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Two new genera and species of sepioline squids (Cephalopoda: Sepiolidae) from Australia

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CHUNG CHENG LU^{1,2,*} AND TAKASHI OKUTANI³

- ¹ Museum Victoria, Melbourne, Victoria 3000, Australia
- ² Department of Life Sciences, National Chung Hsing University, Taichung, Taiwan 402
- ³ #714, Takaishi 4-17-1, Asao-ku, Kawasaki, Japan 215-0003
- * To whom correspondence should be addressed. Email: cclu@nchu.edu.tw

Abstract

Lu, C.C., and Okutani, T. 2022. Two new genera and species of sepioline squids (Cephalopoda: Sepiolidae) from Australia. *Memoirs of Museum Victoria* 81: 1–23.

Two new genera and species of sepioline squid (Cephalopoda: Sepiolidae) are described from Australian waters. *Dextrasepiola taenia* is characterised by having copulatory organs (i.e. the hectocotylised arm in the males and the bursa copulatrix in the females) in the right side of the body. All other known sepiolinids have copulatory organs in the left side of the body. *Amutatiola macroventosa* is characterised by the absence of a hectotylised arm in mature males; instead, it possesses many enormously enlarged suckers on some of the arms of the males. The bursa copulatrix is in the left side of the female body, as in other known sepioline squids. The discovery of these two new taxa indicates that the present definition of Sepiolinae needs to be broadened to accommodate these two new genera.

Keywords

Sepiolinae; Dextrasepiola taenia; Amutatiola macroventosa; Australia.

Introduction

Members of the family Sepiolidae are small to medium size benthic or pelagic cephalopods and are common in tropical, subtropical and temperate waters. Currently, 18 genera are recognised in the following three subfamilies: Heteroteuthinae: Heteroteuthis Gray, 1849, Stoloteuthis Verrill, 1881, Nectoteuthis Verrill, 1883, Iridoteuthis Naef, 1912, and Sepiolina Naef, 1912; (ii) Sepiolinae: Sepiola Leach, 1817, Inioteuthis Verrill, 1881, Euprymna Steenstrup, 1887, Rondeletiola Naef, 1921, Sepietta Naef, 1912, Adinaefiola Bello, 2020, Boletzkyola Bello, 2020, Lusepiola Bello, 2020, and Eumandya Bello, 2020; and (iii) Rossiinae: Rossia Owen, 1834, Semirossia Steenstrup, 1881, Austrorossia Berry, 1918, and Neorossia Boletzky, 1971. For Chonneteuthis Lu and Boucher-Rodoni, 2006, the subfamilial placement is uncertain (Bello, 2020; Lu and Boucher-Rodoni, 2006; Nesis 1987). The three subfamilies are well defined. Table 1 shows the diagnostic characters of these subfamilies.

A member of Sepiolinae was first recorded from Australia by Lu and Phillips (1985) and assigned to the old genus *Sepiola* without specific identification. A dorsal view of a specimen was also presented in Lu and Dunning (1998). The record was accidentally omitted in Lu (2001). In this paper, we describe two new sepioline species and placed them in two new genera

in light of Bello's (2020) revision. These new genera and species appear to belong to Sepiolinae based on the main characters of this subfamily, apart from their peculiar male arm modifications that do not correspond to the normal sepioline hectocotylisation.

Material and methods

All materials examined are listed under each relevant taxon. All except one lot are in the collection of the Museum of Victoria. The materials were all formalin fixed and preserved in 70% ethyl alcohol. All measurements and indices are standard teuthological measurements and indices, following Roper and Voss (1983) and Lu and Boucher-Rodoni (2006), except for nuchal commissure index, which is the width of nuchal commissure expressed as a percentage of the width of mantle at the position of nuchal commissure. Nuchal commissure width is called occipital band width by some authors (e.g. Nesis, 1982). Roper and Voss (1983) used the mantle length as the standard reference size for free funnel index and nuchal commissure index. For arm lengths, arm sucker counts and sucker diameters, left arms were measured or counted. In males, the right arm I was also measured and suckers and sucker stalks counted to ascertain if any modification occurs in right arm I. The maturity stages used in the Tables are those used in Lu and Roper (1979).

Table 1. Comparison of distinguishing characters of subfamilies Heteroteuthinae, Rossiinae and Sepiolinae of the family Sepiolidae (after Nesis, 1982)

	Heteroteuthinae	Rossiinae	Sepiolinae
Anterior ventral mantle edge	extended into projecting ventral shield covering funnel from below and sometimes reaching level of eyes or farther forward; ventral shield with an incision in centre for funnel opening	not extended forward, not covering funnel	not extended forward, not covering funnel
Anterior dorsal mantle edge	fused with head, except in Heteroteuthis	not fused with head	fused with head
Nuchal cartilage	developed in <i>Heteroteuthis</i> ; absent in other genera	developed	no nuchal cartilage
Arms connected by web	3 dorsal pairs of arms joined by deep web	2 dorsal pairs of arms not connected or connected only by shallow web	2 dorsal pairs of arms not connected or connected only by shallow web
Arm suckers	in 2 series; some suckers on lateral arms in males in some taxa greatly enlarged	in 2 or 4 series; no greatly enlarged suckers	in 2 or 4 series; some suckers in males maybe enlarged
Club	narrow or slightly widened, with very small suckers	narrow or widened, with very small, medium or large suckers	narrow or slightly widened, with small suckers
Fins	large, fin length 60–100% of mantle length	moderate size, much shorter than mantle	moderate size, much shorter than mantle
Photophores	on ventral side of ink sac	only one genus, <i>Semirossia</i> , is known to have a bilobed photophore on ink sac	saddle-shaped, two ear-shaped, lens-shaped or absent (<i>Inioteuthis</i>)
Hectocotylisation	usually both dorsal arms hectocotylised	left or both dorsal arms hectocotylised	left dorsal arm hectocotylised
Gladius	absent	present	rudimentary or absent
Habitat	benthic or pelagic	benthic, some species ascend to surface during reproduction	benthic, some species ascend to surface during reproduction

Abbreviations:

CSIRO: Commonwealth Scientific and Industry Research

Organisation of Australia

IYGPT: International Young Gadoid Pelagic Trawl MOV: Museum of Victoria, Melbourne, Victoria, Australia

Q: FRV Courageous of CSIRO

Q47/51: FRV Courageous of CSIRO cruise 47, station 51

SO: FRV Soela of CSIRO

FRV Soela SO1/85/124 (and similar): FRV Soela of CSIRO,

1985 cruise 1, station 124

Systematic description

Class Cephalopoda Cuvier, 1797

Subclass Coleoidea Bather, 1888

Order Sepiolida Fioroni, 1981

Family Sepiolidae Leach, 1817

Subfamily Sepiolinae Leach, 1817

Dextrasepiola n. gen.

Type Species: Dextrasepiola taenia n. gen., n. sp. by monotypy

Diagnosis: Sepiolinae with fins rounded with large anterior lobes, which do not reach the anterior mantle margin; fin length about 50-80% mantle length. Suckers biseriate on all arms. Tentacular club suckers in 4-8 longitudinal series. Nuchal commissure narrow, not reaching over the ocular globes. A pair of dumbbell-shaped photophores on ventral surface of ink sac. Gladius absent. Ventral mantle margin slightly sinuate, without any deep funnel indentation. Right arm I of male hectocotylised. Hectocotylus tripartite: basal part with five suckers in two series, two suckers in dorsal series and three in ventral series; copulatory apparatus long, fleshy, tape like, formed by fusion of two adjoining very elongate sucker stalks, no additional modified structure on the arm (i.e. hook-like stalks); distal to tape-like copulatory apparatus biserial suckers to arm tip (19 suckers in holotype, 23 suckers in paratype 2). Female bursa copulatrix on right side of mantle cavity, open type (cf. Bello, 2020), roughly ear shaped.

Etymology: Generic name Dextrasepiola is derived from Latin dextra meaning right or on the right side plus sepiola meaning a small cuttlefish. The name denotes the unique feature among the Sepiola and its kin having the right dorsal arm hectocotylised instead of the left dorsal one in mature males and the bursa copulatrix in females on the right side of the mantle cavity.

Remarks: The hectocotylisation in Sepiolinae has been thoroughly discussed and illustrated by Bello (2020), Naef (1912a, b; 1923) and Nesis (1982). All known species have the left dorsal arm hectocotylised and the sucker stalks of some suckers are modified into a horn-like or hook-like copulatory organ. The present genus is unique in having the right dorsal arm hectocotylised and the copulatory organ as one thick tape-like structure. In addition, the hectocotylus has the regular tripartite structure typical of most sepioline genera except for *Euprymna* and *Eumandya* (cf. Bello, 2020). The females of all known species of Sepiolinae possess a bursa copulatrix on the left side of the mantle cavity. The present genus is unique in having the bursa copulatrix on the right side of the mantle cavity. This right-handedness of the copulatory organs of both sexes of this genus certainly facilitate copulation in a normal fashion as they are on the same side of the animal.

Dextrasepiola taenia n.gen., n.sp.

Figures 1-5, 13; Table 2

Material examined: Holotype: MOV F80458: Redland Bay, Queensland, 27° 36' S, 153° 19' E, 1.2 m, CSIRO Moreton Bay Survey, J43, Location 31, 10 Aug 1951, 1 male, mature, 8.2 mm mantle length (specimen #1).

Paratype 1: MOV F91359: Redland Bay, Queensland, 27° 36' S, 153° 19' E, 1.2 m, CSIRO Moreton Bay Survey, J43, Location 31, 10 Aug 1951, 1 female, mature, 7.8 mm mantle length (specimen #2).

Paratype 2: MOV F74469: Peel Island, Queensland, 27° 30' S, 153° 21' E, 1.2 m, CSIRO Moreton Bay Survey, J26, Location 41, 10 Aug 1951, 1 male, mature, 6.5 mm mantle length (specimen #3).

Paratype 3: MOV F91361: Peel Island, Queensland, 27° 30' S, 153° 21' E, 1.2 m, CSIRO Moreton Bay Survey, J26, Location 41, 10 Aug 1951, 1 female, mature, 8.7 mm mantle length (specimen #4).

Other material: MOV F91360: Peel Island, Queensland, 27° 30' S, 153° 21' E, 1.2 m, CSIRO Moreton Bay Survey, J26, Location 41, 10 Aug 1951, 2 specimens, poor condition, 1 female, juvenile, 5.4 mm mantle length, 1 specimen, sex indeterminate, 3.9 mm mantle length.

Diagnosis: Small sepioline with right arm I of mature male hectocotylised, copulatory apparatus in the form of a long tapelike process, no hook-like structure on the arm. Females with bursa copulatrix on right side of mantle cavity.

Description: Mantle (figs 1a-c) short dome-shaped, slightly longer than wide, fused with head dorsally for about 25% of width. Anterior ventral mantle margin shallowly concave with lateral projections at position of mantle-funnel connectives. Head wide, slightly narrower than mantle. Nuchal commissure narrow, not reaching beyond level of medial border of eyeball, approximately 25-40% of mantle width at level of nuchal commissure. Eyes large, elliptical, located dorso-laterally on head. Cornea membrane protecting eye attached to skin of head along dorsal margin. Olfactory papilla located behind posterior corner of eye orbit, ventral photosensitive vesicle not found. Funnel long and slender, reaching the level beyond anterior eye margin, free from head for 60-80% of funnel length. Funnel connects to head by an oblique muscle band extending from beneath anterior end of funnel locking cartilage to ventral side of head.

Funnel locking cartilage (fig. 1f) elongated oval with simple, slightly curved depression in the middle, mantle locking cartilage long, low ridge. Dorsal element of funnel organ (fig. 1g) Y-shaped pad with a small papilla at the apex. Behind each ramus is swelling that connects dorsal funnel organ with base

of funnel retractor. Ventral elements of funnel organ (fig. 1g) a pronounced semi-spherical pad, becoming slightly narrower anteriorly, with a mamillar projection slightly posteriorly to centre. Funnel valve well developed on dorsal roof, tongue shaped, located well behind funnel aperture.

Fins (figs 1a-c) circular in outline, anterior border of fins projects forward prominently forming a deep cleft with mantle, anterior fin lobe reaching level halfway between fin insertion and mantle border or to mantle margin, posterior borders of fins convex, less pronounced. Length of fin base about 33% of mantle length.

Arms (figs 1a-c, 2a-c, 3) short, rounded aborally, flatten orally. All arms on both sexes with biserial suckers throughout. Because most suckers are lost, it was impossible to determine the sucker ring dentition and if the enlargement of suckers exists. In males, arm III is the longest and thickest, followed by arm II or arm IV. Right arm I of male (figs 1d-e, 3) with a flat, fleshy, tape-like long process, appeared to be modified sucker stalks of proximal third sucker of dorsal series and proximal fourth sucker of ventral series fused together throughout their length. Length of the process reaches to almost the level of arm tip, thickened along proximal portion ending in a blunt tip. No sucker on the tape-like process of holotype, but a remnant of a tiny sucker on the process of paratype 2 (fig. 3). Distal to the tape-like process, 19 suckers in two series to arm tip on holotype (23 suckers in paratype 2); no hook-like structures on the arm. Left arm I in males and both arms I in females with 28-30 suckers in two series, with no peculiar or unusual development or modification. Arm II with 27-35 suckers in both sexes with no noticeable special development in either sex. In males, arms III thickened proximally, slightly tapers distally to about half of arm length then abruptly tapers distally; swollen proximal part with no suckers except several remnants of suckers; distal part strongly curled towards mouth, with 17-19 suckers. In females, arm III similar to arm II with 21 suckers. Arm IV of both sexes with 26-31 suckers. In males, aboral keel and swimming membrane absent on arms I-III, well developed along whole length of arms IV. In females, aboral keel and swimming membrane present on distal half of arms I and II, and almost whole length of arms III and IV. Webs shallow between all arms except between arms III and IV (web D), which half encloses base of tentacles in both sexes, web E non-existent.

Tentacles weak, longer than arms. Club (fig. 4a) slightly expanded, minute carpal suckers in 4 series, minute manal suckers in 6 series, those on dorsal 2 series larger than the remaining suckers, numerous minute suckers in 8 series on dactylus. Sucker ring dentition of largest club sucker finely toothed around entire minute circle.

Gills with 15–20 lamellae per demibranch, plus a terminal lamella. A pair of dumbbell-shaped, yellowish photophores, opaque with both ends swollen on both sides of ink sac (figs 1g, 4b).

Upper beak (fig. 4d) rostrum slightly curved; jaw angle obtuse; wing long, shoulder (cutting edge) serrated; rostrum dark brown to black, hood, shoulder and dorsal part of lateral wall light brown, posterior part of hood, most of lateral wall unpigmented, transparent.

Table 2. Dextrasepiola taenia n.gen. & n.sp. measurement, counts and indices

Species		Dextrasepiola taenia					
Museum	MOV	MOV	MOV	MOV			
Registration number	F80458	F74469	F91361	F91359			
Specimen number	1	2	3	4			
Type status	Holotype	Paratype 2	Paratype 3	Paratype 1			
Cruise	Moreton Bay Survey	Moreton Bay Survey	Moreton Bay Survey	Moreton Bay Survey			
Station number	J43, Loc.31	J26. Location 41	J26, Location 41	J43. Location 31			
Sex	male	male	female	female			
Maturity	5	5	5	5			
DML (mm)	8.2	6.5	8.7	7.8			
VMLI	93.9	113.8	103.4	102.6			
HLI	29.3	36.9	51.7	43.6			
HWI	75.6	95.4	74.7	88.5			
NCI	26.4	22	40	36.1			
MWI	87.8	90.8	86.2	92.3			
FuLI	53.7	83.1	65.5	70.5			
ruli FuWI	46.3	43.1	47.1	51.3			
Fuwi FFuI	81.8	61.1	61.4	60			
	01.0						
FLI	48.8	67.7	63.2	61.5			
FBLI	35.4	35.4	31	32.1			
FWI	43.9	64.6	44.8	56.4			
A ₁ LI	54.9	84.6	51.7	57.7			
A ₂ LI	67.1	84.6	69	64.1			
A ₃ LI	85.4	107.7	63.2	64.1			
A ₄ LI	54.9	92.3	57.5	51.3			
Arm formula	3.2.1.=4.	3.4.1.=2.	2.3.4.1.	2.=3.1.4.			
A _{R1} LI	67.1	92.3	_	_			
TtLI	85.4	_	137.9	179.5			
CILI	30.5	_	23	38.5			
CIRC	6	_	6	6			
GLI	32.9	46.2	41.4	28.2			
GWI	18.3	29.2	23	21.8			
GiLC	18	20	_	15			
A ₁ SC	28	30	29	30			
A ₂ SC	27	31 right	30	30			
A ₃ SC	-	-	_	27			
A ₄ SC	26	31	29 right	27			
A _{R1} SC	25	29					
CISI	2.2	_	_				
A ₁ SI		4.6					
A ₁ SI A ₂ SI	- -	4.0		- -			
A ₂ SI A ₃ SI	- -						
13.31 A CI		_					
A ₄ SI			_				
SpLI	a:26; b:24.3; c:30.1; d:27.4; e:28.2	_	_	<u> </u> -			
SpWI	a:3.9; b:4.2; c:3.4; d:3.7; e:4.8	_	_				
SpRI	a:20.7; b:22.1; c:19; d:22.2; e:21.6	_	_	_			
CBI	a:33.8; b:36.2; c:30.4; d:34.7; e:33.8		<u> -</u>				
NidGI	-	_	54.4	36.6			

Note: Maturity 4, subadult – sexual characters well distinguished but gonads and accessory organs not completely developed; Maturity 5, adult – sexually mature with spermatophores in Needham's sac in males; ovaries, nidamental and oviducal glands fully developed and ripe, eggs sometimes in oviducts, in females; DML, dorsal mantle length (mm) – measured from anterior-most point of mantle to posterior end of mantle; VMLI, ventral mantle length index – ventral mantle length, measured from anterior border of mantle at ventral midline, to apex of mantle, expressed as a percentage of DML; HLI, head width index – dorsal length of head at level of eyes expressed as a percentage of DML; NCI, nuchal commissure width index – width of nuchal commissure expressed as a percentage of bill, mantle width of mantle at the position of nuchal commissure; MVI, mantle width of mantle width at mantle opening expressed as a percentage of DML; Full, funnel length index – length of funnel from anterior funnel opening to posterior border of funnel measured along ventral midline expressed as a percentage of DML; Full, funnel width index – width of funnel at junction of funnel and head just anterior to funnel locking cartilages expressed as a percentage of DML; Full, funnel width index – length of funnel at junction of funnel and head just anterior to funnel locking cartilages expressed as a percentage of DML; Full, funnel width index – length of fin attachment to head expressed as a percentage of DML; Full, fin base length index – length of fin attachment to mantle expressed as a percentage of DML; ALI, arm II length index – length of arm II expressed as a percentage of DML; ALI, arm II length index – length of arm II expressed as a percentage of DML; ALI, arm II length index – length of arm III expressed as a percentage of DML; ALI, arm II length index – length of arm III expressed as a percentage of DML; ALI, arm II length index – length of arm III expressed as a percentage of DML; ALI, arm II length index – length of arm III expressed

Lower beak (figs 4e, f) wide; rostrum with blunt tip; jaw edge rough, slightly serrated, jaw angle indistinct; blunt tooth on shoulder; no notch in hood; lateral wall without fold or ridge, roughly elongate rhomboidal with lower edge slightly concave, corner faintly produced; rostrum and hood light brown, posterior part of lateral wall and wings transparent. Radula (fig. 4c) seven series, each row with seven unicuspid teeth.

Gladius absent.

Spermatophores (figs 5a, b) small, five spermatophores from the holotype approximately 2–2.5 mm long (spermatophore length index 24–30), greatest width approximately 0.08–0.1 mm

(spermatophore width index 3.4–4.8), sperm reservoir about 0.4–0.5mm (sperm reservoir index 19–22), structure complex, with spiral appearance in ejaculatory apparatus and the sperm mass, cement body 0.72–0.78 mm long (cement body index 30–36), connects to sperm reservoir by a narrow neck, oral end of cement body elongated funnel shaped.

Bursa copulatrix (figs 5c-f) open type, large, roughly earshaped, longer than wide; anteriorly extends medially towards midline, running antero-laterally just below right funnel locking cartilage, reaching posterior end of mantle cavity. Longitudinal opening of bursa close to mantle ventral midline,

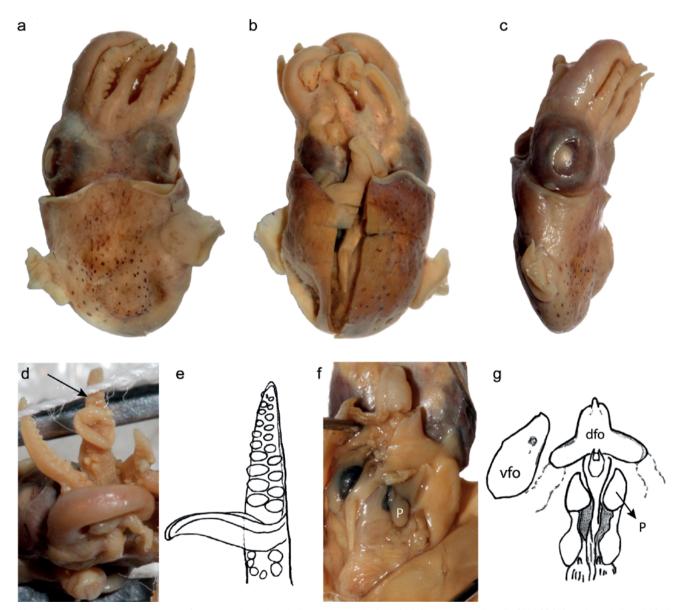


Figure 1. Dextrasepiola taenia n. gen. & n. sp., male: a, dorsal view, holotype (MOV F80458); b, ventral view (MOV F80458); c, lateral view (MOV F80458); d, hectocotylised arm (right arm I; MOV F80458); e, diagram of the hectocotylised arm showing tape-like modification, paratype 2 (MOV F74469; drawn by T. Okutani); f, inside mantle cavity, showing photophores (p) and other organs (MOV F80458); g, diagram of opened funnel and inside mantle cavity showing dorsal funnel organ (dfo), ventral funnel organ (vfo) and photophores (p; MOV F80458; drawn by T. Okutani).

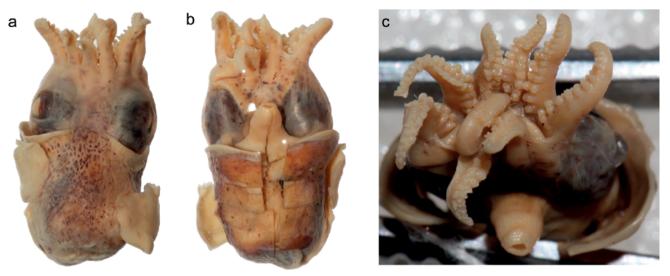


Figure 2. Dextrasepiola taenia n. gen. & n. sp., female, paratype 1 (MOV F91359): a, dorsal view; b, ventral view; c, oral view of arm crown showing sucker arrangements of female.

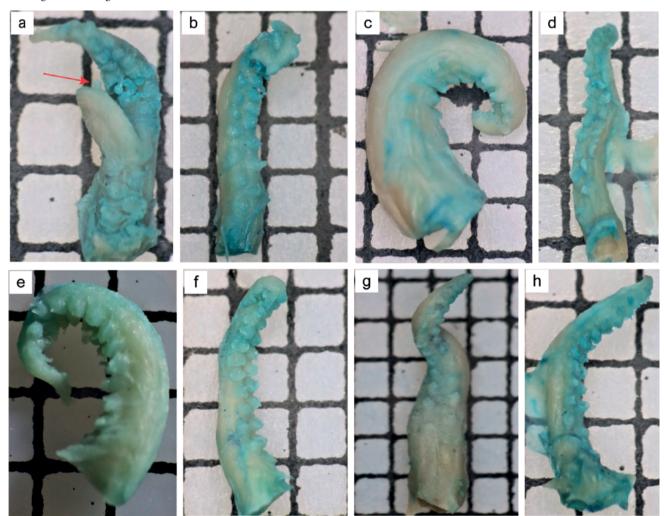


Figure 3. Dextrasepiola taenia n. gen. & n. sp. male, paratype 2 (MOV F74469). Oral view of arms (grids in background: $1 \text{ mm} \times 1 \text{ mm}$): a, right arm I, arrow points to remnant of a tiny sucker; b, right arm II; c, right arm II; d, right arm IV; e, left arm I; f, left arm II; g, left arm III; h, left arm IV.

running along long axis of bursa. Mature females with large nidamental gland, (nidamental gland index 36.6–54.4).

Alcohol-preserved specimens brown in colour, dorsal mantle surface lighter than ventral surface. Dark chocolate-brown chromatophores scattered over brown-coloured background on both dorsal and ventral surfaces of head and mantle, and along aboral surface of all arms. Surfaces of fins devoid of chromatophores and pigmented spots. Skin smooth, lacking sculpture or papillae.

Etymology: Species epithet *taenia* from Latin *taenia* meaning tape-like. The name denotes the tape-like structure in the copulatory apparatus on the hectocotylised arm of the males.

Distribution: Only known from Moreton Bay, Queensland, Australia (fig. 13).

Remarks: This is the only known species in the genus. Due to the poor preservation of the specimens, nearly all suckers are lost or are without sucker rings. The description of sucker ring dentition and spermatophores must wait until better materials are available.

The poor state of preservation resulted in distorted morphology of the specimens studied. This most certainly contributes to the wide range of the morphometric indices listed in Table 2.

Amutatiola n. gen.

Diagnosis: Small Sepiolinae with fins rounded with large anterior lobe, which do not reach the anterior mantle margin; fin length about 40–66% mantle length. Suckers biseriate on all arms. Tentacular club suckers in 4–8 longitudinal series. Nuchal commissure moderately wide, not reaching over the ocular globes, about 38–59% of mantle width. A pair of dumbbell-shaped or elongated kidney-shaped photophores on ventral surface of ink sac. Gladius absent. Ventral mantle margin slightly sinuate, without any deep funnel indentation. No arm in mature males hectocotylised. Some arm suckers in mature males grossly enlarged. Female bursa copulatrix closed type, pouch-like, opening at level of base of left gill.

Type Species: Amutatiola macroventosa n. gen., n. sp. by monotypy.

Etymology: Generic name Amutatiola is derived from Greek a meaning without or absent plus Latin mutatus meaning changed or altered; the ending -ola is the diminutive suffix of sepiola meaning a small cuttlefish. The name denotes the unique feature among the Sepiolinae of having no arm hectocotylised in males.

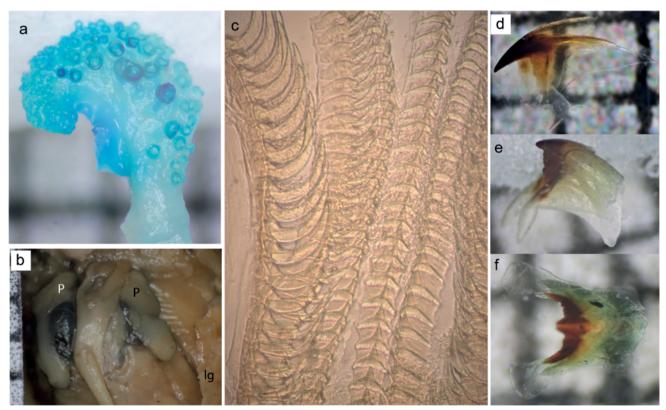


Figure 4. *Dextrasepiola taenia* n. gen. & n. sp. (grids in background: 1 mm × 1 mm): a, left tentacular club, female, paratype 3 (MOV F91361); b, inside mantle cavity: photophores (p), left gill (lg), male, holotype (MOVF80458); c, radula (paratype 1, MOV F91359); d, lateral view of upper beak (MOV F91361); e, lateral view of lower beak (MOV F91361); f, top view of lower beak (MOV F91361).

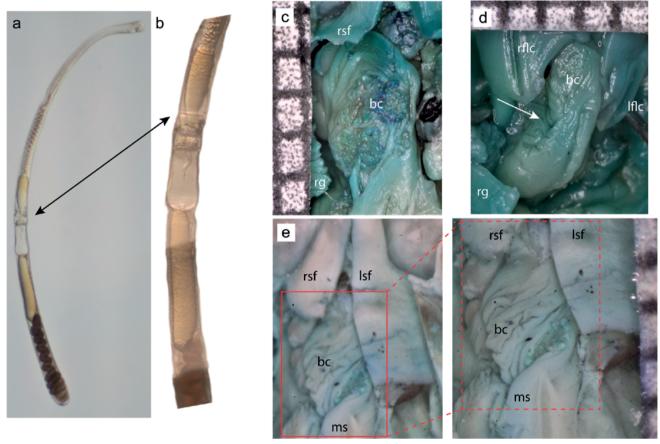


Figure 5. Dextrasepiola taenia n. gen. & n. sp. (grids in background: 1 mm × 1 mm): a, spermatophore from the holotype (MOV F80458); b, close-up of cement body; c, bursa copulatrix, paratype 1 (MOV F31359; bc: bursa copulatrix; rg: right gill; rsf: right side of funnel); d, bursa copulatrix, juvenile (MOV F31360; bc: bursa copulatrix; lflc: left funnel locking cartilage; rflc: right funnel locking cartilage; rg: right gill); e, bursa copulatrix, paratype 3 (MOV F31361; bc: bursa copulatrix; lsf: left side of funnel; ms: mantle septum; rsf: right side of funnel); f, close-up of a portion of e, arrow points to opening of bursa copulatrix.

Amutatiola macroventosa n. gen., n. sp.

Figures 6-13; Tables 3, 4

Material examined: Holotype: MOV F80081: south-east Tasmania, 42° 38.1′ S, 148° 12.4′ E, trawl depth 36–42 m, bottom depth 86–90 m, collected by CSIRO, FRV *Soela* SO1/85/124, 27 Feb 1985, 0331 hr, Rectangular Midwater Trawl with 8 m² mouth area, 1 male, 9.8 mm mantle length, mature (specimen #1).

Paratype 1: MOV F275293: Great Australian Bight, 32° 43' S, 126° 00' E–32° 45' S, 125° 59' E, 40–170 m, collected by CSIRO, FRV *Soela* SO3/80/32, 13 May 1980, 0100 hr, IYGPT, 1 female, 12.2 mm mantle length, mature (specimen #11).

Paratype 2: WAM 3091-83: west side of Irwin Reef, Port Denison, Western Australia, 29° 16' S, 114° 55' E; 7–8 m, collected by N. Sinclair, 4 Apr 1983, Rotenone Station, 1 male, 9.5 mm mantle length, mature (specimen #3).

Paratype 3: MOV F80083: south-east Tasmania, 42° 39.7′ S, 148° 12.1′ E, trawl depth 5–10 m, bottom depth 90–95 m, collected by CSIRO, FRV *Soela* SO1/85/104, 15 Feb 1985, 2034 hr, Rectangular Midwater Trawl with 8 m² mouth area, 1 male, 9.6 mm mantle length, mature (specimen #2).

Paratype 4: MOV F275294: Great Australian Bight, 33° 30' S,

131° 50.0' E–33° 30' S, 131° 53' E, 200–144 m, collected by FRV *Soela* SO3/80/1, 8 May 1980, 1 female, 12.8 mm mantle length, mature (specimen #9).

Paratype 5: MOV F158244: Luck Bay, western point off beach, Cape Le Grand National Park, Western Australia, 33° 59' S, 122° 13' E, 5 m, active over algae, collected by D. Rawlins, J. Finn and M. Norman, 26 April 1998, 1915 hr, hand net, 1 male, 8.8 mm mantle length, mature (specimen #4).

Paratype 6: MOV F275296: Luck Bay, western point off beach, Cape Le Grand National Park, Western Australia, 33° 59' S, 122° 13' E, 5 m, active over algae, collected by D. Rawlins, J. Finn and M. Norman, 26 April 1998, 1915 hr, hand net, 1 female, 6.2 mm mantle length, subadult (specimen #17).

Paratype 7: MOV F275295: Luck Bay, western point off beach, Cape Le Grand National Park, Western Australia, 33° 59' S, 122° 13' E, 5m, active over algae, collect. by D. Rawlins, J. Finn and M. Norman, 26 April 1998, 1915 hr, hand net, 1 male, 8.1 mm mantle length, mature (specimen #5).

Paratype 8: MOV F91362: Luck Bay, western point off beach, Cape Le Grand National Park, Western Australia, 33° 59' S, 122° 13' E, 5 m, active over algae, collected by D. Rawlins, J. Finn and M. Norman, 26 April 1998, 1915 hr, hand net, 1 male, 6.9 mm mantle length, mature (specimen #7).

Table 3. Amutatiola macroventosa n.gen. & n.sp. measurement, counts and indices of male specimens

Species							
Museum	MOV	MOV	WAM	MOV	MOV	MOV	MOV
Registration number	F80081	F80083	3091-83	F158244	F275295	F80087	F91362
Specimen number	1	2	3	4	5	6	7
Type status	Holotype	Paratype 3	Paratype 2	Paratype 5	Paratype 7	_	Paratype 8
Cruise	SO1/85	SO1/85	N. Sinclair, 4 Apr 1983		I- **	_	-
Station number	124	104	4 Apr 1983, Rotenone	<u> </u>	-	_	_
			Station.				
Sex	male	male	male	male	male	male	male
Maturity	5	5	5	5	4	5	4
DML (mm)	9.8	9.6	9.5	8.8	8.1	8	6.9
VMLI	109.2	93.8	102.1	_	88	116.3	103.6
HLI	43.9	47.9	40	49.3	59.6	63.8	54.1
HWI	88.8	70.8	90.5	84.2	87.7	101.3	102
NCI	41.1	38.6	45.8	_	43.7	40.2	50.5
MWI	96.9	91.7	87.4	_	91.6	115	111.4
FuLI	69.4	62.5	70.5	_	81.2	61.3	85.5
FuWI	50	43.8	42.1	34.6	55.1	31.3	58.8
FFuI	60.3	66.7	68.7	_	77.8	61.2	79
FLI	62.2	58.3	53.7	_	54	63.8	64.9
FBLI	35.7	30.2	31.6	30.3	29.8	41.3	52.9
FWI	46.9	38.5	33.7	59.7	48.1	58.8	58.4
A ₁ LI	92.9	87.5	_	140.9	75.3	80	92.4
A ₂ LI	87.8	82.3	82.1	90.9	91	98.8	103.6
A ₃ LI	73.5	83.3	71.6	_	_	88.8	105.2
A ₄ LI	74.5	65.6	73.7	68.2	75.2	77.5	90.9
Arm formula	1.2.4.3.	1.3.2.4.	2.1.4.3.	_	2.1.3.4.	2.3.1.4.	3.2.1.4.
A _{R1} LI	84.7	91.7	76.8	102.3	72.8	100	88.4
TtLI	-	161.8	121.1	_	_	87.5	_
ClLI	24.5	21.9	29.5	22.7	32.1	28.8	26.1
CIRC	6	6	6	6	6–8	6–8	6–8
GLI	42.9	42.7	_	_	40	33.7	46.4
GWI	22.4	16.7	_	_	25.3	16.3	18.8
GiLC	21	21	_	_	17	16	16
A ₁ SC	21	20	19	20	14	28	16
A ₂ SC	30	30	30	32	33	27	28
A ₃ SC	_	_	27	_	24		24
A ₄ SC	29	29	27	21	24	26	22
A _{R1} SC	19	18	17	_	12	25	14
CISI	2.4	1.6		0.6	1.6	2.3	1.9
A ₁ SI	21.4	17.6	19.8	18.6	20.4	11.9	24.2
A ₂ SI	4.7	9.7	5.1	7.3	17.4	_	6.7
A ₃ SI	13.7	8.4	14.5	17.2	20.3	_	20.4
A ₄ SI	4.1	4.8	8.1	5.6	6.3	_	7.4
SpLI	a:36.2; b:33.5; c:35.7; d:34.0		42.7	29.3	_	44.8	_
SpWI	a:6.2; b:6.7; c:5.7; d:6	6.7	5.4	6.6	_	7.0	_
SpRI	a:33.5; b:35.7; c:34; d:43.2	40.3	35.5	37.6	_	27.9	_
CBI	a:20.3; b:22; c:19.1; d:20	19.4	18.5	19.4	-	10.9	_

Note: Maturity 4, subadult – sexual characters well distinguished but gonads and accessory organs not completely developed; Maturity 5, adult – sexually mature with spermatophores in Needham's sac in males; ovaries, nidamental and oviducal glands fully developed and ripe, eggs sometimes in oviducts, in females; DML, dorsal mantle length (mm) – measured from anterior-most point of mantle to posterior end of mantle; VMLI, ventral mantle length index – ventral mantle length, measured from anterior border of mantle at ventral midline, to apex of mantle, expressed as a percentage of DML; HII, head length index – dorsal length of head measured from point of fusion of dorsal arms to anterior tip of dorsal mantle expressed as a percentage of DML; HVI, head width index – greatest width of head at level of eyes expressed as a percentage of DML; NCI, nuchal commissure width index – width of nuchal commissure expressed as a percentage of width of mantle at the position of nuchal commissure; MWI, mantle width index – mantle width at mantle opening expressed as a percentage of DML; Full, funnel length index – length of funnel from anterior funnel opening to posterior border of funnel measured along ventral midline expressed as a percentage of DML; Full, funnel width index – width of funnel at junction of funnel and head just anterior to funnel locking cartilages expressed as a percentage of DML; Full, free funnel index – length of funnel rom the anterior opening to the point of dorsal attachment to head expressed as a percentage of DML; Flat, fin width index – greatest width of a single fin expressed as a percentage of DML; All, arm II length index – length of arm II expressed as a percentage of DML; All, arm II length index – length of arm II expressed as a percentage of DML; All, arm II length index – length of arm II expressed as a percentage of DML; All, arm II length index – length of arm II expressed as a percentage of DML; All, arm II length index – length of arm II expressed as a percentage of DML; All, arm II length

Table 4. Amutatiola macroventosa n.gen. & n.sp. measurement, counts and indices of female specimens

Species					Amutatiola i	macroventosa	$\overline{\imath}$			
Museum	MOV	MOV	MOV	MOV	MOV	MOV	MOV	MOV	MOV	MOV
Registration number	F80084	F275294	F77100	F275293	F77100	F77100	F77100	F80084	F80087	F275296
Specimen number	8	9	10	11	12	13	14	15	16	17
Type status	_	Paratype 4	_	Paratype 1	_	_	_	_	_	Paratype 6
Cruise	O/47	SO3/80	SO1/82	SO3/80	SO1/82	SO1/82	SO1/82	O/47	_	_
Station number	51	1	1	32	1	1	1	51	_	_
Sex	female	female	female	female	female	female	female	female	female	female
Maturity	5	5	4	5	4	4	4	4	4–5	3
DML (mm)	13.2	12.8	12.6	12.2	11.9	11.6	10.6	10.3	9.2	6.2
VMLI	91.7	93	85.7	100	89.9	87.9	89.6	83.5	103.3	90.1
HLI	58.3	44.5	49.2	50.8	52.1	48.3	46.2	48.5	48.9	47
HWI	55.3	64.8	67.5	67.2	68.1	68.1	82.1	64.1	72.8	99.5
NCI	50	55.2	47.6	43	56.5	53.3	59	46.7	54	56.1
MWI	71.2	75	83.3	76.2	86.6	92.2	91.5	72.8	94.6	101.9
FuLI	58.3	62.5	62.2	59	63.1	64.5	74.2	50.5	65.2	89.3
FuWI	44.7	38.3	42.7	39.3	44.5	40.3	45.7	39.8	33.7	53.3
FFuI	79.2	55	63.8	69.4	63.9	60.2	57.2	71.2	66.7	67.8
FLI	49.2	39.8	52.4	50	67.2	53.4	56.6	48.5	64.1	62.6
FBLI	24.2	32.8	27	36.9	32.8	33.6	34	29.1	41.3	35
FWI	34.1	36.7	38.1	36.9	63	38.8	47.2	38.8	52.2	53.5
A ₁ LI	65.9	54.7	47.6	57.4	54.6	64.7	66	58.3	76.1	67.6
A ₂ LI	83.3	78.1	55.6	77.9	67.2	77.6	84.9	63.1	87	93.3
A ₃ LI	_	74.2	67.5	69.7	88.2	90.5	89.6	68	81.5	98.7
A ₄ LI	69.7	66.4	47.6	53.3	63	77.6	66	63.1	76.1	76.6
Arm formula	_	2.3.4.1.	3.2.4.=1.	2.3.4.1.	3.2.4.1.	3.2.=4.1.	3.2.4.=1.	3.2.=4.1.	2.3.4.=1.	3.2.4.1.
TtLI	_	132.8	_	_	_	_	_	_	108.7	-
ClLI	_	27.3	_	_	_	_	_	_	38	32.1
CIRC	_	68	_	_	_	_	_	_	6	68
GLI	40.9	33.6	38.1	38.5	31.9	35.3	40.6	25.2	42.4	35.3
GWI	20.5	14.1	22.2	19.7	16.8	18.1	12.3	15.5	23.9	18.3
GiLC	19	17	17	17	17	17	21	16	18	19
A ₁ SC	32	34	27	30	34	33	32	29	32	29
A_2SC	40	44	26	31	45	44	37	43	35	35
A_3SC	_	34	24	_	38	35	37	33	_	29
A ₄ SC	29	33	31	31	36	38	33	31	_	25
CISI	_	1.2	_	_	_	_	_	_	2.8	2.9
A ₁ SI	3	3.4	4	3.6	4.2	4.3	4.7	4.3	_	5.3
A ₂ SI	3.5	3.4	3.9	3.6	4.1	4.2	4.6	4.3	-	5.8
A ₃ SI	3.3	3.4	3.3	3.8	3.5	3.6	4	3.9	-	5.3
A ₄ SI	3	3.4	3.2	2.7	3.4	3.4	3.8	2.9	-	4.5
NidGI	39.9	41.5	50.6	44	51.3	53.1	56.6	37.2	44.8	_

Note: Maturity 3, juvenile – young specimen in which some sexual characters are distinguished; Maturity 4, subadult – sexual characters well distinguished but gonads and accessory organs not completely developed; Maturity 5, adult – sexually mature with spermatophores in Needham's sac in males; ovaries, nidamental and oviducal glands fully developed and ripe, eggs sometimes in oviducits, in females; DML, dorsal mantle length (mm) – measured from anterior-most point of mantle to posterior end of mantle; VMLI, ventral mantle length index – ventral mantle length, measured from anterior border of mantle at ventral midline, to apex of mantle, expressed as a percentage of DML; HLI, head length index – dorsal length of head measured from point of fusion of dorsal arms to anterior tip of dorsal mantle expressed as a percentage of DML; HUI, head width index – greatest width of head at level of eyes expressed as a percentage of DML; NCI, nuchal commissure width index – width of nuchal commissure expressed as a percentage of DML; Full, funnel length index – length of funnel from anterior funnel opening to posterior border of funnel measured along ventral midline expressed as a percentage of DML; Full, funnel width index – width of funnel at junction of funnel and head just anterior to funnel locking cartilages expressed as a percentage of DML; Full, fire funnel index – length of funnel from the anterior opening to posterior border of funnel locking cartilages expressed as a percentage of DML; Full, fire funnel index – length of a single fin expressed as a percentage of DML; Full, fin length index – length of a single fin expressed as a percentage of DML; A, LI, arm I length index – greatest width of a single fin expressed as a percentage of DML; A, LI, arm I length index – length of arm II expressed as a percentage of DML; A, LI, arm II length index – length of arm II expressed as a percentage of DML; A, LI, arm II length index – length of arm II expressed as a percentage of DML; A, LI, arm II length index – length of arm

Other material: MOV F80087: Franklin Island, South Australia, 32° 27'S, 133° 40'E, sub-light, 4 Apr 1953, 1 male, 8.0 mm mantle length, mature; 1 female, 9.2 mm mantle length, subadult (specimens #6, 16).

MOV F80085: Great Australian Bight, 32° 43' S, 126° 00' E -32° 45' S, 125° 59' E, 40-170 m, collected by CSIRO, FRV *Soela* SO3/80/32, 13 May 1980, 0100 hr, IYGPT, 1 male, 6.6 mm mantle length, subadult; 9 males, 7.7-9.6 mm mantle length, mature; 3 females, 4.7-6.5 mm mantle length, juveniles.

MOV F80086: Great Australian Bight, 33° S, 126° E, 48–50 m, collected by CSIRO, FRV *Soela* S03/80/33, 13 May 1980, IYGPT, 1 male, 7.1 mm mantle length, subadult; 2 males, 8.5–9.8 mm mantle length, mature; 1 female, 12.2 mm mantle length, mature.

MOV F80084: Great Australian Bight, 33° 22' S, 125° 27' E – 33° 23' S, 125° 27' E, 64 m, collected by CSIRO, FRV *Courageous* Q47/51, 7 Apr 1979, 2 females, 10.3–13.2 mm mantle length, mature (specimens #8, 15).

MOV F77100: Bass Strait, 60 km west of Cape Frankland, Flinders Island, 39° 53' S, 147° 03' E, trawl depth 20–60 m, bottom depth 66–68 m, collected by CSIRO, FRV *Soela* SO1/82/1, 16 Jan 1982, 1 female, 5.6 mm mantle length, juvenile; 4 females, 10.6–12.6 mm mantle length, mature (specimens #10, 12, 13, 14; four larger specimens).

MOV F80082: Great Australian Bight, 33° 30' S,

131° 50.0′ E–33° 30′ S, 131° 53′ E, 200–144 m, collected by FRV *Soela* SO3/80/1, 8 May 1980, 9 males, 4.8–7.6 mm mantle length, immature; 3 females, 5.4–6 mm mantle length, immature.

MOV F80080: Great Australian Bight, 32° 22' S, 131° 19' E–32° 17' S, 131° 18' E, 54–68 m, collected by CSIRO, FRV *Soela* SO3/81/41, 6 Aug 1981, 2130 hr, IYGPT, 2 females, 10.4–13.3 mm mantle length, mature.

MOV F158291: Port Victoria Jetty, South Australia, 34° 29' 45" S, 137° 28' 53" E, collected by J. Finn and Mark D. Norman, 21 May 1998, 1 female, 10.9 mm mantle length, mature.

Description: Mantle (figs 6a–c, 7, 8a–b) short dome-shaped with blunt posterior end, slightly longer than wide, muscular, studded by large chromatophores, fused with head dorsally. Anterior ventral mantle margin (figs 6b, 7b, 8b) shallowly concave with blunt lateral projections at position of mantle–funnel connectives, reaching level of posterior margin of eye lens. Head slightly narrower than mantle, head length about 50% of mantle length. Nuchal commissure moderately wide, width 38.6–50.5% of mantle width at commissure in males, 43–59% of mantle width at commissure in females, commissure does not reach beyond medial borders of bulbous eyes.

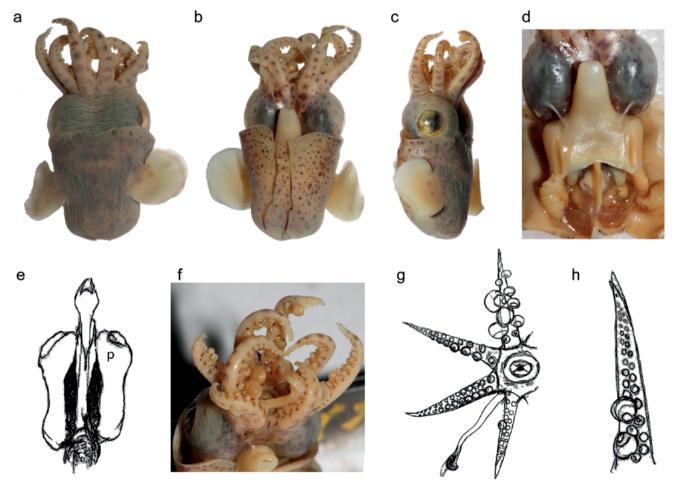


Figure 6. Amutatiola macroventosa n. gen. & n. sp. male, holotype (MOV F80081): a, dorsal view; b, ventral view; c, lateral view; d, inside mantle cavity showing funnel locking cartilages, partial photophores; e, diagram of photophores (p; drawn by T. Okutani); f, arm crown showing arm sucker arrangement; g, diagram of arm crown showing sucker arrangement (drawn by T. Okutani); h, diagram of arm IV showing sucker arrangement (drawn by T. Okutani).

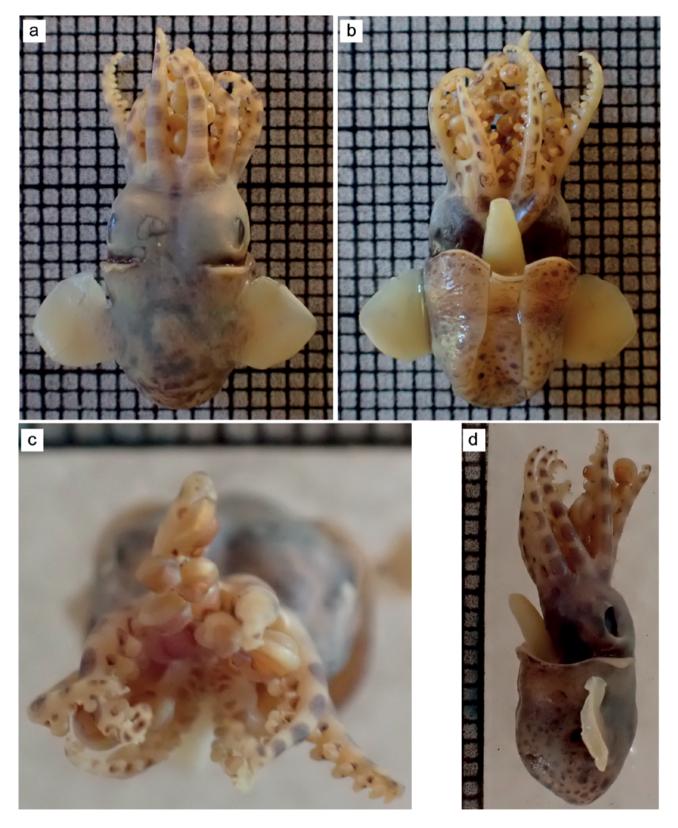


Figure 7. Amutatiola macroventosa n. gen. & n. sp. male, paratype 7 (MOV F275295; grids in background: 1 mm \times 1 mm): a, dorsal view; b, ventral view; c, arm crown showing arm sucker arrangement; d, lateral view.

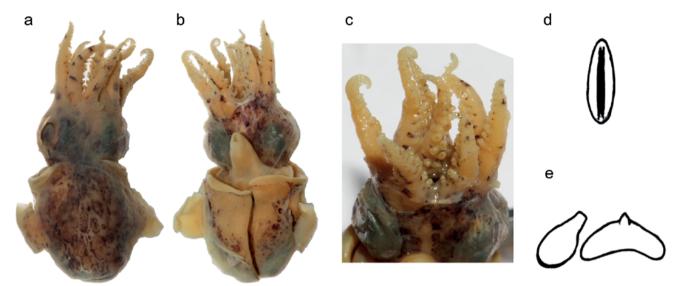


Figure 8. Amutatiola macroventosa n. gen. & n. sp.: a, dorsal view, female, paratype 1 (MOV F275293); b, ventral view, female, paratype 1 (MOV F275293); c, arm crown showing arm sucker arrangement, female, paratype 1 (MOV F275293); d, diagram of funnel locking cartilage, female, paratype 1 (MOV F275293; drawn by T. Okutani); e, diagram of funnel organs, male, paratype 3 (MOV F80083; drawn by T. Okutani).

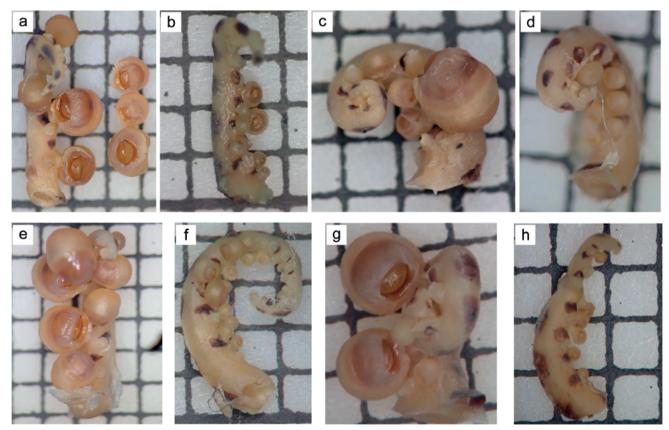


Figure 9. Amutatiola macroventosa n. gen. & n. sp. male, paratype 5 (MOV F158244). Oral views of arms (grids in background: 1 mm \times 1 mm): a, right arm II; b, right arm II; c, right arm III; d, right arm IV; e, left arm I; f, left arm II; g, left arm III; h, left arm IV.

Head almost entirely occupied by a pair of large bulbous eyes with elliptical eye lid. Cornea membrane protecting eye attached to skin of head along dorsal margin. Olfactory papilla located behind posterior corner of eye orbit, ventral photosensitive vesicle not found. Funnel (figs 6b, d, 7b, d, 8b) long and slender, lacking pigmentation, reaching the level beyond anterior eye margin, and free from head for 55–80% of funnel length. Funnel connects to head by an oblique muscle band extending from beneath anterior end of funnel locking cartilage to ventro-posterior corner of eye.

Dorsal funnel organ (fig. 8e) broad V-shaped with a blunt papilla at the apex. A prominent funnel retractor muscle connected funnel near base with ventro-posterior periphery of eye. Ventral elements of funnel organ (fig. 8e) tear drop-shaped pad, narrower anteriorly. Funnel valve well developed on dorsal roof, tongue shaped, located well behind funnel aperture.

Funnel locking cartilage (fig. 8d) elongated oval with simple, slightly curved depression in middle, mantle locking cartilage long, low ridge.

Fins (figs 6a-c, 7a-b, d, 8a-b) circular in outline, attach to mantle at mid-point of mantle, meeting mantle smoothly posteriorly, anterior border of fins project forward prominently forming a deep cleft with mantle, border not reaching level of mantle margin, posterior borders of fins convex, less

pronounced. Length of fin base about 33% of mantle length.

Arms moderately long, rounded aborally, flattened orally, lacking aboral keel and protective membranes. Arm formula inconsistent, in males arm I or II usually longest, arm III or IV usually shortest; in females, arm II or III longest, arm I or IV shortest. Arm suckers biserial with strong sexual dimorphism in sucker sizes and sucker ring dentitions. Web moderately pronounced between arms III and IV. No heteromorphism exists in morphology of right and left arms in males, specifically in the dorsal arms. Webs shallow between all arms except arms IV where no web exists, web D encloses base of tentacles in both sexes.

In males (figs 6f-h, 7, 9), arm I with up to 28 suckers, some suckers in proximal portion of arm enlarged: first to sixth proximal suckers on both dorsal and ventral series enormously enlarged, the third sucker on ventral series the largest, enlarged suckers on ventral series generally larger than dorsal series. Diameter of enlarged suckers exceed arm width. Arm II with up to 32 suckers, of which proximal second to seventh on ventral series slightly enlarged; no enlargement of suckers on dorsal series, suckers gradually reduced in size from proximal to distal end of arm II. Arm III with approximately 27 suckers, first to fourth proximal suckers on ventral series enormously enlarged (1.6 mm in diameter); no enlargement of suckers on dorsal

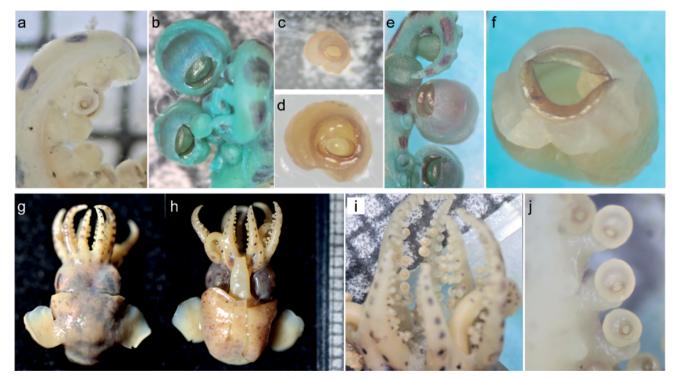


Figure 10. Amutatiola macroventosa n. gen. & n. sp. Sucker ring dentition (grids in background: 1 mm × 1 mm): a, left arm IV of male, paratype 5 (F158244) showing normal (non-enlarged) suckers near arm tip; b, right arm III of male, paratype 5 (F158244) showing sucker ring of enlarged suckers; c, d, normal sucker of left arm II of male, paratype 5 (F158244); e, left arm I of male, paratype 5 (F158244) showing enlarged suckers; f, an enlarged sucker of e showing sucker ring; g, dorsal view of female (F275296) showing non-enlargement of suckers; h, ventral view of female (F275296) showing non-enlargement of suckers; j, close-up of a portion of an arm of i showing sucker ring dentition.

series. Arm IV with approximately 29 normal suckers, no enlargement. Chitinous sucker rings of normal suckers almost at the same level as muscular rim of suckers, sucker ring margin minutely denticulated (figs 10a, c, d). Chitinous sucker rings of enlarged suckers (figs 10b, e, f) extended aborally beyond level of muscular sucker rims, chitinous ring often covered by thin, opaque membrane, sucker ring divided into 2 parts, distal 33–50% of sucker ring long, semicircular shape, proximal portion of sucker ring lower than distal portion, crescent shaped.

Females with more suckers than the corresponding arm in males. Arm I with up to 34 suckers, arm II with up to 45 suckers, arm III with up to 38 suckers and arm IV to 38 suckers. No enlarged sucker in females (figs 8c, 10g-j).

Chitinous sucker rings (figs 10i-j) similar to the non-enlarged suckers in males, sucker rings entire, with minutely denticulated margin.

Tentacle weak, longer than arms. Club slightly expanded, curled due to the presence of the dorsal web, small carpal suckers in 4 series, manal and dactyl suckers small, numerous in approximately 6–8 series, carpal and manal suckers much larger than dactylus suckers, in the central part of club, particularly those on dorsal 2 series slightly larger than others, suckers slightly diminish in size towards club margins and distally (fig. 11a). Sucker ring dentition of largest club sucker finely toothed around entire minute circle.

Gills with 16-21 lamellae per demibranch, plus a terminal

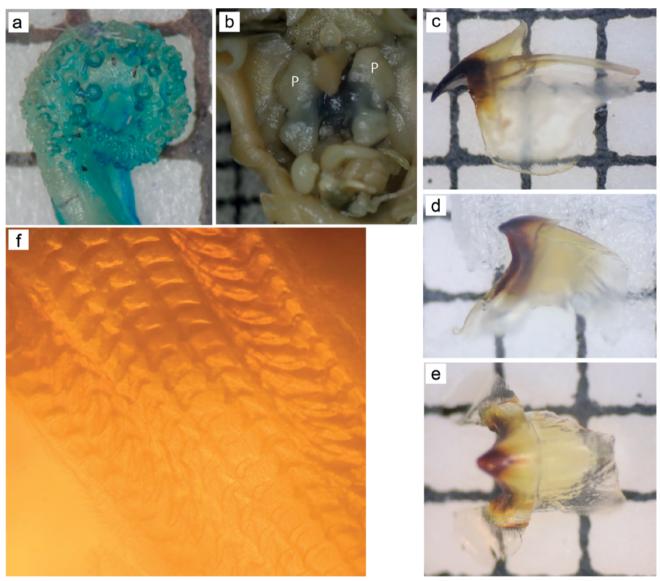


Figure 11. Amutatiola macroventosa n.gen. & n.sp. (grids in background: 1 mm × 1 mm): a, right tentacular club, male, paratype 5 (MOV F158244); b, photophores (p), male, paratype 5 (MOV F158244); c, lateral view of upper beak, female, paratype 1 (MOV F275293); d, lateral view of lower beak, female, paratype 1 (MOV F275293); e, top view of lower beak, female, paratype 1 (MOV F275293); f, radula, female, paratype 1 (MOV F275293).

lamella. A pair of yellowish photophores (figs 6e, 11b), opaque with both ends swollen, dumbbell-shaped or elongated kidney-shaped, on both sides of ink sac.

Upper beak (fig. 11c) rostrum slightly curved with pointed rostral tip; jaw angle obtuse; wing long, shoulder (cutting edge) nearly straight; lateral wall deep; rostrum dark brown to black, hood, shoulder and dorsal part of lateral wall light brown, posterior part of hood, most of lateral wall unpigmented, transparent.

Lower beak (figs 11d, e) wide; rostral tip blunt; jaw edge almost smooth, jaw angle indistinct; blunt tooth on shoulder; no notch in hood; lateral wall without fold or ridge, roughly elongate rhomboidal with lower edge concave, corner faintly produced; rostrum and hood light brown in colour, wings and posterior part of lateral wall transparent. Radula (fig. 11f) 7 series, each row with 7 unicuspid teeth.

Gladius absent.

Spermatophores (fig. 12a) small, 8 spermatophores from 5 individuals approximately 2.6–4.1mm long (spermatophore length index 29.3–42.7), greatest width approximately 0.17–0.25 mm (spermatophore width index 5.4–7), sperm mass moderately long, sperm reservoir about 0.97–1.5 mm (sperm reservoir index 27.9–43.2), structure simple, no obvious ornamental appearance, cement body approximately 0.39–0.75 mm long, connects to sperm reservoir by a narrow neck, oral end of cement body elongated funnel-shaped (cement

body index 11–22), appearance of ejaculatory apparatus plain, without spiral appearance of the preceding species.

Bursa copulatrix closed type, pouch like (Bello, 2020; fig. 12b), opening at level of base of left gill, running dorsally, on a mature female (Paratype 1) anterior end width approximately 2 mm with slit-like opening approximately 1.1 mm long, length of pouch approximately 2.3 mm, some spermatangia visible at opening of bursa. Mature and maturing females with large nidamental gland, (nidamental gland index 37.2–56.6).

Alcohol-preserved specimens brown in colour, dorsal mantle surface slightly darker than ventral surface. Dark blackish brown chromatophores scattered over brown-coloured background on both dorsal and ventral surfaces of head and mantle, and along aboral surface of all arms. Surfaces of fins devoid of chromatophores and pigmented spots, except a semicircular patch of brown chromatophores along fin insertion on dorsal side of fin. Skin smooth, lacking sculpture or papillae.

Etymology: Species epithet macroventosa is derived from Greek makros meaning large plus Latin ventosa meaning suction cup or sucker. The name denotes the presence of the greatly enlarged suckers on some arms of mature males.

Distribution: Flinders Island, Bass Strait, and south-eastern Tasmania to South Australia and the Great Australian Bight to Port Denison, Western Australia (fig. 13).

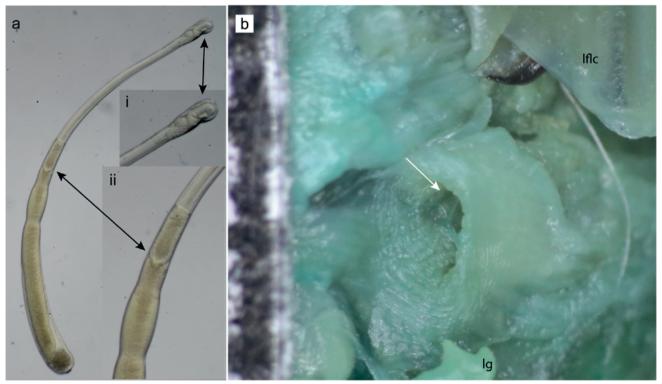


Figure 12. Amutatiola macroventosa n. gen. & n. sp.: a, spermatophore, holotype (MOV F80081) Spermatophore length, 3.55 mm (insets: i, close-up of oral cap; ii, close-up of cement body); b, Bursa copulatrix, paratype 1 (MOV F275293; black scale: 1 mm/division) (lflc: left funnel locking cartilage; lg: left gill); arrow points to the bursa copulatrix entrance.

Remarks: Apart from Dextrasepiola taenia n. sp. described earlier in this paper, all known species of the subfamily Sepiolinae have the left dorsal arm of maturing and mature males hectocotylised and sucker stalks of some suckers in the copulatory apparatus of the hetocotylus modified into horn-like, hook-like, papillae or laminae (Bello, 2020; Naef, 1912a, b; 1923; Nesis, 1982). The present species is unique in having enormously enlarged suckers and lacking a hectocotylised arm bearing highly modified sucker stalks in males. There are some species of Sepiolinae that carry enlarged suckers in hectocotylised arms (Bello, 2020; Naef, 1923), but none is so pronounced as in this species. The female has normal-sized suckers but more of them. In addition to sucker size, strong sexual dimorphism exists in the dentition of the sucker ring: the

dentition of the sucker ring of enlarged suckers in males conspicuously differs from that of the females and the nonenlarged suckers in males.

The structure of the cement body and the sperm mass of the spermatophore of this species is simple in appearance, with no obvious ornamentation, as seen in the preceding species or in *Sepietta oweniana* (d'Orbigny in Férussac and d'Orbigny, 1841; cf. figs 5a, b, 12a; Øresland and Oxby, 2021, figs 59–61).

As in the preceding species, the ranges of the morphometric indices are wide (Tables 3–4). This is certainly due to the range of the state of specimens prior to and during fixation and preservation. With such a wide range of values, it is of dubious value to use them to delineate a specific index for the species.



Figure 13. Distributional map of Dextrasepiola taenia n. gen. & n. sp. (blue) and Amutatiola macroventosa n. gen. & n. sp. (red).

Table 5. Comparison of genera of Sepiolinae (after Bello, 2020 and present results)

					Г	г		Γ	ľ		
	_	[Steenstrup, 1887	Septend Naef, 1912	Naef, 1921	Bello, 2020	Bello, 2020 Bello, 2020	0		,	Amutationa n.gen.
	- 1	nalf	led; fin h half le length	rounded or bluntly angled laterally; fin length about half mantle length	bluntly angled laterally; fin length about half mantle length	_ +	1	vith large anterior lobe, may reach anterior mantle margin; fin length about 50–66% mantle mantle	_ #	rounded with large anterior lobe, not reaching anterior mantle margin; fin length about 50–80% mantle length	rounded with large anterior lobe, not reaching anterior mantle margin; fin length about 40-66% mantle length
Arm suckers	iate on I to III at least imally on IV	biseriate on all arms	4 longitudinal series, exceptionally in 8 series	biseriate on all arms	biseriate on all arms	biseriate on all arms	biseriate on lall arms	te on	biseriate on all arms	biseriate on all biseriate on all arms	biseriate on all arms
Club suckers	linal	8–10 longitudinal	numerous 12 or more minute suckers longitudinal in a few tens of series longitudinal series series		16 longitudinal series	8 longitudinal series	8 4–8 longitudinal longitudinal series series		6–14 longitudinal series	4-8 longitudinal series	4–8 Iongitudinal series
Nuchal commissure (mantle-head occipital band)	narrow, not reaching over ocular globes	narrow, not reaching over ocular globes	ding over r globes	narrow, not narrow, not reaching over reaching over ocular globes ocular globes		narrow, not reaching over ocular globes	narrow, not reaching over ocular globes	narrow, not reaching over ocular globes	broad, extending over ocular globes	narrow, not reaching over ocular globes, about 25–40% of its width	moderately wide, not reaching over ocular globes, about 38–59% of its width
Photophores on ventral surface of ink-sac	one pair, kidney-shaped	absent	one pair, kidney-shaped	absent	one single, bipartite, oval-shaped	one pair, kidney- shaped	one single, cordiform	one pair, kidney- shaped	one pair, kidney- shaped	one pair, dumbbell- shaped	one pair, dumbbell- shaped or elongated kidnev-shaned
Gladius		absent	absent	present,	absent	present,	absent	absent	absent	absent	absent
Ventral mantle	slightly sinuate, without any deep funnel indentation	slightly sinuate, is without any deep is funnel indentation	slightly sinuate, without any deep funnel indentation	any nnel ion	slightly sinuate, without any deep funnel indentation	ep ion iy	slightly sinuate, without any deep funnel indentation	slightly sinuate, without any deep funnel indentation	faintly sinuate slightly or with sinuate, slightly deep without funnel deep fu indentation indenta	any nnel iion	slightly sinuate, without any deep funnel indentation
Hectocotylized left arm I arm in male tripartite	left arm I, tripartite	left arm I, tripartite	left arm I, thicker than right arm I, bipartite	left arm I, tripartite	left arm I, tripartite	left arm I, tripartite	left am I, I	left arm I, tripartite	bipartite	right arm I, tripartite	No hectocotylized arm; some arm suckers in mature males grossly enlarged

Amutatiola n.gen.	Ī	1
Dextrasepiola Amutatiola n.gen. n.gen.	with five suckers in two series	long, fleshy, tape-like, formed by fusion of two adjoining sucker stalks, no trace of suckers on tape-like structure, no hook-like structure on arm
0	occupying 50–66% of arm, with regular suckers	pedicel of 3rd long, fleshy, sucker in tape-like, ventral series formed by lengthened, fusion of two papilla-like, adjoining may bear sucker stalks vestigial no trace of suckers at its suckers normal structure, no normal hook-like structure on arm
Lusepiola Bello, 2020	with four regular suckers in two series	with pedicel of 3 modified sucker in sucker-less ventral serie pedicels: two lengthened, ventral papilla-like pedicels may bear hom-like, vestigial aligned, sucker at its directed tip, other distally and suckers slightly normal laterally, and reach other and directed ventrally, adhering to oral arm surface and to base of both ventral homs to form a concave pad
Boletzkyola Lusepiola Bello, 2020 Bello, 2020	with one incomplete transverse series of suckers (only ventral one is present)	
Adinaefiola Boletzkyola Lusepiola Bello, 2020 Bello, 2020 Bello, 202	either with three suckers, two ventral and one dorsal, or two ventral suckers only	with modified suckerless pedicels: two ventral pedicels horn- or two dorsal pedicels separate from ventral ones, fused with each other and distally directed between two series of suckers of distal part, additional dorsal pedicels projecting toward right arm I
Rondeletiola Naef, 1921	with three suckers, two ventral and one dorsal	with transverse formation of two ventral and two dorsal modified suckerless pedicels all four of them fused at their bases, ventral-most strongly developed hook-like, others hardly developed, dorsal pedicels forming most part of transverse crest
Sepietta Naef, 1912	with three or four suckers, two ventral and one or two dorsal	with with transverse transv formation of format two wentral two ventral and two dorsal modified suckerless pedicels of pedices of development, bases, all four of ventral-most them fused a strong their bases, development hook-shaped dorsal hook-shaped dorsal hook-shaped dorsal development pedice formin part of part of transverses.
Euprymna Steenstrup, 1887	occupying 20–50% of arm, with regular suckers	1—3 modified pedicels lengthened papilla-like, may bear vestigial suckers, in third to fifth position of ventral sucker series
Inioteuthis Verrill, 1881	with three suckers, two ventral and one dorsal	broadly enlarged, ear-shaped, involving about list devental modified sucker pedicels; dorsal spedicels; dorsal spedicels dorsally ioined by a broad web proximally crossing arm oral face to reach ventral formation of three hom-like pedicels, connected with each other by narrow web, so that a webbed structure delimits meso-proximally a hollow; proximal hom-like pedicels of ventral row followed distally by a void hence by a bout four deeply modified pedicels combined into a trough-like formation
Sepiola Leach, 1817	with three suckers, two ventral and one dorsal	with transverse formation of two ventral and two dorsal modified suckerless pedicels, all four of them lengthened and fused with each other throughout their length (few additional dorsal modified pedicels may be present mesially to transverse formation)
	Basal part of hectocotylus	apparatus apparatus

Amutatiola n.gen.	1	closed type, pouch-like, opening at level of base of left	Amutatiola macroventosa gen. nov., sp. nov. by monotypy
Dextrasepiola Amutatiola n.gen. n.gen.	biserial suckers to arm tip (19 suckers in holotype, 23 suckers in paratype 2)	open type, roughly ear-shaped	Dextrasepiola taenia gen. nov., sp. nov. by monotypy.
Eumandya Bello, 2020	occupying 33–50% of arm distally, with lengthened columnar sucker pedicels, closely packed longitudinally bearing reduced suckers and not connected with each other by any web	pouch-like	Euprymna pardalota Reid, 2011, designated by Bello
Bello, 2020 Bello, 2020	with sucker pedicels of both series leaf-like, lengthened, widened, triangular- or squarish-shaped, flattened proximodistally, their bases inserted transversally on arm oral surface, except for distalmost suckers with regular short pedicels; in seeveral preserved specimens distal part rodated towards right dorsal arm dorsal arm	pouch-like	Sepiola birostrata Sasaki, 1918, designated by Bello (2020)
Bello, 2020 Bello, 202	with several suckers missing proximally in ventral row and four enlarged suckers in dorsal series	pouch-like with wide opening	Sepiola knudseni Adam, 1984, designated by Bello (2020)
Adinaefiola Bello, 2020	with some enlarged suckers in either ventral or both series	roughly ear-shaped, devoid of cover	Sepiola ligulata Naef, 1912, designated by Bello (2020)
Rondeletiola Naef, 1921	first two ventral suckers lacking, some proximal suckers enlarged in both series	roughly ear-shaped, devoid of cover	Sepietta minor Naef, 1912, by monotypy
Sepietta Naef, 1912	with some proximal suckers of dorsal row enlarged, wide space between two sucker series	roughly ear-shaped, devoid of cover	Sepiola oweniana d'Orbigny in Férussac & d'Orbigny, 1841, by monotypy
Euprymna Steenstrup, 1887	occupying 50–80% of arm distally, with lengthened columnar sucker pedicels, closely packed to form longitudinal palisades, bearing at tip embedded suckers that are partially covered by fleshy caps, mumber of palisades proximally equal to that of regular sucker rows but regular sucker rows but reduced toward arm extremity	pouch-like	Inioteuthis morsei Verrill, 1881, by subsequent designation
Inioteuthis Verrill, 1881	with several enlarged suckers in ventral series, first one very large, laying on trough-like structure of copulatory apparatus	pouch-like	Inioteuthis japonica Verrill, 1881, by subsequent designation
Sepiola Leach, 1817	with some enlarged suckers in dorsal series	roughly ear-shaped, devoid of cover	Sepiola rondeletii Leach, 1817, by monotypy
	Distal part of hectocotylus	Female bursa copulatrix	Type species

Note: AS, Aegean Sea; CS, Catalan Sea; EA, eastern Atlantic Ocean; IO, Indian Ocean; Indo-Pac, Indo-Pacific; MS, Mediterranean Sea; NEA, north-eastern Atlantic Ocean; NS, North Sea; Pac, Pacific Ocean; RS, Red Sea.

Discussion

Bello (2020) revised the subfamily Sepiolinae based on analyses of the structures of the hectocotylised arms, and split the old *Sepiola* Leach, 1817, into four genera: *Sepiola* Leach, 1817, *Adinaefiola* Bello, 2020, *Boletzkyola* Bello, 2020, and *Lusepiola* Bello, 2020. The genus *Euprymna* Steenstrup, 1887, was split into two genera: *Euprymna* and *Eumandya* Bello, 2020. According to Bello's (2020) revision, Sepiolinae includes nine genera, of which seven genera – *Sepiola*, *Adinaefiola*, *Boletzkyola*, *Inioteuthis*, *Lusepiola*, *Rondeletiola* and *Sepietta* – have a tripartite hectocotylus, and the remaining two genera – *Euprymna* and *Eumandya* – are characterised by the hectocotylus (left arm I) with sucker-stalks in its distalmost portion modified into a palisade-like structure.

Both new genera, *Dextrasepiola* and *Amutatiola*, share some basic features with the other members of Sepiolinae: mantle fused dorsally with head, biseriate arm suckers, bilobed kidney- or dumbbell-shaped visceral light organ (the latter two features are deemed plesiomorphic character states by Bello, 2020), reduced arm web, ventral mantle does not produce into a ventral shield (unlike in Heteroteuthinae) and small body size.

Dextrasepiola n. gen. also shares the same type of hectocotylisation with the tripartite-hectocotylus genera, but it conspicuously differs from the other because of its unique peculiarity that the right dorsal arm of the male is modified into a copulatory arm instead of the left one. In this genus, the copulatory apparatus is also unique in being formed by two suckerless stalks modified and fused into a tape-like structure. Amutatiola n. gen. is also unique among Sepiolinae in lacking an evident hectocotylised dorsal arm in male and instead having some arm suckers enormously enlarged. Table 5 shows the comparison of features of all 11 genera of Sepiolinae.

In a recent report, Sanchez et al. (2021) concluded that the subfamily Sepiolinae is split into Indo-Pacific and Atlantic-Mediterranean lineages, the former characterised by a closed type bursa copulatrix, and the latter by an open type bursa. The discovery of the *Dextrasepiola taenia* n. gen. and n. sp., (i.e. a sepioline genus and species with an open type bursa copulatrix) is not consistent with that systematic-biogeographic pattern.

With Amutatiola macroventosa n. gen. and n. sp., the lack of a normal sepioline hectocotylus in males is a unique feature which co-occurs with the enlargement of several suckers in the male arms. The enlargement of some suckers is also found in the mature males of several species of Euprymna (Norman and Lu, 1997), as well as in some Rossiinae and Heteroteuthinae (Nesis, 1982). Contrary to Dextrasepiola taenia n. gen. and n. sp., females of Amutatiola macroventosa n. gen. and n. sp. display a closed bursa copulatrix, which parallels the other Indo-Pacific sepioline genera and species.

Based on the present results and descriptions of the new sepioline genera and species, the definition of the subfamily Sepiolinae should be widened to include *Dextrasepiola* and *Amutatiola*. This can be done by amending the character state of Hectocotylisation for Sepiolinae in Table 1 to "left or right (in *Dextrasepiola*) dorsal arm hectocotylised or no hectocotylisation (in *Amutatiola*)" and by adding the character "bursa copulatrix" as "bursa copulatrix in female on left side of

mantle cavity in all Sepiolinae except *Dextrasepiola* (on right side)". Subfamilies Heteroteuthinae and Rossinae do not have well-differentiated bursa copulatrix, spermatophores are implanted on the body or on a patch of wrinkled tissue near the opening of the oviduct (Hoving, et al., 2008, 2009; Naef, 1923).

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References

- Bello, G. 2013. Description of a new sepioline species, *Sepiola bursadhaesa* n. sp. (Cephalopoda: Sepiolidae), from the Catalan Sea, with remarks and identification key for the *Sepiola atlantica* group. *Scientia Marina* 77: 489–499.
- Bello, G. 2020. Evolution of the hectocotylus in Sepiolinae (Cephalopoda: Sepiolidae) and description of four new genera. European Journal of Taxonomy 655: 1–53
- Bello, G. and Salman, A. 2015. Description of a new sepioline species, Sepiola boletzkyi n.sp. (Cephalopoda: Sepiolidae), from the Aegean Sea. European Journal of Taxonomy 144: 1–12.
- Heij A. de, and Goud J. 2010. *Sepiola tridens* spec. nov., an overlooked species (Cephalopoda: Sepiolidae) living in the North Sea and north-eastern Atlantic Ocean. *Basteria* 74: 51–62.
- Hoving, H.J.T., Laptikhovsky, V., Piatkowski, U., and Önsoy, B. 2008. Reproduction in *Heteroteuthis dispar* (Rüppell, 1844) (Mollusca: Cephalopoda): a sepiolid reproductive adaptation to an oceanic lifestyle. *Marine Biology* 154: 219–230.
- Hoving, H.J.T., Nauwelaerts, B., Van Genne, B., Stamhuis, E.J., and Zumholz, K. 2009. Spermatophore implantation in Rossia moelleri Steenstrup, 1856 (Sepiolidae; Cephalopoda). Journal of Experimental Marine Biology and Ecology 372: 75–81.
- Lu, C.C. 2001. Cephalopoda. Pp.129–308 in: Wells, A. and Houston,
 H.W.K. (eds) Zoological Catalogue of Australia. Vol. 17.2.
 Mollusca: Aplacophora, Polyplacophora, Scaphopoda,
 Cephalopoda. CSIRO Publishing: Melbourne. xii, 353 pp.
- Lu, C.C., and Boucher-Rodoni, R. 2006. A new genus and species of sepiolid squid from the waters around Tonga in the central South Pacific (Mollusca: Cephalopoda: Sepiolidae). *Zootaxa* 1310: 37–51.
- Lu, C.C., and Dunning, M.C. 1998. Subclass Coleoidea Bather, 1888. Pp.
 499–563 in: Beesley, P.L., Ross, G.J.B., and Wells, A. (eds)
 Mollusca: The Southern Synthesis. Fauna of Australia. Volume 5.
 CSIRO Publishing: Melbourne. Part A. xvi, 563 pp.
- Lu, C.C., and Phillips, J.U. 1985. An annotated checklist of the Cephalopoda from Australian waters. Occasional Papers of the Museum of Victoria 2: 21–36.
- Lu, C.C., and Roper, C.F.E. 1979. Cephalopods from deepwater dumpsite 106 (Western Atlantic): vertical distribution and seasonal abundance. Smithsonian Contributions to Zoology 288: 1–36.
- Naef, A. 1912a. Teuthologische Notizen. 3. Die Arten du Gattungen Sepiola und Sepietta. Zoologischer Anzeiger 39: 262–271.
- Naef, A. 1912b. Teuthologische Notizen. 7. Zur Morphologie und Systematik der Sepiola- und Sepietta- Arten. Zoologischer Anzeiger 40: 78–85.

- Naef, A. 1923. Die Cephalopoden, Systematik. Fauna und Flora des Golfes von Neapel 35: 1–863. Israel Program for Scientific Translation: Jerusalem [English translation].
- Nesis, K.N. 1982. Cephalopods of the world. English Translation from Russian. Levitov, B.S. (Transl.), Burgess, L.A. (ed.) (1987). T.F.H. Publications: Neptune city. 351 pp.
- Norman, M.D., and Lu, C.C. 1997. Redescription of the southern dumpling squid *Euprymna tasmanica* and a revision of the genus *Euprymna* (Cephalopoda: Sepiolidae). *Journal of the Marine Biological Association of the United Kingdom* 77: 1109–1137.
- Øresland, V., and Oxby, G. 2021. A photo-illustrated dissection guide for bobtail squids. Divers and Scientists West Coast Sweden, Guide No.1. 122 pp.
- Roper, C.F.E., and Voss, G.L. 1983. Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum of Victoria* 44: 48–63.
- Sanchez, G., Fernández-Álvarez, F.Á., Taite, M., Sugimoto, C., Jolly, J., Simakov, O., Marlétaz, F., Allcock, L., and Rokhsar, D. 2021. Phylogenomics illuminates the evolution of bobtail and bottletail squid (order Sepiolida). *Communications Biology* 4: 819.
- Sanchez G., Jolly J., Reid A., Sugimoto C., Azama C., Marlétaz F., Simakov O., and Rokhsar D.S. 2019. New bobtail squid (Sepiolidae: Sepiolinae) from the Ryukyu islands revealed by molecular and morphological analysis. *Communications Biology* 2: 465.