated proximally by a wedge of scales for up to half their length. At distal end of each radial shield, above genital plates, a spiny process points upwards. Proximalmost arm segments lack dorsal plates, covered instead by skin, which ruptured in the preparation process, but was undamaged originally. In vivo, the genital plates and ventral disk are attached to this part of the arms. Dorsal arm plates at their distal edge twice as wide as long, proximal and lateral edges forming a convex bow, distal edge straight; plates on consecutive joints touch barely. Four arm spines proximally, dorsalmost spine longest, longer than an arm joint; spines tapering gradually into a blunt tip, edges slightly rugose, longitudinal grooves running towards the tip from about mid-length. Distal arm spines slightly hook shaped with distal thorn, long open groove at one side, bordered by small thorns.

Ventral disk covered by scales similar to dorsal disk; bursal slits lined by bar-like genital plates, wich are exposed due to the raised disk. Oral shields elongated drop-shaped with acute proximal point and convex distal edge; one shield slightly larger, with hydropore to the side of its distal edge, marking it as the madreporite. Adoral shields wing-like flaring, reaching around the oral shield and separating it from the arm. Jaws narrow, bearing three oral papillae to either side; a small oval infradental to either side of the dental plate, a similar papilla at the oral plate and a low, wide papilla at the adoral shield, no buccal scale. Ventral arm plates pentagonal, slightly wider than long, with obtuse proximal angle, straight lateral edges, concave distal edge; consecutive plates not touching. Single elongated tentacle scale on ventral arm plate, as long as lateral edge of ventral plate.

Remarks. The Lifou specimens agree well with Koehler's (1922) original description and images and the description by Cherbonnier & Guille (1978). This species was described in the genus *Amphipholis* and still remained there until now, although Clark (1970) remarked on its affinities with *Amphiodia* and was undecided on its generic position. However, she had access only to the single type specimen that lacked the dorsal disk. The nature of the disk scalation and the presence of spiny processes were therefore unknown to her. Cherbonnier & Guille (1978) found complete specimens at Madagascar and for the first time described the dorsal disk including the spiny processes, but although they remarked on its great similarities with *Amphiodia*, they kept it in *Amphipholis* solely on the basis of the widened outer oral papilla. The extremely long arms, fine disk scalation, long, partially

separated radial shields, the single elongated, ventrally placed tentacle scale, and the number and placement of the oral papillae all point to *Amphiodia*; the thorny processes distal to the radial shields are similar to those found in the subgenus *Amphispina* (Stöhr *et al.* 2010). The only character in common with *Amphipholis* is the widened third oral papilla, which is usually shorter in *Amphiodia*, but in *A. loripes* it is not as high and operculiform as in *Amphipholis* (see above) and the jaws appear longer and narrower as in that genus. Weighing the combined evidence it is highly likely that the distal papilla is a convergent rather than homologous structure. The subgenus *Amphispina* is characterized by spiny marginal scales, which are lacking in all known specimens of *A. loripes*. However, as Stöhr *et al.* (2010) have shown, this character is highly variable and the radial processes may be the only spiny scales present in some individuals of species of *Amphispina*. It is also likely that the marginal spines have been reduced completely in some species. Therefore, I propose to transfer *A. loripes* to *Amphiodia* (*Amphispina*).

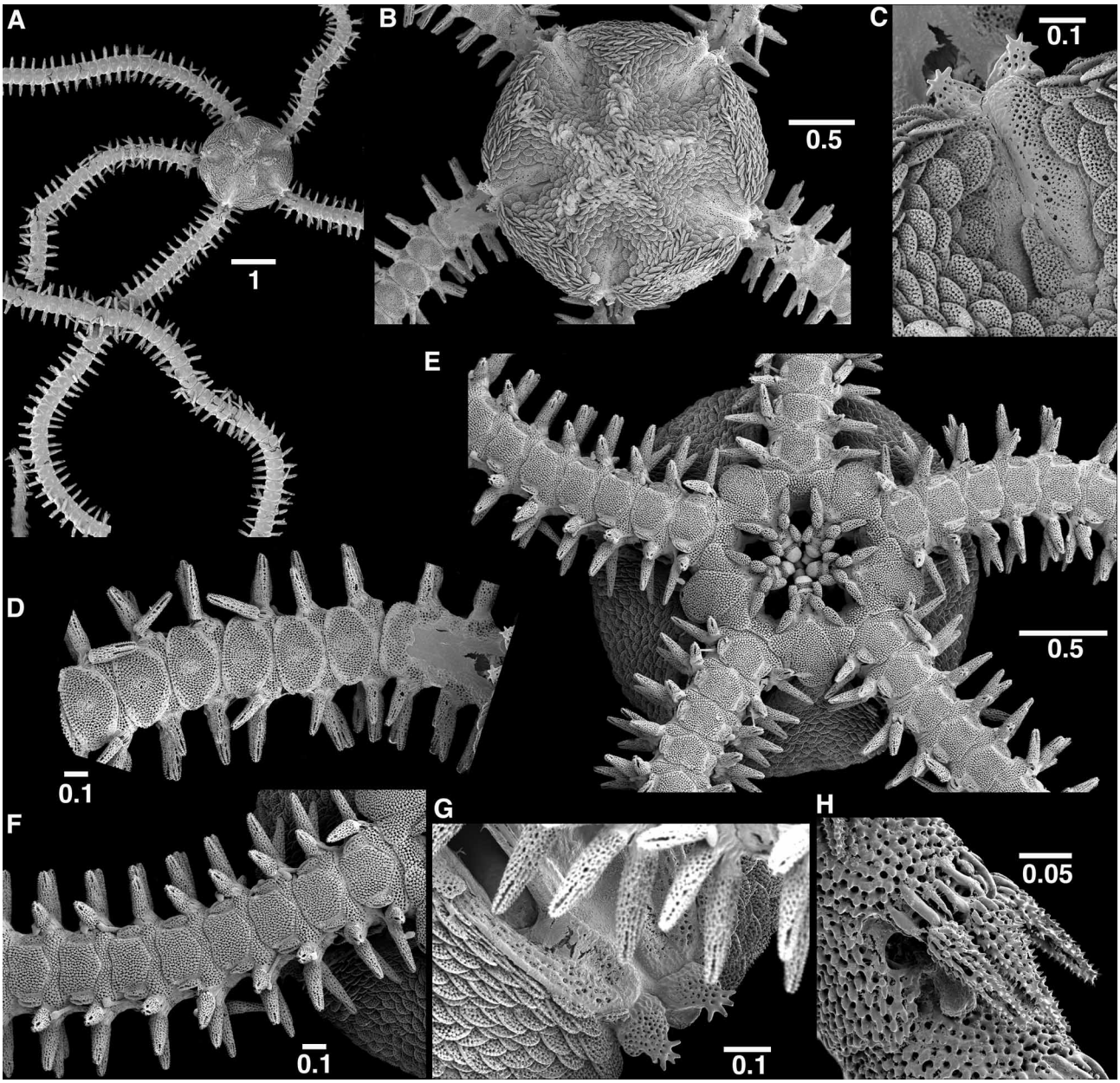

FIGURE 13. SEM images of *Amphiodia* (*Amphispina*) *loripes*. A, habitus; B, dorsal aspect; C, radial shields with spiny processes; D, dorsal arm; E, ventral aspect; F, ventral arm; G, genital slits and ventral aspect of radial shield processes, H, arm spines. Scale bars in millimetre.

Family Ophionereididae Ljungman, 1867

Genus *Ophionereis* Lütken, 1859

***Ophionereis degeneri* (A.H. Clark, 1949)**
Figure 14A, 15

Material. Sta. 1455: 1 spm; sta. 1456: 2 spms; sta. 1450: 1 spm; sta. 1465: 3 spms (1 used for SEM); sta. 1467: 2 spms.

Description. At 4.5 mm dd dorsal disk covered by round, imbricating scales of uniform size. Radial shields small, overlapped and separated by scales. Dorsal arm plates trapezoidal, twice as wide as long, distal edge shorter than proximal, contiguous. Stereom with bead-like structure. Supplementory dorsal arm plates half-circle shaped, conspicuous, as long as lateral edges of ventral plates. Three blunt arm spines, shorter than an arm joint.

Ventral disk covered by scales similar to dorsal disk. Oral shield triangular to spearhead-shaped, longer than wide, madreporite larger, possibly deformed in figured specimen. Aboral edge of bursal slit lined with granule-like genital papillae along its entire length, visible at distal edge of radial shield from above. Ventral arm plates axe-shaped, twice as wide as long, dorsal edge twice as wide as proximal edge, concave, lateral edges indented for tentacle pores. Single large oval tentacle scale.

Dental plates rectangular, flat, externally four tooth sockets visible, two dorsal ones with a pair of deeper fenestrations, only dorsalmost socket completely perforating plate, visible internally, ventral sockets low depressions. Oral plates with smooth irregular rectangular abradial muscle attachment area, adradial distal “hinge” with numerous horizontal bars and grooves. Proximal lateral arm plates 1.5 times as wide as long, spine articulations u-shaped, internally a small hole near tentacle pore. Vertebrae zygospondylous, with proximal depression and distal projection (keel), dorsal surface with longitudinal groove. Radial shield triangular, distal edge shorter than proximal edge, lateral edge (towards adjacent shield) longest, with distal strong ball-like condyle.

Colouration in ethanol a mottled light and dark brown on dorsal disk, radial shields lighter, arms variegated light brown with dark bands.

Remarks. One of the largest spms with a dd of 4.5 mm was selected for examination in comparison with *O. porrecta*. *Ophionereis degeneri* is superficially similar to *O. porrecta*, but it can be distinguished by a number of characters. The dorsal disk scalation is coarser and lacks the differentiation into smaller central scales and larger marginal radial scales observed in *O. porrecta* (see below). The supplementary dorsal arm plates are conspicuously larger, the arm spines shorter and at least proximally the ventral spines are flat and wide with a truncated tip, in contrast to the conically tapered spines of *O. porrecta*. The distal edge of the ventral arm plates is concave, while it is slightly convex in *O. porrecta*. The oral shield is longer than wide, while it is as wide as long in *O. porrecta*. Also the internal skeleton shows differences in the perforations of the dental plate, the shape of the oral plate and the radial shield, but since only one specimen of each species has been examined, more data are necessary to determine intraspecific variation of these characters. In addition, *O. degeneri* does not grow larger than 7 mm dd (Clark & Rowe 1971), whereas *O. porrecta* reaches a size of more than 10 mm dd.

Devaney (1974a) synonymized *O. degeneri* with *O. porrecta* without explanation. Guille and Ribes (1981) considered their small specimens as juveniles of *O. porrecta*, although they exhibited characters of *O. degeneri* and apparently no comparisons with young *O. porrecta* were made. The Lifou material shows that at a size of 4.5 mm dd both species can be distinguished without doubt and there is no reason to believe that smaller specimens of *O. porrecta* would show characters of *O. degeneri* that then somehow vanish during further development. In the Lifou material, the smallest specimen of *O. porrecta* measured 3.2 mm dd and was clearly identifiable by its disk scalation, longer arm spines and smaller accessory arm plates. The size range of *O. degeneri* was 2.6– 4.5 mm dd and all of these showed the distinguishing characters of the species. The size of disk scales is usually relatively larger in small juvenile brittle stars, which can cause difficulties in identification, particularly at stages that have not yet developed the supplementary arm plates. In large specimens the size of these supplementary plates varies and may approach either species. However, the shorter arm spines in *O. degeneri* and the larger marginal disk plates in *O. porrecta* are reliable characters.

According to T. O'Hara, *O. degeneri* is similar to *O. lineata* H.L. Clark, 1946, *O. terba* Baker & Devaney, 1981 and *O. novaezelandiae* Mortensen, 1936 (recognized as different from *O. fasciata* Hutton, 1872 by O'Hara), but they all have small accessory dorsal arm plates (O'Hara, personal communication).

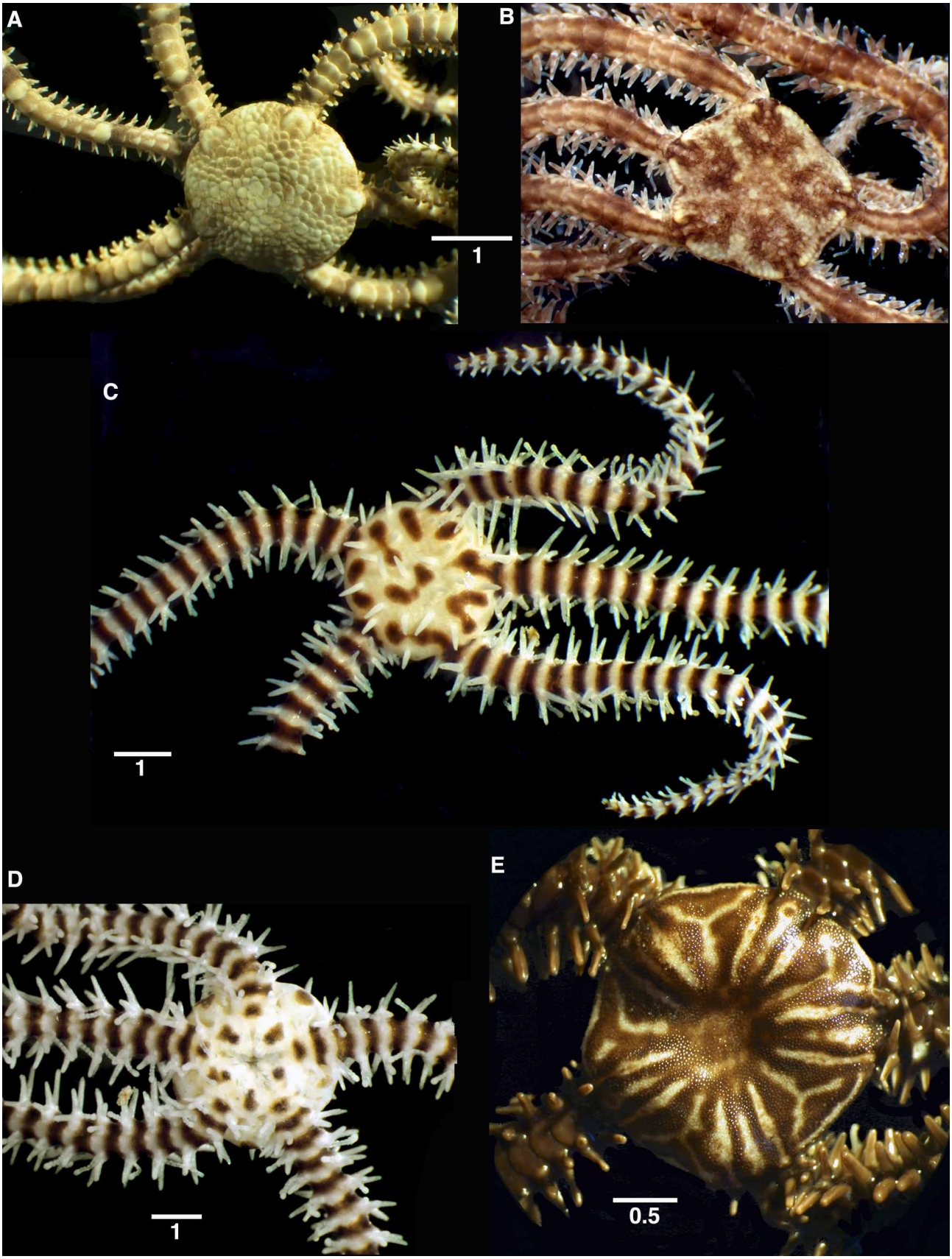

FIGURE 14. A, *Ophionereis degeneri*, dorsal aspect. B, *Ophionereis porrecta*, dorsal aspect. C, D, *Ophiomastix caryophyllata*, juvenile; C, dorsal aspect; D, ventral aspect. E, *Ophiocoma erinaceus*, probably night colouration. Scale bars in millimetre.

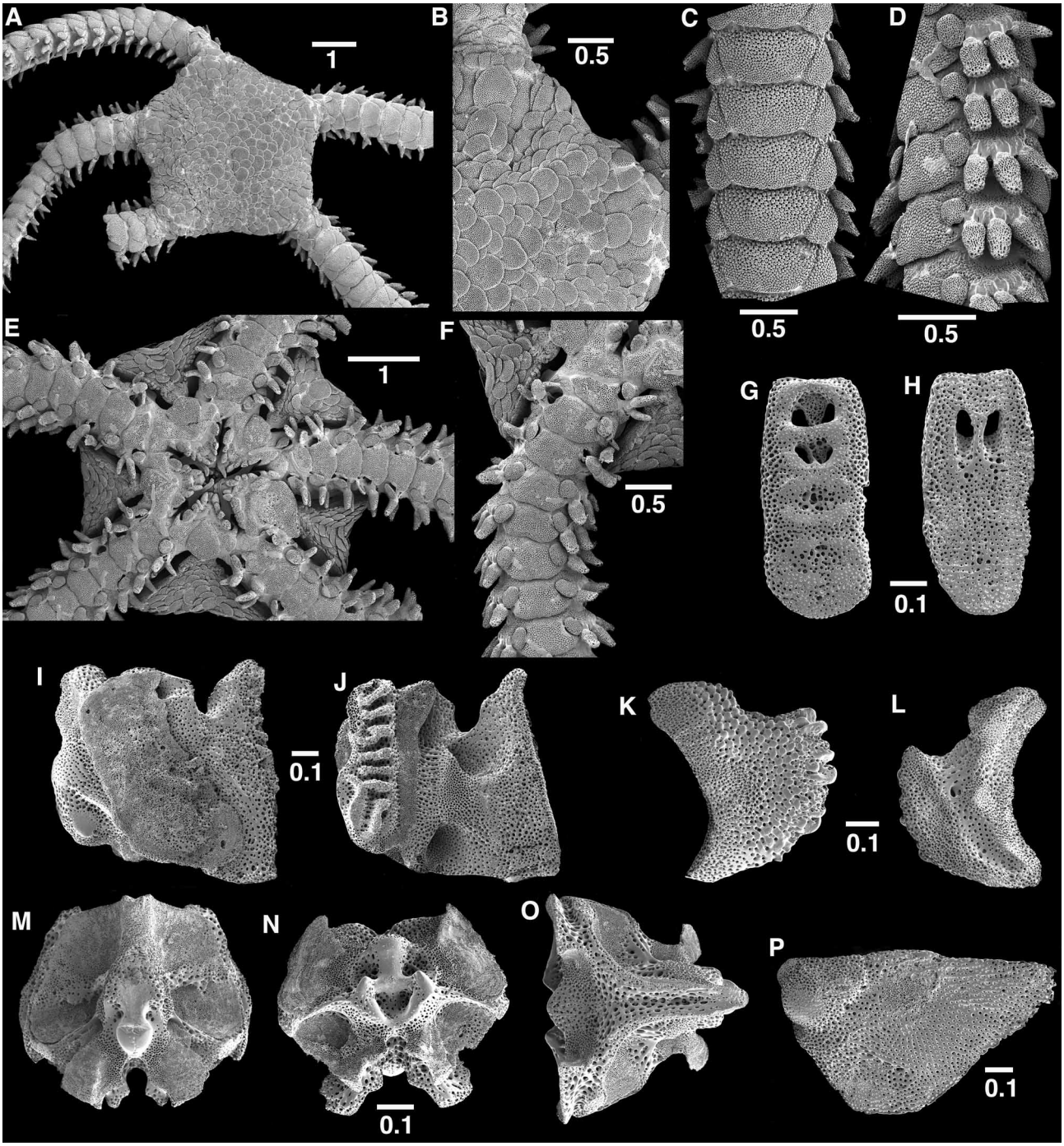

FIGURE 15. SEM images of *Ophionereis degeneri*, 4.5 mm disk diameter. A, dorsal aspect; B, dorsal interradius; C, dorsal arm; D, lateral arm; E, ventral aspect; F, ventral arm; G, dental plate, external; H, dental plate, internal; I, oral plate, abradial; J, oral plate, adradial; K, proximal lateral arm plate, external; L, proximal lateral arm plate, internal; M–O, proximal vertebra; M, distal face; N, proximal face; O, dorsal; P, radial shield, internal. Dental plates orientated with dorsal end up; oral plates with distal end to the left; radial shield with proximal end to the left. Scale bars in millimetre.

Distribution. This is a species of shallower shelf areas, at Lifou it was found at 15–90 m depth. Its true geographic distribution is unknown due to the taxonomic confusion, which has probably resulted in it being reported as *O. porrecta* in many cases. Both species occur in sympatry at least in part of their range. With just nine specimens of *O. degeneri* found at Lifou, the species seems to be more limited in its distribution and possibly narrower in its ecological requirements or more difficult to collect due to a cryptic life-style (living in holes in dead coral; T. O'Hara personal communication). This is a new record for New Caledonia.

***Ophionereis porrecta* Lyman, 1860**
Figure 14B, 16

Material. Sta. 1411: 1 spm; sta. 1422: 5 spms; sta. 1429: 1 spm; sta. 1446: 2 spms; sta. 1450: 1 spm; sta. 1451: 1 spm; sta. 1453: 1 spm; sta. 1455: 1 spm; sta. 1456: 1 spms; sta. 1461: 5 spms; sta. 1462: 1 spm; sta. 1465: 6 spms (1 used for SEM); sta. 1466: 5 spms; sta. 1467: 4 spms; sta. 1468: 1 spm; sta. 1469: 1 spm.

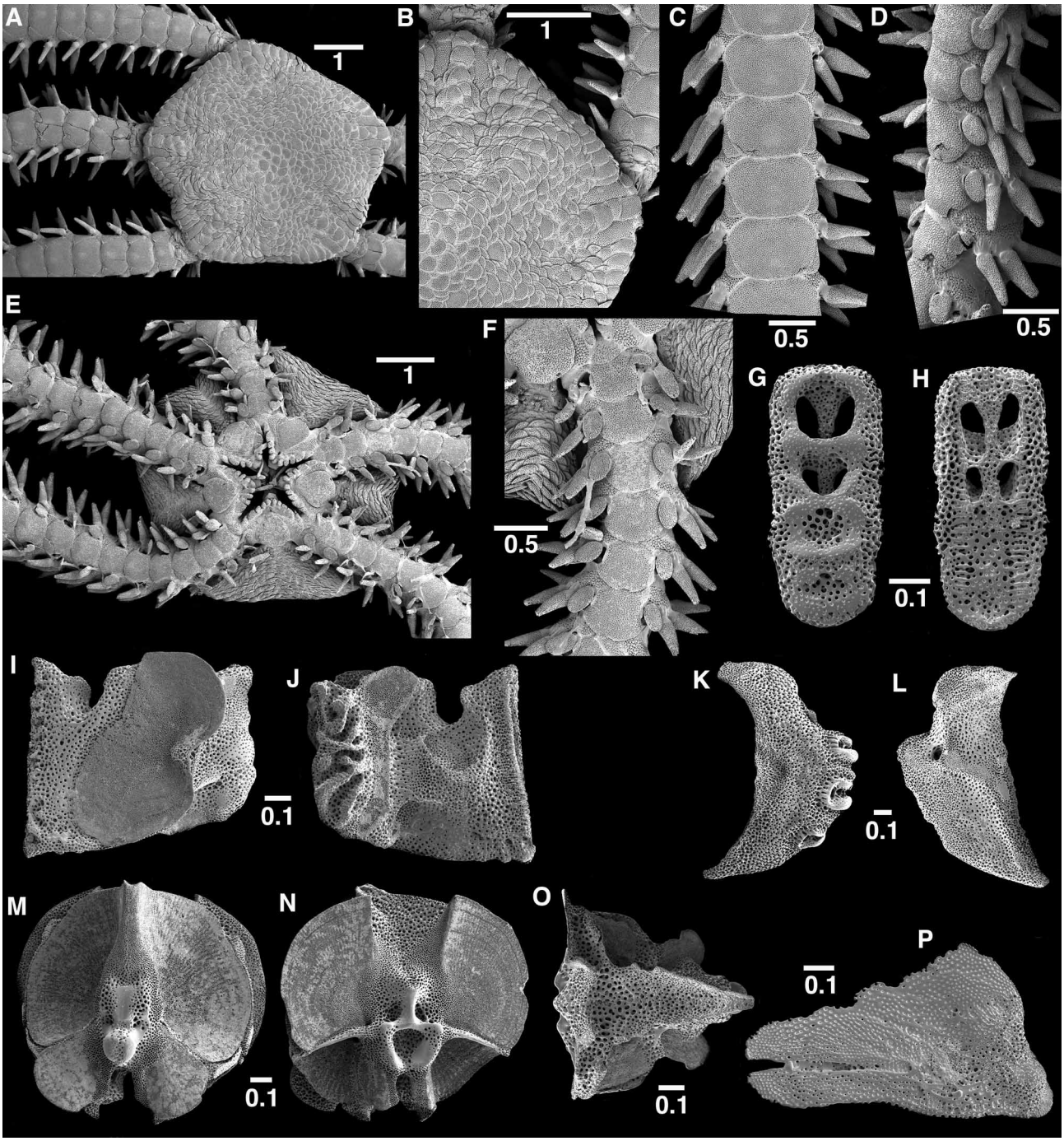

FIGURE 16. SEM images of *Ophionereis porrecta*, 4.5 mm disk diameter. A, dorsal aspect; B, dorsal interradius; C, dorsal arm; D, lateral arm; E, ventral aspect; F, ventral arm; G, dental plate external; H, dental plate, internal; I, oral plate, adradial, proximal end left; J, oral plate, adradial, proximal end right; K, L, proximal lateral arm plates, K, external, L, internal; M–O, proximal vertebra; M, distal face; N, proximal face; O, dorsal; P, radial shield, internal, proximal end right. Scale bars in millimetre.

Description. At 4.5 mm dd, disk covered by small round imbricating scales. Interradially at disk edge larger scales, increasing in size towards radial shields. Small oval radial shields, overlapped and separated by disk scales. Dorsal arm plates trapezoidal, distal edge shorter than proximal edge, 1.5 times as wide as long. Supplementary dorsal arm plates small, half as long as lateral edges of ventral plates. Arm spines three, conical, as long as an arm joint.

Ventral disk covered by small, round imbricating scales. Oral shield spearhead-shaped, as wide as long, madreporite larger, with hydropore at right laterodistal edge. Ventral arm plates slightly axe-shaped, distally little wider than proximally, distal and proximal edge convex, lateral edges concave. Single large oval tentacle scale.

Dental plate with four tooth sockets, both ventral sockets shallow depressions, dorsal ones each with a pair of oval fenestrations, completely perforating the plate, but smaller on the internal side, separated by a septum. Oral plates with smooth ear-shaped abradial muscle attachment area, adradial "hinge" with irregular bars and grooves. Proximal lateral arm plates twice as wide as long, spine articulations u-shaped, internally a large hole near the tentacle pore. Vertebrae zygospondylous, with deep proximal depression and distal projection (keel), dorsal surface depressed. Radial shield elongated triangular, with long inner edge (towards adjacent shield), short distal and long proximal outer edge, proximal half divided by longitudinal incision, distally with weak ball-like condyle.

Remarks. For comparison with *O. degeneri* a small spm of 4.5 mm dd was selected, incidentally from the same sample. In this sample there also was the smallest *O. porrecta* of the material, at 3.2 mm dd, and a same size *O. degeneri*. The size range over all samples was 3.2–10 mm dd, and thus O. porrecta reaches about twice the size of O. degeneri. *Ophionereis porrecta* can be distinguished from *O. degeneri* by the large marginal radial dorsal disk scales, the longer, tapered arm spines, the smaller supplementary dorsal arm plates, the convex distal edge of the ventral arm plates and by the oral shield being as wide as long. For further discussion see under *O. degeneri*. The sympatric occurrence of both species at similar size in the same sample further corroborates their validity as separate species.

Distribution. At Lifou this species was found at depths of 4–130 m. Its true geographical distribution cannot be determined since it has often been confused with *O. degeneri*, but it appears to be a common species in the tropical Indo-Pacific. Since more than four times as many (38) specimens of *O. porrecta* as of *O. degeneri* were collected at Lifou, it appears to be the more common and more widely distributed species of the two, possibly with wider ecological tolerances or more easily collected.

Family Ophiocomidae Ljungman, 1867

Genus *Ophiomastix* Müller & Troschel, 1842

Remarks. Among the species of *Ophiomastix* found at Lifou, *O. ornata* Koehler, 1905 is an interesting find. According to Devaney (1978) it is unusual among its congeners, because of the lack of enlarged arm spines, a character otherwise typical of *Ophiomastix*, and in that the arm spines are hollow, a character it shares with *Ophiocoma pusilla* (Brock, 1888). *Ophiomastix ornata* is characterized also by compressed spindle-shaped disk spinelets.

Ophiomastix caryophyllata Lütken, 1869 is a conspicuously patterned (Fig. 13C, D) member of the genus, found only once at Lifou, as a juvenile specimen. The most common species of *Ophiomastix* is *O. variabilis* Koehler, 1905, found at 12 collecting sites.

Distribution. *Ophiomastix ornata* was previously known from the type specimen from southeastern Borneo and two specimens from the island of Bikini, at depths of 35–55 m. It is a new record for New Caledonia and the known depth range has increased to 25–200 m. This appears to be a rare species with wide distribution. *Ophiomastix variabilis* is a widespread Indo-Pacific species, whereas *O. caryophyllata* may be rarer.

Genus *Ophiocoma* L. Agassiz, 1835

Figure 17A–D, L, M

Remarks. Seven species of *Ophiocoma* were found at Lifou (Table 2). Of these, *O. macroplaca* (H.L. Clark, 1915), *O. doederleini* de Loriol, 1899 and *O. schoenleinii* Müller & Troschel, 1842 are new records for New Cale-

donia. Benavides-Serrato & O'Hara (2008) showed that *O. schoenleinii* is a distinct species, separate from *O. erinaceus*, with which it had been synonymized before (Devaney 1970). Therefore, previous records of *O. erinaceus* from New Caledonia may include specimens of *O. schoenleinii* and the distribution of both species cannot be assessed. These dark brown to black coloured species are distinguished by *O. erinaceus* having two tentacle scales and red tube feet (white in alcohol), whereas *O. schoenleinii* has a single tentacle scale and grey tube feet (alive as well as in alcohol).

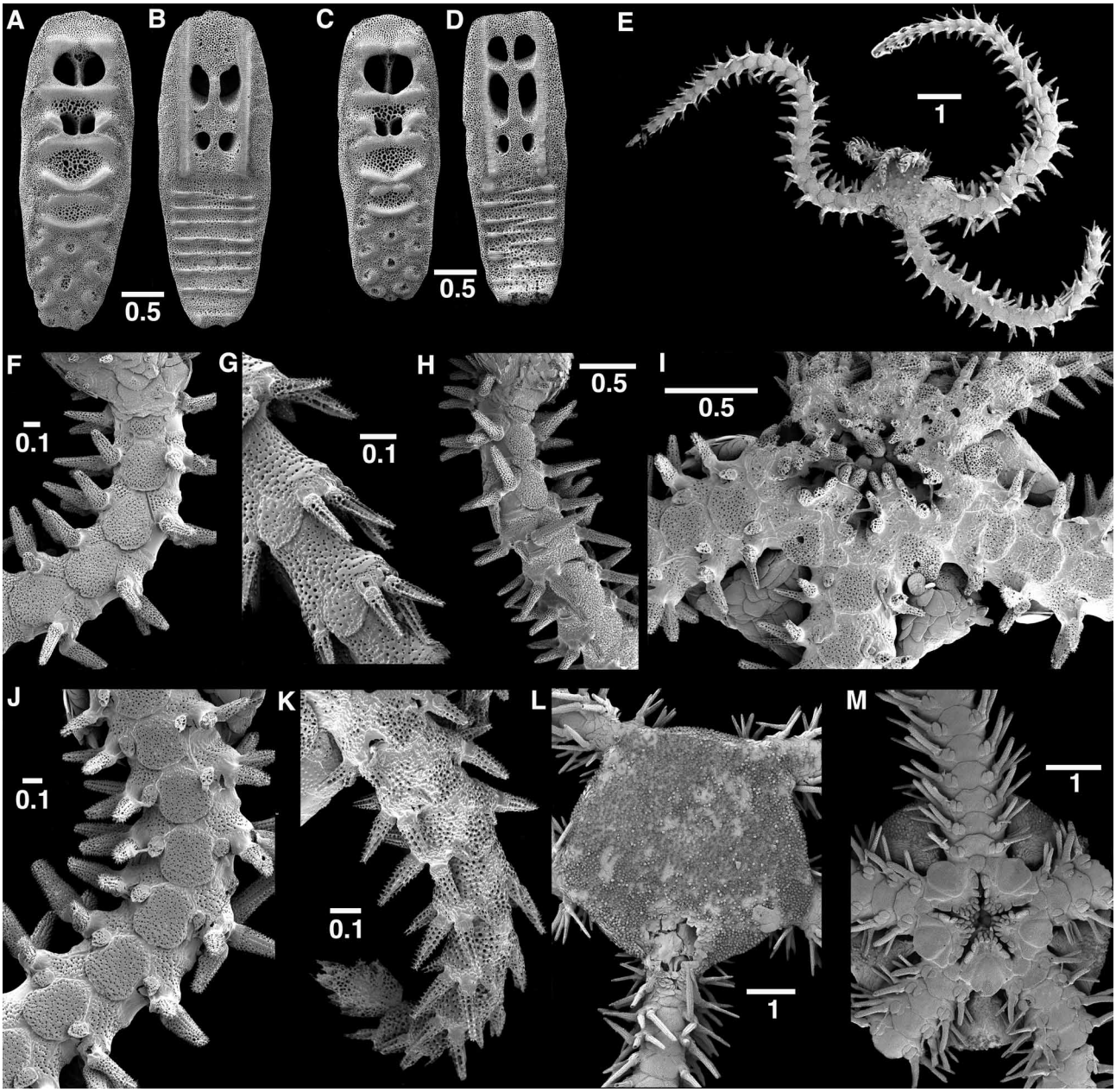

FIGURE 17. SEM images of Ophiocomidae. A, B, *Ophiocoma erinaceus*, dental plate; A, external, B, internal. C, D, *Ophiocoma schoenleinii*, dental plate; C, external, D, internal. E–K, *Ophiocomella sexradia*, F–H, J, large arm; E, dorsal aspect; F, dorsal arm proximal; G, dorsal arm distal; H, lateral arm; I, ventral aspect; J, ventral arm; K, small, regenerating arm. L, M, *Ophiocoma pusilla*, L, dorsal aspect; M, ventral aspect. Dental plates orientated with dorsal end up. Scale bars in millimetre.

The differences in the dental plates shown by Benavides-Serrato & O'Hara (2008) are confirmed here at a smaller size of 15–16 mm dd. The internal surface of the dental plate in *O. erinaceus* lacks the dorsalmost perforations at this size, which are already present in *O. schoenleinii*. As additional character to separate these and a third dark species, *O. cynthiae* Benavides-Serrato & O'Hara, 2008, the authors suggested the extent of granules covering the ventral disk. In *O. erinaceus*, the granules are supposed to persist from the disk edge almost to the oral shields,

in *O. schoenleinii* only as a wedge near the disk margin and in *O. cynthiae* they are absent (Benavides-Serrato & O'Hara 2008). In the Lifou material one specimen that clearly belongs to *O. schoenleinii*, according to all other characters, has a fully granulated disk, another shows a wedge extending to the oral shield. Some specimens of *O. erinaceus* on the other hand show a short wedge and specimens of 7 mm dd lack granules altogether, but in *O. erinaceus* disk granules first appear at a size of 7.5 mm dd (Devaney 1970). One of the syntypes of *O. erinaceus* (ZMB Ech 921) that I have examined in the Museum für Naturkunde in Berlin lacks granules on the ventral interradius. This character may therefore be less reliable and size-dependent. However, it cannot be ruled out that the syntype series includes both species, which would require selection of a lectotype to stabilize the concept of *O. erinaceus*.

Several *O. erinaceus* were preserved in what must be their night colour pattern; light brown to beige, radiating lines on a dark brown dorsal disk, similar to that shown for *O. erinaceus* by O'Hara *et al.* (2004). Unfortunately, the collection notes do not record the time of preservation, but since collecting and preserving in the field went on until midnight it is highly likely that these animals were preserved at night. Hendler (1984) demonstrated colour-changes related to time of day in four species of *Ophiocoma*, in some of which the presence of photoreceptors was shown later (Aizenberg *et al.* 2001). Nothing is known about the presence of calcitic microlenses in *O. erinaceus*.

Ophiocoma macroplaca is distinguished from other species in the *scolopendrina*-group of *Ophiocoma* and most importantly from *O. scolopendrina* (Lamarck, 1816) by the presence of four spines on the third arm joint. In the Lifou specimens this character is rarely present on all arms in the same individual. As reviewed by Devaney (1970), this species has caused some taxonomic confusion, because the tiny holotype had few elongated granules or spinelets on the disk. In the Lifou specimens, the disk granules vary somewhat in size and shape. A specimen with 11 mm disk diameter has a dense covering of small round granules measuring about 100:130µm (width:height) intermingled with larger conical granules of 130:170 µm, while a specimen of 6 mm disk diameter has mostly low round granules and few, scattered, about twice as large, conical granules. Other specimens have mostly low round granules, with larger conical ones restricted to the disk margin. The Lifou specimens of *O. scolopendrina* have only low, round granules, about as high as wide, widely spaced. In addition, *O. scolopendrina* is restricted to the littoral zone (Devaney 1970) and has at Lifou only once been collected deeper than 5 m, whereas *O. macroplaca* was not found shallower than 4 m and as deep as 150–200m. One of the specimens of *O. macroplaca* is almost white, presumably night colouration.

Ophiocoma pusilla differs from other species of *Ophiocoma* by its small size and hollow arm spines, a character also found in Ophiacanthidae and in *Ophiomastix ornata*.

Genus *Ophiocomella* A.H. Clark, 1939

Ophiocomella sexradia (Duncan, 1887)

Figure 17E–K

Material. Sta. 1410: 1 spm.

Remarks. This small specimen may easily be mistaken for *Ophiocnida* or *Dougaloplus*, both genera of Amphiuridae with spiny disk. Clark (1970) alluded briefly to the similarity between *Dougaloplus* and *Ophiocomella* when she suggested that *Dougaloplus dividua* (Matsumoto, 1917) may be synonymous with *O. sexradia*, but she never followed up on that idea. I have not examined any *Dougaloplus* species, but *Ophiocomella* does not have the parallel-ridge arm spine articulation typical for Amphiuridae (Martynov 2010a), but a large rounded articulation that suggests it is correctly assigned to Ophiocomidae. Morphological similarity may thus be due to convergent evolution, but a revision of *Dougaloplus* is needed to decide. Unusual for ophiocomids, the spines on the distal arm are thorny and slightly hook-shaped, which may support the hypothesis of a close relationship between Ophiacanthidae and Ophiocomidae proposed by Martynov (2010b). The species is usually hexamerous and fissiparous, although specimens with seven and five arms have been reported (Devaney 1970). Devaney (1974) suggested that *O. sexradia* may be a species complex due to its high morphological variability and wide geographical distribution, but no further investigations have yet been conducted to answer this question.

Distribution. Widely distributed across the Indo-Pacific, littoral to 15 m.

Family Ophiolepididae Ljungman, 1867

Genus *Ophiozonella* Matsumoto, 1915

***Ophiozonella hexactis* sp. nov.**
Figure 18

Type material. Holotype on SEM stub, sta. 1461, New Caledonia, Loyalty Islands, Lifou, reef Shelter, 20°54'S, 167°02.1'E, 100–120 m [MNHN IE-2009-9209]. 1 paratype, sta. 1467, in ethanol [SMNH-Type-8081].

Other material. SOL4934 14Gr23, Australia, Joseph Bonaparte Gulf, 10°18.517'S, 129° 37.01'E, 87 m [MoV-F171262]; SS10/2005 96, Australia, Kalbarri, 27°48.48'S, 113°17.82'E, 123–112 m [MoV-F111958]; SS10/2005 105, Australia, Zuytdorp, 27°8.01'S, 112°46.06'E, 414–405 m [MoV-F111983].

Etymology. The specific name is derived from the Greek words *hex* meaning six and *actis* meaning ray.

Holotype description. Disk irregular hexamerous, a larger and a smaller half, showing clear signs of fission, 1.4–2.0 mm dd. All arms broken, at least 2 times dd, three smaller, three larger. Disk covered by round, imbricating scales, irregularly placed, centrodorsal clearly distinguishable. Radial shields hardly larger than disk scales, round, contiguous except at proximal end, overlapped by disk scales. Dorsal arm plates rounded triangular with straight distal edge, consecutive plates widely separated by lateral plates. No accessory dorsal arm plates. Two conical arm spines, about 1/3 as long as an arm joint, distally turning into multi-toothed hooks.

Ventral disk covered by small, round imbricating scales. Genital slits do not extend to the disk edge. The six jaws all vary in the size of the plates and papillae. Oral papillae consist of a pointed apical papilla, three low oval lateral papillae at dental and oral plate, and a wide low distal papilla at oral plate and adoral shield edge. Adoral shields elongated triangular with flaring distal ends. Oral shields all of different size, the largest elongated triangular with straight edges and a hydropore on its proximal part, a tiny triangular one, a broken triangular one possibly with hydropore, another medium sized rounded triangular one with hydropore, a tiny pentagonal one and a drop-shaped one with convex distal edge. Second tentacle pore completely inside the mouth angle. Ventral arm plates pentagonal, about as long as distal width, with strongly concave lateral edges, slightly convex distal edge, consecutive plates widely separated by lateral plates. A single large, round tentacle scale at each pore. Spine articulation of two parallel ridges, connected proximally.

Paratype variations. The paratype measures 1.6–1.7 mm dd, and resembles the holotype in the disk scalation, arm plates and oral frame. It has likewise three smaller and three larger arms and a distorted disk showing signs of regeneration after fission. The younger arms are longer than in the holotype and on the distalmost joints the dorsal spine is distinctly hook-shaped. One of these arms has an intact tip with an elongated conical terminal plate with distal opening.

Remarks. Matsumoto (1915) erected *Ophiozonella* to separate deep water forms from littoral forms placed in *Ophiozona*, now a synonym of *Ophiolepis* (Devaney 1974b). One of the main differences between *Ophiozonella* and *Ophiozona*/*Ophiolepis* is supposed to be the absence of a distinct trio of plates distal to each pair of radial shields in *Ophiozonella* (but see below). The new species lacks these plates and its large disk scales and oral and adoral shields also fit with the description of *Ophiozonella*. It also lacks accessory dorsal arm plates that are typical for *Ophiolepis* (Matsumoto 1915; Devaney 1974b). The genus until now included 31 species (Stöhr & O'Hara 2007), which are rather heterogeneous in appearance. The type species, *O. longispina* (H.L. Clark, 1908), is a large species reaching more than 10 mm dd, with well differentiated skeleton of numerous plates and scales. Other species are small, a few millimetres in diameter, with reduced skeleton and paedomorphic appearance, such as *O. novaecaledoniae* Vadon, 1990. The new species is the only hexamerous, fissiparous species in the genus and thus distinguished from all others. Its maximum size is unknown, but many fissiparous ophiuroids are small and need a long time to reach their final size due to repeated fission and regeneration (Mladenov & Emson 1988).

The genus *Ophiozonoida* bears great resemblance to *Ophiozonella*. According to the description of the type species *Ophiozonoida picta* H.L. Clark, 1915, it is distinguished by infradentally placed apical mouth papillae, erect arm spines, a single large tentacle scale and small scales interspersed with larger plates on the dorsal disk (Clark 1915). Since Spencer & Wright (1966) synonymized *Ophiotylos* with *Ophiozonoida*, the genus includes six species, most of which are small, under 5 mm in disk diameter. Liao &Clark (1995) remarked that the species previously assigned to *Ophiotylos* may actually be misidentified young of *Ophiolepis*, due to their small size and

underdeveloped skeleton. The remaining species may likewise be young of *Ophiolepis* or *Ophiozonella*, except for the type species *O. picta*, which has been reported with up to 10 mm disk diameter (Mortensen 1924). Among the unidentified species from Lifou, the *Ophiozonella* sp. from sta. 1440 (Table 2) has a colour pattern similar to the image of *O. obscura* Koehler, 1922 shown in Koehler (1930) and agrees in most characters with it, except at a disk diameter of 3.8 mm it is larger than Koehler's specimen and it has small scales between the larger disk plates, which suggests it may be the young of an *Ophiolepis*. Further examination and revision of all species of *Ophiozonoida* are needed to resolve their status.

Distribution. Known from Lifou, northern Australia (Timor Sea) and southwest Australia (Indian Ocean). Most of the species of *Ophiozonella* live in the deep sea, from a few hundred to several thousand meters deep. However, the locality (Uraga Channel, Japan) of the type species, *O. longispina*, was only 128 m deep. The holotype of *Ophiozonella hexactis* **sp. nov.** was collected at 100–120 m, the paratype at just 90 m, and the Australian material at 87–414 m.

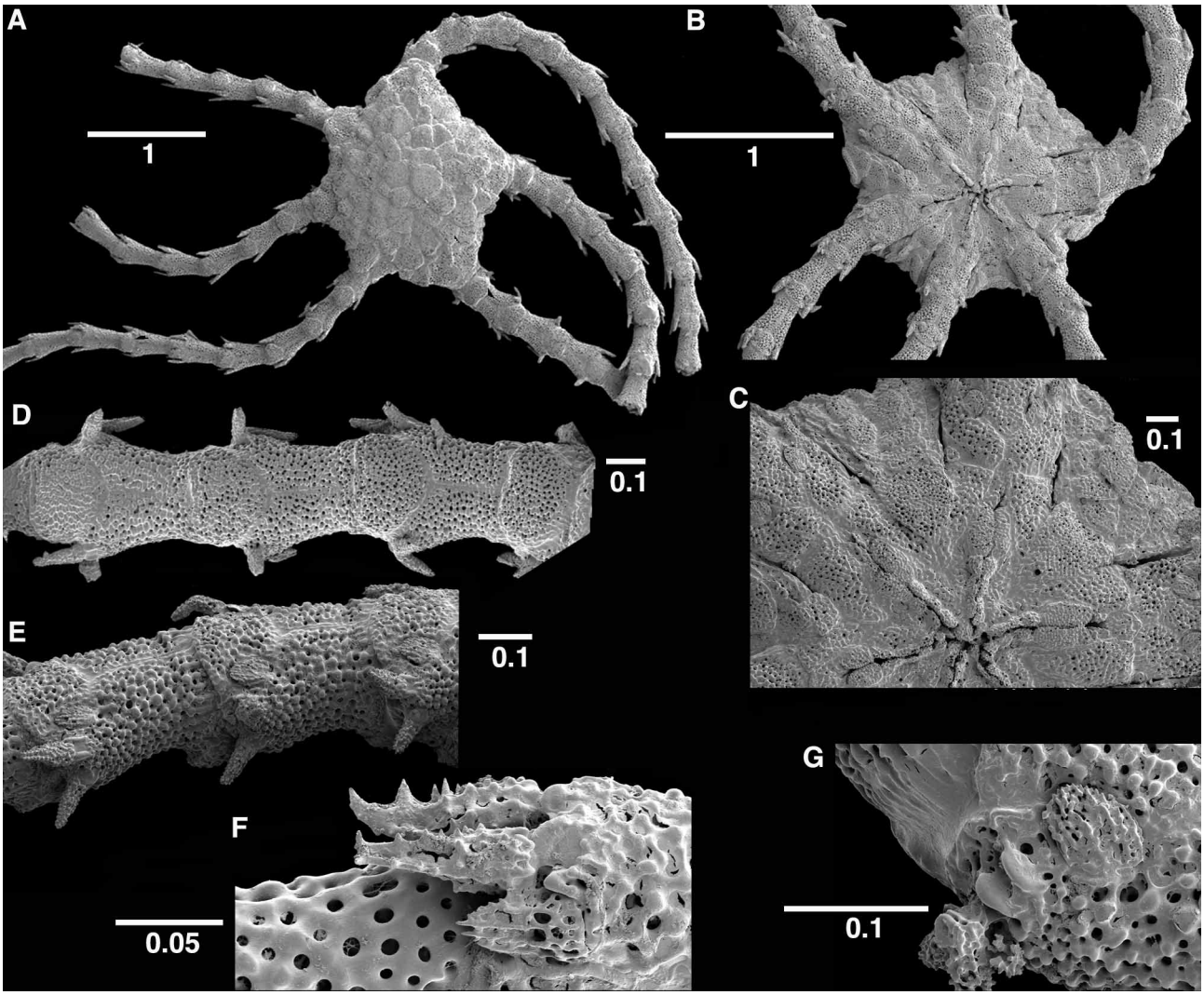

FIGURE 18. SEM images of *Ophiozonella hexactis* nov. sp., holotype MNHN IE-2009-9209. A, dorsal aspect, showing signs of regeneration with three smaller and three larger arms and an irregular disk; B, ventral aspect; C, oral frame and ventral interradii, note the large distal oral papilla; D, dorsal arm; E, ventrolateral arm; F, hook-shaped distal arm spines; G, arm spine articulation and tentacle scale. Scale bars in millimetre.

Ophiozonella projecta (Koehler, 1905)

Figure 19

Material. Sta. 1461: 2 spms; sta. DW1648: 1 spm; sta. DW1650C: 7 spms.

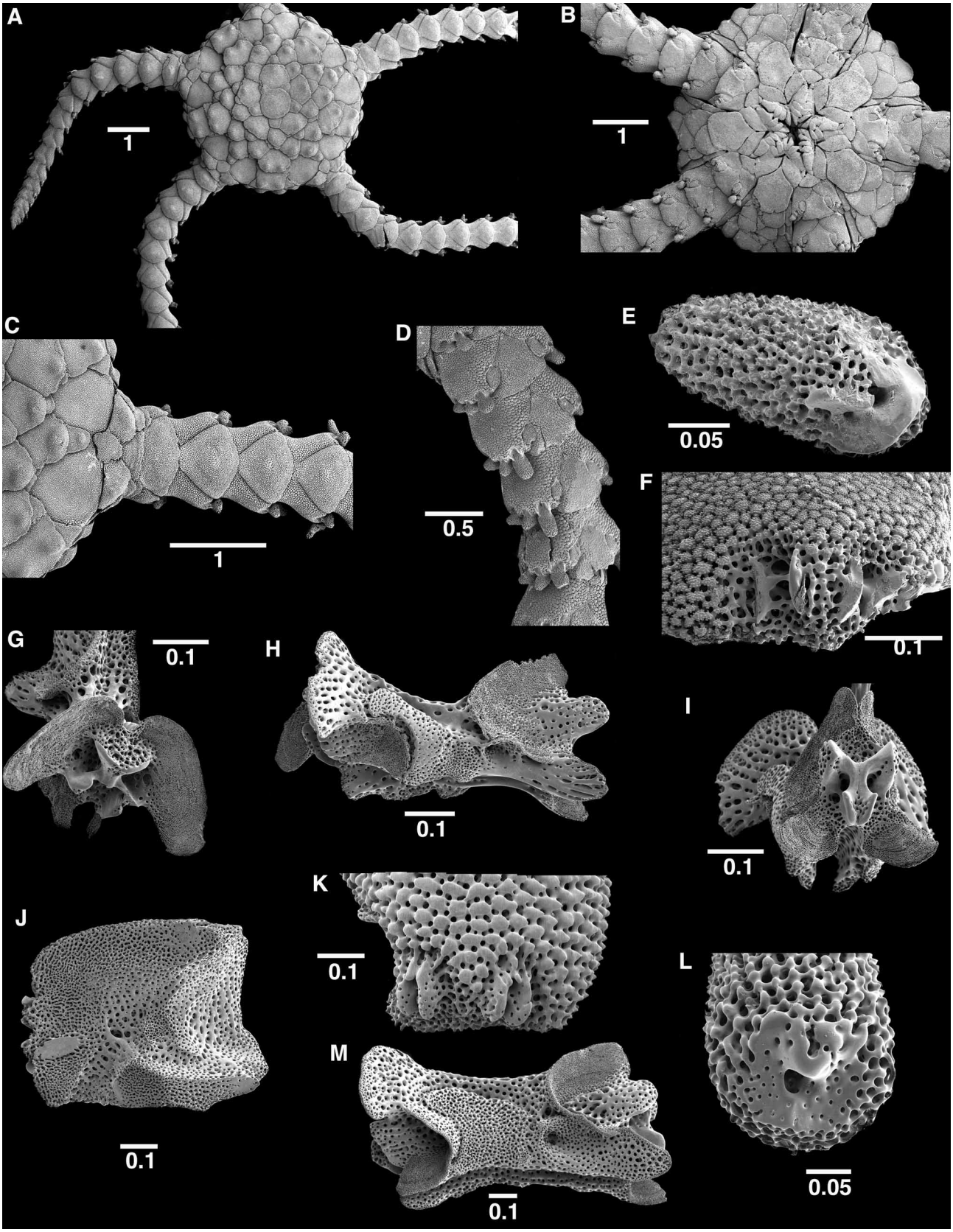

FIGURE 19. SEM images, A–J, *Ophiozonella projecta*. A, dorsal aspect; B, dorsal arm, note the triplet of plates at the arm base; C, ventral aspect; D, ventrolateral arm; E, arm spine, articulating end; F, spine articulation on lateral arm plate; G, proximal vertebra, proximal face; H, proximal vertebra, lateral aspect; I, proximal vertebra, distal face; J, proximal lateral arm plate, internal aspect. K–L, *Ophiozonella longispina*. K, spine articulations on lateral arm plate; L, arm spine, articulating end; M, distal vertebra, lateral aspect. Scale bars in millimetre.

Comparative material. Syntypes (as *Ophiozona projecta*), Siboga sta. 96, Philippines, Sulu Archipel, SE of "Perlbank", 15 m, [ZMA U.Ech O. 2569] and Siboga sta. 142, Obi Major (Moluccas), Mouiallge de Laiwu, 23 m, [ZMA U.Ech O. 2570]. *Ophiozonella longispina* (H.L. Clark, 1908), Vega Expedition 1878-80, Japan, Honshu, Yeddo bay, 119 m, 11.10.1879 [SMNH-108072].

Remarks. The Lifou specimens agree well with the syntypes. The colouration is light brown and preserves well in alcohol. They are characterized by tuberculous, more or less convex, dorsal disk plates, a distinct trio of plates distal to the radial shields and three small, blunt arm spines, of which the ventralmost one is distinctly larger than the other two. The microstructure of the arm plates shows a grainy surface. The proximal arm vertebrae are elongated, similar to distal vertebrae of *O. longispina*, suggesting a paedomorphic condition in *O. projecta*. The spine articulation consists of two narrow parallel ribs and differs from the thicker, rounded, at one end connected ribs that comprise the articulation of *O. longispina*; another possible indication of paedomorphosis. In placing this species in *Ophiozonella*, Matsumoto (1915) contradicts himself immediately after describing the genus as lacking the trio of plates distal to the radial shields (typical for *Ophiolepis*), since these are obvious in the syntypes. The validity of this character is thus doubtful. *Ophiolepis* is also differentiated from *Ophiozonella* by its larger dorsal disk plates being encircled by small scales. However, in juvenile *Ophiolepis superba* H.L. Clark, 1915 (the generic type) these scales are absent (Cherbonnier & Guille 1978). The partially paedomorphic appearance of the small species *O. projecta*, the presence of a trio of plates distal to the radial shields, and its occurrence at rather shallow depths suggest that the affinities between *Ophiozonella* and *Ophiolepis* may need to be re-investigated. The species may also be mistaken for an *Ophiozonoida* (see above), further emphasizing the need for taxonomic revision of all these forms.

Distribution. The species has a wide distribution, from Japan to the Philippines and New Caledonia, for which it is a new record. The four syntype localities in the original description (Koehler 1905) range across depths of 15–113 m, whereas the specimens from Lifou were collected at depths of 100–260 m.

Genus *Actinozonella* gen. nov.

Etymology. The name is derived from the Greek words *aktinos* meaning ray, eluding to the pattern of disk plates of the type species resembling spokes of a wheel, and *zonella* (Greek = little belt) referring to the affinities of this genus with *Ophiozonella*. Gender feminine.

Type species. *Ophiomastus texturatus* Lyman, 1883

Description. As type species.

Actinozonella texturata (Lyman, 1883), new combination

Figure 20

Ophiomastus texturatus Lyman, 1883: 247–248, pl. IV, figs 49–51.
Ophioglypha humilis Koehler, 1904: pl. VII, figs 1–3. New synonymy.
Ophiozonella humilis – Koehler 1930: 254.
Amphiophiura humilis – H.L. Clark 1915: 310.

Type locality. Fiji, off Matuku, "Challenger" sta. 173, 19°9'35"S, 179°41'50"E, 315 fms (=576 m), coral mud, 24 July 1874, dredged.

Material. Sta. 1468: 1 spm; sta. 1650C: >50 spms.

Description. Figured specimen from sta. 1650C with dorsal disk 4.7 mm dd, covered with a round centrodorsal plate, encircled by 7 small trapezoidal plates, an outer circle of 10 larger pentagonal plates, interradial columns of 2–3 rectangular plates, interspersed by a few smaller plates at the outer circle. Radial shields triangular, about half of disk radius long, completely separated by series of 4 rectangular plates similar to the interradial series. The distalmost of these radial plates forms the centre of a trio of plates on the arm base distal to the radial shields. Dorsal arm plates contiguous, fan-shaped, slightly wider than long, with convex to angular dorsal edge. Lateral arm plates massive. All plates with tuberculous microstructure. Three short conical arm spines, about as long as half an arm joint, appressed.

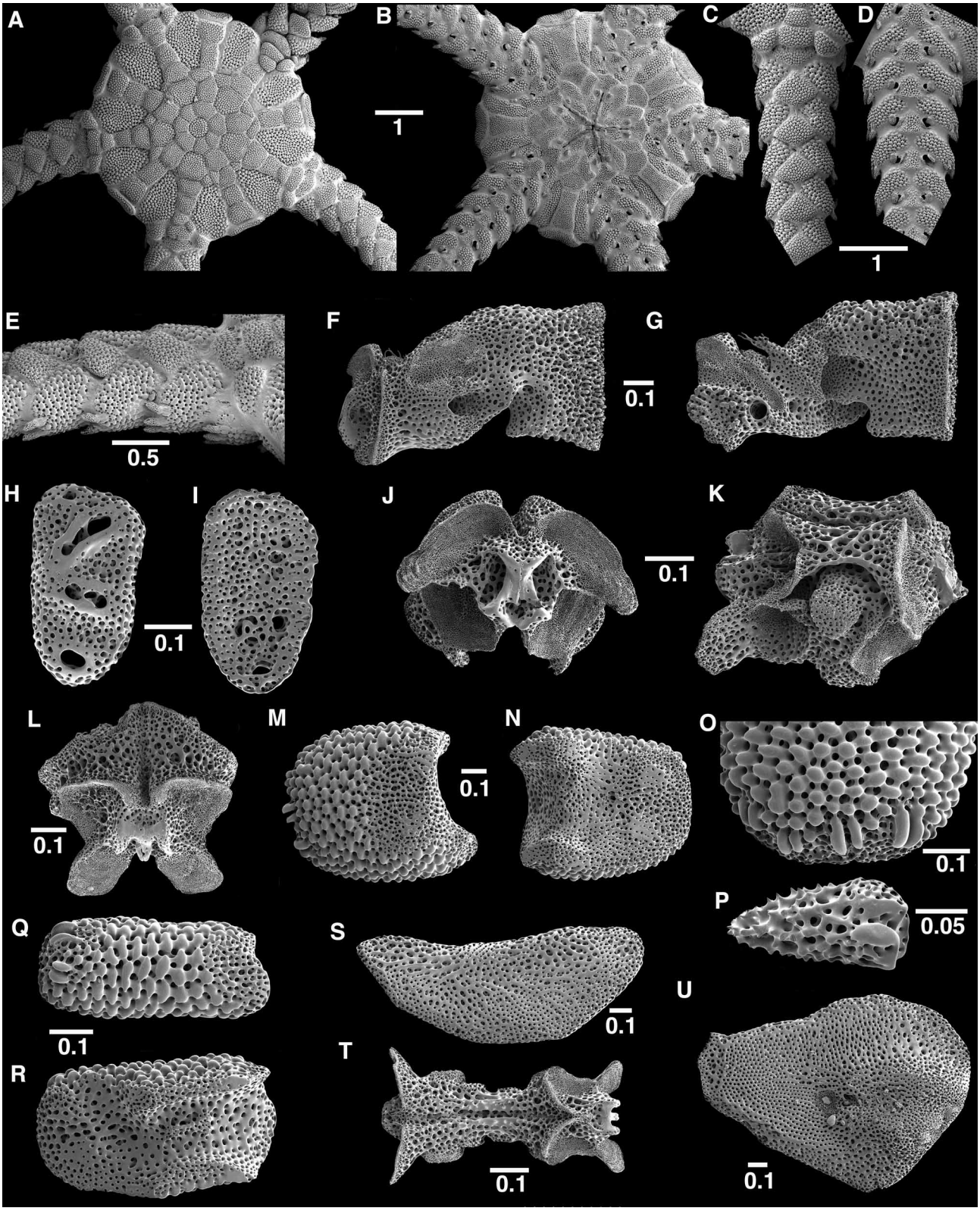

FIGURE 20. SEM images of *Actinozonella texturata*. A, dorsal aspect; B, ventral aspect; C, dorsal arm; D, ventral arm; E, dorsolateral arm; F, oral plate (half-jaw), abradial aspect; G, oral plate, adradial aspect; H, dental plate, external; I, dental plate, internal; J, proximal vertebra, proximal face; K, proximal vertebra, lateral aspect; L, proximal vertebra, distal face and dorsal; M, proximal lateral arm plate, external; N, proximal lateral arm plate, internal; O, spine articulations on lateral arm plate; P, arm spine, showing articulation; Q, distal lateral arm plate external; R, distal, lateral arm plate internal; S, abradial genital plate; T, distal vertebra, dorsal; U, radial shield, internal. Oral plates and radial shield orientated with distal end left, dental plates with dorsal side up. Scale bars in millimetre.

Ventral disk covered by a wide marginal plate that is the extension of the distal dorsal interradial plate, a narrow rectangular plate three times as long as wide, and two large genital plates as long as the entire interradius. Genital slits restricted to proximalmost arm joint, inconspicuous, lacking papillae. Jaws with small papilliform apical papilla and three low, wide, scale-like lateral papillae. Adoral shields curved, distally flaring, abutting the proximal edges of the oral shield, not separating it from the arm. Oral shield fan-shaped with acute proximal angle and convex distal edge, slightly wider than long. Ventral arm plates small, slightly wider than long, widely separated by lateral plates, pentagonal with straight distal edge and convex lateral edges. A single round tentacle scale at each pore, on the lateral plate. Tentacle pores along entire arm.

Internal skeleton: oral plates elongated and strongly arched, with a small round abradial muscle attachment area. Dental plate somewhat cup-shaped convex, dorsal tooth fenestration elongated and placed at an angle, middle one shorter and almost horizontal, ventral one an oval opening. On internal side of dental plate several holes indicate positions of ventral and middle fenestration, but not the dorsal one. Proximal vertebrae with typical zygospondylous articulation and not elongated much, with wide, winglike proximal muscle flanges. Their lateral structure shows a complex pattern of muscle flanges, a central process and grooves. Proximal lateral arm plates about as long as high, strongly convex, with a tuberculous external stereom, except where two plates meet and overlap ventrally. Internal side strongly excavated proximally, bearing two smooth distal patches and a slightly off-centre nerve opening. Spine articulations on proximal arm consist of two parallel ribs with muscle and nerve opening between them. Distalwards lateral plates more and more elongated and more convex. Abradial genital plate massive, with convex outer and straight inner edge. An adradial genital plate was not identified and may be absent. Radial shields on the same animal differ in shape, some with a straight inner edge and some with an almost rhombic shape. Their internal side is depressed distally, but shows no obvious socket to form a joint with the genital plate.

Variations. The scalation pattern of the dorsal disk is highly variable in the sample at hand. In smaller specimens the scales in the circle next to the centrodorsal are smaller and their number varies from four to eight. When there are five of them they are placed interradially and this is most likely the basic, undisturbed pattern. These are cleary secondary plates developing after the primaries and probably other plates. The larger radial plates in the following circle are present in all specimens and most likely represent the primary plates. Several specimens lack distinct circles of plates. Instead, the centre of the disk is covered by a random looking assortment of unidentifiable plates. This may suggest regeneration after damage. One specimen from sta. 1650C is hexamerous with a deformed disk on which the primaries cannot be distinguished.

Remarks. It should be noted that Lyman (1883) included this and two other Indo-Pacific species from the "Challenger" expedition in his report on the "Blake" expedition to the West Indies. He particularly remarked on the pattern of the disk plates with 11 central plates and ten radiating lines of single plates, which are a unique characteristic of this species, clearly visible also in Koehler's (1904) illustration. *Actinozonella texturata* and *O. humilis* are thus conspecific. A new genus is proposed for this species, since it does not fit well with either *Ophiomastus* or *Ophiozonella*, nor with any other known genus, which is also reflected by the fact that the species has been transferred between several genera. *Ophiomastus* is described as the disk being covered with little more than the primary plates and all included species show a strongly paedomorphic morphology, suggesting that some may actually be the juveniles of other species. *Actinozonella texturata* has a larger number of disk plates.

Actinozonella differs from *Ophiozonella* in the shape of the oral papillae, particularly the absence of an operculiform distal papilla, the presence of a superficial second tentacle pore and the small tentacle scales. This species may be placed in the family Ophiuridae, subfamily Ophiurinae, due to its superficial second oral papilla, a character regarded as critical for this subfamily. However, the absence of genital papillae and an arm comb, the short genital slits, the large disk plates and the trio of plates distal to the radial shields are similar to genera in the family Ophiolepididae (compare *Ophiozonella* above). Indeed, *A. texturata* had originally been placed in that family, since Matsumoto (1915) placed *Ophiomastus* in Ophiolepididae, subfamily Ophiomastinae. Koehler (1930) recognized these affinities when he revised his original opinion on *O. humilis*. Matsumoto (1917) remarked on the juvenile appearance of many species in Ophiolepididae, and the position of the second tentacle pore outside the mouth used to delimit Ophiurinae is a juvenile character (Sumida *et al.* 1998; Stöhr 2005). Its validity as a character for family delimitation is thus questionable. Pending a much needed revision of Ophiurinae and Ophiolepididae, since all other characters point to Ophiolepididae, I propose to place *A. texturata* in this family.

***Ophiomusium* Lyman, 1869**
Figure 21

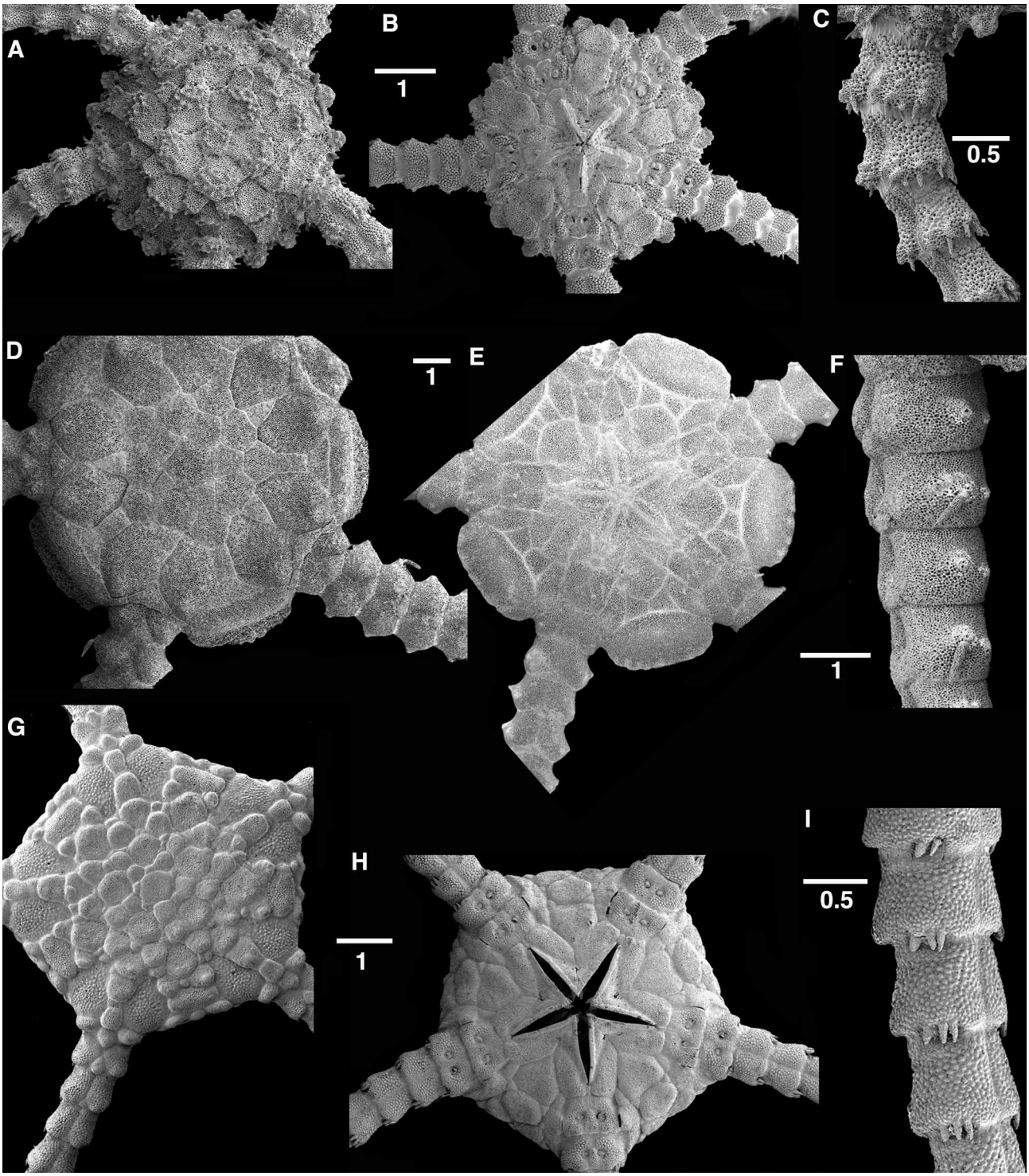

FIGURE 21. SEM images of species of *Ophiomusium*. A–C, *O. relictum*, A, dorsal aspect, B, ventral aspect, C, arm in lateral view. D–F, *O. luetkeni*, D, dorsal aspect, E, ventral aspect, F, arm in lateral view. G–I, *O. scalare*, G, dorsal aspect, H, ventral aspect, I, arm in lateral view. Scale bars in millimetre.

Remarks. *Ophiomusium* is a moderately large genus with 72 described species (Stöhr & O'Hara 2007), but many of them are morphologically similar and difficult to identify. They present a juvenile appearance with few disk plates, wide, block-like mouth papillae, absence of ventral and dorsal arm plates beyond a few proximal arm joints, and tentacle pores restricted to proximal joints or not obvious on the distal arm. The arm spines are usually few and

shorter than an arm joint. The position of the second tentacle pore inside the mouth slit is however not a juvenile character. Four species, previously unknown from New Caledonia, have been identified from Lifou (Table 2). Among them, *O. relictum* Koehler, 1904 has a conspicuously rough appearance, with tuberculous plates on disk and arms. *Ophiomusium scalare* Lyman, 1878 has numerous, tumid disk scales and arm plates. As Koehler (1922) remarked, *O. morio* Koehler, 1922 is similar to *O. simplex* Lyman, 1878, but distinguished by fewer disk scales and lack of small plates between oral shield and the large ventral interradial plate.

Ophiomusium luetkeni Lyman, 1878

Fig. 21D–F

Ophiomusium luetkeni Lyman, 1878: 114, pl. 5 figs 138–140; Guille 1981: 453; Guille & Vadon 1986: 173–174.
Ophiomusium impurum Koehler, 1904: 64, pl. 10 figs 8–10 [new synonymy].

Material. Sta. CP1646: 20 spms; sta. DW1650C: 1 spm.

Comparative material. *Ophiomusium impurum* (possibly syntype, but status unclear), MNHN Ec Os 22102, 8 mm dd, Indonesia, Sunda Islands.

Remarks. The disk of *O. luetkeni* has a high, boxy appearance and a conspicuously large marginal plate in each interradius, with a prominent transverse ridge. It is distinguished from other species of *Ophiomusium* by the small spine on the dorsal part of the lateral arm plate. These spines have fallen off in most of the specimens at hand, but the articulation is clearly visible. Koehler (1930) failed to notice the similarity between his *O. impurum* and *O. luetkeni*, maintaining both, but in recent works *O. luetkeni* was used, without synonymizing them. The putative type of *O. impurum* cannot be distinguished from the description of *O. luetkeni*. O'Hara confirmed their conspecificity after examining both types (personal communication).

Discussion

Contrary to expectations, the ophiuroid fauna of Lifou is composed of shallow as well as deep species, well in accordance with their known preferences. Despite the intensity of the collecting effort, a large proportion (45%) of the identified species appear to be ecologically rare, since they were found only once, 33% were also numerically rare and represented by a single specimen. This finding is well in line with that for molluscs collected off the northwest coast of New Caledonia (Bouchet *et al.* 2002), where 20% of the species were represented by single specimens, 48% with five or fewer and 33% at single stations. Preliminary results from "Atelier Lifou 2000" indicate that 26–29% of all species were found at single stations, 22% with single specimens and 49% with five or fewer (Bouchet *et al.* 2001).

Including the new species, 58 species have been found for the first time in the New Caledonia region, increasing the diversity by 40% to a total of 205 ophiuroid species. The overlap between Lifou and previously documented areas is only 36 species (25%), but this may be due to the fact that the large number of samples collected by previous expeditions and housed in the storage of the Muséum national d'Histoire naturelle in Paris have not been completely analyzed and documented. The latest detailed study (O'Hara & Stöhr 2006) dealt with only two families of deep-water ophiuroids, leaving 15 more families to examine.

In part, the observed high diversity may be caused by the intense sampling efforts around New Caledonia in the past 40 years, but it also reflects the unusual species richness of the region, well documented above all for molluscs and attributed to the extraordinary geomorphological heterogeneity of the region (Bouchet *et al.* 2008). The actual number of species will almost certainly increase, since some of the specimens collected at Lifou still remain to be identified or possibly described.

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APPENDIX

Works that have used *Euryale* as a valid generic name for an ophiuroid in the past 50 years (1961–2010).

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