

A NEW GENUS AND TWO NEW SPECIES OF MESOBENTHIC OCTOPUSES FROM AUSTRALIA AND NEW CALEDONIA

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ABSTRACT

Trawl surveys off Western Australia and seamounts south of New Caledonia at depths between 375 and 545 m have yielded two species of a previously unknown genus of benthic octopus (Family: Octopodidae). *Histoctopus* n. gen. is described here and contains two new species, *Histoctopus discus* and *Histoctopus zipkasae* n. spp. The most distinctive morphological feature of this new genus is extreme web margin development along the length of the arms, widening towards the distal tips. Of all benthic octopuses, such web margin development only occurs in this new genus and three other distinct genera, *Graneledone*, *Pteroctopus* and *Velodona* (from comparable depths, typically >200 m). Due to significant morphological differences between these two genera and *Histoctopus*, we propose that the shared web margin development reflects convergence that is peculiar to a deeper-water habitat. The function of these web extensions remains unknown; they may aid in ensnaring or enveloping prey and/or provide lift while jet swimming off the seafloor.

INTRODUCTION

Over the past 30 years, slope and deep-water trawl surveys in the Australasian region by French and Australian researchers have been uncovering diverse and largely unknown assemblages of benthic organisms (Bouchet & Metivier, 1982; Richer de Forges, 1990; Richer de Forges, Koslow & Poore, 2000; Valdéz, 2001a, b; Valdéz & Gosliner, 2001). Amongst the material collected have been many new and distinctive benthic octopus taxa (Norman, Hochberg & Lu, 1997; Norman, Boucher & Hochberg, 2004; Norman, Hochberg & Boucher-Rodoni, 2004, 2005).

In Australia, trawl surveys by the Australian Commonwealth Scientific and Research Organization (CSIRO) between 1982 and 1989 at depths of 375–458 m on the Northwest Shelf off northern Western Australia collected a distinctive new mesobenthic octopus with extreme web margin development. Around the same time, repeated visits (1986, 1989, 2001) by French researchers to a seamount system, the Sponge Bank off New Caledonia, yielded a second species with similar web development from depths of 500 to 545 m. The mature males of this second species possess dramatically enlarged suckers.

In 2005, deployment of still and video camera equipment at depth off the Western Australian coast by the CSIRO captured images of live individuals of the new Australian species foraging over soft sediment and low-relief rocky areas at depths of 384 to 449 m.

On detailed examination, dissection and description, it was clear that these two species represented members of a new mesobenthic genus, described here as *Histoctopus* n. gen. The presence of an ink sac clearly distinguished this taxon from other deeper water genera that lack an ink sac, namely *Benthoctopus* Grimpe, 1921 and *Bathypolypus* Grimpe, 1921. The presence of two rows of suckers per arm clearly distinguished it from deep-water genera that possess a single row of suckers,

such as *Graneledone* Joubin, 1918, *Microeledone* Norman, Hochberg & Boucher-Rodoni, 2004, *Thaumeledone* Robson, 1930, *Bentheledone* Robson, 1932 and *Velodona* Chun, 1915. The closest morphological similarities are with the mesobenthic genera *Scaevargus* Troschel, 1857 and *Galeoctopus* Norman, Boucher & Hochberg, 2004.

Recent molecular studies indicate that the genus *Octopus* as it has historically been treated is paraphyletic (Guzik, Norman & Crozier, 2005; Strugnell *et al.*, 2005). It represents a catchall genus encompassing diverse and unrelated groups. As a consequence, the genus has recently been restricted to *Octopus sensu stricto*, containing the type species, *Octopus vulgaris* Cuvier, 1797, and members of the 'Octopus vulgaris species group' (see Norman & Hochberg, 2005). Distinct subgenera and species groups within the family Octopodidae that had previously been placed in the genus *Octopus* are now being reevaluated, with a number being raised to generic rank (i.e. Huffard & Hochberg, 2005 for *Amphioctopus*; Norman & Hochberg, 2005a for *Abdopus*; Norman & Hochberg, 2005b for *Thaumoctopus*; Hochberg, Norman & Finn, 2006 for *Wunderpus*).

MATERIAL AND METHODS

Indian Ocean specimens examined in this study originated from CSIRO benthic trawl surveys by the FRV *Soela* in 1982 and 1984 and from observers on board commercial fishing vessels (FV *Courageous*, *Striker* and *Surefire*) in 1988 and 1989. Still images of live octopuses were obtained by CSIRO on board the FRV *Southern Surveyor* in 2005, using headrope still and video cameras.

Pacific Ocean material examined in this study resulted from research campaigns off New Caledonia and the Coral Sea: CHALCAL 2, 1986; SMIB 4, 1989; NORFOLK 1, 2001. Three gear types were used in capture of this species: Waren dredge, ('Drague Waren', station code: DW), Fish trawl ('chalut à perche', station code: CP) and shrimp trawl ('chalut à panneaux [crevettes]', station code: CC).

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Table 1. Comparison of slope and deep-water genera that possess an ink sac with *Octopus s.s.* (Octopodidae).

	<i>Octopus s.s.</i> Cuvier, 1797	<i>Histoctopus</i> n. gen.	<i>Scaevurgus</i> Troschel, 1857	<i>Pteroctopus</i> Fisher, 1882	<i>Galeoctopus</i> Norman <i>et al.</i> , 2004	<i>Velodona</i> Chun, 1915
Source	Unpubl. data	This study	Norman <i>et al.</i> (2005)	Norman <i>et al.</i> (1997) and unpubl. data	Norman <i>et al.</i> (2004)	Unpubl. data
Number of species	10 +	2	6 +	2	1	1
Max mantle length (ML) in mm	250	107	90	130	37	150
Number of sucker rows	2	2	2	2	2	1
Hectocotylyzed arm side	Right	Right	Left	Left or right	Right	Right
Arm length (× ML)	3–6	2.4–3.7	2–3.3	2.8–3.8	2.7–4.4	3–4.5
Arm formula	3 = 2 > 4 > 1	4 = 3 = 2 > 1	3 = 2 > 4 > 1	Subequal	4 = 3 = 2 > 1	1 > 2 > 3 > 4
Gill lamellae count	6–11	8–9	8–13	8–10	10–11	9–11
Flared distal webs	Absent	Present	Absent	Present	Absent	Present
Stylet mineralization*	Absent	Present	Present	Absent	Absent	Absent
Pallial aperture (% circumference)	Wide (c. 50%)	Wide (c. 50%)	Wide (c. 50%)	Narrow (<40%)	Wide (c. 50%)	Wide (c. 50%)
Funnel Organ shape	W	W	W	V V	W	V V
Enlarged suckers on arms of males	Arms 2–3 +	All arms	Arms 2–3 +	Absent	Absent	Absent
Ligula shape	Triangular to spoon-shaped with open groove	Spoon- to leaf-shaped with open groove	Double-peanut shaped, deep groove	Broad, conical with open groove	Barrel-shaped with transverse lug-lined pit as ligula groove	Elongate triangular with open groove and thick margins
Ligula length(% HAL)	typically <3%**	4.5–8	5–14	5–11	11–20	6–9
Calamus length (% of ligula length)	15–60	40–60	20–70	30–45	55–75	30–34
Terminal shape	Linear	T-shaped	Linear	Linear	6-shaped	6-shaped
Terminal organ diverticulum size	Small	Large	Small	Small	Moderate	Moderate
Spermatophore length (× ML)	0.3–0.8	0.9–1.6	1.2–1.6	0.5–0.9	0.7–1.2	0.8–1.1
Sperm cord	Single	Plaited double	Plaited double	Single	Single	Single
Lateral ridge	Absent	Absent	Present	Absent	Present	Absent

HAL, hectocotylyzed arm length. *Mineralization often dissolves in unbuffered preservation, presence indicates detection in at least some specimens. **4.5 % in a single member species, *O. tehuelchus*.

Type material for the new species described here is lodged in the cephalopod collections of Museum Victoria (MV), Melbourne, Australia and the Muséum national d'Histoire naturelle (MNHN), Paris.

Morphological characters and measurements used in the descriptions below follow Roper & Voss (1983) and Norman & Sweeney (1997). Where sufficient specimens exist, ranges are presented as 'minimum–mean–maximum'. Diagnoses and descriptions presented here are based on submature and mature specimens. Data for juvenile material are not included here as counts and relative measurements [such as sucker counts and arm lengths *vs* mantle length (ML)] undergo considerable ontogenetic change in the early growth stages of octopuses and can cause overlap in otherwise valid diagnostic characters.

SYSTEMATIC DESCRIPTIONS

Family Octopodidae d'Orbigny, 1840

Histoctopus new genus

Type species: Histoctopus zipkasae n. gen., n. sp.

Etymology: From the Greek 'histos' for web or tissue, referring to the wide and flared web margins characteristic of members of this new genus.

Diagnosis: Small to medium-size mesobenthic species. Mantle muscular, globose to rounded ovoid. Stylets present, long, chitinous (mineralized). Arms: muscular, medium length, 2.5–3.8 times ML; approximately equal in length, lateral arms slightly shorter (typically $2 > 3 > 4 > 1$ or $3 > 2 > 4 > 1$). Arm autotomy at distinct plane absent. Web: moderate to deep, deepest around 20–30% of longest arm; approximately equal in depth, slightly deeper on lateral arms (typically $B = C = D = E = A$). Web margins on ventral arms very wide, form loose semi-transparent membranes in preserved material. Interbranchial web pouches absent. Suckers in two rows. Enlarged suckers present on all arms in mature males. Funnel organ W-shaped. Gills with eight to nine lamellae per demibranch. Radula with nine elements, seven rows of teeth plus marginal plates. Rhachidian tooth with two to three lateral cusps in asymmetrical seriation. Posterior salivary glands moderate to large, approximately equal in length with buccal mass. Distinct crop present as side-branch off oesophagus. Ink sac and anal flaps present. Third right arm of male hectocotylized, 75–85% length of opposite arm. Ligula of moderate size, 4.5–8% of hectocotylized arm length, triangular to spoon-shaped with open groove and lacking raised transverse laminae. Calamus large and pronounced, *c.* 40–60% of ligula length. Terminal organ (penis) large and T-shaped with diverticulum longer than distal portion. Spermatophores large (equal to or longer than ML), bulbous with swollen short sperm reservoir containing few coils (<10) of sperm cord coiled in a double strand. Distal tip of spermatophore storage sac with reticulate glandular tissue. Eggs (where known) of moderate size (6.5–8 mm, 7–9% of ML). Colour patterns orange brown dorsally, cream ventrally. Transverse rows of small white papillae/leucophores visible on dorsal mantle in live animal and in some preserved material. False eye-spots (ocelli) absent. Skin sculptured with evenly spaced small rounded papillae. Skin ridge around lateral margin of mantle absent.

Taxonomic remarks: *Histoctopus* n. gen. is discriminated from other octopodid genera that possess an ink sac in Table 1. The genus *Octopus* s.s. Cuvier, 1797 is clearly distinguished by the absence of extreme web margin development (*vs* present in *Histoctopus*), a small ligula (*c.* <3 *vs* 4.5–8%), a simple linear terminal organ with small diverticulum (*vs* a T-shaped terminal organ with large diverticulum), absence of a distinct

swollen glandular organ on the proximal spermatophore storage sac (*vs* present), and small, almost linear spermatophores with a singly coiled sperm cord (*vs* large bulbous spermatophores with a double-plaited sperm cord in *Histoctopus*).

The glandular organ on the spermatophore storage sac is reported for the first time. It is possible that this tissue produces some form of lubricant to aid the transmission of the large bulbous spermatophores.

Flared distal web margins occur in three other deeper-water octopodid genera, *Velodona* Chun, 1915, *Graeledone* Joubin, 1918 and *Pteroctopus* Fisher, 1882. The genera *Velodona* and *Graeledone* are easily distinguished from *Histoctopus* by the possession of only a single row of suckers. The genus *Pteroctopus* is also easily distinguished by its semi-gelatinous skin (*vs* muscular in *Histoctopus*), very narrow mantle opening (<40% of mantle circumference *vs c.* 50%), narrow-limbed VV funnel organ (*vs* a broad-limbed W) and paired elongate supraocular papillae over each eye (*vs* absent). At least one *Pteroctopus* species also has left-handed hectocotylyzation (*vs* right in *Histoctopus*).

The genus *Histoctopus* shares certain morphological characters with the mesobenthic octopus genera *Scaevargus* Troschel, 1857 and *Galeoctopus* Norman, Boucher & Hochberg, 2004.

Histoctopus and *Scaevargus* possess large (and typically mineralized) stylets and a double-plaited sperm cord. Males of *Scaevargus* are easily distinguished by left-handed hectocotylyzation (*vs* right-handed in *Histoctopus*), a bulbous peanut-shaped ligula with deep ligula groove (compared with an open

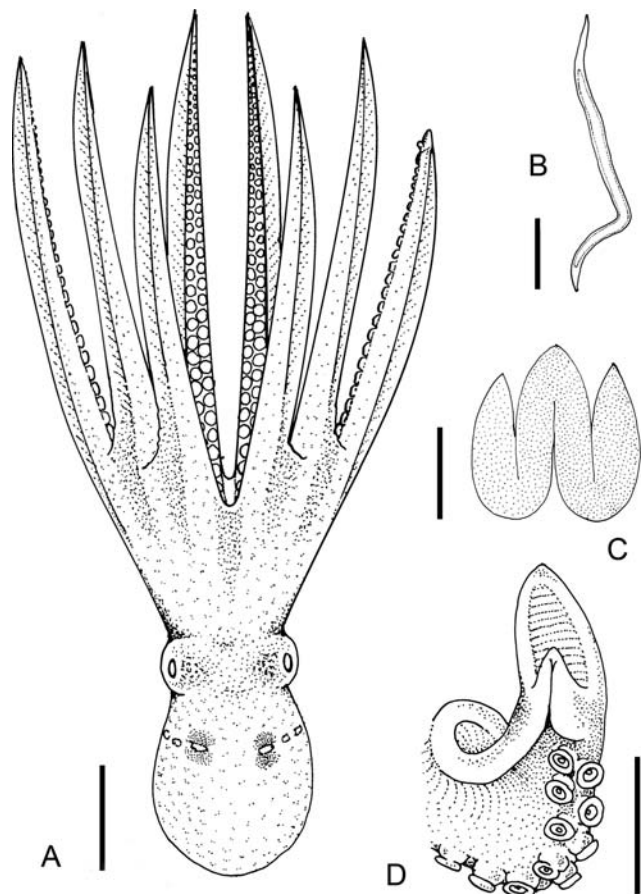


Figure 1. *Histoctopus discus* n. gen., n. sp. **A.** Dorsal whole animal, 41.2 mm ML male paratype (MNHN 2109). **B.** Stylet, 44.4 mm ML paratype (MNHN 2108). **C.** Funnel organ, 46.7 mm ML paratype (MNHN 2109). **D.** Ligula, 46.7 mm ML paratype (MNHN 2109). Scale bars: **A** = 20 mm; **B** = 10 mm; **C** = 5 mm; **D** = 5 mm.

triangular to spoon-shaped ligula), and possession of a lateral mantle ridge (*vs* absent in *Histoctopus*).

Histoctopus and *Galeoctopus* share similar arm lengths, arm formulae and spermatophore lengths (relative to ML); however, they differ in that *Galeoctopus* lacks flared web margins, enlarged suckers, and a glandular organ on the tip of the spermatophore storage sac. It also possesses a significantly shorter hectocotylied arm (*c.* 40–60% of opposite arm length *vs c.* 80% in *Histoctopus*), a lateral mantle skin ridge and a unique large, barrel-shaped ligula (11–20% of arm length) with a deep transverse ligula groove, the floor of which contains paired raised papillae. The spermatophores of *Galeoctopus* are narrow with singly coiled sperm cord in 50–90 coils (*vs* bulbous with <10 doubly coiled sperm cord whorls).

In general, body form, skin patterns and sculpture, the genus *Histoctopus* is similar to *Scaevurgus* and *Galeoctopus*. The origins of (and phylogenetic relationships among) these taxa remain unknown and await thorough molecular and biogeographic analyses.

Histoctopus discus new species (Figs 1–4)

Type Material: Holotype: New Caledonia South: M: 51.5 mm ML, MNHN 3803, Norfolk Ridge, Sponge Bank, N/O 'Alis', Campagne NORFOLK 1, stn CP1687, 24°54'S, 168°22'E, 539–545 m, coll. Lozouet, Boisselier and Richer-IRD, 23 June 2001. Paratypes: New Caledonia South: 1M: 44.4 mm ML, MNHN 2108, Sponge Bank, N/O 'Coriolis', CHALCAL 2, stn. CC1, 24°55'S, 168°22'E, 500 m, coll. Bouchet, Metivier and Richer de Forges, 28 Oct 1986. 2M: 46.7, 41.2 mm ML, MNHN 2109, Sponge Bank, N/O 'Alis', Campagne SMIB 4, stn. DW34, 24°55'S, 168°22'E, 510–515 m, coll. ORSTOM, 7 March 1989.

Etymology: Latin for disk or circular plate, referring to the enlarged plate-like suckers found in mature males of this species.

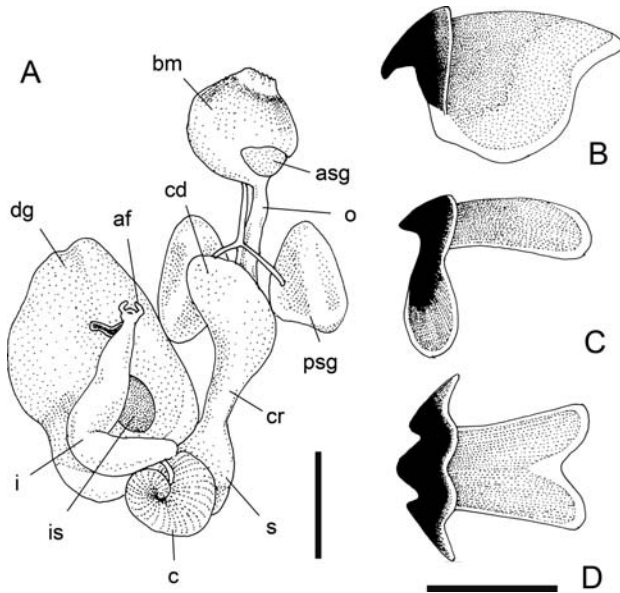


Figure 2. *Histoctopus discus* n. gen., n. sp. **A–E.** Digestive components of 46.7 mm ML male (MNHN 2109). **A.** Digestive tract. Abbreviations: af, anal flaps; asg, anterior salivary gland; bm, buccal mass; c, caecum; cd, crop diverticulum; cr, crop; dg, digestive gland; i, intestine; is, ink sac; o, oesophagus; psg, posterior salivary gland; s, stomach. **B.** Lateral view of upper beak. **C.** Lateral view of lower beak. **D.** Ventral view of lower beak. Scale bars: **A** = 10 mm; **B–D** = 5 mm.

Diagnosis: Small to moderate-sized species, ML to at least 51 mm. Arm lengths approximately three times ML (longest 2.8–3.5 × ML). Arms approximately equal in length, dorsal arms slightly shorter. Web sectors very thin and membranous, deep, up to 30% of longest arm length. Webs approximately equal in depth, lateral webs slightly deeper. Webs extend as membranous flared margins along entire length of all arms (including hectocotylied arm), very well developed in distal 25% of arm length with arm tips free. Suckers forming two rows. Suckers to around 145 on normal arms. Hectocotylied arm with 72–79 suckers. Three to five extremely enlarged and flattened suckers present on all arms of mature males, diameter up to 21% of ML at level of 6th to 10th proximal sucker. Large W-shaped funnel organ. Eight and nine gill lamellae per demibranch. Ink sac and anal flaps present. Third right arm hectocotylied. Ligula small to moderate (5.6 and 8.0% of arm length in two intact mature males), spoon to leaf-shaped with wide, open groove, floor with around 10–12 simple transverse creases. Calamus large and prominent, around 50% of ligula length (44.4–59.7%). Spermatophores large (1.2–1.6 × ML), few (1–4 in three mature males). Females unknown. Colour pattern: Orange brown dorsally, cream ventrally, four darker brown patches as two pairs on anterior dorsal mantle separated by strip of cream-coloured papillae. Skin sculpture: Small, round papillae uniformly scattered on all dorsal surfaces; slightly larger papilla present on posterior tip of mantle. Larger supraocular papillae absent. Lateral mantle ridge absent.

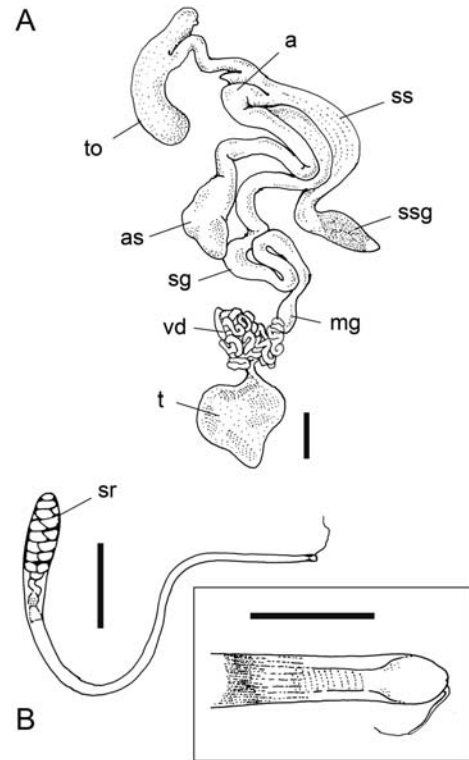


Figure 3. *Histoctopus discus* n. gen., n. sp. **A, B.** Male reproductive system of 44.4 mm ML paratype (MNHN 2108). **A.** Reproductive tract. Abbreviations: a, appendix; as, accessory spermatophoric gland; mg, mucilaginous gland; sg, spermatophoric gland; ss, spermatophore storage sac; ssg, spermatophore sac gland; t, testes; to, terminal organ; vd, vas deferens. **B.** Spermatophore. Inset: oral cap end of spermatophore. Abbreviation: sr, sperm reservoir. Scale bars: **A** = 10 mm; **B** = 10 mm (inset 2 mm).

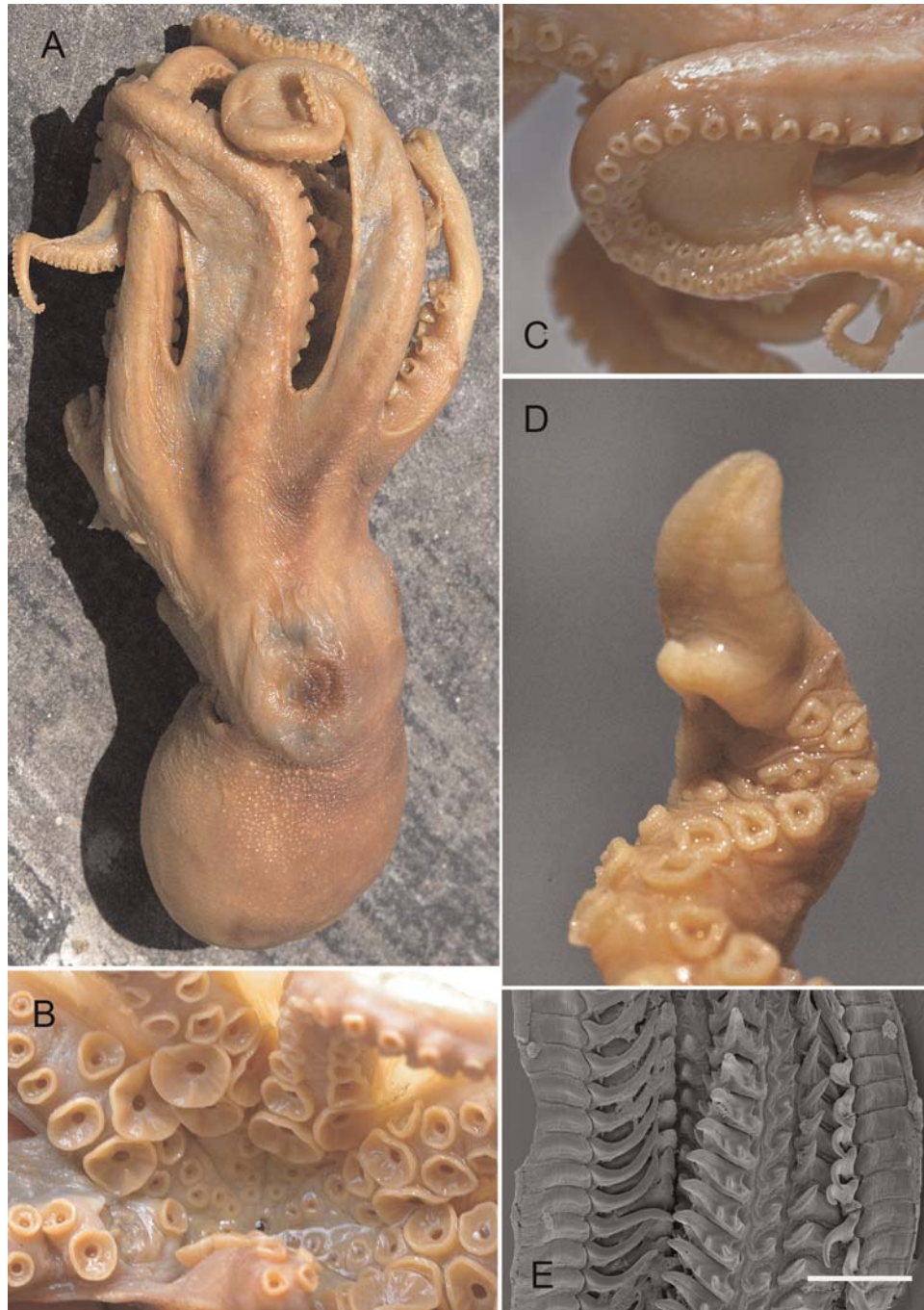


Figure 4. *Histoctopus discus* n. gen., n. sp. **A.** Left dorso-lateral view of whole animal, 46.7 mm ML male paratype (MNHN 2109). **B.** Enlarged suckers of 44.4 mm ML male paratype (MNHN 2108). **C.** Close-up of web margins on arms 2 and 3, 46.7 mm ML male paratype (MNHN 2109). **D.** Hectocotylus of 51.5 mm ML male holotype (MNHN 3803). **E.** Radula from 46.7 mm ML male paratype (MNHN 2109). Scale bar **E** = 0.5 mm. (This figure appears in colour in the online version of *Journal of Molluscan Studies*.)

Description: Counts and measurements are presented in Table 2. The following description is based on four males (three mature and one late submature).

Medium-size muscular species (Figs 1A, 4A); ML to at least 51.1 mm, total length to at least 238 mm; weight to at least 96 g. Mantle ovoid to pear-shaped, longer than wide (width 76.0–83.0–91.2% of ML). Head wide (60.4–63.8–70.7% of ML; 72.6–76.9–79.4% of mantle width). Skin firm, sculptured and pigmented. Eyes large. Stylets: large, robust, mineralized rods (Fig. 1B), length around 40% of ML (20 mm in 51.1 and

44.4 mm ML males, MNHN 3803 and 2108). Mantle opening wide, *c.* 50% of circumference of body at level of opening. Funnel: moderate length, *c.* 40% of ML (38.2–39.5–46.2% of ML), free portion moderate to long, *c.* 40–50% of funnel length (31.1–38.6–44.7%). Funnel organ: W-shaped (Fig. 1C), lateral limbs slightly shorter than (or equal to) median ones (lateral limbs 73.7–84.7–100.0% of median limbs); occupies *c.* 60% (49.7–57.3–63.4%) of funnel length.

Arms: moderate length, around 3 times ML (2.8–3.5 times ML); moderately robust, sub-cylindrical along length, tapering

Table 2. *Histoctopus discus* n. gen., n. sp.: counts and measurements (mm).

Repository	MNHN	MNHN	MNHN	MNHN
Catalogue number	3803	2108	2109	2109
Status	Holotype	Paratype	Paratype	Paratype
Sex	Male	Male	Male	Male
Maturity	Mature	Mature	Mature	Submature
Total length	238	210	171 +	170
Total wet weight (g)	95.7	75.1	49.1	39.4
Dorsal mantle length	51.1	44.4	46.7	41.2
Ventral mantle length	39.0	37.7	33.7	26.1
Mantle width	41.7	40.5	35.5	34.3
Head width	32.6	31.4	28.2	24.9
Funnel length	19.5	20.5	16.4	15.8
Free funnel length	8.7	7.0	5.1	7.7
Funnel organ length				
Lateral limb	9.7	10.4	7.3	7.5
Medial limb	9.7	13.0	9.9	8.8
Web depths (L, R)				
A	25	19	25	18
B	32, 32	30, 25	30, d	24, 27
C	d, 37	36, 35	29, d	29, 34
D	38, 35SpG	36, 34SpG	d, d	35, 33SpG
E	31	31	D	25
Web depth formula	C = D > B = E > A	C = D > B = E > A		C = D > B = E > A
Arm lengths (L, R)				
1	152, 160	143, d	118, d	90, 102
2	175, 163	154, 154	116d?, d	114, 114
3	d (L)	d (L)	112 (L)	117 (L)
Hc (R)	127	113	d	99
4	161, 157	147, d	d, d	106, 115
Arm length formula	2 > 4 = 1 or subequal	2 > 4 > 1 or subequal	subequal	4 = 3 = 2 > 1
Arm width	9.5	8.5	7.4	6.4
Sucker diameter	8.3	9.3	7.4	4.5
Sucker counts (L, R)				
Hc	72	78	79	78
4	141, –	141, –	138, –	145, –
Gill count (outer/inner demibranch)	8/–, 9/–	c. 8–9, c. 8–9	9/9, 9/9	8/9, 9/9
Stylet length	20	20.1	–	–
Ligula length	7.1	9.0	6.2	3.8
Calamus length	3.2	4.0	3.7	2.5
Terminal organ length	39.5	29.5	D	Submature
Diverticulum length	30.6	16.7	D	Submature
Spermatophore count	3, 1TO	3, 1TO	1	Submature
Spermatophore length	69	69	54	Submature
Spermatophore width	3.7	3.8	3.2	Submature
Spermatophore reservoir length	14	20.2	15.8	Submature
Spermatophore cord whorls	c. 8	c. 7–8	c. 9	Submature

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; SpG, spermatophore groove; TO, terminal organ; +, arm tip missing; –, not measured.

evenly to fine tips. Arm autotomy at base of arms absent. Dorsal arms slightly shorter in material examined, remainder subequal. Suckers in two rows. Three to five extremely enlarged suckers on all arms in mature males (to around 15–20% of ML: 16.2–20.9% in three mature males), at level of sixth to tenth proximal suckers (Fig. 4B). Up to 145 suckers on intact arms (only known for males, 138–145).

Webs of moderate depth (deepest webs 21.7–29.9% of longest arm in intact males). Lateral webs slightly deeper than other sectors, web formula typically C = D > B = E > A. Webs margins well developed on all arms, widened as paddle-

like flares in distal quarter of normal arms, with extreme tips of arms free of web (Fig. 4C).

Third right arm of males hectocotylized. Modified arm relatively short, approximately 2.5 times ML (2.4–2.5 times ML in intact material) and 85% length of opposite arm in only male with both third arms undamaged. Ligula (Figs 1D, 4D) of small to moderate size (5.6 and 8.0% of arm length in two intact mature males), spoon to leaf-shaped with wide, open groove, floor with around 10–12 simple transverse creases. Calamus large and proud, around 50% of ligula length (44.4, 45.1, 59.7%). 72–79 suckers on hectocotylized arm.

Gills with 8–9 lamellae on both inner and outer demibranchs, plus terminal lamella.

Digestive tract (Fig. 2A): Anterior salivary glands of moderate size, *c.* 60% of length of buccal mass. Posterior salivary glands of moderate size, slightly larger than buccal mass (112% in 49.4 mm ML male, MNHN 2109), *c.* 50% of digestive gland length (49.2% in same specimen). Crop with distinct diverticulum. Stomach bipartite. Caecum coiled in single whorl, distinctly striated. Digestive gland roughly ovoid. Ink sac present, deeply embedded. Anal flaps present. Upper beak (Fig. 2B) with hooked rostrum and moderate hood (40.5% of upper beak length in same specimen). Lower beak with rounded rostrum, narrow hood and relatively parallel lateral walls separated in approximately posterior 15%, although pigmentation gives appearance of deeper fork (Fig. 2C, D). Radula with seven teeth and two marginal plates in each transverse row (Fig. 4E). Rhachidian tooth with two to three 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 reproductive tract (Fig. 3A): Terminal organ ('penis') in mature male very large, around two-thirds of ML (66.4 and 77.3% in two undamaged mature males), T-shaped with diverticulum longer than distal portion. Spermatophore storage sac with unique darkly pigmented large glandular mass on posterior tip, termed here the 'spermatophore storage gland' (SSG, Fig. 3). Spermatophores: (Fig. 3B) large, longer than ML (54–69 mm, 1.2, 1.4 and 1.6 times ML), few (1–4). Sperm reservoir: wide (4.9, 5.1, 5.3% of length) short, under one-third of spermatophore length (20.3, 29.3, 29.3%). Sperm cord: robust double strand of around seven to nine loose coils. Ejaculatory apparatus simple, without coils. Central section of ejaculatory apparatus with regular ridged coils, potentially armed with small teeth (not distinct in material examined).

Female material unknown.

Basal colour of preserved specimens typically orange brown dorsally and cream ventrally. Orange-brown colour over eyes with blue-black subdermal colour. Four darker brown patches on dorsal mantle behind head as pairs separated by strip of cream-coloured papillae (Fig. 1A). Aboral web sectors A, B and C dark red brown, darker colour not extending onto aboral arms or lateral web extensions. Small dark chromatophores evenly scattered amongst papillae over all dorsal surfaces. Small founder chromatophores widely scattered on anterior half of ventral mantle.

Skin sculptured with evenly spaced, small rounded papillae forming low granular texture over all surfaces (Fig. 4A). No enlarged papillae evident over eyes. Single, slightly larger papilla on posterior tip of mantle, often white in colour. Papillae texture pronounced above eyes. Lateral ridge absent.

Skin colour and sculpture of live animal unknown.

Life history: Nothing is known of the biology of this species. The extreme sucker enlargement found in this species suggests some special use in courtship behaviour (see Discussion).

Distribution: Southwest Pacific Ocean; only known from Sponge Bank, Norfolk Ridge, south of New Caledonia. Collected at depths of 500 to 545 m.

Remarks: See below.

***Histoctopus zipkasae* new species**

(Figs 5–8)

Type material: Holotype: Western Australia, Northwest Shelf: 1M: 61.6 mm ML, MV F164025, FRV 'Soela', SO1/84/18, 18°44'S, 117°00'E, 404 m, coll. CSIRO, 30 Jan 1984. Paratypes: Western Australia, Northwest Shelf: 1M, 54.6 mm

ML, MV F164024, FV *Surefire*, SF1/88/02, 18°25'S, 117°48'E, 375 m, 0700–1000 h, coll. CSIRO, 21 Aug 1988. 1M, 58.5, 2F, 36.5, 71.1 mm ML, MV F164034, FV *Surefire*, SF1/88, 17°45'S, 118°32'E, 420 m, 1000–1300 h, coll. CSIRO, 27 Aug 1988. 1M, 62.7 mm ML, MV F164031, FV *Courageous*, CR1/89/03, 18°33'S, 117°53'E, 380 m, 1305 h, coll. CSIRO, 8 Feb 1989. 1F: 69.4 mm ML, MV F164035, FRV *Soela*, SO1/84/12, 18°53'S, 116°10'E, 458 m, coll. CSIRO, 29 Jan 1984. 1M, 73.8 mm ML, MV F164020, FV *Striker*, shot 1, 16°59'S, 120°10'E, 411 m, 0200–0700 h, coll. Sue Morris, CSIRO, 3 Apr 1989. 2F, 89.3, 107.7 mm ML, MV F164036, FRV *Soela*, SO4/82, 18°01'S, 118°23'E, 376 m, 2030 h, coll. CSIRO, 1 Aug 1982.

Other material examined: Western Australia, Northwest Shelf: 1F, 53.7 mm ML, MV F164033, FV *Surefire*, SF1/88/02, 18°25'S, 117°48'E, 375 m, 0700–1000 h, coll. CSIRO, 21 Aug 1988. 1F, 70.8 mm ML, MV F164082, FV *Surefire*, SF1/88, 18°36'S, 117°20'E, 425 m, 1215–1515 h, coll. CSIRO, 20 Aug 1988. 1F, 72.0, mm ML, MV F164032, FV *Surefire*, SF1/88, 18°35.8'S, 117°20'E, 428 m, 1700–2000 h, coll. CSIRO, 20 Aug 1988.

Remote video still images: Western Australia: Off Kalbarri, 27°56.58'S, 113°05.18'E, RV *Southern Surveyor*, SS07/2005/96, 424 m, 01:27 h, image coll. CSIRO, 30 July 2005, data ID: 45922. Off Abrolhos Islands, 29°01.23'S, 113°47.32'E, RV *Southern Surveyor*, SS07/2005/107, 384 m, 06:46 h, image coll. CSIRO, 31 July 2005, data ID: 56337. Off Abrolhos Islands, 29°01.35'S, 113°47.31'E, RV *Southern Surveyor*, SS07/2005/107,

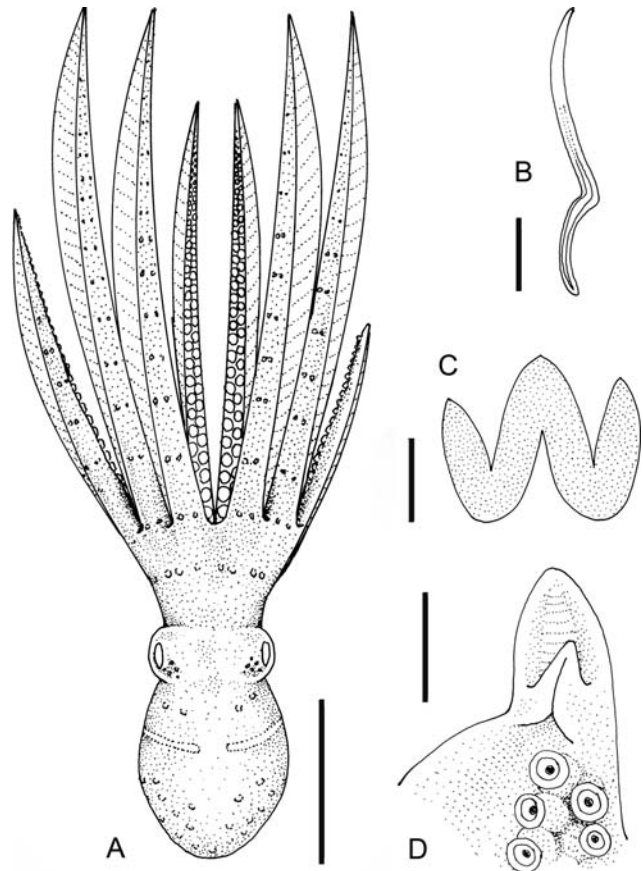


Figure 5. *Histoctopus zipkasae* n. gen., n. sp. **A–D.** 61.6 mm ML male holotype (MV F164025). **A.** Dorsal whole animal. **B.** Stylet. **C.** Funnel organ. **D.** Ligula. Scale bars: **A** = 50 mm; **B–D** = 5 mm.

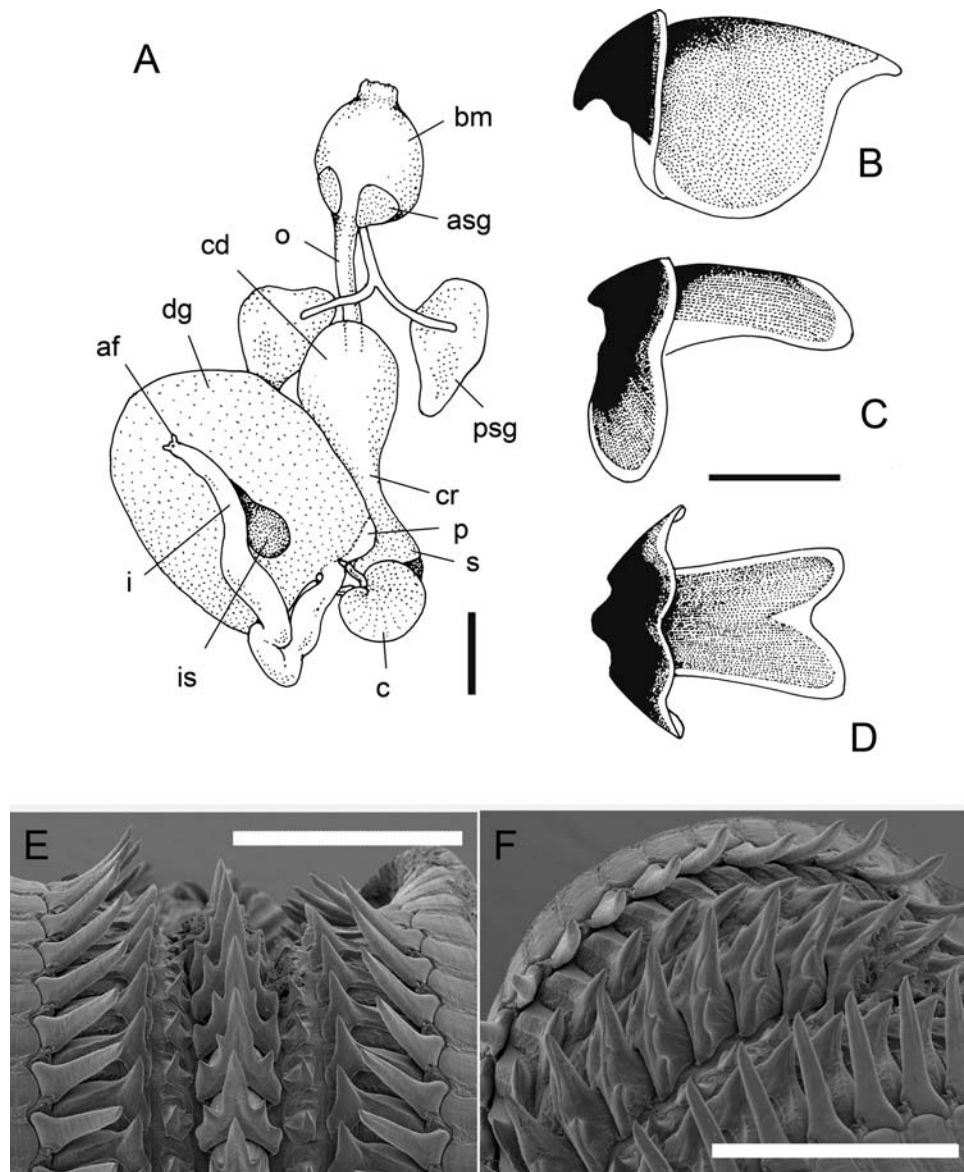


Figure 6. *Histioctopus zipkasae* n. gen., n. sp. **A–F.** Digestive components of 62.7 mm ML male (MV F164031). **A.** Digestive tract. Abbreviations as in Figure 2 plus p, pancreatic tissue. **B.** Lateral view of upper beak. **C.** Lateral view of lower beak. **D.** Ventral view of lower beak. **E., F.** Radula. Scale bars: **A** = 10 mm; **B–D** = 5 mm; **E, F** = 1 mm.

415 m, 06:51 h, image coll. CSIRO, 31 July 2005, data ID: 56629. Off Jurien Bay, 29°50.88'S, 114°22.02'E RV *Southern Surveyor*, SS07/2005/125, 401 m, 02:15 h, image coll. CSIRO, 2 Aug 2005, data ID: 67222. Perth Canyon, 32°00.19S, 115°11.29'E, RV *Southern Surveyor*, SS07/2005/217, 449 m, 00:47 h, image coll. CSIRO, 2 Aug 2005, data ID: 120359.

Etymology: *zipkasae*, after the senior author's wonderful wife, Karen Zipkas.

Diagnosis: Medium-sized species, ML to at least 107 mm. Arm lengths approximately three times ML (longest 2.4–3.7 × ML). Arms approximately equal in length, dorsal arms slightly shorter. Web sectors very thin and membranous, deep, up to 30% of longest arm length. Webs approximately equal in depth, lateral webs slightly deeper. Webs extend as membranous flared margins along entire length of arms, very well developed towards arm tips. Suckers forming two rows. Sucker counts to around 168 on normal arms. Hectocotylized arm

with 66–68 suckers. Two to three slightly to moderately enlarged and flattened suckers present on all arms of mature males, diameter up to 15% of ML at level of 7th to 13th proximal sucker. Large W-shaped funnel organ. Gill count nine lamellae per demibranch. Ink sac and anal flaps present. Third right arm hectocotylized. Ligula small to moderate size (4.5–6.2% of arm length), spoon-shaped with robust rims and wide, open groove, floor with around 10–12 simple transverse creases. Calamus large and prominent, 34.7–59.7%. Spermatophores large (0.9–1.1 × ML) and few (3–8). Distal oviducts thickened along length. Eggs of moderate size (6.5–7.8 mm, 7.2–9.1% ML). Colour pattern: Pink orange dorsally, cream ventrally. Orange-brown basal colour on first three arm pairs. Two transverse rows of small white spots on dorsal mantle. Regularly spaced white spots present along aboral midline of first three arm pairs. Skin sculpture: Small, round papillae uniformly scattered on all dorsal surfaces; larger supraocular papillae absent. Lateral mantle ridge absent.

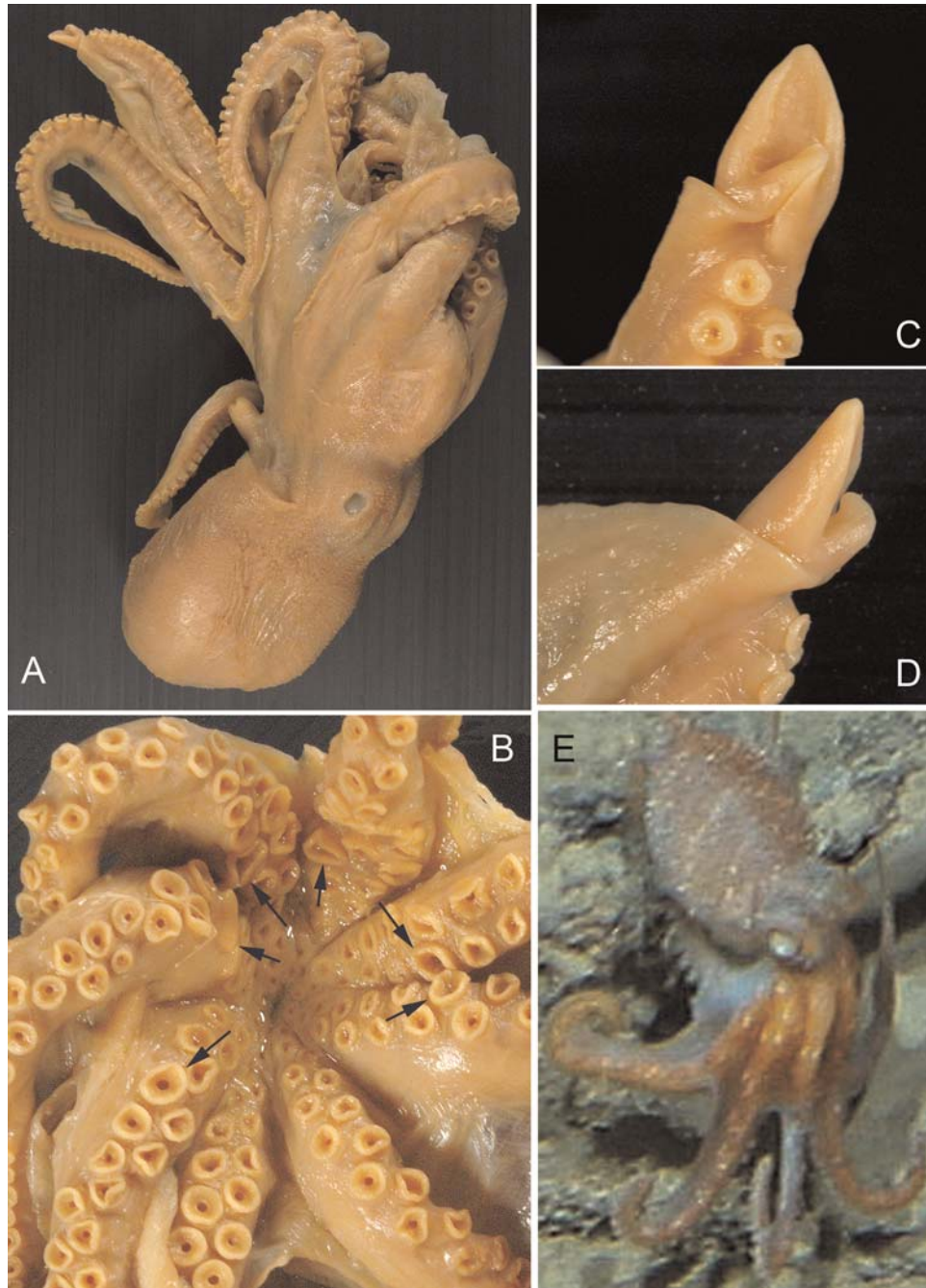


Figure 8. *Histioctopus zipkasae* n. gen., n. sp. **A–D.** 61.6 mm ML male holotype (MV F164025). **A.** Left lateral view of whole animal. **B.** Oral view of arm crown showing slightly enlarged suckers (arrows). **C, D.** Hectocotylus. **E.** Live animal image from CSIRO tow camera, 401 m, off Jurien Bay, Western Australia, photo: B. Barker, CSIRO.

Distribution: Indian Ocean, off Western Australia from Perth Canyon to Northwest Shelf (Fig. 9), trawled at depths of 375–458 m. Video records from 384–449 m.

Remarks: *Histioctopus zipkasae* is distinguished from *Histioctopus discus* in that it is larger (to 107 mm *vs* 51 mm in *H. discus*), has higher sucker counts on the normal arms (149–168 *vs* 138–145) yet lower sucker counts on the hectocotylyzed arm (66–68 *vs* 72–79), shorter hectocotylyzed arm relative to ML (1.7–1.9 \times ML *vs* 2.4–2.5), smaller enlarged suckers (to 15 *vs* to 20%), and smaller spermatophores relative to ML (0.9–1.1 \times ML *vs* 1.2–1.6). See summary in Table 5.

DISCUSSION

The new genus and its two new species described here were collected on the continental slope and seamounts at depths of between 375 and 545 m. Of all the benthic octopuses in the world, the distinctive form of flared distal web margins found in *Histioctopus* species is reported in only three other octopus genera, *Velodona* (Fig. 10A), *Pteroctopus* (Fig. 10B–D) and *Graneledone* (*G. antarctica* in Vecchione, Allcock & Piatkowski, 2005). The first two taxa occur in comparable depths to *Histioctopus*, typically 200–750 m. The third occurs to depths of more than 2000 m (Voss, 1976). The function of these distal

Table 3. *Histioctopus zipkasae* n. gen., n. sp.: counts and measurements (mm) of male material.

Repository	MV	MV	MV	MV	MV
Catalogue number	F164025	F164020	F164031	F164024	F164034
Status	Holotype	Paratype	Paratype	Paratype	Paratype
Maturity	Mature	Mature	Mature	Mature	Mature
Total length	278	291	d	265	272
Total wet weight (g)	136	89	83	60	79
Dorsal mantle length	61.6	73.8	62.7	54.6	58.5
Ventral mantle length	50.2	58.5	51.0	50.6	52.2
Mantle width	47.8	46.8	39.7	d	42.6
Head width	32.9	26.6	29.9	d	30.4
Funnel length	22.0	25.3	23.8	d	20.7
Free funnel length	7.2	11.1	5.4	d	6.5
Funnel organ length					
lateral limb	9.2	InD	InD	d	InD
medial limb	10.3	InD	InD	d	InD
Web depths (L, R)					
A	25	28	d	34	d
B	d, d	39, 39	d, d	d, 35	d, d
C	38, d	39, 43	d, d	d, 32	33, d
D	43, d	d, 38SpG	d, d	30, d	35, 31
E	30	33	d	30	29
Web depth formula	D > B > E > A	C = B > E > A	d	d	E > D > C
Arm lengths (L, R)					
1	d, 196	164, d	d, d	196, 197	d, d
2	168, 200	188, 198	d, d	200, d	d, d
3	138 (L)	d (L)	d (L)	148 (L)	d (L)
Hc (R)	118	123	117	106	d
4	178, 186	171, 172	d, d	169, 160	d, 193
Arm length formula	2 = 1 > 4 > 3?	2 > 4 > 1	d	1 = 2 > 4 > 3	d
Arm width	10.0	8.6	8.7	7.8	9.4
Sucker diameter	7.2	7.0	5.0	4.3	8.8
Sucker counts (L, R)					
1	–	–	–	–	–
2	–, 157	–	–	152, –	–
3	–	–	–	–	–
Hc	68	67	67	66	d
4	–	–, c. 150	–	–	–, 149
Gill count (outer/inner demibranch)	9/9, 9/9	c. 9, c. 9	c. 9, c. 9	9/? , 9/?	c. 9, c. 9
Stylet length	20.4	21.2	21.2	19.6	21.1
Ligula length	8.5	7.2	7.2	4.8	D
Calamus length	5.0	2.5	4.3	2.3	D
Terminal organ length	28.4	39.2	d	33.3	30.7
Diverticulum length	19.0	–	d	d	D
Spermatophore count	5, 1TO	4, 1TO	2, 1TO	2, 1TO	7, 1TO
Spermatophore length	c. 70	68	d	d	58
Spermatophore width	3.4	3.5	d	3.0	3.1
Spermatophore reservoir length	c. 20	14	d	d	13.2
Spermatophore cord whorls	D	~6	d	d	c. 5 +

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; SpG, spermatophore groove; TO, terminal organ; –, not measured.

web margin expansions is unknown but may be associated with feeding and/or locomotion.

Many shallow-water octopuses use proximal web sectors to ensnare prey by enveloping boulders or small coral heads and using the arm tips to flush prey into the webs and waiting suckers. *Octopus cyanea* and *Octopus maorum* use such techniques (Norman, 2000). Similar techniques are used by other octopus species to capture small prey (i.e. *Wunderpus photogenicus*,

Hochberg *et al.*, 2006; *Vulcanoctopus hydrothermalis*, Voight, 2005). The flared distal web margins with free distal arm tips in *Histioctopus*, *Velodona* and *Pteroctopus* may be used to forage for and snare prey while extending the arms over areas of soft sediment.

An alternative hypothesis is that the extreme web development in these three mid-depth genera relates to swimming behaviour. These flared webs may provide lift to the arms

Table 4. *Histoctopus zipkasae* n. gen., n. sp.: counts and measurements (mm) of female material.

Repository	MV	MV	MV	MV	MV
Catalogue number	F164036	F164036	F164034	F164028	F164035
Status	Paratype	Paratype	Paratype	–	Paratype
Maturity	Gravid	Gravid	Gravid	Submature	Submature
Total length	383	386	310	347	240
Total wet weight (g)	243	206	132	133	114
Dorsal mantle length	107.7	89.3	71.1	70.8	69.4
Ventral mantle length	86.9	74.0	59.8	55.2	58.3
Mantle width	62.8	58.0	47.8	50.1	48.3
Head width	38.6	40.2	30.1	34.1	37.5
Funnel length	34.0	34.5	25.9	d	23.6
Free funnel length	11.5	17.4	11.5	d	5.5
Funnel organ length					
Lateral limb	InD	InD	InD	InD	11.2
Medial limb	InD	InD	InD	InD	13.3
Web depths (L, R)					
A	42	36	30	30	28
B	d, d	57, 59	34, 39	35, 45	32, 47
C	d, 53	57, 62	45, 47	39, 45	48, 48
D	d, 50	57, d	d, d	39, 39	45, d
E	d	d	d	33	32
Web depth formula	C = D > A	B = C = D > A	C > B > A	B = C = D > E > A	B = C > D > E > A
Arm lengths (L, R)					
1	d, 258	214, 207	d, d	173, 178	153, d
2	225, 255	d, 274	222, d	220, 257	167, 157
3	225, d	233, 219	208, d	191, d	d, 150
4	205, 240	d, d	d, 215	237, 225	d, 167
Arm length formula	1 = 2 > 4 > 3	2 > 3 > 1	4 = 3 = 2	2 = 3 > 1	4 = 2 > 3 = 1
Arm width	11.2	11.1	9.5	11.3	10.8
Sucker diameter	4.3	5.5	5.3	5.6	4.8
Sucker counts (L, R)					
1	–	–	–	–	–
2	–	–	165, –	–, 160	168, –
3	164, –	–, c. 153	166, –	–	–
4	–	–	–	–	–
Gill count (outer/inner demibranch)	9/?, 9/?	InD, InD	9/9, 9/9	?/9, 9/?	9/?, 9/?
Stylet length	29.7	26.5	–	–	–
Egg length	7.8	6.5	6.5	Submature	Submature
Egg width	1.7	1.8	1.8	Submature	Submature

A–E, web sectors starting from dorsal sector; d, damaged/distorted; InD, indistinct; L, left; R, right; n/a, not applicable; –, not measured.

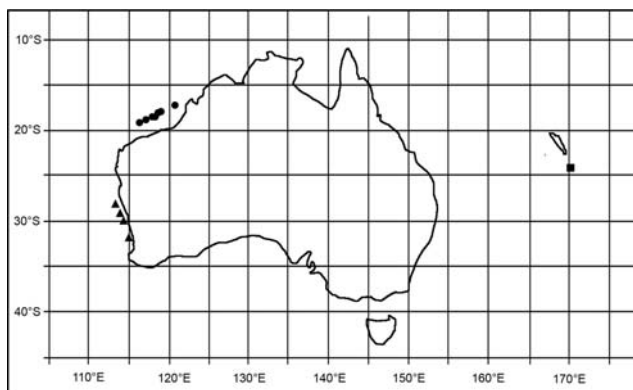


Figure 9. Known distribution for the genus *Histoctopus* n. gen. Symbols: circle, *H. zipkasae* material examined; triangle, *H. zipkasae* video records; square, *H. discus* material examined.

while jet swimming, potentially for energy efficient swimming. Until live observations are made of all three genera, these suggestions remain speculative.

Sucker enlargement found in mature males of *Histoctopus*, particularly the extreme enlargement in *H. discus*, is unusual. The presence of enlarged suckers only in males suggests a reproductive function for these modified suckers. Packard (1961) reported that enlarged suckers in mature males of the shallow-water species, *Octopus vulgaris*, were used for visual displays as a signal to females of state of maturity and cues for mating. With poor light penetration at depth (the two known members of *Histoctopus* occurring at 375–545 m), enlarged suckers are less likely to function as visual reproductive cues. Instead, these larger suckers may act as tactile [or even chemosensory, Voight (1991)] indicators of sexual identity and maturity.

The genus *Histoctopus* is described here based on two species from comparable depths in Western Australia and a seamount south of New Caledonia. Norman *et al.* (2005) reported

Table 5. Morphological comparison of new *Histioctopus* species.

	<i>H. discus</i>	<i>H. zipkasae</i>
Maximum size (mm ML)	51	107
Arm length (× ML)	2.8–3	2.4–3.7
Sucker count	138–145	149–168
Hectocotylyzed arm sucker count	72–79	66–68
Enlarged suckers on all arms of males	3–5, very large	2–3, slightly enlarged
Enlarged sucker size (% ML)	16–21	8–15
Hectocotylyzed arm length (× ML)	2.4–2.5	1.7–1.9
Ligula length (% HAL)	5.6, 8.0	4.5–6.2
Calamus length (% LL)	44–60	35–60
Spermatophore length	54–69	58–70
Spermatophore length (× ML)	1.2–1.6	0.9–1.1

ML, mantle length; HAL, hectocotylyzed arm length; LL, ligula length.

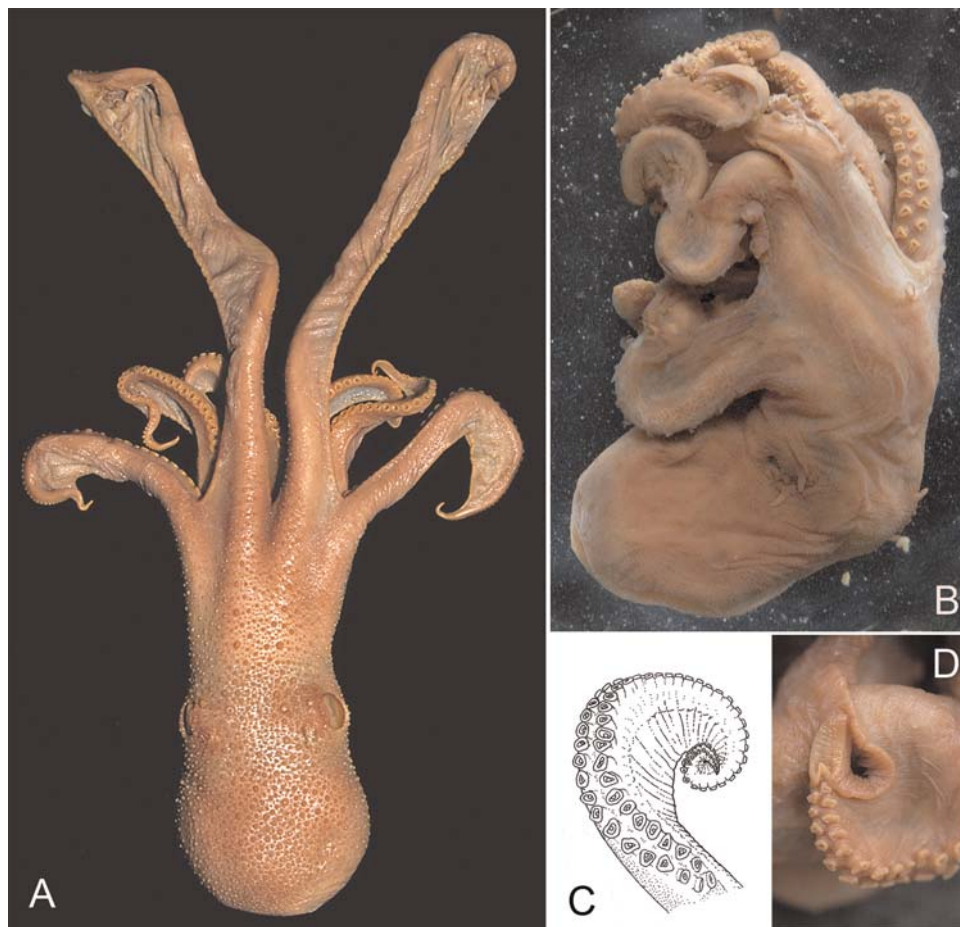


Figure 10. Other octopodid genera with flared distal web margins. **A.** *Velodona togata*, whole animal, South Africa Museum, Cape Town. **B–D.** *Pteroctopus* sp., Muséum National d’Histoire Naturelle, Paris, **B.** Whole animal. **C.** Distal arm tip. **D.** Hectocotylyzed arm. (This figure appears in colour in the online version of *Journal of Molluscan Studies*.)

regional endemism at parallel latitudes and depths for five species of the genus *Scaevargus* in the area surrounding New Caledonia [*Scaevargus* spp.: 19–25°S latitude, depth: 230–530 m; *Histioctopus* spp. 18–19°S (Western Australia), c. 25°S (New Caledonia), depth: 375–545 m]. Norman *et al.* (2005) also reported undescribed *Scaevargus* species from off the Western Australian coast. Biogeographic links between the Western Australian continental slope and New Caledonian

seamounts merit further investigation. It is possible that these taxa share palaeo-austral origins and affinities.

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