A REVISION OF THE DEEP-WATER OCTOPUS GENUS *SCAEURGUS* (CEPHALOPODA: OCTOPODIDAE) WITH DESCRIPTION OF THREE NEW SPECIES FROM THE SOUTHWEST PACIFIC OCEAN

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(Received 12 January 2004; accepted 28 January 2005)

ABSTRACT

Deep-water trawl surveys on seamounts around New Caledonia yielded 62 specimens of the little-known genus, *Scaeurgus*. Members of this genus of octopuses typically occur at depths of 200–500 m in temperate and tropical latitudes worldwide. Prior to this study, *Scaeurgus* was considered to contain one to two species. The new material from New Caledonia contained a surprising diversity of *Scaeurgus* species from a small area: three distinct new species are described and limited material of a further two taxa is reported. A pygmy member of this genus is reported for the first time. Distributions of these new taxa are consistent with reports of high endemism on the seamount systems in this region. Fifty-eight of the 62 specimens were collected from seamounts, with four of the five taxa unique to a single seamount.

INTRODUCTION

Taxonomic history

Members of the genus *Scaeurgus* form an easily recognized group of upper bathyal benthic octopuses. They typically occur on seamounts and continental slopes at depths between 100 and 500 m (Nesis, 1987). This genus has been collected worldwide from tropical and temperate latitudes in all major oceans (Fig. 11A). To date, however, it has been known primarily from two regions: the Atlantic Ocean (and Mediterranean Sea) and off islands in the Hawaiian Archipelago.

Prior to the present study, two species had been named, *Scaeurgus unicirrhus* Chiaie, 1839–1841 in Férussac & d'Orbigny, 1838–1848 and *S. patagiatus* Berry, 1913. *Scaeurgus unicirrhus* was described by Chiaie while he was based in Naples, Italy, and the type locality is presumed to be near Naples. *Scaeurgus unicirrhus* occurs in at least the Mediterranean Sea and northeast Atlantic Ocean (Mangold, 1998). In the Mediterranean Sea it typically occurs at depths of around 100–400 m, but is also recorded from 50–500 m. *Scaeurgus patagiatus* was described from Hawaii at depths of around 200–300 m.

These species names (or combinations of both) have been applied to reports of this genus elsewhere. *Scaeurgus unicirrhus* has been reported from western and southern Atlantic Ocean: Florida (Voss, 1951); off Cuba (Voss, 1955); Brazil (Voss, 1964; Palacio, 1977); and Namibia (Sanchez & Alvarez, 1988). Robson (1921), (1929) and Nesis (1993a) reported *S. unicirrhus* from the Saya de Malha Bank in the Indian Ocean (approximately 11° S, 62° E) at depths of 225 and 175–250 m, respectively. Nesis (1993a) referred to his material as transitional in form between *S. unicirrhus* and *S. patagiatus*. Oommen (1967) provided limited descriptions of four additional specimens (two of each sex) under the name *S. unicirrhus*, from off the Malabar Coast of southern India captured at depths of 250–300 m. Outside Hawaii, *Scaeurgus patagiatus* has been reported from Japan (Sasaki, 1920, 1929; Okutani, Tagawa & Horikawa, 1987) and the East China Seas (Okutani *et al.*, 1987). Kubodera & Yamada (1998) reported '*S.* cf. *patagiatus*' from the South and East China Seas. Kubodera & Lu (2002) added records of *Scaeurgus* sp. from Taiwan.

Nesis (1990) demoted the name *patagiatus* to a subspecies ranking, reporting six specimens of *S. unicirrhus patagiatus* from five seamounts in the Nazca and Sala y Gómez ridges in the southeast Pacific Ocean (approximately 25° S, 85–100° W). This material was collected from depths between 162 and 440 m.

The majority of the records listed above provide insufficient morphological data to compare with our material and the previously named species.

How many species?

Robson (1929) proposed that *S. unicirrhus* and *S. patagiatus* were synonyms and that there was only a single circum-global species, *S. unicirrhus*: a decision supported by subsequent authors (Voss, 1951; Roper, Sweeney & Nauen, 1984; Nesis, 1987; Sanchez & Alvarez, 1988). This decision was based on limited material using few diagnostic characters (size, mantle and head width, and arm length). Toll (1988) examined sucker counts of specimens attributed to these two species and found consistent differences on both normal and hectocotylized arms, independent of animal size. As a consequence Toll recognized these taxa as distinct species. Toll's graphs show that hectocotylized arm sucker counts were: *S. unicirrhus* 60–70, *S. patagiatus* 80 + .

Our examination of material of *S. unicirrhus* and *S. patagiatus* from the regions of their original description (Mediterranean Sea and Hawaii, respectively; see Supplementary Data) found no obvious distinguishing characters and only slight differences in two characters: hectocotylized arm sucker counts (82–87 *vs* 85–93, respectively) and number of sperm cord whorls (38–44 *vs* 26–28) (Table 4). We did not find the marked difference in sucker counts between these species reported by Toll (1988). Both species had hectocotylized arm sucker counts in excess of 80 (82–87 and 85–93, respectively). The discrepancy between our sucker counts and Toll's may relate to his source for *unicirrhus*

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 doi:10.1093/mollus/eyi033
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material, listed as 'Florida, Caribbean and Mediterranean' (p. 210). The senior author of the present study examined Voss's cephalopod collection in Miami in 1993 and noted 15 lots of *Scaeurgus* from the western Atlantic Ocean. We believe that Toll's counts are based solely on this material, which differs from the eastern Atlantic and Mediterranean taxon and may constitute a distinct species.

A lack of mature material in good condition for the two previously named taxa prevents further resolution of the *unicirrhus/patagiatus* problem, as is the case for many of the published reports of *Scaeurgus* from elsewhere around the world (Fig. 11A). To aid resolution of the identity of material in the Atlantic Ocean currently being treated under the name *S. unicirrhus*, we designate a neotype for this species, a mature male from off Banyuls, France, in the western Mediterranean Sea.

Our study

Obtaining material of deep-water benthic octopuses such as *Scaeurgus* is extremely difficult. Most species described to date from depths of greater than 200 m are based on few or single specimens. This is due to limited research trawling at these depths, use of commercial fisheries gear that is inappropriate for collecting benthic invertebrates, and poor retention and preservation of the rare octopus captures. In recent years, octopus material has typically been frozen on board (often crushed under other catches), resulting in distorted or damaged specimens of limited value.

The extensive bathyal surveys conducted in the Pacific Ocean over the past two decades by the Muséum National d'Histoire Naturelle in Paris (MNHN) and L'Institute de Recherche pour le Developpement (IRD, formerly ORSTOM) are exceptional, as they surveyed thousands of deep water sites using gear that sampled benthic organisms from a wide range of habitats. All cephalopod material was retained and preserved appropriately. As a result, these campaigns have generated the world's largest collection of well-preserved deeper water benthic cephalopods. Amongst material collected around New Caledonia and in the Coral Sea is the best collection to date of *Scaeurgus*. Over the past 18 years, 62 specimens of this genus were collected in 11 of the 29 MUSORSTOM campaigns in this region. These campaigns sampled at depths between 15 and 1000 m, collecting specimens from depths of 230–530 m.

None of the *Scaeurgus* material collected by the MUSORSTOM campaigns belongs to either of the previously described species. The collection contains three distinct new species, described here, with limited material of two additional species. *Scaeurgus unicirrhus* and *S. patagiatus* are compared to each other and the new taxa. Based on this extensive collection, the genus is redefined. The high diversity of *Scaeurgus* species around New Caledonia is discussed in relation to endemism on seamounts in the region.

MATERIAL AND METHODS

Trawl campaigns were carried out on board three N/O vessels, Alis, Coriolis and Vauban. Three gear types captured octopods: Waren dredge (drague Waren, station code: DW), beam trawl (chalut à perche: CP) and otter trawl for fish (chalut à panneaux: CH).

Type material for the new species described here is lodged in the Muséum National d'Histoire Naturelle (MNHN), Paris. Additional comparative material was examined from the Natural History Museum, London (BMNH), Santa Barbara Museum of Natural History (SBMNH), Californian Academy of Sciences (CASIZ), National Museum of Natural History, Smithsonian Institution (USNM) and the Institut Royal des Sciences Naturelles de Belgique (IRSNB).

Morphological characters and measurements used in the descriptions below follow Norman & Sweeney (1997) and Norman, Hochberg & Lu (1997). State of maturity is classified as immature, submature or mature. In immature specimens, reproductive organs are not visible or are tiny. Submature specimens have developed reproductive ducts (visible as distinct terminal organ or oviducts), but lack spermatophores or a swollen ovary. Mature males possess functional spermatophores. Mature females possess a large ovary, which occupies a third or more of the mantle cavity and contains distinct individual eggs. Diagnoses and descriptions presented here are based on submature and mature specimens. Data for juvenile and immature material are not included as counts and relative measurements (such as sucker counts and arm lengths versus mantle length) undergo considerable ontogenetic change in the early growth stages and can cause overlap in otherwise valid diagnostic characters. Abbreviations in descriptions: F, female; M, male; ML, mantle length.

SYSTEMATIC DESCRIPTIONS

Family Octopodidae d'Orbigny, 1840

***Scaeurgus* Troschel, 1857**

Scaeurgus Troschel, 1857: 51.
Titanotus Troschel (manuscript name in Troschel, 1857: 53; unavailable).

Diagnosis: Benthic octopuses of small to moderate size, mantle length to 90 mm. Mantle ovoid, encircled by low keel or ridge. Large stylets present, often mineralized. Body covered with regular numerous rounded papillae, dense on dorsal surfaces, present but less dense on ventral mantle, absent from aboral surface of fourth arm pair and ventral half of third arms from midline. Arms short, two to three times mantle length. Arm autotomy absent. Webs moderately deep, deepest around 25–30% longest arms. Interbrachial web pouches absent. Suckers biserial, medium sized and slightly to distinctly enlarged in males of different species. Modification of suckers on non-hectocotylized arm tips of males absent. Left third arm hectocotylized, slightly shorter than opposite arm (~80%). Copulatory organ of moderate size with fleshy thick-rimmed elongate ligula, often peanut-shaped. Calamus small to very large (up to 70% ligula length). Funnel organ W-shaped. Gills with 8–14 lamellae per outer demibranch. Ink sac and anal flaps present. Crop diverticulum well developed. Visceral mass membrane with scattered founder chromatophores present on at least dorsal surface, typically also on ventral surfaces. Radula: rhachidian with one to two cusps on either side (typically two), in asymmetrical seriation. Terminal organ of male linear, with simple short swollen diverticulum. Spermatophores with double-strand coiled sperm cord, forming a braided pattern. Spermatophores produced in low numbers (<10). Distal oviducts fleshy and swollen, opening midway along mantle cavity septum. Four paired black spots on mantle, anterior pair on lateral mantle adjacent to mantle aperture and dorsal to lateral skin ridge. Posterior pair on posterior tip of mantle dorsal to lateral ridge, faint in some species. Diamond of primary papillae present on dorsal mantle. Single large papilla present over each eye and large papilla present on posterior tip of mantle. Dorsal white spots (*sensu* Packard & Sanders, 1971) visible in live animals and some preserved material.

Type species: *Octopus cocco* Verany, 1846 [=*Scaeurgus unicirrhus* (Chiaie, 1839–1841)].
Distribution: Atlantic, Indian and Pacific Oceans, generally at tropical and subtropical latitudes (Fig. 11A). Typically on

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seamounts and continental/oceanic slopes at depths of 200–500 m. Shallowest depth record 50 m (Mangold, 1998).

Taxonomic remarks: The taxonomic history of the genus *Scaeurgus* is convoluted. Troschel (1857) defined the genus based on hectocotylization of the third left arm (*vs* the more typical right-hand form found in most benthic octopuses). Troschel placed two species in his new genus, a new species *S. titanotus* and *S. cocco* (Verany, 1846) (misspelled *coccoi*). Subsequent authors (Naef, 1923; Robson, 1929; Mangold, 1998) recognized *S. titanotus* as a junior synonym of *Pteroctopus tetracirrhus* (Chiaie, 1830) and *cocco* as a junior synonym of *Scaeurgus unicirrhus* (Chiaie, 1839–1841).

In 1882, P. Fischer introduced the genus *Pteroctopus* for the single species, *P. tetracirrhus* Chiaie, 1830. Unaware of (or disregarding) Fischer's genus, a number of authors over the next 50 years continued to use Troschel's genus *Scaeurgus* for *unicirrhus* and *tetracirrhus* (summary in Naef, 1923). Naef (1923) raised doubts as to the validity of placing these two very different taxa in the same genus, solely on the basis of a left-handed hectocotylized arm. Naef suggested affinities between *tetracirrhus* and a right-handed species, *Octopus hoylei* (Berry, 1909) from Hawaii. Despite these doubts, Naef still placed both *unicirrhus* and *tetracirrhus* in the tentative subgenus *Octopus* ('*Scaeurgus*'). Robson (1929) agreed with Naef's analysis and returned *tetracirrhus* to *Pteroctopus*.

Today, the names *Scaeurgus unicirrhus* and *Pteroctopus tetracirrhus* are in common usage and are widely recognized as valid and distinct taxa. The genera (and species) are clearly distinguished by numerous morphological characters (see Roper *et al.*, 1984).

Confusion exists, however, over the type species of *Scaeurgus*, its resolution having significant taxonomic implications. In his list of cephalopod generic names, Hoyle (1910) used page priority ('sp. first named') to designate *S. titanotus* (=*Pteroctopus tetracirrhus*) as the type species of *Scaeurgus*. Under the International Code of Zoological Nomenclature (ICZN, 1999: art. 24.2.1), Hoyle constitutes the First Reviser and thus his type determination is considered valid. As a result, *tetracirrhus* Chiaie, 1830 (the type species of the genus *Pteroctopus*) becomes the type species for the older generic name, *Scaeurgus*. If we follow strict convention, there are three implications: (1) the genus *Pteroctopus* should be placed in the synonymy of the genus *Scaeurgus*, (2) *tetracirrhus* should be treated as a species of *Scaeurgus*, and (3) a new genus should be coined for *unicirrhus*, *patagiatus* and the new taxa reported here.

If we read between the lines, it appears that Robson (1929) was aware of this name priority issue and chose to disregard it: 'As I think it is quite clear that Troschel's *titanotus* is delle Chiaje's [sic] *tetracirrhus*, and as it is proposed to maintain Fischer's genus [*Pteroctopus*], it follows that *unicirrhus* must be regarded as the genotype of *Scaeurgus*' (p. 191–192). Robson and subsequent authors followed this convention through to the present day (Sweeney & Roper, 1998).

Due to the long usage of the two names *Pteroctopus* and *Scaeurgus* and their component species, particularly in the Mediterranean Sea, we believe disruption of these generic names will only cause unnecessary confusion. We propose that page priority be suppressed in the interest of prevailing usage, and to maintain the historical conventions since Robson (1929) that *unicirrhus* remain the type species for *Scaeurgus*. As a result, *tetracirrhus* would be retained as the type species for the distinct genus *Pteroctopus*. A submission to ICZN supporting this proposal is pending.

The original diagnostic character proposed for *Scaeurgus* by Troschel was left-handed hectocotylization. Several authors have added additional diagnostic characters to the genus. Robson (1921) described the fleshy and thickened distal oviducts. Robson (1929) expanded the definition to include: a large ligula with inrolled sides and prominent calamus; a penis with a long diverticulum; and subequal arm and web formulae. Sasaki (1929) defined the genus as follows. 'A pair of subtile (sic) horny stylets present internally. Left third arm hectocotylized. First part of spermatophoric gland marked off from the remaining by a strong constriction at least in the Japanese specimen examined by me.' Hochberg, Nixon & Toll (1992) further expanded the diagnosis to include the lateral mantle ridge and a body densely covered in rounded papillae, as well as providing general body and arm proportions.

We consider diagnostic characters of *Scaeurgus* to be: hectocotylization of the third left arm; a lateral skin ridge around the mantle; a fleshy ligula with thick-rimmed ligula groove, often peanut-shaped; spermatophores that contain a double strand of sperm cord, forming a braided appearance; muscular fleshy openings to the distal oviducts located approximately midway along the length of the pallial septum; large stylets (approximately 30–40% mantle length); a skin sculpture of regular rounded papillae over dorsal surfaces; two pairs of large black spots on the dorsal mantle; rachidian tooth of radula with one to two cusps on either side (typically two), in asymmetrical seriation.

***Scaeurgus unicirrhus* Chiaie, 1839–1841**

Octopus unicirrhus Chiaie, 1839–1841, in Férussac & d'Orbigny, 1834–1848: 70.
Octopus cocco Verany, 1846: 17, pl. 4.
Scaeurgus coccoi—Troschel, 1857: 57 (error for *cocco*).
Octopus '*Scaeurgus*' *unicirrhus*—Naef, 1923: 713.
Scaeurgus unicirrhus—Robson, 1929: 192. Mangold-Wirz, 1963: 45. Roper *et al.*, 1984: 215. Mangold, 1998: 526.

Neotype: 1M: 40.4 mm ML, MNHN 3819, off Banyuls, Catalane Sea, France, 'S.u. 94/1', from private collection of Katharina Mangold, Laboratoire Arago, Banyuls, 1994.

Other material examined: see Supplementary Data.

Remarks: As the original type of *unicirrhus* does not exist (Sweeney & Roper, 1998, and examination of relevant museum collections by the senior authors), we designate a mature male collected from the Catalane Sea as the neotype.

***Scaeurgus tuber* new species**

(Figures 1–3, 10A, 10B, 10G)

Holotype: M: 19.1 mm ML, MNHN 2135, Jumeau Ouest, Norfolk Ridge, south of New Caledonia, southwest Pacific Ocean, N/O *Alis*, BERYX 2 campagne, stn CP 44, 23°41′ S, 168°01′ E, 230–250 m, 20 Oct 1992.

Paratypes: Norfolk Ridge, South of New Caledonia: 3M: 13.3–19.3 + 1F: 15.5 mm ML, MNHN 2137, Aztec (=Antigonia) Bank, N/O *Alis*, SMIB 8, stn DW184, 23°18′ S, 168°05′ E, 305–320 m, 31 Jan 1993. 1M: 18.0 mm ML, MNHN 2124, Jumeau Ouest, N/O *Alis*, Campagne BATHUS 3, CP 805, 23°41′ S, 168°01′ E, 278–310 m, 27 Nov 1993. 1M: 16.9 mm ML, MNHN 3811, Banc Azteque (=Antigonia), N/O *Alis*, SMIB 8, stn DW 184, 23°18′ S, 168°05′ E, 305–320 m, 31 Jan 1993. 2M: 15.1, 15.7 mm ML, MNHN 2129, Banc Jumeau Ouest, N/O *Alis*, Campagne SMIB 8, stn DW174, 23°40′ S, 168°01′ E, 235–240 m, 29 Jan 1993. 1F: 23.8 mm ML, MNHN 3792, Banc Jumeau Ouest, N/O *Alis*, LITHIST, stn CP16, 23°43.2′ S, 168°16.2′ E, 379–391 m, 12 Aug 1999. 1F: 18.7 mm ML, MNHN 3804, small mount just north of Stylaster, N/O *Alis*, Campagne NORFOLK 1, stn DW1658, 23°26′ S, 167°50′ E, 320–336 m, 19 June 2001.

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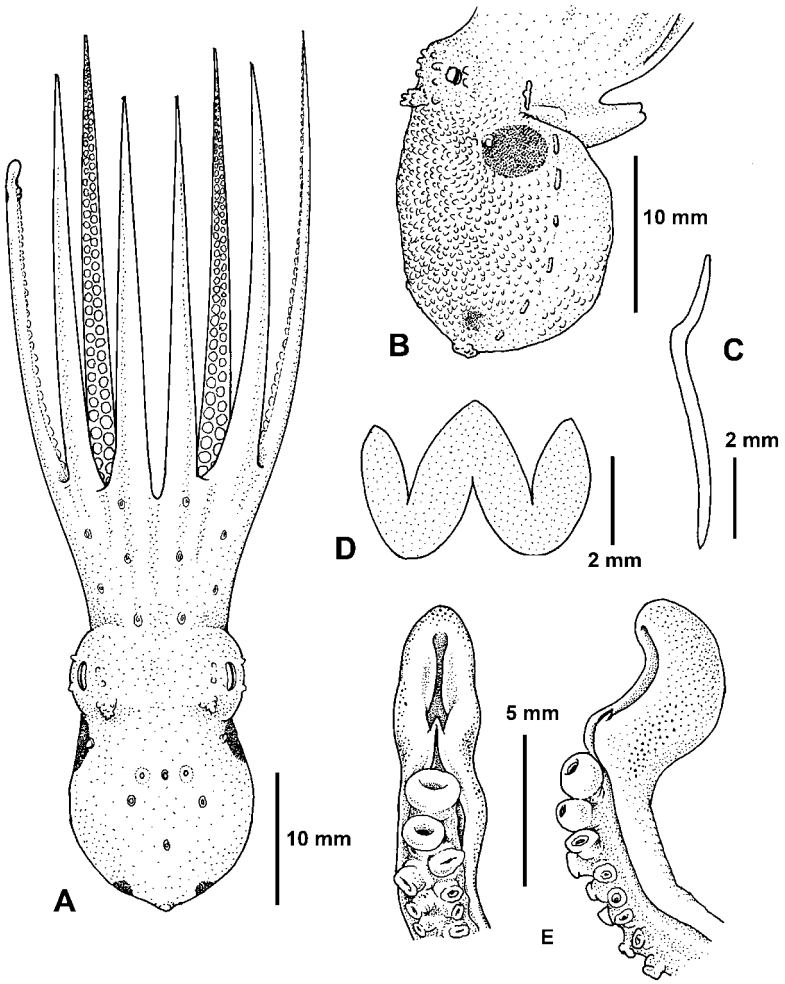

Figure 1. *Scaeurgus tuber* new species. **A.** Dorsal view of 18.0 mm ML male (MNHN 2124). **B, C.** 19.8 mm ML female (MNHN 2136). **B.** Lateral mantle. **C.** Stylet. **D, E.** 19.1 mm ML male holotype (MNHN 2135). **D.** Funnel organ. **E.** Copulatory organ.

Other material examined: 13 additional specimens (see Supplementary Data).

Etymology: *tuber* (Latin) referring to the swollen tubular suckers on distal tip of male hectocotylized arm.

Diagnosis: Small, muscular (ML to 24 mm) with short arms (2.1–2.8 × ML) of approximately equal length. Deepest web 24–35% longest arm. Lateral webs slightly deeper than dorsal and ventral web sectors. Normal arms with 100–130 suckers (male: 107–115; female: 113–128). Hectocotylized arm with 54–63 suckers. Three to four enlarged suckers present in males on all arms (at level of 8–12th proximal suckers), diameter to 16% mantle length (10.7–15.7%). Gills with 8–10 lamellae per demibranch. Third left arm hectocotylized. Ligula large (10–14% arm length) with thick-rimmed groove; calamus small (20.7–43.6% length of ligula). Distal one to three suckers on hectocotylized arm significantly enlarged as tall and swollen cylinders. Spermatophores small (9–12 mm), approximately 60% mantle length (55–68%). Distal oviducts long and convoluted. Eggs 1.7–2.6 mm, around 10% mantle length (9–11%). Remnants of lateral mantle ridge present as short ridge under anterior black spot followed by a line of larger papillae through to the posterior mantle papilla. Formalin-fixed specimens with orange-brown to cream base colour with pronounced pair of anterior mantle black spots. Posterior black spot pair present on mantle, but fainter and smaller than anterior pair. Visceral mass membrane with founder chromatophores on dorsal surfaces only.

Description: The following description is based on five mature males and five females (two mature and three submature). Small species (Fig. 1A, B); mantle length (ML) to at least 24 mm, total length to at least 95 mm; weight to at least 9 g (Table 1). Mantle ovoid to round, longer than wide (width 66.7–79.9% ML, 85.7 in gravid female). Head wide (60.8–74.5% ML; 82.7–102.4% mantle width). Skin firm. Eyes moderate in size. Stylets present, typically clear but mineralized in several animals (Fig. 1C), length around 35% ML (30.6–36.4%). Mantle opening wide, around 50% circumference of body at level of opening. Funnel of moderate length, approximately 40% mantle length (37.9–46.7% ML), free portion moderate to long, 25.3–54.1% funnel length. Funnel organ W-shaped (Fig. 1D), outer limbs shorter than median ones (outer limbs 73.2–91.9% median limbs). Funnel organ occupies approximately 60% (47.6–66.2%) funnel length. Arms moderate length, 2.1–2.8 times ML. Arms of moderate width, sub-cylindrical along length, taper gradually to thin tips. Arms approximately equal in length. Suckers in two rows, moderate sized in females, around 8–10% mantle length; three to four enlarged suckers present in males on all arms (at level of 8–12th proximal suckers), up to 16% mantle length

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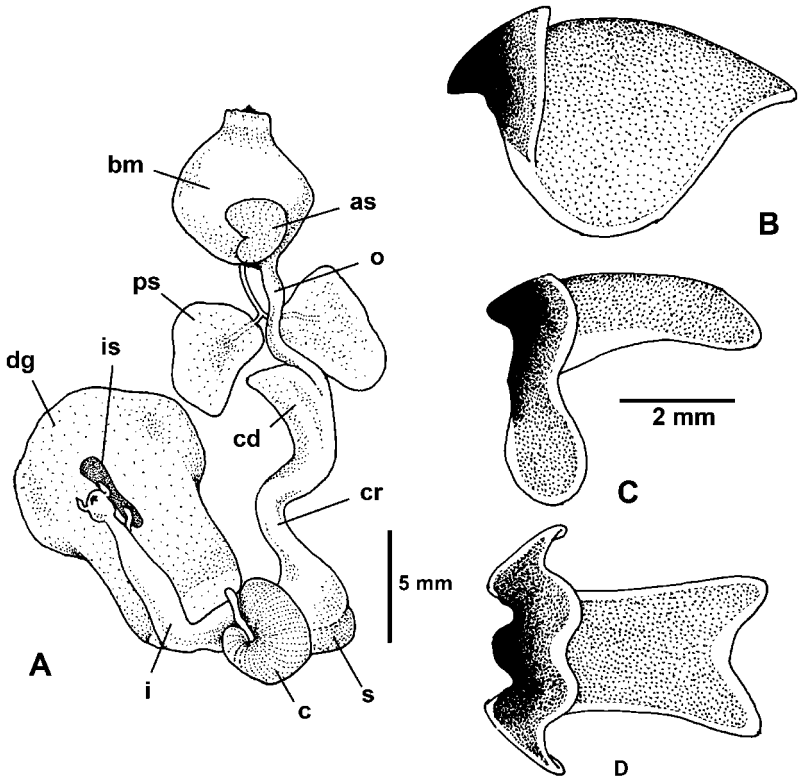

Figure 2. *Scaeurgus tuber* new species. **A.** Digestive tract of 21.0 mm ML female (MNHN 2126). **B–D.** Beaks of same specimen. **B.** Upper beak, lateral view. **C.** Lower beak, lateral view. **D.** Lower beak, ventral view. Abbreviations: as, anterior salivary glands; bm, buccal mass; c, caecum; cd, crop diverticulum; cr, crop; dg, digestive gland; i, intestine; is, ink sac; o, oesophagus; ps, posterior salivary gland; s, stomach.

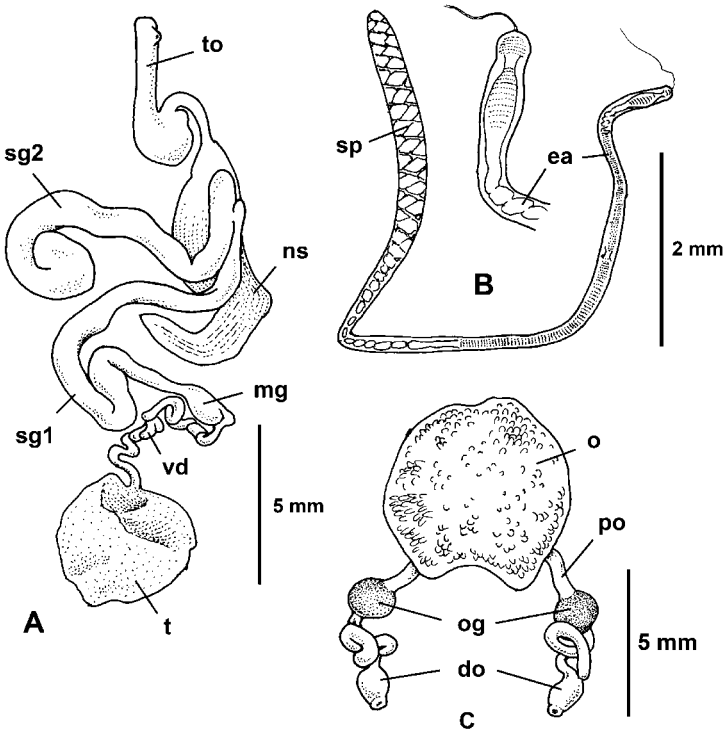

Figure 3. *Scaeurgus tuber* new species. **A, B.** Reproductive system of 19.1 mm ML male holotype (MNHN 2135). **C.** Ovary of 21.0 mm ML female (MNHN 2126). Abbreviations: Male reproductive tract: mg, mucilaginous gland; ns, Needham's sac; sg1, spermatophoric gland; sg2, accessory spermatophoric gland; t, testis; to, terminal organ ('penis'); vd, vas deferens. Spermatophore: ea, ejaculatory apparatus; sr, sperm reservoir. Female reproductive tract: do, distal oviducts; o = ovary; og, oviducal gland; po, proximal oviduct.

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Table 1. *Scaeurgus tuber* new species. Counts and measurements (mm).

Repository	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN
Catalogue number	2135	2137	2124	3811	2129	3792	2125	2136	2136	3804
Status	Holotype	Paratype	–	Paratype	Paratype	Paratype	–	–	–	Paratype
Sex	Male	Male	Male	Male	Male	Female	Female	Female	Female	Female
Maturity	Mature	Mature	Mature	Mature	Mature	Gravid	Submature	Submature	Submature	Mature
Total length	77	65	70	64	57	95	86	86	75	60
Total wet weight (g)	5.0	4.7	3.7	3.4	2.2	8.7	6.0	6.1	5.5	4.1
Dorsal mantle length	19.1	19.3	18.0	16.9	15.7	23.8	22.2	21.4	19.8	18.7
Ventral mantle length	15.7	15.8	14.3	13.0	11.5	16.7	16.6	15.6	15.3	13.3
Mantle width	13.5	13.1	12.7	13.5	11.7	20.4 gravid	14.8	16.8	15.3	14.9
Head width	13.5	13.1	13.0	12.1	11.7	16.6	13.5	13.9	13.2	13.0
Funnel length	8.2	7.4	8.4	7.8	6.7	9.9	9.1	8.1	8.9	7.8
Free funnel length	2.5	4.0	3.4	2.4	2.1	4.7	2.3	4.2	3.1	3.5
Funnel organ length										
lateral limb	3.3	3.9	3.0	3.4	2.7	4.4	4.4	d	3.6	3.7
medial limb	3.9	4.9	4.1	3.7	3.7	5.5	5.5	d	4.7	4.4
Web depths (L R)										
A	12	11	10	8	9	14	13	17	13	12
B	13 11	12 12	12 11	10 11	9 10	12 15	13 15	17 14	16 15	13 12
C	13 14	11 11	12 12	11 11	10 11	15 16	17 15	17 13	18 15	12 13
D	11SpG 11	10SpG 12	12SpG 12	12SpG 12	10SpG 9	d d	18 16	13 15	15 13	14 13
E	10	11	10	10	9	12	15	12	13	13
Arm lengths (L R)										
1	d 50	38 34	41 41	d 39	34 34	d d	51 54	60 52	48 52	46 43
2	53 d	41 36	43 44	44 d	36 35	57 64	57 54	d 53	50 50	47 44
3	d (R)	40 (R)	46 (R)	d (R)	37 (R)	66 57	54 58	60 52	51 50	46 47
Hc	38 (L)	34 (L)	37 (L)	31 (L)	29 (L)	n/a	n/a	n/a	n/a	n/a
4	46 45	39 39	d 45	43 44	36 35	60 59	57 58	57 53	51 d	47 48
Arm width	4.0	3.9	3.1	2.9	2.2	4.1	3.7	3.0	3.5	2.6
Sucker diameter	3.0	2.6	2.0	1.8	1.8	2.2	2.2	2.1	2.0	1.5
Sucker counts (L R)										
1	–	–	–	–	–	–	–	–	–	–
2	–	–	–	–	–	–	–	–	–	–
3	d (R)	110 (R)	113 (R)	d (R)	107 (R)	112 114	117 128	124 122	113 112	113 114
Hc	59 (L)	54 (L)	63 (L)	63 (L)	58 (L)	n/a	n/a	n/a	n/a	n/a
4	110	–	–	-115	–	–	–	–	–	–
Gill count (outer/inner demibranch)	9/9 9/9	9/9 9/9	InD 9/InD	InD 8/9	InD	10/9 InD	10/10 10/10	InD 9/9	InD/9 9/9	InD
Stylet length	6.7	6.0	6.1	6.0	4.8	–	~7	7.0	7.2	–
Ligula length	4.9	4.6	3.9	3.1	2.9	n/a	n/a	n/a	n/a	n/a
Calamus length	1.8	1.1	1.7	0.7	0.6	n/a	n/a	n/a	n/a	n/a
Terminal organ length	4.9	4.9	4.1	3.8	2.6	n/a	n/a	n/a	n/a	n/a
Diverticulum length	–	1.7	–	–	–	n/a	n/a	n/a	n/a	n/a
Spermatophore count	7+1 (TO)	7+1 (TO)	+1 (TO)	1	1	n/a	n/a	n/a	n/a	n/a
Spermatophore length	11	12	11	11.5	8.6	n/a	n/a	n/a	n/a	n/a
Spermatophore width	0.4	0.5	0.4	0.4	0.4	n/a	n/a	n/a	n/a	n/a
Spermatophore reservoir length	4.5	4.7	4.0	4.1	3.6	n/a	n/a	n/a	n/a	n/a
Spermatophore cord whorls	Braided	Braided	Braided	Braided	Braided	n/a	n/a	n/a	n/a	n/a
Egg length	n/a	n/a	n/a	n/a	n/a	2.6	Submature	Submature	Submature	1.7
Egg width	n/a	n/a	n/a	n/a	n/a	0.6	n/a	n/a	n/a	0.4
Egg count	n/a	n/a	n/a	n/a	n/a	Hundreds	n/a	n/a	n/a	Hundreds

A–E: web sectors starting from dorsal sector; d, damaged/distorted; InD, indistinct; Hc, hectocotylized arm of male; L, left; R, right; n/a, not applicable; sub., submature; TO, terminal organ; –, not measured.

(10.7–15.7%). Around 100–130 suckers on intact arms (males 107–115, females 113–128). Webs deep (deepest webs 24.2–35.3% longest arm). Webs approximately equal in depth, ventral and dorsal web sectors often shallower. Webs extend as narrow membranous margins for at least half of arm length, not developed at arm tips.

Third left arm of males hectocotylized. Modified arm short, approximately twice mantle length (1.8–2.1 ML) and around

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80% length of opposite arm (78.4–85.0). Ligula large (10.0–13.5% arm length); elongate spoon-shaped with thick-rimmed deep ligular groove (Fig. 1E). Distal one to three suckers on hectocotylized arm significantly enlarged as tall, swollen cylinders (Fig. 1E). Calamus small, sharp, around 30% ligula length (20.7–43.6%). Hectocotylized arm with 54–63 suckers. Gills with 8–10, typically 9, lamellae on both inner and outer demibranchs, plus terminal lamella.

Digestive tract (Fig. 2A). Anterior salivary glands well developed, longest axis 60% buccal mass length. Posterior salivary glands moderate sized, longest axis slightly shorter than buccal mass length (84.4% in 21.0 mm ML female, MNHN 2126), approximately 40% digestive gland length (41.5% in same female). Crop with distinct diverticulum. Stomach bipartite. Caecum with 1–1.5 whorls, distinctly striated. Digestive gland ovoid to lobed. Ink sac embedded in digestive gland. Anal flaps present. Dorsal surface of visceral mass membrane with an even scatter of numerous large dark founder chromatophores. Ventral surface of membrane lacks chromatophores. Upper beak (Fig. 2B) with short, slightly hooked rostrum and moderate hood, hood length 38.2% total upper beak length in 21.0 mm ML female (MNHN 2126). Lower beak (Fig. 2C, D) with rounded rostrum and relatively parallel lateral walls. Rear border moderately concave, medial length 83.5% total length in same specimen. Radula with seven teeth and two marginal plates in each transverse row (Fig. 10G, H). Rhachidian tooth with one to two lateral cusps, typically two, on each side of large medial cone; lateral cusps in asymmetrical seriation, migrating from lateral to medial position over approximately five to six transverse rows.

Male genitalia (Fig. 3A). Terminal organ ('penis') in mature males small, around one quarter ML (16.7–25.7%); curved with small diverticulum. Spermatophores (Fig. 3B) small (9–12 mm, 54.8–68% ML), produced in low numbers (1–7 in spermatophore storage sac). Sperm reservoir less than half spermatophore length (35.7–41.9%), double strand of sperm cord coiled in around 20 whorls; forms braided effect. Ejaculatory apparatus of linear large core with numerous transverse creases, lacking inward-pointing teeth (unarmed). Oral tip with internal ovoid swelling with distinct internal ridges.

Genitalia of submature female (Fig. 3C). Distal oviducts convoluted, swollen. Oviduct openings broad, fleshy suggesting that this is the location of sperm storage. Oviducts of gravid female (MNHN 3792) distorted but swelling and convolutions of distal oviducts still evident. Oviducal glands with distinct radial chambers. Eggs small, mature ovarian eggs 1.7–2.6 mm long in material examined. Egg length around 10% mantle length based on available material (10.9, 9.1%).

Base colour orange-brown dorsally and lighter cream ventrally, irregular darker brown markings scattered across dorsal mantle and arm crown in some specimens. Pair of large well-defined dark brown to black round spots present on mantle, one each on anterior lateral mantle adjacent to mantle aperture (Fig. 1B). Small faint pair of black spots visible on posterior dorsal mantle in some specimens, not as pronounced as in other members of genus (Fig. 1B). Pair of dorsal white spots (*sensu* Packard & Sanders, 1971) visible on dorsal mantle of well-preserved specimens.

Skin sculptured in numerous rounded papillae in regular texture over entire dorsal surfaces and along aboral surfaces of arms 1–3, present on ventral mantle but less dense and less pronounced (Figs 1B, 10A, B). Diamond of four small primary papillae present on dorsal mantle (Fig. 1A). Longitudinal row of three larger papillae down aboral midline of arms 1–3 (Fig. 1A). Single large branched papilla over each eye, along with several smaller papillae. Large papilla dorsal to each anterior black spot. Large posterior mantle papilla present. Lateral ridge present, well defined at margin of mantle aperture but continues as line of broken short ridges along lateral mantle to posterior papilla (Fig. 1B). Short longitudinal ridge present on lateral head, one under each eye.

Distribution: New Caledonia and Norfolk Ridge, trawled between 230 and 391 m (Fig. 11B).

Remarks: Scaeurgus tuber clearly belongs in this genus on the basis of its left-hand hectocotylized arm, mantle black spots, braided spermatophores, large stylets and remnants of a lateral ridge. The attributes of this pygmy species lead to revision of the characters seen as defining this genus. It differs from the other member species in that it has fewer gill lamellae (8–10 *vs* 12–13), a broken lateral ridge, a reduced calamus, enlarged distal suckers on the hectocotylized arm and reduced posterior mantle black spots. Egg size relative to mantle length further separates *S. tuber* from the other species: *S. tuber*: 9.1–10.9%; *S. jumeau*: 6.0–6.2%; *S. nesisi*: 3.0–3.6%; *S. unicirrhus*: 3.1%.

***Scaeurgus jumeau* new species**

(Figures 4–6, 10C, D, H)

Holotype: M: 30.7 mm ML, MNHN 2141, East Jumeau Bank, Norfolk Ridge, South New Caledonia, N/O *Alis*, BATHUS 3, stn. CP814, 23°48′ S, 168°17′ E, 444–530 m, 28 Nov 1993.

Paratypes: East Jumeau Bank, Norfolk Ridge, South New Caledonia: 1M: 31.9 + 1F: 43.8 mm ML, MNHN 3793, N/O *Alis*, Campagne LITHIST, stn CP14, 23°42.2′ S, 168°15.8′ E, 378–402 m, 12 Aug 1999. 1M: 41.0 mm ML, MNHN 2144, N/O *Alis*, Campagne SMIB 8, stn. DW179, 23°46′ S, 168°17′ E, 400–405 m, 30 Jan 1993. 1F: 43.3 mm ML, MNHN 3806, N/O *Alis*, Campagne NORFOLK 1, stn CP1705, 23°46′ S, 168°17′ E, 400–465 m, 25 June 2001. 1M: 39.0 mm ML, MNHN 3807, N/O *Alis*, Campagne NORFOLK 1, stn CP1706, 23°44′ S, 168°17′ E, 383–394 m, 25 June 2001. 3F: 32.9–37.5 mm ML, MNHN 2143, N/O *Alis*, BATHUS 3, stn. CP811, 23°41′ S, 168°15′ E, 383–408 m, 28 Nov 1993.

Other material examined: Two additional specimens (see Supplementary Data).

Etymology: Named after the single seamount, East Jumeau Bank, on which this species has been found.

Diagnosis: Moderate sized, muscular (ML to 44 mm) with short arms (2.2–2.7 × ML) of approximately equal length. Deepest web 25–32% longest arm. Lateral webs slightly deeper than dorsal and ventral web sectors. Normal arms with around 140–150 suckers (male: 135–141; female: 137–154). Hectocotylized arm with 72–78 suckers. Two to three slightly enlarged suckers present in males on arms 2 and 3 (11–13th proximal suckers), around 12% mantle length (8.8–12.6%). Gills with 12–13 lamellae per demibranch. Third left arm hectocotylized. Ligula of moderate size (7.3–9.5% arm length), peanut-shaped with thick-rimmed groove; calamus very large (50.6–68.2% length of ligula). Distal suckers on hectocotylized arm not enlarged. Spermatophores of moderate size (18–36 mm), over half mantle length (59–92%). Distal oviducts of moderate length and straight. Eggs 2.6–2.7 mm, around 6% mantle length (6.0–6.2%). Continuous lateral mantle ridge present. Base colour orange brown to cream with both pairs of mantle black spots obvious. Visceral mass membrane with founder chromatophores on dorsal and ventral surfaces.

Description: The following description is based on four mature males and three females (two mature and one submature).

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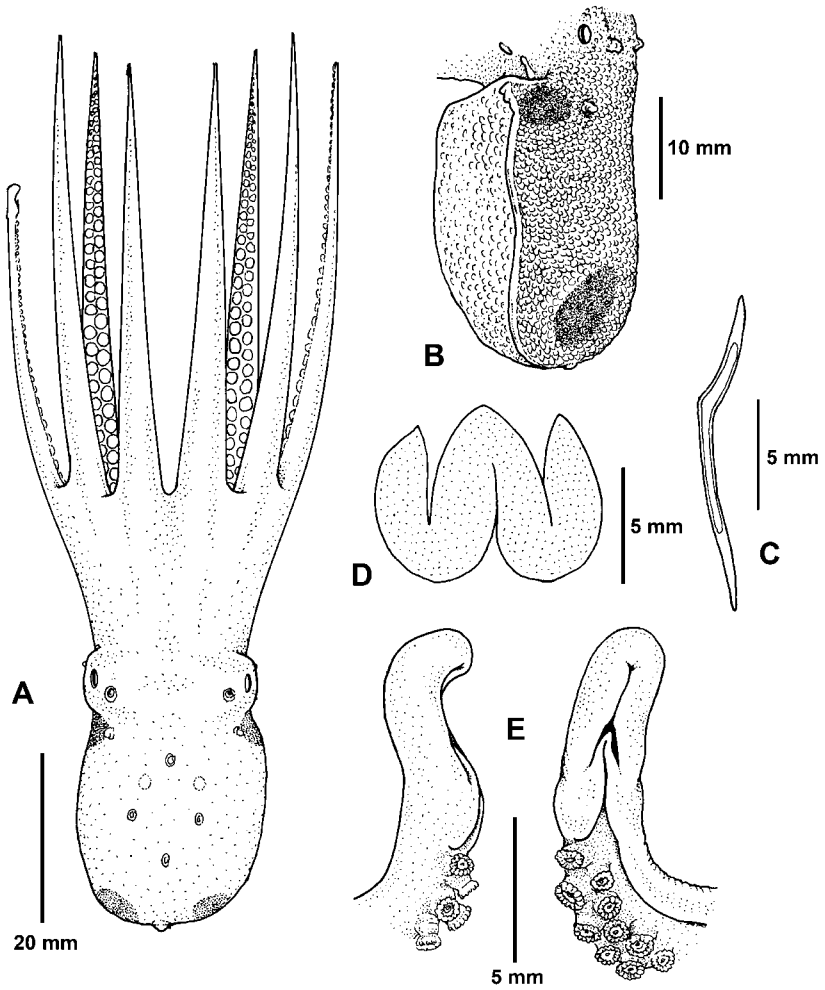

Figure 4. *Scaeurgus jumeau* new species. **A.** Dorsal view of 30.7 mm ML male holotype (MNHN 2141). **B.** Lateral mantle of 35.0 mm ML female paratype (MNHN 2143). **C.** Stylet of 43.8 mm ML female paratype (MNHN 3793). **D.** Funnel organ of 32.9 mm ML female (MNHN 2143). **E.** Copulatory organ of 41.0 mm ML male paratype (MNHN 2144).

Small to moderate sized species (Fig. 4A); mantle length (ML) to at least 44 mm, total length to at least 160 mm; weight to at least 40 g (Table 2). Mantle elongate ovoid, slightly flattened dorso-ventrally and longer than wide (width 58.7–73.5% ML). Head wide (49.5–61.9% ML; 73.3–84.4% mantle width). Skin firm. Eyes moderate to small in size. Stylets present, typically clear but mineralized in several animals (Fig. 4C), length around 40% ML (32.0–39.1%). Mantle opening wide, around 50% circumference of body at level of opening. Funnel of moderate length, approximately 40% mantle length (30.5–40.4% ML), free portion moderate to long, 26.0–51.5% funnel length. Funnel organ W-shaped (Fig. 4D), outer limbs slightly shorter than median ones (outer limbs 80.2–95.7% median limbs). Funnel organ occupies approximately 60% (57.4–68.1%) of funnel length. Arms moderate length, 2.2–2.7 × ML. Arms of moderate width, sub-cylindrical along length, taper gradually to thin tips. Arms approximately equal in length. Suckers in two rows, moderate sized in females, around 8% mantle length (6.9–8.3%); two to three slightly enlarged suckers present in males on arms 2 and 3 (11–13th proximal suckers), around 12% mantle length (8.8–12.6%). Around 140–150 suckers on intact arms (males 135–141, females 137–154). Webs deep (deepest webs 24.8–32.3% longest arm). Webs approximately equal in depth, ventral web often the shallowest. Webs extend as narrow membranous margins for at least half of arm length, not developed at arm tips.

Third left arm of males hectocotylized. Modified arm short, approximately twice mantle length (2.0–2.2 × ML) and around 80% length of opposite arm (85.6, 81.1). Ligula of moderate size (7.3–9.5% arm length), elongate, peanut-shaped with deep ligular groove (Fig. 4E). Calamus very large, narrow and sharp, over 50% ligula length (50.6–68.2%). Hectocotylized arm with 72–78 suckers. Gills with 12–13 lamellae on both inner and outer demibranchs, plus terminal lamella.

Digestive tract (Fig. 5A). Anterior salivary glands small, longest axis 45% buccal mass length. Posterior salivary glands moderate sized, longest axis slightly shorter than buccal mass length (82.0% in 41.0 mm ML male paratype, MNHN 2144), approximately 40% digestive gland length (36.4% in same male). Crop with distinct diverticulum. Stomach bipartite. Caecum coiled with 1–1.5 whorls, distinctly striated. Digestive gland ovoid to lobed. Large ink sac embedded in digestive gland. Anal flaps present. Ventral and dorsal surfaces of visceral mass membrane with an even scatter of numerous small dark chromatophores. Upper beak (Fig. 5B) with a short, slightly hooked rostrum and moderate hood, hood length 34.4% total upper beak length in 41.0 mm ML male paratype (MNHN 2144). Lower beak (Fig. 5C, D) with rounded rostrum and almost parallel lateral walls. Rear border moderately concave,

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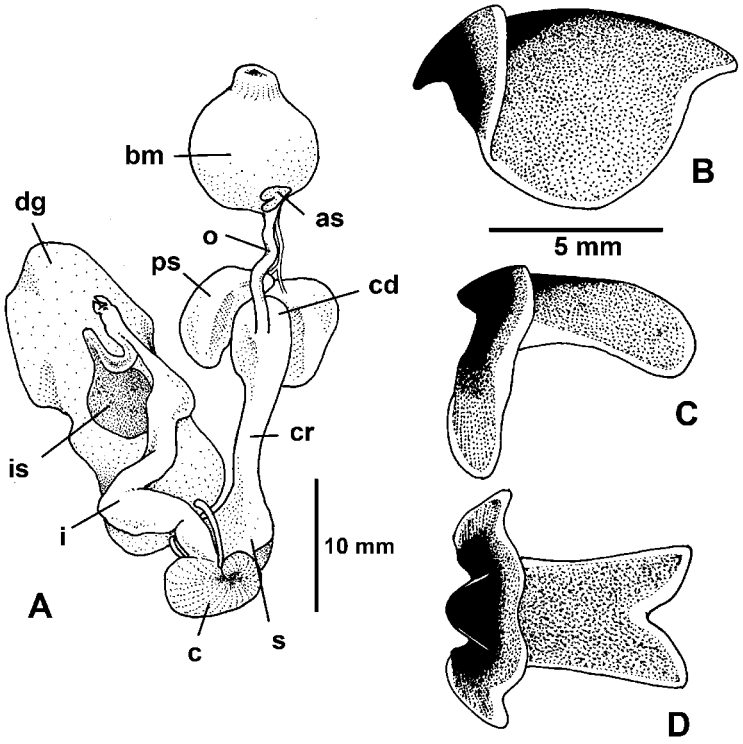

Figure 5. *Scaeurgus jumeau* new species. **A.** Digestive tract of 41.0 mm ML male paratype (MNHN 2144). **B–D.** Beaks of same specimen. B. Upper beak, lateral view. C. Lower beak, lateral view. D. Lower beak, ventral view. Abbreviations as in Figure 2.

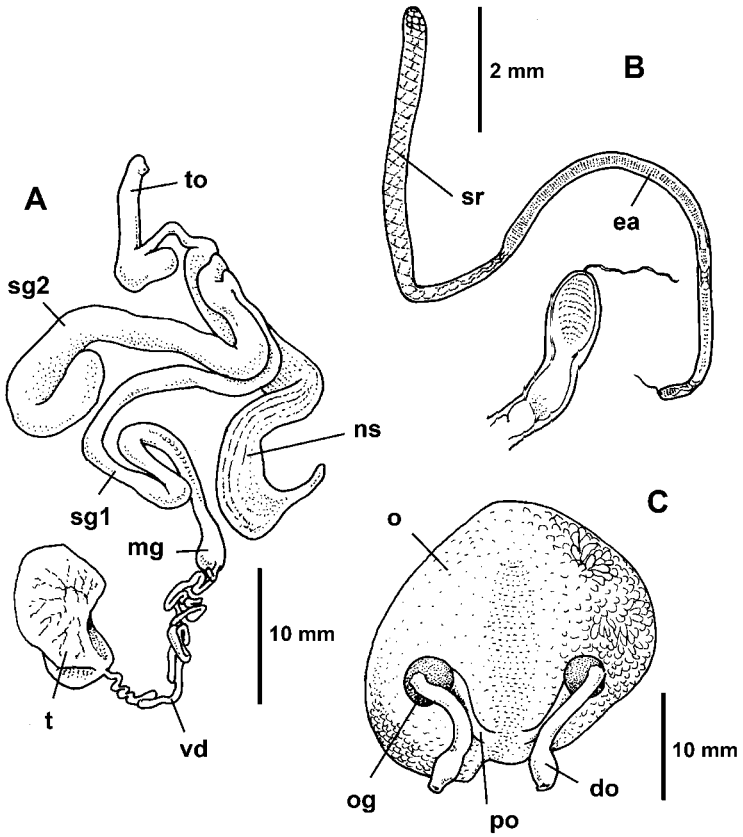

Figure 6. *Scaeurgus jumeau* new species. **A.** Reproductive tract of 41.0 mm ML male paratype (MNHN 2144). **B.** Spermatophore of 39.0 mm ML male paratype (MNHN 3807). **C.** Ovary of 43.8 mm ML female paratype (MNHN 3793). Abbreviations as in Figure 3.

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Table 2. *Scaeurgus jumeau* new species. Counts and measurements (mm).

Repository	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN
Catalogue number	2144	3807	2141	3793	3793	3806	2143
Status	Paratype	Paratype	Holotype	Paratype	Paratype	Paratype	Paratype
Sex	Male	Male	Male	Male	Female	Female	Female
Maturity	Mature	Mature	Mature	Mature	Mature	Mature	Submature
Total length	155	151	114	125	160	157	121
Total wet weight (g)	33.5	23.3	18.0	12.7	39.9	32.3	20.0
Dorsal mantle length	41.0	39.0	30.7	31.9	43.8	43.3	37.5
Ventral mantle length	31.2	25.6	26.7	25.7	33.9	29.5	29.5
Mantle width	29.6	24.5	21.5	20.1	32.2	30.3	22.0
Head width	24.2	19.8	19.0	15.8	23.6	23.0	19.4
Funnel length	15.2	11.9	11.9	11.5	17.7	d	13.2
Free funnel length	5.5	3.9	5.0	4.3	4.6	d	6.8
Funnel organ length							
lateral limb	9.0	5.9	6.5	6.1	9.7	d	7.3
medial limb	9.4	7.2	8.1	6.6	10.3	d	8.8
Web depths (L R)							
A	24	d	19	15	27	30	23
B	25 25	22 d	21 20	20 14	26 24	34 31	24 23
C	25 26	24 25	20 19	20 16	28 27	31 33	24 24
D	26SpG 25	26SpG 23	20SpG 18	19SpG 23	30 27	d 33	24 26
E	22	22	16	d	25	25	22
Arm lengths (L R)							
1	105 104	105 d	74 74	75 67	105 104	93 90	76 56
2	104 105	95 97	70 77	77 81	d d	94 95	74 79
3	104 (R)	d (R)	74 (R)	84 (R)	104 106	97 105	79 81
Hc	89 (L)	82 (L)	60 (L)	55 regen(L)	n/a	n/a	n/a
4	95 100	88 86	74 69	d 77	d 109	98 d	80 70
Arm width	7.4	7.0	5.6	4.5	6.4	6.6	5.8
Sucker diameter	4.9	4.9	3.3	2.8	3.5	3.0	3.1
Sucker counts (L R)							
1	–	–	–	–	–	–	–
2	–	137 -	–	–	–	–	–
3	135	–	138	141	−142	134 137	150 136
Hc	78	72	77	76	n/a	n/a	n/a
4	–	–	–	–	−154	–	–
Gill count (outer/inner demibranch)	12/12 12/12	12/13 12/13	12/12 12/12	12/12 12/d	13/12 12/12	12/- 12/-	12/12 12/12
Stylet length	15.5	15	12	11	14	–	14
Ligula length	7.7	7.8	4.4	4.8	n/a	n/a	n/a
Calamus length	3.9	5.0	3.0	2.9	n/a	n/a	n/a
Terminal organ length	9.5	–	–	–	n/a	n/a	n/a
Diverticulum length	–	–	–	–	n/a	n/a	n/a
Spermatophore count	4+1 (TO)	7 + 1(TO)	1	2 + 1(TO)	n/a	n/a	n/a
Spermatophore length	30	36	18	21	n/a	n/a	n/a
Spermatophore width	0.8	0.9	0.6	0.7	n/a	n/a	n/a
Spermatophore reservoir length	13.7	16	InD	9	n/a	n/a	n/a
Spermatophore cord whorls	Braided	Braided	Braided	Braided	n/a	n/a	n/a
Egg length	n/a	n/a	n/a	n/a	2.7	2.6	1.5 Submature
Egg width	n/a	n/a	n/a	n/a	0.7	0.7	0.7
Egg count	n/a	n/a	n/a	n/a	1000+	1000+	1000+

A–E, web sectors starting from dorsal sector; d, damaged/distorted; InD, indistinct; Hc, hectocotylized arm of male; L, left; R, right; n/a, not applicable; sub., submature; TO, terminal organ; –, not measured.

medial length 74.4% total length in same specimen. Radula with seven teeth and two marginal plates in each transverse row (Fig. 10I, J). Rhachidian tooth with two lateral cusps on each side of large medial cone; lateral cusps in asymmetrical seriation, migrating from lateral to medial position over approximately seven transverse rows.

Male genitalia (Fig. 6A). Terminal organ ('penis') in mature males small, around one quarter ML (23.2%); generally linear

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with small diverticulum. Spermatophores (Fig. 6B) large (18–36 mm, 58.6–92.3% ML), produced in low numbers (1–7 in spermatophore storage sac). Sperm reservoir less than half spermatophore length (42.8–45.7%), double strand of sperm cord coiled in around 30–35 whorls; forms braided effect. Ejaculatory apparatus of linear large core with numerous transverse creases, lacking inward pointing teeth (unarmed). Oral tip with internal ovoid swelling with distinct internal ridges.

Genitalia of mature female (Fig. 6C). Distal oviducts almost linear, swollen and fleshy at genital opening. Oviducts open into the mantle cavity at approximate midpoint of medial septum. Distal oviduct appears to be seminal receptacle in this species. Eggs small, mature ovarian eggs 2.6–2.7 mm long in material examined. Egg length around 6% mantle length based on available material (6.0, 6.2%).

Base colour orange brown dorsally and lighter cream ventrally, irregular darker brown markings scattered across dorsal mantle and arm crown in some specimens. Four large dark brown to black round spots present as two pairs on mantle, one pair on posterior mantle, other pair on anterior lateral mantle adjacent to mantle aperture (Fig. 4B). Skin sculptured in numerous rounded papillae in regular texture over all dorsal surfaces and along aboral surfaces of arms 1–3, less dense on ventral mantle (Fig. 4B). Diamond of four small primary papillae present on dorsal mantle (Fig. 4A). Single large papilla over each eye, along with several smaller papillae. Large papilla dorsal to each anterior black spot. Large posterior mantle papilla present. Lateral ridge present, continuous along entire lateral mantle (Fig. 4B). Short longitudinal ridge present on lateral head, one under each eye.

Distribution: Only known from East Jumeau Bank, Norfolk Ridge, trawled between 378 and 530 m.

Remarks: Scaeurgus jumeau is clearly distinguished from *S. nesisi* by sucker counts in submature and mature animals: normal arms: M: 135–141, 160–179 respectively; F: 137–154, 168–194. Sucker count on the hectocotylized arm also separates *S. jumeau* from *S. unicirrhus*, *S. patagiatus* and *S. nesisi*: 72–78 *vs* 82–87, 85–93 and 93–98, respectively.

***Scaeurgus nesisi* new species**

(Figures 7–9, 10E, F, I)

Holotype: M: 40.6 mm ML, MNHN 2142, Nova Bank, Coral Sea, south-west Pacific Ocean, N/O *Coriolis*, MUSORSTOM 5, stn. CP319, 22°24′ S, 159°17′ E, 320–325 m, 13 Oct 1986.

Paratypes: Nova Bank, Coral Sea: 3M: 48.2–53.1 + 2F: 55.0, 56.3 mm ML, MNHN 2147, CHALCAL, N/O *Coriolis*, ORSTOM, stn CH2, 22°35′ S, 159°18′ E, 330m, 28 July 1984. 6M: 16.3–33.4 + 6F: 17.4–44.1 mm ML, MNHN 2145, N/O *Coriolis*, MUSORSTOM 5, stn CP318, 22°27′ S, 159°21′ E, 330m, 13 Oct 1986.

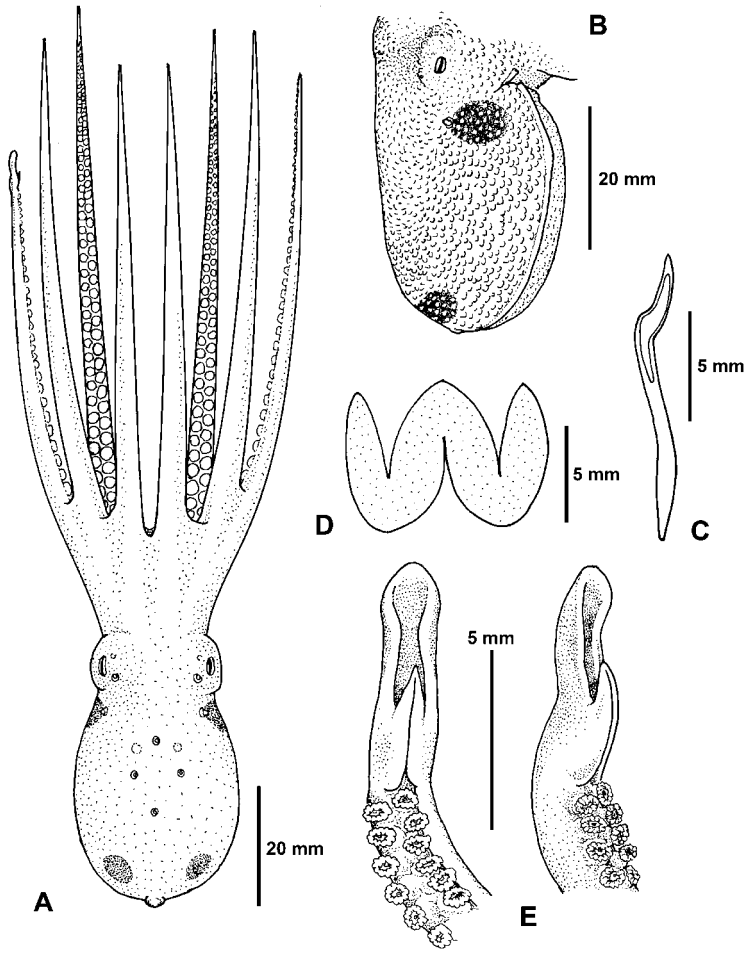

Figure 7. *Scaeurgus nesisi* new species. **A, B.** 30.7 mm ML male holotype (MNHN 2141). **A.** Stylized dorsal view filling in two missing arms. **B.** Lateral mantle. **C, D.** 44.1 mm ML female (MNHN 2145). C. Stylet. D. Funnel organ. **E.** Copulatory organ of 40.6 mm ML male holotype (MNHN 2142).

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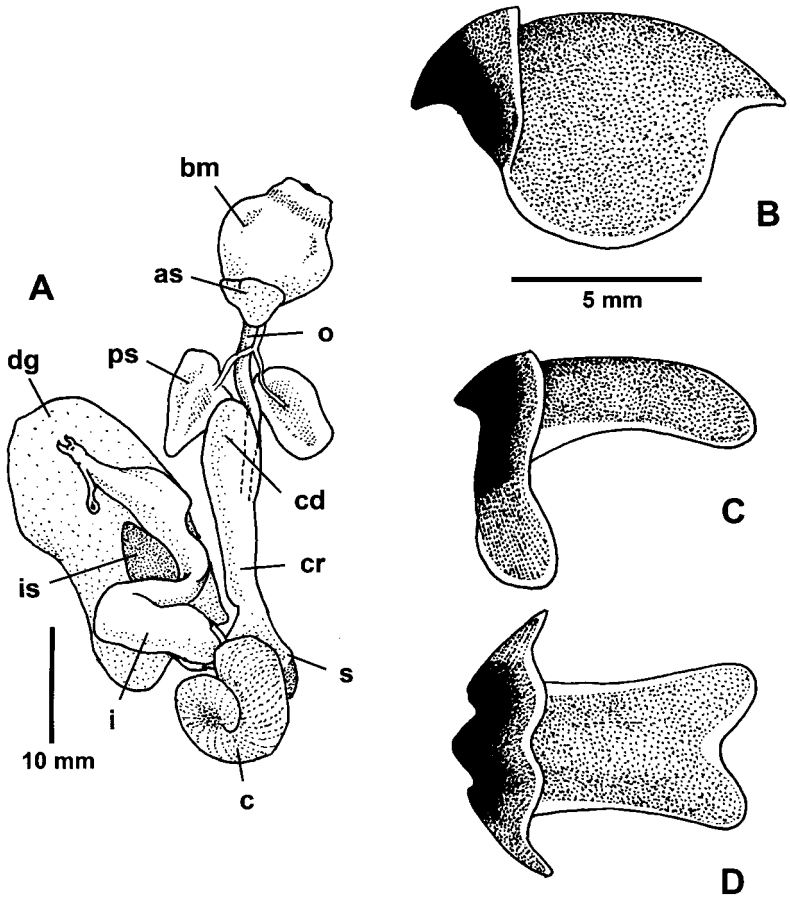

Figure 8. *Scaeurgus nesisi* new species. **A.** Digestive tract of 44.1 mm ML female paratype (MNHN 2145). **B–D.** Beaks of same specimen. **B.** Upper beak, lateral view. **C.** Lower beak, lateral view. **D.** Lower beak, ventral view. Abbreviations as in Figure 2.

Other material examined: Total of five additional specimens (see Supplementary Data).

Etymology: *Named* in honour of the late great teuthologist, Kir Nesis (who recently passed away; he will be sorely missed).

Diagnosis: Moderate sized muscular species (ML to 56 mm) with short arms (2.5–3.0 × ML) of approximately equal length. Deepest web 20–30% longest arm. Lateral webs slightly deeper than dorsal and ventral web sectors. Normal arms with around 170–190 suckers (male: 160–179; female: 168–196). Hectocotylized arm with 93–98 suckers. Two to three enlarged suckers present in larger males on arms 2 and 3 (around 11–13th proximal suckers), to 14% mantle length (8.4–14.1%). Gills with 12–13 lamellae per demibranch. Third left arm hectocotylized. Ligula of moderate size (5.1–8.6% arm length), peanut-shaped with thick-rimmed groove; calamus very large (47.5–57.9% length of ligula). Distal suckers on hectocotylized arm not enlarged. Spermatophores of moderate size (20–30 mm), around half mantle length (49–62%). Distal oviducts of moderate length and straight. Mature eggs small, 1.6–1.7 mm, around 3% mantle length (3.0–3.6%). Continuous lateral mantle ridge present. Base colour orange brown to cream with both pairs of mantle black spots obvious. Visceral mass membrane with founder chromatophores on dorsal and ventral surfaces.

Description: The following description is based on five males (three mature, two submature) and four females (two mature and two submature). Moderate sized species (Fig. 7A); mantle length (ML) to at least 56 mm, total length to at least 214 mm; weight to at least 56 g (Table 3). Mantle elongate ovoid, slightly flattened dorso-ventrally and longer than wide (width 60.2–70.7% ML). Head wide (47.1–55.5% ML; 70.0–82.8% mantle width). Skin firm. Eyes moderate to small in size. Stylets present, typically clear but mineralized in several animals (Fig. 7C), length around 30% ML (24.9–38.9%). Mantle opening wide, around 50% circumference of body at level of opening. Funnel of moderate length, approximately one third of mantle length (32.6–36.5% ML), free portion moderate to long, 24.4–65.9% funnel length. Funnel organ W-shaped (Fig. 7D), outer limbs shorter than median ones (outer limbs 77.1–92.8% median limbs). Funnel organ occupies approximately 60% (56.9–64.7%) of funnel length.

Arms moderate length, around 2.5–3 times mantle length (2.5–3.0 × ML). Arms of moderate width, sub-cylindrical along length, taper gradually to thin tips. Arms approximately equal in length. Suckers in two rows, moderate sized in females, around 8% mantle length (7.6–8.2%); 2–3 enlarged suckers present in larger males on arms 2 and 3 (around 11–13th proximal suckers), up to 14% mantle length (8.4–14.1%). Around 170–190 suckers on intact arms (males to 160–179, females to 168–196). Webs moderate to deep (deepest webs 20.2–29.9% longest arm). Webs approximately equal in depth, ventral or dorsal web sectors often the shallowest. Webs extend as narrow membranous margins for at least half of arm length, not developed at arm tips.

Third left arm of males hectocotylized. Modified arm short, approximately twice mantle length (1.8–2.4 × ML) and shorter than opposite arm (70.9–95.2). Ligula of moderate

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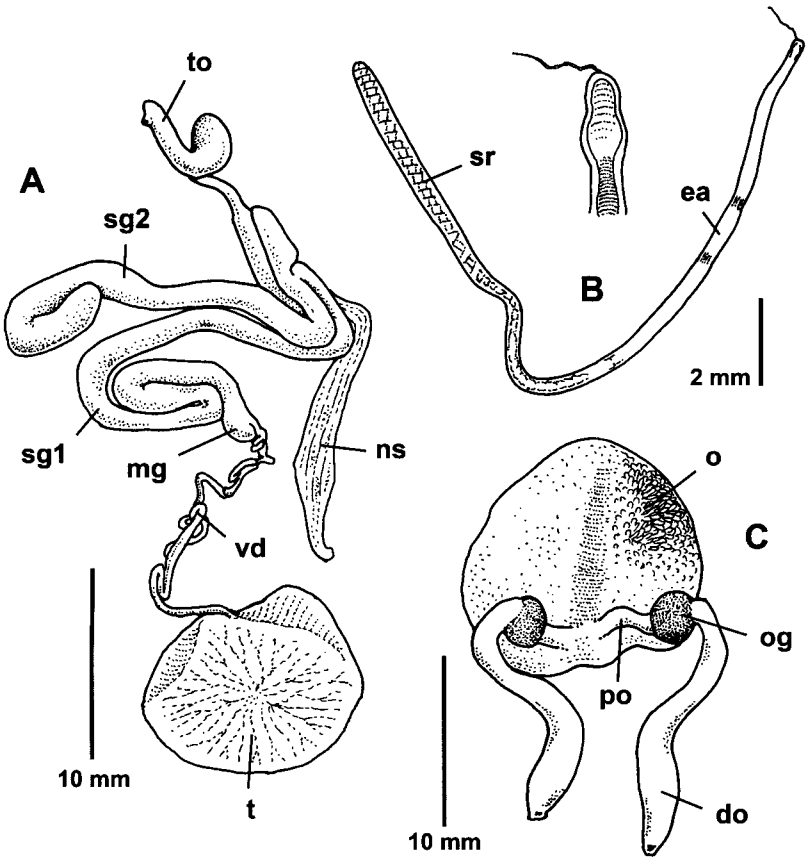

Figure 9. *Scaeurgus nesisi* new species. **A, B.** 40.6 mm ML male holotype (MNHN 2142). **A.** Reproductive tract. **B.** Spermatophore. **C.** Ovary of 44.1 mm ML female paratype (MNHN 2145). Abbreviations as in Figure 3.

size (5.1–8.6% arm length); elongate, peanut-shaped with deep ligular groove (Fig. 7E). Calamus very large, narrow and sharp, around 50% ligula length (47.5–57.9%). Hectocotylized arm with 93–98 suckers.

Gills with 12–13 lamellae on both inner and outer demibranchs (rarely 14), plus terminal lamella.

Digestive tract (Fig. 8A). Anterior salivary glands moderate to large, longest dimension 46.0% length of buccal mass in 44.1 mm ML female (MNHN 2145). Posterior salivary glands moderate sized, longest dimension 75.4% length of buccal mass in same female (36.2% digestive gland length). Crop with distinct diverticulum. Stomach bipartite. Caecum coiled with 1–1.5 whorls, distinctly striated. Digestive gland approximately ovoid. Ink sac and anal flaps present.

Upper beak (Fig. 8B) with a short, slightly hooked rostrum and moderate hood, hood length 37.0% total upper beak length in 44.1 mm ML female paratype (MNHN 2145). Lower beak (Fig. 8C, D) with rounded rostrum and relatively parallel lateral walls. Rear border moderately concave, medial length 87.8% total length in same specimen.

Radula with seven teeth and two marginal plates in each transverse row (Fig. 10K, L). Rhachidian tooth with one to two lateral cusps, typically two, on each side of large medial cone. Lateral cusps in asymmetrical seriation, migrating from lateral to medial position over approximately seven transverse rows.

Male genitalia (Fig. 9A). Terminal organ ('penis') in mature male small to moderate, up to one third of ML (14.7–35.1%); curved with moderate diverticulum. Spermatophores (Fig. 9B) large (20–30 mm, 49.3–62.2% ML), produced in low numbers (1–6 in spermatophore storage sac). Sperm reservoir less than half spermatophore length (35.0, 37.0%), double strand of sperm cord coiled in around 25–30 whorls; forms braided effect. Ejaculatory apparatus of linear large core with numerous transverse creases, lacking inward pointing teeth (unarmed). Oral tip with internal ovoid swelling with distinct internal ridges.

Genitalia of mature female (Fig. 9C). Distal oviducts almost linear, swollen and fleshy at genital opening. Oviducts open into mantle cavity at approximate midpoint of medial septum. It appears that the distal oviducts act as the seminal receptacle in this species. Eggs small, mature ovarian eggs 1.6–1.7 mm long in material examined. Egg length around 3% mantle length based on available material (3.0, 3.6%).

Base colour uniform orange-brown dorsally and lighter cream ventrally. Four large dark brown to black round spots present on mantle, one pair on posterior mantle, other pair on anterior lateral mantle adjacent to mantle aperture (Figs 7A, B, 10F). Skin sculptured in numerous rounded papillae in regular texture over entire dorsal surfaces, less dense on ventral mantle (Figs 7B, 10F). Some papillae on dorso-lateral anterior mantle fused into short irregular longer patches. Single large papilla over each eye, along with several smaller papillae. Large papilla dorsal to each anterior black spot. Large posterior mantle papilla present. Lateral ridge present, continuous along entire lateral mantle (Fig. 10F). Short longitudinal ridge present on lateral head, one under each eye, extending as broken line down midline of third arms.

Distribution: Nova Bank, Coral Sea, trawled at depths between 295 and 340 m.

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Table 3. *Scaeurgus nesisi* new species. Counts and measurements (mm).

Repository	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN
Catalogue number	2147	2147	2142	2145	2145	2147	2145	2147	2145
Status	Paratypes	Paratype	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Sex	Male	Male	Male	Male	Male	Female	Female	Female	Female
Maturity	Mature	Mature	Mature	Submature	Submature	Mature	Mature	Submature	Submature
Total length	208	197	154	132	115	207	184	214	149
Total wet weight (g)	56.0	38.6	26.6	15.7	14.4	51.0	36.2	54.0	22.0
Dorsal mantle length	48.2	53.1	40.6	33.4	31.9	56.3	44.1	55.0	39.9
Ventral mantle length	37.9	47.2	34.7	28.2	25.7	45.3	34.7	33.9	31.2
Mantle width	34.0	d	26.8	22.7	22.4	d	31.2	35.5	24.0
Head width	23.8	d	22.1	18.8	17.7	d	22.5	d	18.8
Funnel length	17.6	17.3	13.8	11.9	11.5	19.3	16.0	19.0	14.0
Free funnel length	11.6	8.2	6.2	2.9	3.5	6.2	5.5	9.4	6.2
Funnel organ length									
lateral limb	InD	InD	6.2	7.0	5.4	InD	7.6	InD	7.7
medial limb	InD	InD	8.0	7.7	7.0	InD	9.1	InD	8.3
Web depths (L R)									
A	27	23	d	18	19	36	23	31	17
B	d 30	21 31	d 18	19 21	18 22	d 37	25 26	35 27	20 19
C	29 27	25 d	d 27	22 23	18 18	d 36	32 26	36 26	21 21
D	32SpG d	32SpG 40	23SpG 25	23SpG 23	17SpG 19	d 32	d 25	40 33	21 20
E	31	37	25	18	14	d	24	28	17
Arm lengths (L R)									
1	d 124	109 d	d 98	d d	78 79	135 d	d 127	135 110	101 103
2	128 d	116 121	d 106	93 90	78 74	132 114	d d	143 127	104 d
3	d (R)	134 (R)	100 (R)	83 (R)	74 (R)	d 115	130 117	128 114	104 94
Hc	113 (L)	95 (L)	84 (L)	79 (L)	65 (L)	n/a	n/a	n/a	n/a
4	146 132	118 125	108 102	80 80	74 76	d 140	116 121	144 125	104 d
Arm width	d	7.0	6.2	4.6	5.5	d	6.9	7.5	5.9
Sucker diameter	6.8	5.2	3.6	2.8	3.1	4.5	3.6	4.2	3.1
Sucker counts (L R)									
1	–	–	–	–	–	–	–	–	–
2	–	–	–	–	–	168 -	–	–	–
3	–	176	177	170	160	−168	196 194	171 -	180 171
Hc	93	94	93	98	98	n/a	n/a	n/a	n/a
4	173 179	–	–	–	–	–	–	175 –	–
Gill count (outer/inner demibranch)	13/d d/d	12/12 12/12	13/13 13/13	13/13 13/13	13/14 13/13	12/- 12/-	13/13 13/13	13/- 13/13	12/12 12/13
Stylet length	16	–	–	13	–	14	13	–	15
Ligula length	9.7	5.7	6.2	4.0	3.6	n/a	n/a	n/a	n/a
Calamus length	4.7	3.3	3.5	1.9	2.0	n/a	n/a	n/a	n/a
Terminal organ length	16.9	9.7	–	–	4.7	n/a	n/a	n/a	n/a
Diverticulum length	InD	2.4	–	–	–	n/a	n/a	n/a	n/a
Spermatophore count	6 + 1(TO)	3 + 1(TO)	2+1 (TO)	Submat	Submat	n/a	n/a	n/a	n/a
Spermatophore length	30	∼27	20	n/a	n/a	n/a	n/a	n/a	n/a
Spermatophore width	0.9	0.6	0.5	n/a	n/a	n/a	n/a	n/a	n/a
Spermatophore reservoir length	InD	∼10	7	n/a	n/a	n/a	n/a	n/a	n/a
Spermatophore cord whorls	Braided	Braided	Braided	n/a	n/a	n/a	n/a	n/a	n/a
Egg length	n/a	n/a	n/a	n/a	n/a	1.7 ov	1.6 ov	Submature	Submature
Egg width	n/a	n/a	n/a	n/a	n/a	0.5	0.3	Submature	Submature
Egg count	n/a	n/a	n/a	n/a	n/a	1000 +	1000 +	Sub mature	Sub mature

A–E, web sectors starting from dorsal sector; d, damaged/distorted; InD, indistinct; Hc, hectocotylized arm of male; L, left; R, right; n/a, not applicable; sub., submature; TO, terminal organ; –, not measured.

Remarks: Amongst the new species, *Scaeurgus nesisi* is the closest in morphology to the two previously described species. It differs by a combination of higher hectocotylized arm sucker counts (93–98 *vs* 82–86 and 85–93), smaller spermatophores (both in actual size and size relative to mantle length, see Table 4) and smaller eggs (1.6–1.7 *vs* 2.0–2.5). It is further distinguished from *S. unicirrhus* by a lower number of sperm cord whorls (25–30 *vs* 38–44).

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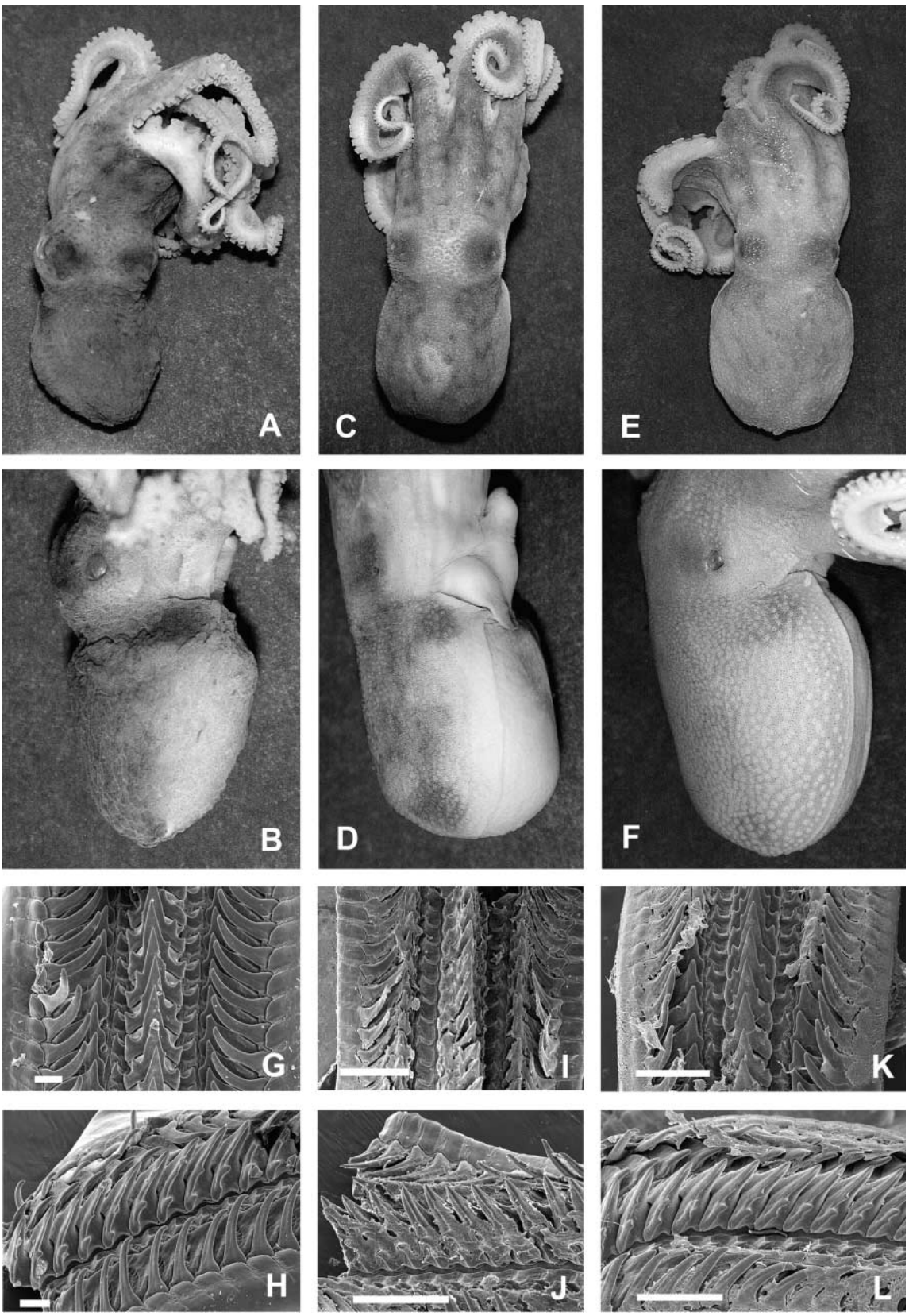

Figure 10. A, B. *Scaeurgus tuber* new species, 19.1 mm ML male holotype (MNHN 2135). **A.** Dorsal view. **B.** Lateral mantle. **C, D.** *Scaeurgus jumeau* new species. **C.** Dorsal view of 30.7 mm ML male holotype (MNHN 2141). **D.** Lateral mantle of 31.5 mm ML female (MNHN 2146). **E, F.** *Scaeurgus nesisi* new species, 40.6 mm ML male holotype (MNHN 2142). **E.** Dorsal view. **F.** Lateral mantle. **G–L.** Scanning electron microscope images of radulae. **G, H.** *Scaeurgus tuber* new species, 21.0 mm ML female (MNHN 2126). **I, J.** *Scaeurgus jumeau* new species, 41.0 mm ML male paratype (MNHN 2144). **K, L.** *Scaeurgus nesisi* new species, 44.1 mm ML female paratype (MNHN 2145) Scale bars: **G, H** = 0.1 mm; **I, J**=5 mm; **K, L**=5 mm.

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Table 4. Comparison of new *Scaeurgus* species with named species.

Character	*S. tuber*	*S. jumeau*	*S. nesisi*	sp. 1	sp. 2	*S. unicirrhus*	*S. patagiatus*	'*S. patagiatus*' of Sasaki, 1929
Synonyms	–	–	–	–	–	*cocco* Verany, 1846	Scaeurgus sp. Berry, 1909	–
No. of specimens for data	5M, 5F	4M, 3F	5M, 4F	1M, 1F	2F	6M, 1F	6M, 3F	1M
Maximum size: ML	24	44	56	21	20	90 (Mangold-Wirz, 1963)	63	57
Maximum size: TL	95	160	214	76	–	255 (64 mm ML)	254	235
Head width/ML (%)	60.8–74.5	49.5–61.9	47.1–55.5	62.3, 72.1	–	40.0–51.5	41.3–54.3	57.9
Arm length/ML (%)	2.1–2.8	2.2–2.7	2.5–3.0	2.0, 2.4	–	2.3–2.9	2.6–3.3	3.0
Sucker diameter F	8.0–10.1	6.9–8.3	7.6–8.2	9.1	–	6.5–7.0	6.7–9.8	–
Enlarged suckers	M: 8–12th All arms	M: 11–13th Arms 2, 3	M: 11–13th Arms 2, 3	M: 8–11th All arms	–	M: 12–15th All arms	M: 12–15th Arms 2, 3	M: 15–18th All arms
Sucker diameter M	10.7–15.7	8.8–12.6	8.4–14.1	8.5	–	7.8–10.0	9.1–12.5	18.9
Sucker count F	114–128	137–154	168–194	124	156	187	173–210	–
Sucker count M	107–115	135–141	160–179	114	–	176–198	173–189	~180
Hecto sucker count	54–63	72–78	93–98	72	–	82–87	85–93	76
Gill count	8–10	12–13	12–13	12–13	12–13	12–13	11–12	12
Ligula length index	10.0–13.5	7.3–9.5	5.1–8.6	7.7	–	8.1–10.4	7.3–8.4	9.6
Calamus length index	20.7–43.6	50.6–68.2	47.5–57.9	39.1	–	42.9–60.3	50–56	39.5
Inflated distal suckers	Present	Absent	Absent	Absent	–	Absent	Absent	Absent
Spermatoph. length	9–12	18–36	20–30	Submature	–	34–45	30–45	50
Spermatoph. length/ML	55–68	59–92	49–62	–	–	65–84	65–71	88
Sperm cord whorls	Braided ~20	Braided 30–35	Braided 25–30	–	–	Braided 38–44	Braided 26–28	Braided 40–46
Egg length	1.7–2.6	2.6–2.7	1.6–1.7	Submature	–	2.0–2.5	2.0–2.5	–
Egg length/ML	9.1, 10.9	6.0, 6.2	3.0, 3.6	Med-large	Submature	3.1	?	–
Mantle black spots	4	4	4	4	–	4	4	–
Lateral mantle ridge	Broken	Continuous	Continuous	Continuous	Continuous	Continuous	Continuous	Faint, interrupted

M, male; F, female; ML, mantle length; TL, total length.

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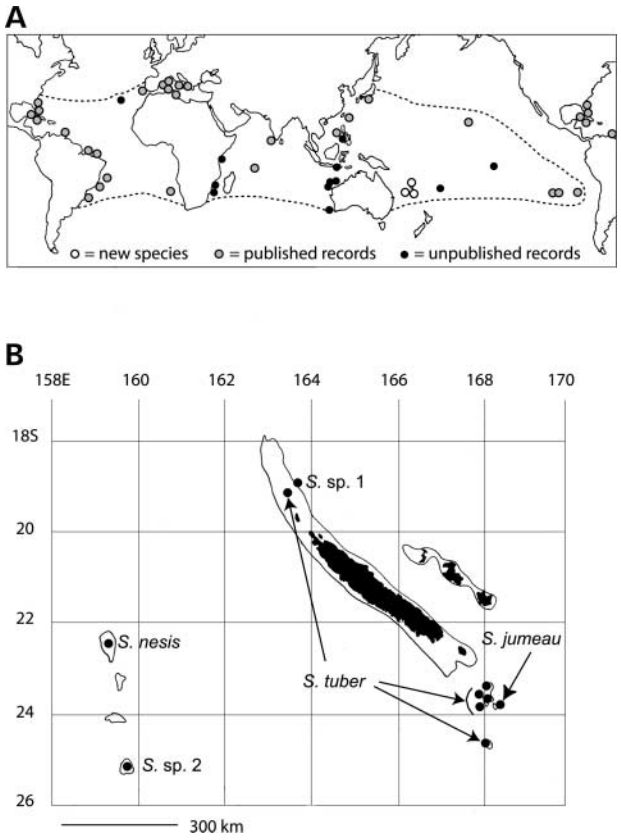

Figure 11. A. Known geographic distribution of members of the genus *Scaeurgus (*unpublished records based on museum material examined by the authors). **B.** Distributions of new members of the genus *Scaeurgus* around New Caladonia.

Scaeurgus sp. 1

Material examined: Northern New Caledonia, Grand Passage: 1M: 19.9 mm ML, MNHN 2156, deep site in midst of shallow water survey, Secteur de Belep, stn 1152 (MUSORSTOM shallow-water survey), 18°58′ S, 163°24′ E, 335 m, coll. B. Richer, ORSTOM, 29 Oct 1989. 1F: 20.8 mm ML, MNHN 2568, N/O *Vauban*, MUSORSTOM 4, stn. CP192, 18°59′ S, 163°25′ E, 315 m, coll. Bouchet and Richer de Forges, 19 Sept 1985.

Description: Small muscular species (ML to 20 mm) with short arms (2.0–2.4 × ML) of approximately equal length. Normal arms with around 120 suckers (male: 114; female: 124). Hectocotylized arm with 72 suckers. Approximately 4 enlarged suckers present in larger males on all arms (around 8–11th proximal suckers), to 8.5% mantle length. Gills with 12–13 lamellae per demibranch. Third left arm hectocotylized. Ligula of moderate size (7.7% arm length), peanut-shaped with thick-rimmed groove. Calamus very large (39.1% length of ligula). No enlargement of distal suckers on hectocotylized arm. Spermatophores unknown. Eggs appear large in submature ovary. Continuous lateral mantle ridge present. Base colour orange brown to cream with both pairs of mantle black spots obvious. Visceral mass membrane with founder chromatophores on dorsal and ventral surfaces.

Distribution: Grand Passage, Northern New Caledonia, trawled at depths between 295 and 340 m.

Remarks: *Scaeurgus* sp. 1 is similar in size and normal arm sucker counts with the pygmy species *S. tuber*, but is clearly distinguished by higher gill counts (12–13 *vs* 8–10), absence of enlarged distal suckers on the hectocotylized arm, and a continuous lateral ridge (versus a broken lateral ridge in *tuber*). Sucker counts and the location of enlarged suckers in the male clearly distinguish *Scaeurgus* sp. 1 from the remaining *Scaeurgus* species.

Scaeurgus sp. 2

Material examined: Coral Sea, Banc Capel: 1F: 15.4 mm ML, MNHN 2153, N/O *Coriolis*, MUSORSTOM 5, stn CP268, 24°45′ S, 159°39′ E, 280 m, Bouchet, Metivier and Richer, 9 Oct 1986; 1F: 20.2 mm ML, MNHN 2158, N/O *Coriolis*, MUSORSTOM 5, stn CP269, 24°47′ S, 159°37′ E, 280 m, Bouchet, Metivier and Richer, 9 Oct 1986.

Distribution: Banc Capel in the Coral Sea. Both specimens trawled from 280 m.

Remarks: This taxon is represented by two small submature females with 12–13 gill lamellae, a continuous lateral ridge and developing eggs. Data on these specimens is provided in Table 4. The *Scaeurgus* sp. 2 females are much smaller for their stage of maturity (15.4 and 20.2 mm ML) compared with the larger *Scaeurgus nesisi* from further north. The third right arm of the larger female has 156 suckers, separating it from the other two small species, *S. tuber* and *S.* sp. 1. Additional material of this taxon is required before its status can be further resolved.

DISCUSSION

We recognize that there are at least four species in the genus *Scaeurgus*: our three new species (*S. tuber*, *S. jumeau* and *S. nesisi*) and at least one species from the unresolved *unicirrhus/patagiatus* issue. *Scaeurgus* species 1 and 2 also appear distinct and are likely to constitute additional new species.

The large number of distinct taxa encountered in the present study from a small area of the southwest Pacific Ocean raises the likelihood that considerably more species exist in this genus than had been previously suspected. As such, many of the published records listed require detailed re-examination to resolve their identifications. In addition to Toll's western Atlantic material, Sasaki's (1929) *patagiatus* from Japan seems different from both *patagiatus* and *unicirrhus* in sucker counts, enlarged sucker size, ligula size, calamus size and spermatophore size (see Table 4). Similarly, specimens reported from Valdivia Bank off Namibia as *S. unicirrhus* by Sanchez & Alvarez (1988) differed in size and arm length from both the northern Atlantic and Hawaiian material. Additional material from throughout the range of this genus (Fig. 11A) is the subject of ongoing studies.

Pygmy species

At least one of the new *Scaeurgus* species, *S. tuber*, is a pygmy species, mature at tiny sizes (ML <25 mm). *Scaeurgus* spp. 1 and 2 may also constitute pygmy species but are only represented by late submature individuals (all <25 mm ML). These taxa support the hypothesis that pygmy taxa have arisen more than once in the evolution of benthic octopuses, tiny representatives occurring in multiple octopodid lineages (Norman, 2000).

Biogeography

The genus *Scaeurgus* occurs on seamounts and continental slopes at depths between 50 and 500 m. Depth distributions of the new taxa fell between 230 and 530 m (*S. tuber*: 230–391 m; *S. jumeau*:

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378–530 m; *S. nesisi*: 295–340 m; *S.* sp. 1: 295–340 m; *S.* sp. 2: 280 m). Nesis (1993b) suggests that this genus is more typically found on seamounts than on continental slopes.

This genus occurs at tropical and subtropical latitudes worldwide, except in the East Pacific region (Fig. 11A). Nesis (1990) provides the most easterly report of *Scaeurgus* in the Pacific Ocean, from the Nazca and Sala y Gómez submarine ridges in the southeast Pacific Ocean (~25° S, 85–100° W). Parin, Mionov & Nesis (1997) discussed a potential biogeographic barrier midway along this 1600 km long submarine mountain range, at around 83–84° W. These authors proposed that this may represent the eastern limit of the Indo-West Pacific influence on the seamount fauna, the fauna further east showing East Pacific and South American affinities. The six *Scaeurgus* specimens captured in the surveys reported by Nesis (1990) were all collected west of this break.

In our study, the new *Scaeurgus* species showed restricted geographic distributions. Fifty-eight of the 62 *Scaeurgus* specimens collected by MUSORSTOM/IRD were trawled off seamounts. The remaining four specimens were collected on the slopes of the New Caledonia land mass and belonged to two species (*S. tuber* and *Scaeurgus* sp. 1). The 58 seamount specimens came from seven individual seamounts.

Each seamount bore a single *Scaeurgus* species. *Scaeurgus jumeau*, *S. nesisi* and *Scaeurgus* sp. 2 were each found on their own seamount. *Scaeurgus* sp. 1 was found on the northern end of the New Caledonia land mass. Only one species occurred on more than one seamount. The smallest species, *S. tuber*, was the most widely distributed, occurring on the continental slopes of New Caledonia as well as on three seamounts: Aztec (=Antigonia), West Jumeau and Mont A. The presence of this species on both the New Caledonian slopes and Aztec may be explained by the relatively shallow isthmus (200–400 m deep) between these locations. According to data available at time of publication, the sea floor between Aztec to Jumeau West is unchartered so it is unclear if there is a potential saddle at an appropriate depth joining these mounts. Mont A, however, is surrounded by a bathyal plain at around 1600 m. The presence of *S. tuber* on several seamount systems including the isolated Mont A suggests that planktonic dispersal of young may be occurring in this pygmy species. Hatchlings of *S. tuber (*and the other new species) are unknown.

Based primarily on shallow-water octopuses, Boletzky (1992) proposed that egg size relative to body size indicates hatchling mode. Eggs less than 10% mantle length develop into planktonic hatchlings while larger eggs (>10% ML) develop into benthic hatchlings. *Scaeurgus unicirrhus* from the Mediterranean Sea have an egg to mantle length ratio of around 3% and have been reported as having planktonic hatchlings (Boletzky, 1984). If we follow Boltezky's proposal, the distributions and relative egg sizes in the new *Scaeurgus* species are counterintuitive. Those that appear to have the most restricted distributions have the smallest relative egg sizes: *S. jumeau* (1.6–1.7 mm, 3.0–3.6% ML) and *S. nesisi* (2.6–2.7 mm, 6.0–6.2% ML). Although the eggs of *S. tuber* are small (1.7–2.6 mm), they are large relative to body size (around 10% mantle length), a relative size at the cusp between Boltezky's two hatchling modes.

Interpretations of egg size and hatchling behaviour in deeper water octopuses may be more complicated than in shallow waters because of the potential for lecithotrophic planktonic hatchlings: free-swimming juveniles stocked with yolk for non-foraging dispersal in deep-sea currents, as occur in many non-cephalopod deep-sea invertebrate species (Gage & Tyler, 1992). Collection of open-water and deep-water planktonic samples in this region could shed light on the dispersal strategies of these new taxa.

The high number of *Scaeurgus* species reported here from a relatively small area, supports hypotheses of high endemism on seamounts in this region. Richer de Forges, Koslow & Poore (2000) reviewed the seamount faunas of the southeast Coral Sea and Tasman Sea and found high endemism (29–34% of the fauna). These authors suggested that 'low species overlap between seamounts in different portions of the region indicates that the seamounts in clusters or along ridge systems function as "island groups" or "chains", leading to highly localized species distributions and apparent speciation between groups or ridge systems that is exceptional for the deep sea' (p. 944). It is clear that there is still much to learn of the seamount faunas of this region.

ACKNOWLEDGEMENTS

This study would not have been possible without the financial and moral support of both the Muséum National d'Histoire Naturelle, Paris and the Australian Biological Resources Study, Environment Australia. In Paris, we warmly thank Guy Boucher, Bernard Metivier, Dominique Doumenc, Marie-Paule Bruneaux, Delphine Pichon, Nadia Ameziane, Marc Eleaume. In Banyuls, Jean-Yves Bodiou and Marie Therese Panouse, and in Basel, Katharina Mangold. The authors wish to thank Janet Voight and an anonymous reviewer for constructive comments on the manuscript. Many thanks to Mike Sweeney for alerting us to the nomenclatural problems of the genus; Claude Massin of the Institut Royal des Sciences Naturelles de Belgique, Brussels for loan material; Joan Clarke for assistance with electron microscopy; Daniel Geiger, Natural History Museum of Los Angeles County for translation of Troschel's original descriptions; Julian Finn for comments on the manuscript; and Karen Zipkas for assistance with morphological descriptions.

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