FOLIA MALACOLOGICA
Folia Malacol. 26(3): 125–147
ISSN 1506-7629 (print) • ISSN 2300-7125 (on-line)
The Association of Polish Malacologists
Faculty of Biology, Adam Mickiewicz University
Bogucki Wydawnictwo Naukowe
Poznań, September 2018
https://doi.org/10.12657/folmal.026.014

A NEW SPECIES OF *SEPIA* (CEPHALOPODA: SEPIIDAE) FROM SOUTH AFRICAN WATERS WITH A RE-DESCRIPTION OF *SEPIA DUBIA* ADAM ET REES, 1966

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ABSTRACT: A new species of cuttlefish *Sepia shazae* n. sp. is described from South Africa. It is one of the commonest small *Sepia* species in South African waters occurring from 29°48'S in the north to 25°E in the east, between 200 and 700 m (only the third *Sepia* species recorded deeper than 600 m). It is recognised by: four papillae clusters dorsally on the head between the eyes; tubercles, warts and prominent clusters dorsally on mantle; skin between these structures smooth and shiny; cuttlebone lightly calcified, thin and fragile with thin inner cone and broad outer cone. *S. shazae* has been confused with *Sepia dubia* Adam et Rees, 1966 and is well represented in the holdings of the Iziko Museum, Cape Town (SAMC) as "*S. dubia*(?)". *S. dubia* is re-described here on the basis of the second known individual, and is recognised by: four turret-clusters on dorsal head; two turrets transversely on mid-dorsal mantle; small warts covering dorsal body; cuttlebone heavily calcified, exceptionally broad, especially posterior phragmocone and outer cone. The holotype of *S. shazae* is deposited in the South African Institute of Aquatic Biodiversity (SAIAB) and paratypes in SAMC and the Natural History Museum (NHMUK), London. The new individual of *S. dubia* is deposited in SAIAB (the holotype is housed in NHMUK).

KEY WORDS: small cuttlefish, new species, re-described species, South African waters, *Sepia*, *Hemisepius*

INTRODUCTION

Sepia (Sepiidae) and *Octopus* (Octopodidae) are two exceptionally speciose genera in the class Cephalopoda, a class that is renowned for containing many monotypic genera. Currently *Sepia* contains 106 nominal species (WORMS 2018). The following species groups of uncertain status (sometimes referred to as sub-genera) have been recognised within *Sepia*: *Sepia* s. str., *Acanthosepion, Rhombosepion, Anomalosepia, Doratosepion* and *Hemisepius* (KHROMOV 1998a).

The genus *Hemisepius* was erected by STEENSTRUP in 1875 for *Hemisepius typicus* Steenstrup, 1875. Without much explanation ADAM & REES (1966) relegated *Hemisepius* to subgeneric status within *Sepia*, containing *S. (H.) typica* and *S. (H.) dubia* Adam et Rees, 1966. ROELEVELD (1972) discussed the relationship among southern African sepiids in some detail. She retained the subgenus *Hemisepius* with only two species (*S. typica* and *S. dubia*), while noting that *S. robsoni* (Massy, 1927) and *S. faurei* Roeleveld, 1972 share a number of characters with *Hemisepius* and may represent intermediate links "in the transition from *Sepia* to *Hemisepius*" (p. 257). The discovery of *S. pulchra* Roeleveld et Liltved, 1985 raised the number of small sepiids in this problematic group to five. ROELEVELD & LILTVED (1985) noted that although these five small sepiids share a number of characters, there are also some worrying morphological differences in important structures such as cuttle-

Ministry of Science and Higher Education
Republic of Poland

Folia Malacologica is funded by the Ministry of Science and Higher Education, Republic of Poland, under agreement no 534/P-DUN/2018 of April 4th, 2018 allocated to the activities for disseminating science:
Task 1: Preparation of English versions of publications (sum funded by DUN 12,000 PLN) and
Task 2: Digitalisation of publications and scientific monographs to enable their open access in the Internet (sum funded by DUN 11,070 PLN).

bones and armature of arms. Despite this conclusion, KHROMOV (1998a) retained *Hemisepius* as a separate unit containing *S. typica*, *S. dubia*, *S. pulchra*, *S. faurei* and *S. robsoni*, with the following characteristics: "Mantle length at maturity <30 mm. Anterior ventral mantle emargination deep, either rectangular or trapezoidal. Dorsal mantle margin slightly produced anteriorly, short, wide. Suckers biserial on all arms. Spine absent. Inner cone markedly reduced, with short limbs."

We have participated in numerous demersal surveys conducted in southern African waters by RS Africana (1982–2017) and R/V Dr Fridtjof Nansen (2000–2016). Extensive new small sepiid material was collected during these surveys and only a fraction of this material has been used in the present paper. It is hoped that this material in its entirety will help to chart research towards resolving the status and relationships between the small sepiids that have traditionally been placed in the so-called *Hemisepius* complex. These small sepiids appear to form a hitherto unrecognised large group (or groups) of mostly deep water cephalopods, including *S. shazae* n. sp. a species that is very common and widely distributed in the southern Benguela and is only now recognised as a new to science.

MATERIAL AND METHODS

Specimens of *Sepia shazae* were collected using bottom trawls during the course of demersal research surveys conducted off the west and south coasts of South Africa by the research vessels RS Africana and R/V Dr Fridtjof Nansen. Details of bottom trawl gear, trawling, sorting and processing of the catch, and references thereof are given in AXELSEN & JOHNSEN (2014), although note that they erroneously record the codend mesh size of the gear deployed by the RS Africana, the correct mesh sizes are 112 mm codend with 35 mm small mesh liner.

Measurements and counts (see: Table 1 for definitions) follow ROELEVELD (1972), ROELEVELD & LILTVED (1985), and LU & REID (1997) and were taken from preserved specimens. Dorsal (ML) and ventral (MLv) mantle length was measured to the nearest mm below using slide callipers. Fin length (FL) was measured by placing a thread along the base of the fin from the anterior edge and marking the position of the posterior end of the fin, the length of the thread was then measured on a metal ruler. All other measurements were taken using dividers or a graticule in a stereo dissecting microscope at 10× magnification. Sucker diameters were measured at 40× magnification. Weights were taken from preserved specimens.

Table 1. Description of measurements and counts. Definitions follow ROELEVELD (1972), ROELEVELD & LILTVED (1985) and LU & REID (1997)

Abbreviation	Definition
AL1–AL4	**Arm Length**: length of the right (rt) or left (lt) arm of each designated (1 to 4) arm pair, measured from the inner base of the most proximal sucker to the tip of the arm.
AMH	**Anterior Mantle to Head:** length of anterior projection of the dorsal mantle margin measured along the midline from the anterior-most point of the dorsal mantle to a transverse line joining the posterior-most points of the dorsal mantle margin on either side of the midline
AS1–AS4	**Arm Sucker diameter**: diameter of the largest sucker on the right (rt) or left (lt) arm of each designated (1 to 4) arm pair
ASC1–ASC4	**Arm Sucker Count**: total number of suckers on the right (rt) or left (lt) arm of each designated (1 to 4) arm pair
ASl4	**Arm Sucker left 4**: diameter of the largest sucker on the hectocotylised (left ventral) arm
ASl4m	**Arm Sucker left 4 minimum**: diameter of the smallest (modified) sucker on the hectocotylised arm
CES	**Club Edge Suckers**: number of suckers along the edge of the club from the basal sucker to the most distal sucker
ClRC	**Club Row Count**: number of suckers in a single transverse row across the middle of the tentacular club
ClS	**Club Sucker diameter**: diameter of the largest sucker on the tentacular club
CS#	**Club Sucker count**: total number of suckers on a tentacular club
CTR#	**Club Transverse Row Number**: number of transverse rows of suckers on the tentacular club
FFu	**Free Funnel length**: measured from the anterior funnel opening to the dorsal attachment of the funnel to the head
FIa	**Fin Insertion anterior**: distance from the anterior mantle margin to the anterior junction of fin and mantle
FIp	**Fin Insertion posterior**: distance between the posterior junction of the left and right fins with the mantle

Table 1 continued

FL	**Fin Length**: measured from anterior to posterior insertion along the curve of the mantle at the base of the fin
FuL	**Funnel Length**: measured along the ventral midline from the anterior funnel opening to the posterior margin (the ventral mantle has to be cut to expose the posterior edge of the funnel)
FW	**Fin Width**: measured from the lateral edge of the mantle to the free edge of the fin
HcL	**Hectocotylus Length**: length of the hectocotylised (left ventral) arm measured from the inner base of the most proximal sucker to the tip of the arm
HL	**Head Length**: from the anterior tip of the nuchal cartilage to the anterior edge of the dorsal interbranchial membrane between the dorsal arm pair
HW	**Head Width**: the greatest width of the head (generally across the eyes)
L	**Length** of the cuttlebone along the mid-line
MHL	**Modified Hectocotylus Length**: of the modified (proximal) portion of the hectocotylus measured from the inner base of the most proximal sucker to the inner base of the first normal sucker
ML	**Mantle Length (dorsal)**: measured along the midline from the anterior edge of the dorsal mantle to the posterior end of the mantle
MLv	**Mantle Length (ventral)**: measured along the midline from the midpoint of the ventral emargination to the posterior end of the mantle
Tcl	**Tentacular club length**: measured from the basal sucker to the tip of the club
TL	**Tentacle Length**: measured from the point of emergence from the tentacular sac to the tip of the club
TrRC	**Transverse Row Count**: Number of suckers in a single longitudinal row across the tentacular club

Bodies of most small sepiids in southern African waters have various complex skin patterns that are important for correctly determining species. We therefore developed the following new definitions (or their new combinations) for some of these structures:

- **Warts** are simple, solid, rounded, flat, and low excrescences on the skin, that may be quite large.
- **Tubercles** are simple projections or protuberances, that are sharp or rounded. They may be very long, or short, but never flat.
- **Papillae** are prominent, complex protuberances in following forms:
  - **Turrets** (see: Roeleveld & Liltved, 1985) where tubercles and/or warts are on top of each other;
  - **Clusters** where tubercles and/or warts are next to each other, forming a distinct unit;
  - **Turret-clusters** where turrets and clusters are combined in one distinct unit.

Most of the photographs were taken using Canon EOS 7D Mk I and Mk II cameras, or Canon EOS 650 camera coupled with Nikon stereomicroscope using a specially engineered ring. Images of sucker rings and spermatophore were taken using a Nikon SMZ18 stereomicroscope with a P2-SHR Apo1x lens and NIS Elements D 4.60.00 (build1171) 64bit software. Images of the radula of *S. shazae* and *S. dubia* were taken using a Nikon SMZ1500 stereo dissecting microscope fitted with a Nikon U3 Digital Sight camera system and the Nikon Imaging Systems Basic Research software package.

Abbreviations for museums holding material are: BMNH – specimens at NHMUK catalogued prior to 1992; NHMUK – Natural History Museum London, UK; SAIAB – South African Institute of Aquatic Biodiversity, Grahamstown, South Africa; SAMC – Iziko, South African Museum in Cape Town, South Africa.

SYSTEMATIC ACCOUNTS

SEPIA SHAZAE SP. NOV.

(Figs 1–27, Tables 2–3)

Sepia sp. A (Leslie & Lipinski 2018: p. 345)

Holotype (Fig. 1): SAIAB 205824 – mature male ML 30 mm, TW 6.2 g. R/V Dr Fridtjof Nansen demersal survey 2011401, 06 Feb. 2011, Station 94, 31°06'06.0"S, 16°34'06.0"E to 31°05'12.0"S, 16°33'42.0"E, bottom trawl 286–285 m.

Paratypes: NHMUK 20180276 – male ML 22 mm, TW 3.1 g. R/V Dr Fridtjof Nansen demersal survey 2013401, 04 Feb. 2013, Station 99, 31°24'06.0"S, 16°41'24.0"E to 31°25'30.0"S, 16°42'00.0"E, bottom trawl 299–302 m; NHMUK 20180278 – female ML 32 mm, TW 7.3 g. R/V Dr Fridtjof Nansen demersal survey 2008401, 10 Feb. 2008, Station 1529, 33°15'24.0"S, 17°15'36.0"E to 33°17'00.0"S, 17°16'00.0"E, bottom trawl 465–441 m; SAIAB 205826 – male 28 mm, 4.6 g, R/V Dr Fridtjof Nansen demersal survey 2011401, 06 Feb. 2011, Station 93, 31°04'06.0"S, 16°39'30.0"E

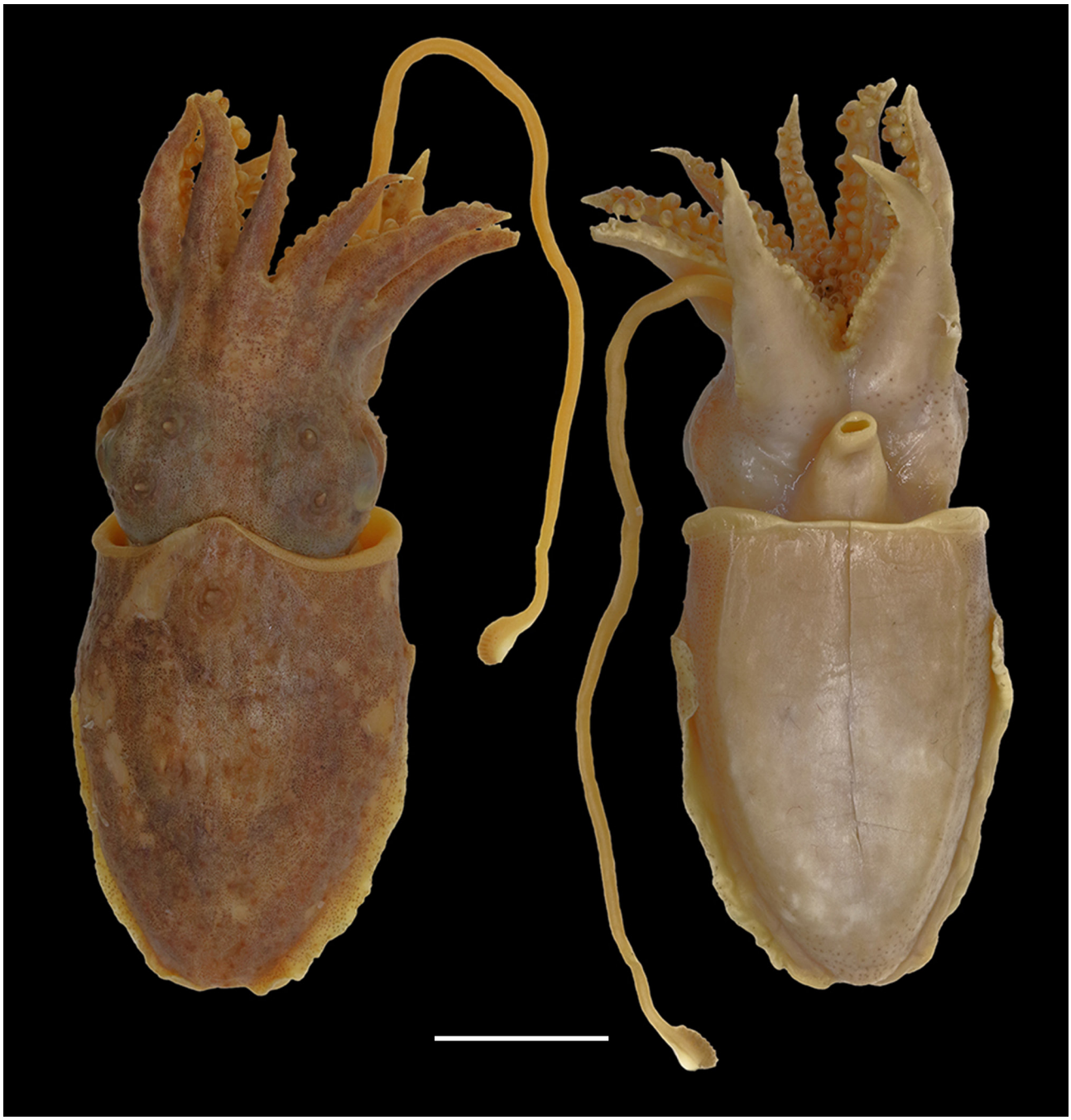


Fig. 1. Dorsal (left) and ventral (right) views of the holotype of *Sepia shazae* sp. nov. (SAIAB 205824, male ML 30 mm). Scale bar 10 mm

to 31°02'42.0"S, 16°38'36.0"E, bottom trawl 256–254 m; SAIAB 205827 – female ML 29 mm, TW 6.3 g and SAIAB 205822 – female ML 31 mm TW 9.0 g, R/V Dr Fridtjof Nansen demersal survey 2013401, 07 Feb. 2013, Station 116, 30°30'48.0"S, 15°25'00.0"E to 30°29'42.0"S, 15°23'36.0"E, bottom trawl 301 m; SAMC A090207 – male ML 30 mm, TW 6.6 g. R/V Dr Fridtjof Nansen demersal survey 2006402, 20 Feb. 2006, Station 1265, 31°46'00.0"S, 16°56'00.0"E to 31°45'30.0"S, 16°54'30.0"E, bottom trawl 285–279 m; SAMC A090208 – female ML 28 mm, TW 6.6 g. R/V Dr Fridtjof Nansen demersal survey 2012401, 15 Feb. 2012, Station 102, 31°04'00.0"S, 15°58'24.0"E to 31°03'30.0"S, 15°56'36.0"E, bottom trawl 357–354 m.

Additional material: NHMUK 20180277 – 1 male: 22 mm 2.8 g, 5 females: 19 mm 2.6 g, 21 mm 3.6 g, 26 mm 4.4 g, 27 mm 5.6 g, 29 mm 5.8 g, R/V Dr Fridtjof Nansen demersal survey 2013401, 04 Feb. 2013, Station 99, 31°24'06.0"S, 16°41'24.0"E to 31°25'30.0"S, 16°42'00.0"E, bottom trawl 299–302 m (same station as NHMUK 20180276); NHMUK 20180279 – 1 male: 26 mm 4.3 g, 2 females: 27 mm 7.1 g, 30 mm 6.2 g, R/V Dr Fridtjof Nansen demersal survey 2008401, 10 Feb. 2008, Station

Table 2. Measurements (mm), weight (g) and counts recorded for characters of the holotype and of the smallest, average and largest non-type male and female *Sepia shazae* sp. nov. examined (selected from the whole material available). See: Table 1 for a description of the characters

Catalogue number	SAIAB 205824 Holotype	SAIAB 206657	SAIAB 206659	SAIAB 206661	SAIAB 206658	SAIAB 206656	SAIAB 206659
Sex	M	M	M	M	F	F	F
Maturity	V	V	V	V	IV	V	V
Weight	6.2	2.2	4.4	4.4	1.7	7.0	7.9
ML	30	17	23	29	17	27	33
MLv	28	16	22	24	17	26	31
HL	15	10	13	15	11	15	17
HW	16	12	12	14	10	13	17
AMH	1.9	1.4	2.3	2.2	1.4	1.3	2.9
FL	25	12	19	23	18	27	30
FW	2.4	1.3	1.5	2.6	1.0	1.4	2.9
FIa	5.2	3.8	4.3	3.3	3.3	3.8	4.8
FIp	2.2	1.9	1.4	2.4	1.1	1.4	3.8
FFu	4.8	3.3	3.8	5.0	3.3	4.5	3.8
FuL	11	9	9	10	8	12	13
AL1-rt	14	7	10	11	7	12	13
AL2-rt	15	7	13	13	7	11	14
AL3-rt	15	8	14	14	8	11	14
AL4-rt	17	10	13	13	9	12	14
HcL	15	10	13	14	–	–	–
MHL	9	5	8	10	–	–	–
TL	66	34	43	56	–	77	64
Tcl	3.1	3.2	3.0	4.2	–	3.8	3.9
AS1-rt	0.9	1.2	0.6	0.7	0.5	0.6	0.7
AS2-rt	1.2	1.0	1.0	1.3	0.5	0.7	0.7
AS3-rt	1.1	1.0	0.9	1.1	0.6	0.6	0.7
AS4-rt	1.1	0.9	0.6	0.9	0.5	0.6	0.6
ASl4	0.9	0.6	0.6	0.6	–	–	–
ASl4m	0.2	0.2	0.2	0.1	–	–	–
ClS	0.3	0.4	0.2	0.3	–	0.3	0.3
ASC1-rt	30	18	33	24	36	37	44
ASC2-rt	28	23	42	24+	40	52	50
ASC3-rt	31	25	45	36	51	46	50
ASC4-rt	46	32	46	37+	50	29+	60
CS#	56	46	53+	53	n/a	56+	48
CTR#	15	–	12	–	–	14	14
CES	18	–	16	19	–	16	18

1529, 33°15'24.0"S, 17°15'36.0"E to 33°17'00.0"S, 17°16'00.0"E, bottom trawl 465–441 m (same station as NHMUK 20180278); SAIAB 205828 – 3 males: 22 mm 3.6 g, 28 mm 5.3 g, 28 mm 5.9 g, 2 females: 29 mm 6.3 g, 33 mm 7.1 g, R/V Dr Fridtjof Nansen demersal survey 2011401, 06 Feb. 2011, Station 94, 31°06'06.0"S, 16°34'06.0"E to 31°05'12.0"S 16°33'42.0"E, bottom trawl 286–285 m (same station as holotype); SAIAB 206675 – 3 females: 27 mm 5.9 g, 27 mm 6.4 g, 28 mm 6.8 g, R/V Dr Fridtjof Nansen demersal survey 2013401, 07 Feb. 2013, Station 116, 30°30'48.0"S, 15°25'00.0"E to 30°29'42.0"S, 15°23'36.0"E, bottom trawl 301 m (same station as for paratypes SAIAB 205827 and SAIAB 205822); SAIAB 206665 – 1 female: 34 mm, 8.0 g, R/V Dr Fridtjof Nansen demersal survey 2007404, 05 Apr. 2007, Station 1399, 30°43'18.0"S, 15°25'24.0"E to 30°42'06.0"S, 15°24'24.0"E, bottom trawl 399–397 m; SAIAB 206664 – 1 male: 22 mm 2.3 g, R/V Dr Fridtjof Nansen demersal survey 2007402, 05 April 2007, Station 1400, 30°40'24.0"S, 15°25'00.0"E to 30°39'36.0"S, 15°24'12.0"E, bottom trawl 346–344 m; SAIAB 2066660 – 1 male: 19 mm 2.4 g, 1 female: 34 mm 8.5 g, R/V Dr Fridtjof Nansen demersal survey 2004401, 25 April 2004, Station TS 830–025, 28°54'00.0"S, 14°24'00.0"E, bottom trawl

Table 3. Minimum (Min), maximum (Max), mean, standard deviation (Std) and sample size (n) for mantle length (ML, mm) and indices (expressed as proportion of ML except for MHL, which is reported as proportion of Hcl) for male and female *Sepia shazae* sp. nov. examined. The values recorded for the holotype are given for comparison. Individuals for measurements were selected from the whole material available. Main criterion was the biological condition (not all specimens can be measured). See: Table 1 for a description of the characters

Character	Males						Females				
	Holotype	Min	Max	Mean	Std	n	Min	Max	Mean	Std	n
ML	30	17	30	24.4	3.84	14	17	33	27.6	4.45	16
MLv	0.93	0.83	0.98	0.92	0.05	14	0.74	0.99	0.90	0.08	16
HL	0.50	0.50	0.65	0.58	0.05	14	0.49	0.71	0.58	0.06	16
HW	0.53	0.48	0.71	0.56	0.06	14	0.44	0.60	0.53	0.05	16
AMH	0.06	0.04	0.10	0.07	0.02	14	0.03	0.13	0.08	0.03	16
FL	0.83	0.69	0.94	0.82	0.08	14	0.70	1.03	0.85	0.10	16
FW	0.08	0.05	0.09	0.07	0.01	14	0.05	0.12	0.08	0.02	16
FIa	0.17	0.11	0.25	0.18	0.03	14	0.12	0.22	0.16	0.03	16
FIp	0.07	0.04	0.12	0.07	0.02	14	0.03	0.20	0.08	0.04	14
FFu	0.16	0.13	0.24	0.17	0.03	14	0.11	0.22	0.17	0.03	16
FuL	0.38	0.34	0.52	0.43	0.05	14	0.37	0.49	0.42	0.04	16
AL1-rt	0.46	0.38	0.51	0.45	0.04	14	0.34	0.44	0.38	0.03	16
AL2-rt	0.50	0.40	0.60	0.50	0.05	13	0.38	0.53	0.42	0.04	16
AL3-rt	0.52	0.46	0.66	0.55	0.06	14	0.37	0.57	0.43	0.05	16
AL4-rt	0.56	0.45	0.62	0.55	0.05	14	0.38	0.56	0.47	0.04	16
HcL	0.50	0.48	0.70	0.56	0.06	14	–	–	–	–	–
MHL	0.66	0.54	0.73	0.65	0.05	14	–	–	–	–	–
TL	2.19	1.81	2.47	2.07	0.20	11	1.58	2.83	2.06	0.39	11
Tcl	0.10	0.09	0.19	0.14	0.03	13	0.11	0.23	0.15	0.04	12
AS1-rt	0.030	0.024	0.069	0.031	0.011	14	0.019	0.031	0.023	0.004	16
AS2-rt	0.040	0.034	0.058	0.044	0.007	14	0.019	0.033	0.025	0.004	16
AS3-rt	0.036	0.034	0.058	0.041	0.006	14	0.019	0.034	0.024	0.005	16
AS4-rt	0.036	0.025	0.052	0.036	0.007	14	0.016	0.030	0.024	0.004	16
ASl4	0.030	0.018	0.035	0.025	0.004	14	–	–	–	–	–
ASl4m	0.007	0.003	0.012	0.008	0.002	14	–	–	–	–	–
ClS	0.010	0.007	0.023	0.011	0.005	13	0.007	0.023	0.014	0.006	12
ASC1-rt	30	18	41	30.3	5.5	14	19	44	35.1	7.6	15
ASC2-rt	28	23	43	34.8	6.6	13	34	55	46.5	6.8	16
ASC3-rt	31	25	48	39.9	6.7	14	33	64	49.6	9.1	16
ASC4-rt	46	32	58	48.1	6	13	29	63	53	9.1	12
CS#	56	46	58	53.5	3.9	10	48	59	53.7	3.6	11
CTR#	15	10	15	12.4	1.5	9	7	15	12.9	2.3	10
CES	18	15	20	16.9	1.7	12	15	18	16.3	1.2	12

434–435 m; SAIAB 206657 – 3 males: 16 mm 2.2 g, 21 mm 3.7 g, 27 mm 5.3 g, 4 females: 20 mm 3.2 g, 21 mm 4.6 g, 23 mm 4.3 g, 24 mm 5.1 g, R/V Dr Fridtjof Nansen demersal survey 2008401, 09 Feb. 2008, Station 1527, 33°04'12.0"S, 17°31'06.0"E to 33°05'48.0"S, 17°31'12.0"E, bottom trawl 336–345 m; SAIAB 206663 – 1 female: ML 26 mm TW 6.4 g, R/V Dr Fridtjof Nansen demersal survey 2011401, 29 Jan. 2011, Station 46, 33°13'24.0"S, 17°17'42.0"E to 33°11'54.0"S, 17°17'54.0"E, bottom trawl 407–398 m; SAMC A090209 – 2 males: 22 mm 4.1 g, 22 mm 4.1 g, 1 female 25 mm 4.8 g, R/V Dr Fridtjof Nansen demersal survey 2006402, 20 Feb. 2006, Station 1265, 31°46'00.0"S, 16°56'00.0"E to 31°45'30.0"S, 16°54'30.0"E, bottom trawl 285–279 m (same station as SAMC A090207); SAMC A090210 – 1 female: 26 mm 5.3 g, R/V Dr Fridtjof Nansen demersal survey 2012401, 15 Feb. 2012, Station 102, 31°04'00.0"S, 15°58'24.0"E to 31°03'30.0"S, 15°56'36.0"E, bottom trawl 357–354 m (same station as SAMC A090208).

Diagnosis

Cuttlebone lightly calcified, thin and fragile; anterior part (~30% of length) triangular, pointed; posterior part broad, oval, rounded posteriorly; spine absent; thin chitin flange all round; last septum elevated (occupies ~20% of length); distinct mid-dorsal longitudinal ridge; phragmocone well defined, striae borderline approximately straight or slightly convex; inner cone thin, extends anteriorly into striated zone,

ventral part reduced; outer cone very broad, width decreasing anteriorly into upper limbs that end close to anterior tip of cuttlebone. Head with four papillae clusters dorsally between eyes with prominent tubercle in centre of each cluster; transverse tubercle row between eyes; 3–4 transverse tubercle rows dorsally at base of arms. Prominent tubercles on slightly raised triangular patch anterio-ventral of each eye, ventral tubercle largest. Dorsal mantle usually with three prominent clusters, but sometimes only large, long central tubercles present; one cluster on dorsal midline near anterior mantle margin, two medially on either side of midpoint of dorsal midline. Mantle covered in irregularly placed tubercles and few warts; skin between clusters, tubercles and warts smooth, shiny.

D e s c r i p t i o n

Small species; mean±SD ML males 24.4 ±3.84 mm, females 27.6 ±4.45 mm (Table 3). Mantle rather elongated, oval (more round in smaller animals), dorso-anterior margin generally straight wide Λ-shape (varies from close to 90° to broad angle, Fig. 2), ventro-anterior margin entire or slightly and broadly emarginated in both sexes (Fig. 3). Ventral margins of mantle with distinct keels (Fig. 3), keels

Fig. 2. Variation in dorsal colour and of the shape of the dorsal mantle margin in *Sepia shazae* sp. nov. From left to right: SAIAB 206661, female ML 29 mm; SAIAB 206665, female ML 33 mm; SAIAB 206675, female ML 28 mm; NHMUK 20180279, male ML 26 mm. Scale bar 10 mm

Fig. 3. Variation in the shape of the ventral mantle margin in *Sepia shazae* sp. nov. From left to right: deep, angular emargination (SAIAB 206657, male ML 27 mm); shallow, rounded emargination (SAIAB 206675, female ML 28 mm); entire (SAIAB 206674, male ML 28 mm). Scale bar 10 mm

Fig. 4. Dorsal aspect of the head of the *Sepia shazae* sp. nov. holotype showing the two pairs of supra-orbital papillae clusters and rows of tubercles across the head and bases of the arms (SAIAB 205824, male ML 30 mm). Scale bar 10 mm

Fig. 5. Lateral view of the *Sepia shazae* sp. nov. showing the two prominent papillae clusters above the eyes and the large papillae cluster anterio-dorsally on the mantle (SAIAB 206657, male 27 mm). Scale bar 10 mm

Fig. 6. Dorsal mantle of the *Sepia shazae* sp. nov. holotype showing the prominent papillae clusters on the dorsal mantle (SAIAB 205824, male ML 30 mm). Scale bar 10 mm

iridescent blue in fresh specimens. Fins narrow, ending well before anterior mantle margin (FIa 11–25%); small gap between fins posteriorly.

Head width equal to mantle opening width, appears elongated because of membrane joining arm bases; eyes prominent, protruding; neck narrow (Figs 1, 2, 4). Tentacle pouch prominent, stored tentacles sometimes visible through skin. Buccal membrane without suckers.

Colour in preservative highly variable, very pale to dark grey or reddish brown (Fig. 2). Skin covered by various structures (papillae, tubercles and warts); smooth, shiny between structures. Skin sculpture (excrescence) species-specific, although quite variable. Four papillae clusters, each with prominent (rarely flattened, unobtrusive) central tubercle dorsally on head between eyes (Figs 4–5); transverse tubercle row between the eyes in occipital region; 3–4 transverse tubercle rows dorsally on head anterior to eyes at arm bases (some rows may be difficult to see). Single small tubercles along arm pairs I–III. Prominent tubercles on flat triangular raised structure anterio-ventral to each eye, ventral tubercle (at triangle tip) largest (Fig. 5). Usually three prominent papillae clusters (sometimes only large, long central tubercles present) dorsally on mantle (Fig. 6), one on dorsal midline near anterior mantle margin, two medially in transverse row midway between dorsal and posterior mantle edges; smaller clusters (usually two pairs) may be present dorsally on posterior mantle. Mantle also covered in mostly irregularly placed tubercles and a few warts.

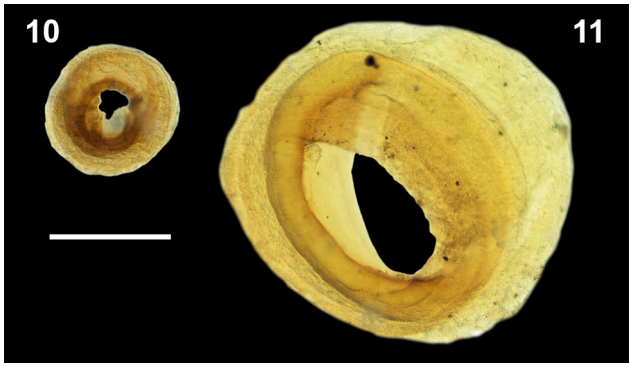
Tentacular stalk very long (up to ~2.5× ML), club tiny (Fig. 7) with subequal small suckers in eleven diagonal rows of four suckers each. Protective membranes relatively narrow, well separated. Natatory membrane well developed, broad, continuing along tentacular stalk for about 1/3 of club length.

Arms robust, stout, subequal in length (Figs 8–9), relatively long, strong membrane joining pair I proximally for about 40%, membrane becoming gradually shallower between subsequent arms, absent ventrally between arms IV. Protective membranes well developed. Suckers globose, biserial on all arms (sometimes in crowded zigzag pattern appearing tetraserial on arms III and IV, especially in females, considerable variability in this regard among various individuals (see: Remarks). Sucker rings on club (Fig. 11) and arms (Fig. 10) smooth.

Arms and especially their armature modified in mature males, sub-distal suckers (usually 3 pairs) enlarged on arms II–III (Fig. 9). Left ventral arm IV hectocotylised (Figs 12–13): basal dorsal sucker normal size; next 15 to 16 pairs of minute marginal suckers with diameter decreasing gradually distally; fleshy transverse folds running between marginal sucker pairs; 3–4 pairs of sub-distal suckers enlarged;

Fig. 7. Dorsal (right) and ventral (left) views of the club of *Sepia shazae* sp. nov. (SAIAB 205828, female 29 mm). Scale bar 10 mm

Figs 8–9. Arms of *Sepia shazae* sp. nov.: 8 – female (SAIAB 206659, ML 33 mm); 9 – male (SAIAB 206659, ML 28 mm). Scale bar 10 mm



Figs 10–11. Suckers of *Sepia shazae* sp. nov. (SAIAB 205828, female ML 29 mm): 10 – club sucker from the middle of the manus (6th row) of the right club; 11 – sucker from right arm IV, ventral, 3rd pair from the base. Scale bar 200 μm

Fig. 12. Suckers at tip of hectocotylised arm of male *Sepia shazae* sp. nov. (SAIAB 206662, male ML 19 mm). Scale bar 1 mm

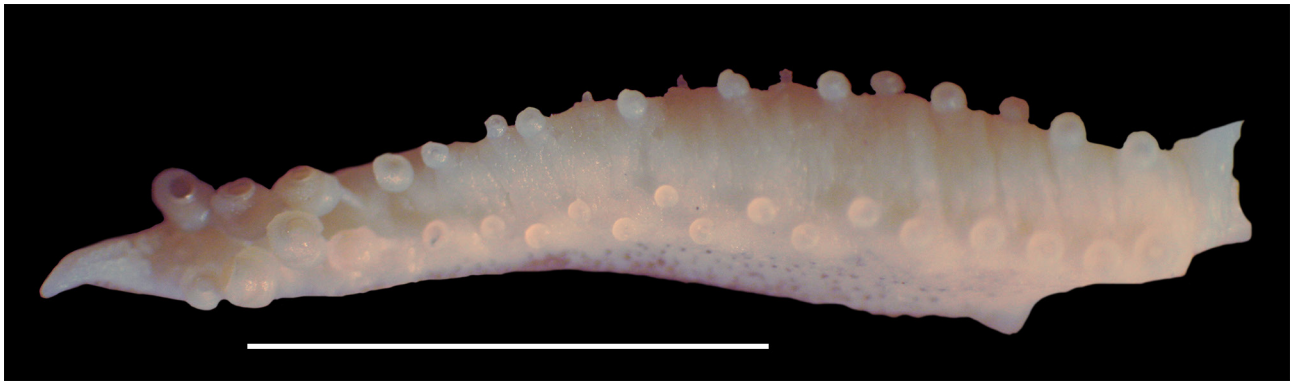


Fig. 13. Hectocotolised left arm IV of *Sepia shazae* sp. nov. (SAIAB 206662, male ML 19 mm). Scale bar 5 mm

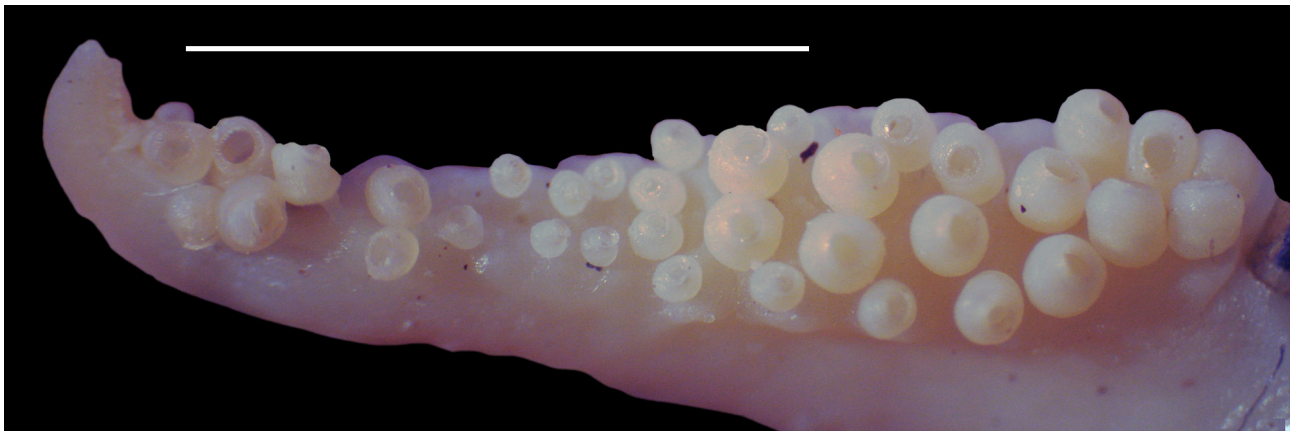
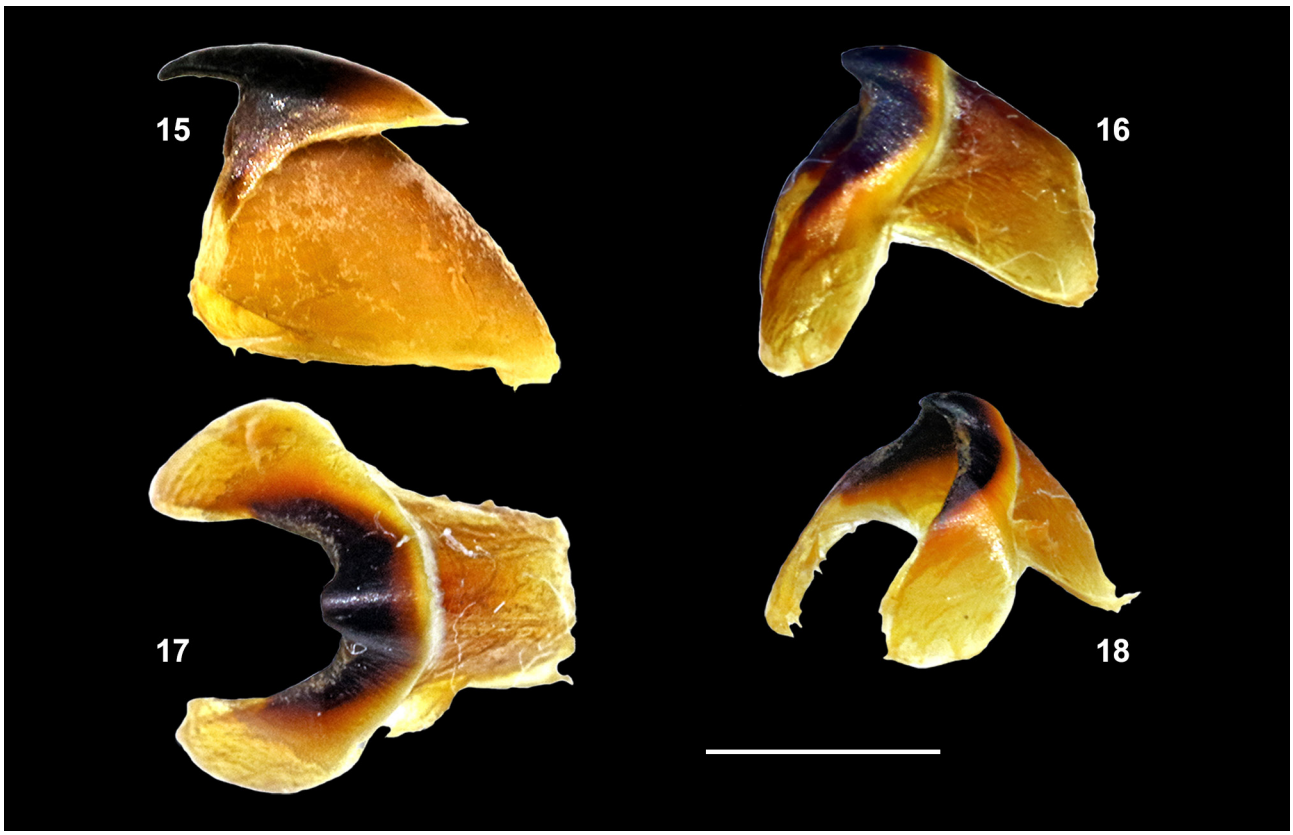


Fig. 14. Right arm of IV of male *Sepia shazae* sp. nov. (SAIAB 206662, male ML 19 mm). Scale bar 5 mm

hectocotylus tip with biserial small suckers (Fig. 12). Right ventral arm also modified (Fig. 14), sucker arrangement from base to tip: two pairs of biserial normal suckers; two rows of three suckers each; three rows of tetraserial suckers, with marginal suckers of reduced diameter; three pairs of small suckers; 3–4 rows of enlarged biserial suckers; 6–10 rows tiny biserial suckers to tip.

Beaks small, fragile, of typical sepiid proportions. Upper beak (Fig. 15): rostrum blunt, relatively short, slightly hooked, length slightly greater than width, rostrum angle curved; hood high above crest posteriorly; jaw edge straight, jaw angle 90°; lateral wall posterior edge slightly curved; only rostrum and anterior part of hood dark. Lower beak (Figs 16–18): rostrum short, blunt, jaw angle rounded, broad, >90°, cutting edge straight; hood low on crest; crest slightly curved; crest and lower edge of lateral wall at slight angle; posterior edge of lateral wall straight and rounded; only rostrum, anterior part of hood and anterior part of shoulders dark.

Radula simple homodont, with 7 teeth per row. Rhachidian teeth small, squat, bluntly triangular; lateral teeth roughly similar; marginal teeth very



Figs 15–18. Beaks of *Sepia shazae* sp. nov. (SAIAB 206660, female ML 33 mm): profile aspect of upper beak (15) and profile (16), top (17) and oblique (18) aspects of lower beak. Scale bar 5 mm

long, 6–7 times longer than rhachidian teeth, distally curved, sharp (Fig. 19).

Spermatophores (Fig. 20) have not been shown to have species-specific characteristics (but see: Remarks).

Locking cartilages: funnel component semi-oval, with internal margin almost straight (Fig. 21), groove not very deep, simple, without additional median cleft; mantle component simple, not prominent (Fig. 22).

Funnel with valve. Funnel organ well defined: dorsal part with anterior ridge and papilla; arms relatively long, thick and fleshy (Fig. 23); ventral part simple, elongated oval (Fig. 24).

Cuttlebone: lightly calcified, thin and fragile, with thin chitin flange all round; anterior ~30% triangular and pointed; broad, oval and round posteriorly (Figs 25–26); spine absent. Last septum elevated, ~20% of length, distinct longitudinal ridge mid-dorsally. Phragmocone well defined, striae borderline approximately straight or slightly convex. Inner cone thin, anteriorly extends into striated zone, ventral portion reduced. Outer cone broad, width decreasing anteriorly into upper limbs that end close to anterior tip of cuttlebone. Cuttlebone sexually dimorphic, broader in females than males (Fig. 26). Length to width ratio: males ~2.0 (range 1.8–2.1; n=7); females ~1.7 (range 1.6–1.9; n=12).

R e m a r k s

In size range investigated this small species (largest known specimen is 33 mm ML) is sexually mature at 23–30 mm ML (males), and 20–33 mm ML (females). Juveniles have not been recorded. The holotype (Fig. 1) and most of the paratypes are mature.

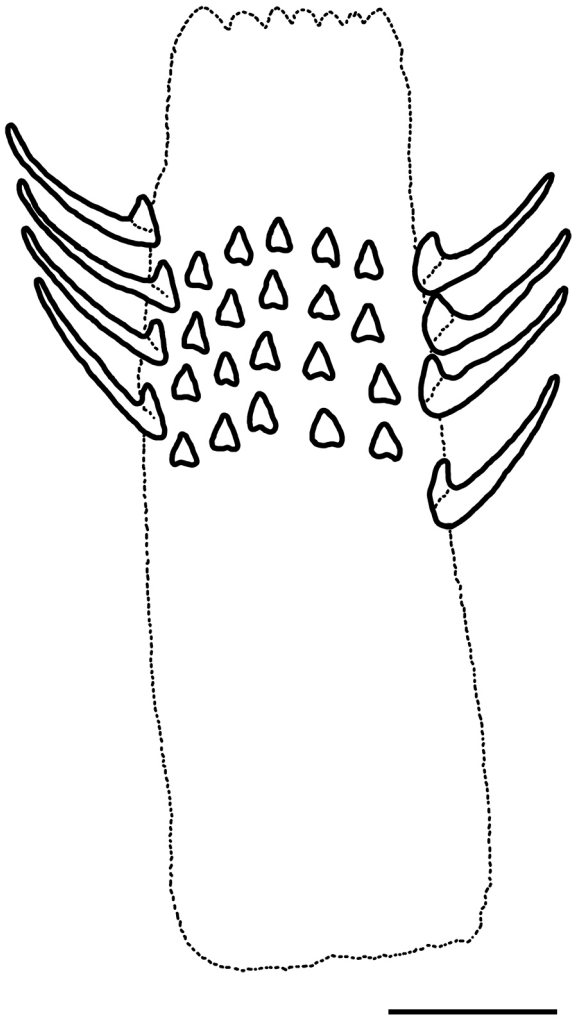


Fig. 19. Radula of *Sepia shazae* sp. nov. (SAIAB 206660, female ML 33 mm). Based on a photograph. Scale bar 20 μm

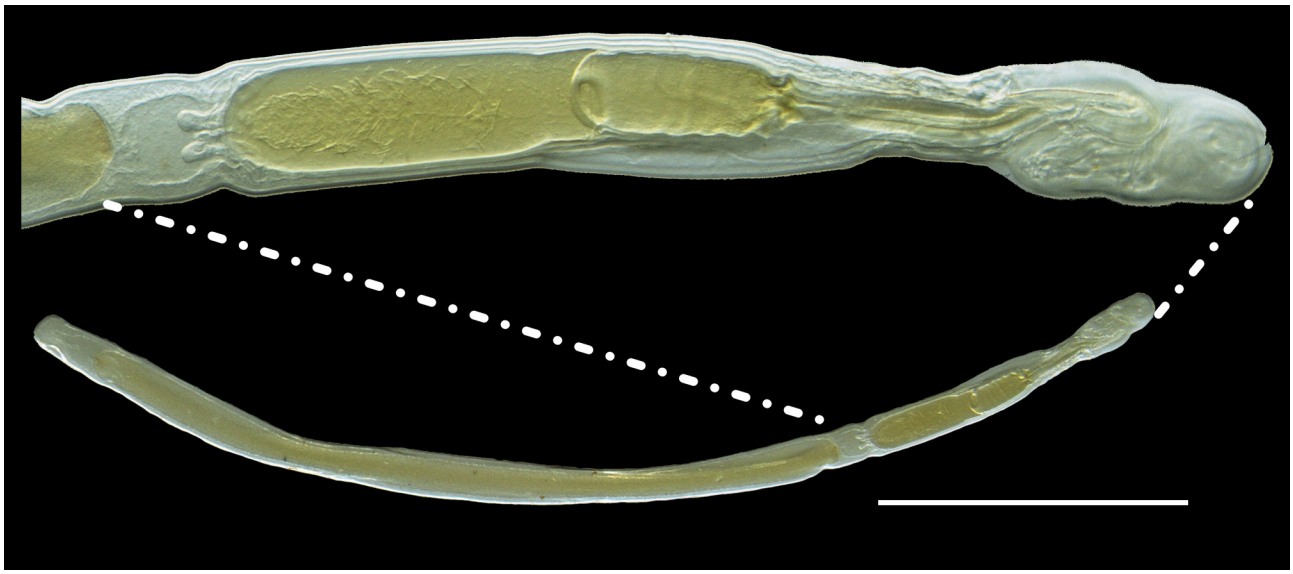
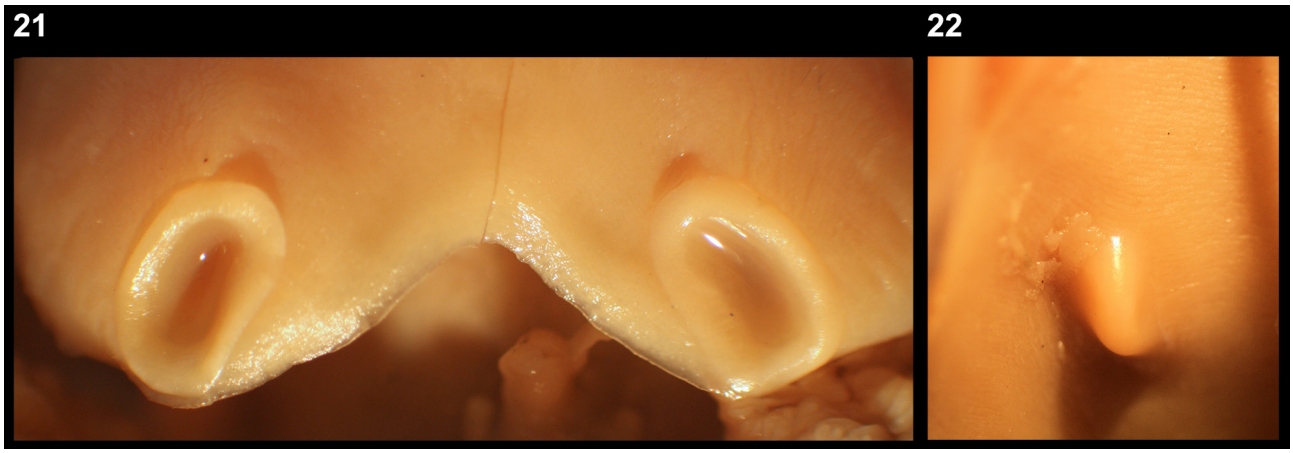


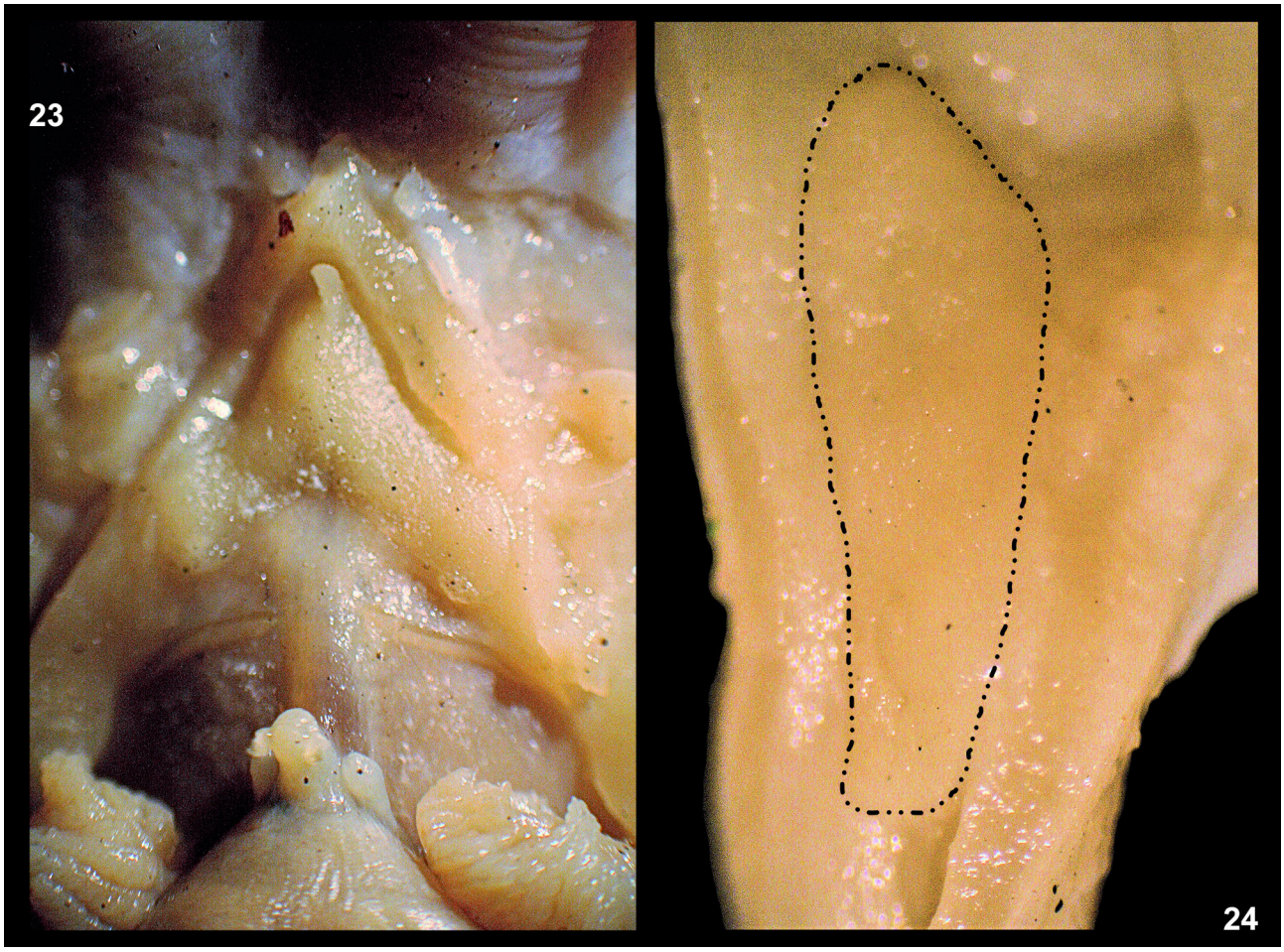
Fig. 20. Spermatophore of *Sepia shazae* sp. nov. (SAIAB 206659, male ML 28 mm) with an insert showing an enlargement of the cement body, oral connective complex and ejaculatory apparatus



Figs 21–22. Funnel (21) and mantle (22) cartilages of the funnel/mantle locking mechanism of *Sepia shazae* sp. nov. (SAIAB 206659, female ML 29 mm)

Observed natural variation and sexual dimorphism that could aid identification in the field has been included in the description.

There is considerable variability in the total number of suckers, especially in females (Table 3). Most of this variability appears to stem from variation in the number of small to minute suckers at the tips of the arms, which could be the result of injury or regeneration. We could not test this in females because the sucker diameter decreases gradually over the length of the arm. Males possess a group of enlarged suckers near the tip of arms II and III (see for example: Fig. 9) that provides a convenient landmark. For a sample of eight males we calculated the absolute



Figs 23–24. Funnel organ of *Sepia shazae* sp. nov. (SAIAB 206659, female ML 29 mm): 23 – dorsal component of the funnel organ; 24 – ventral component, cut off from the dorsal component (indicated by the dotted line)

Figs 25–26. Cuttlebones of a male and female *Sepia shazae* sp. nov.: 25 – cuttlebone of male (SAIAB 206672, male ML 31 mm), dorsal (left) and ventral (right); 26 – cuttlebone of female (SAIAB 206671, female 29 mm) dorsal (left) and ventral (right). Scale bar 10 mm

deviation from the mean number of suckers for the proximal (from the basal up to and including the last enlarged sucker) and distal region of arms II and III. We found that the overall mean absolute deviation for the distal region was 1.75× that of the proximal region.

The morphology of spermatophores of *S. shazae* differs little from published accounts of other members of the genus (see for example: Roeleveld & Liltved 1985 or Lu & Reid 1997). However, the relative proportions of the three basic components (sperm mass, cement body and ejaculatory apparatus) are known to differ among sepiids (Lu & Reid 1997: fig. 6 vs. fig. 14), as has been shown for other cephalopods (e.g. Voss 1969: p. 725). In small sepiids, sperm mass is relatively long and other parts relatively short, but not to the extreme shown for example by Australian *S. senta* Lu et Reid, 1997 (Lu & Reid 1997: p. 294).

The combination of: small size at maturity (ML seldom larger than 30 mm); anterior mantle margin slightly produced, short and wide; biserial suckers on all arms; lack of posterior spine on the cuttlebone place this species in the so-called *Hemisepius*-group together with *S. dubia*, *S. faurei*, *S. pulchra*, *S. robsoni*, and *S. typica* (part of the *Hemisepius* diagnosis by Khromov 1998a).

Sepia shazae is easily distinguished from *S. faurei*, *S. robsoni* and *S. typica* by the following characters: dorsal mantle lacking large, complex structures and either almost completely smooth (*S. robsoni*), sparsely papilose (*S. typica*) or densly tuberculate (*S. faurei*); cuttlebone partially (*S. typica*) or completely (*S. robsoni, S. faurei*) chitinised; distal third of the dorsal arms devoid of suckers and finger-like (*S. faurei* and *S. robsoni*); the lateral fleshy keel on the ventral mantle pierced by 10–12 pairs of pores (unique to *S. typica*).

Sepia shazae is distinguished from *S. dubia* by the following characters. Mantle more elongated, length to width ratio >1.5 (Figs 1–3) compared to <1.2 (Figs 28–29). Dorsal mantle in *S. shazae* bears three prominent papillae clusters, one on the dorsal midline near the anterior mantle margin, the other two close to the midpoint of the dorsal midline and scattered tubercles with a few warts, no turrets (Figs 5–6) whereas *S. dubia* has two large prominent turrets close to the midpoint of the dorsal midline and a minimum of four smaller turrets anterior and two posterior to those prominent structures and numerous irregular warts (Figs 29–30). There are two supra-orbital papillae clusters, each with a prominent central tubercle and three prominent tubercles on a flat raised structure anterio-ventral to each eye in *S. shazae* (Figs 4–5). In contrast, *S. dubia* has two supra-orbital turret-clusters and a single turret-cluster anterio-ventral to each eye (Figs 29–30). The funnel component of the funnel locking cartilage is less complex with a shallower groove in *S. shazae* (Fig. 21) than in *S. dubia* (Fig. 40).

Distribution

S. shazae is a common near endemic to South Africa, known only from the southern Benguela System. Occurs from 29°48'S in southern Namibia to 25°E on the South Coast of South Africa (Fig. 27). Recorded from 200 to 700 m depth. This is the third

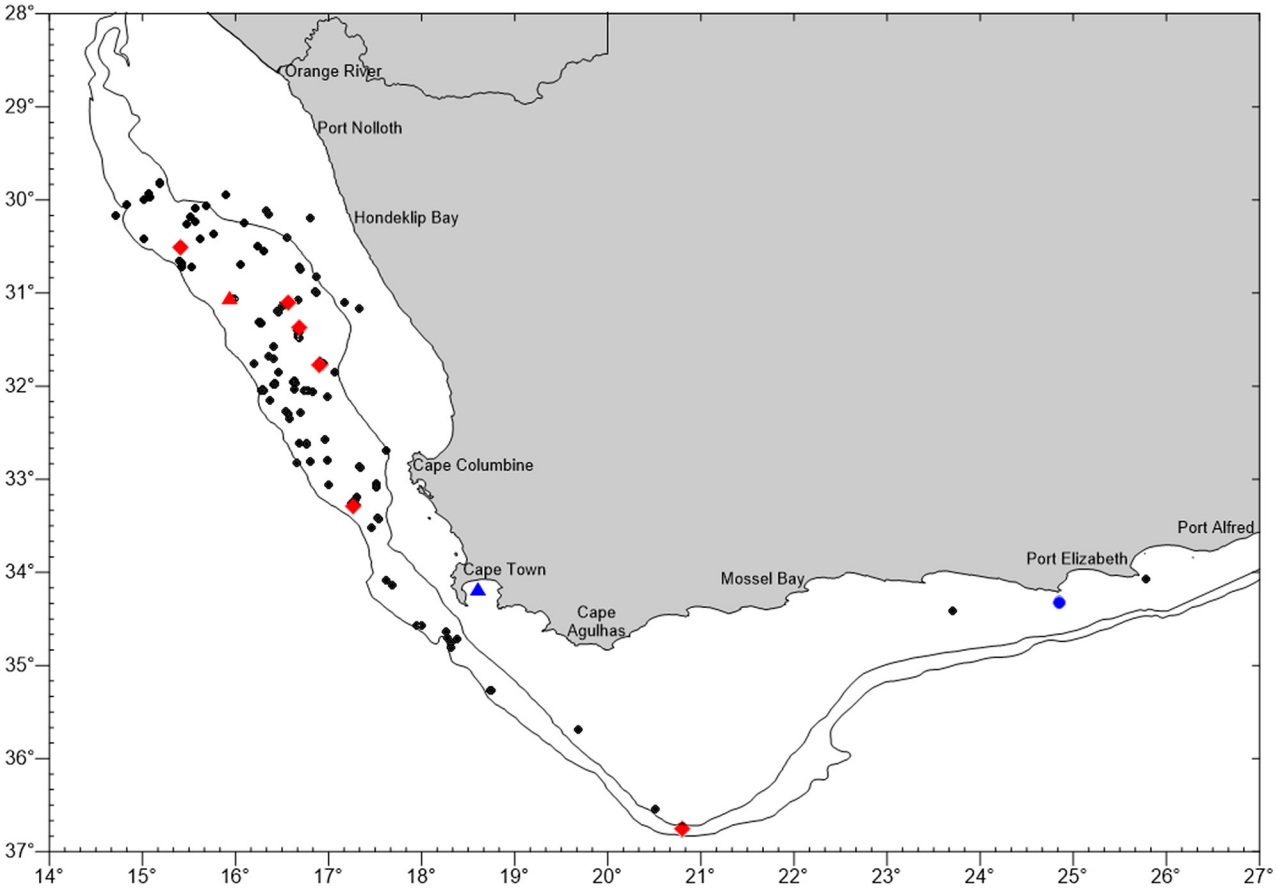


Fig. 27. Chart showing the location of all survey trawls where *Sepia shazae* sp. nov. specimens were recorded (black dots) during bottom trawl research surveys off the coast of South Africa, and the localities for the *S. shazae* holotype (red triangle) and paratypes (red diamonds) and for the *S. dubia* holotype (blue triangle) and the only other known specimen (blue circle). The contour lines show the 200 and 500 m isobaths

species of *Sepia* that occurs so deep. The others are *S. hedleyi* Berry, 1918 that occurs up to 1,092 m, and *S. cultrata* Hoyle, 1885 that occurs up to 803 m (JEREB & ROPER, 2005), both Australian endemics.

E t y m o l o g y

Sepia shazae is named to honour Ms. Sharon ("Shaz") du Plessis, for many years Chief Technician and then Liaison Officer (Research Vessels) in the Fisheries Management Branch of the Department of Agriculture, Forestry and Fisheries, Cape Town, South Africa. She collected numerous small sepiids during many research cruises in which she participated.

SEPIA DUBIA ADAM ET REES, 1966

(Figs 28–49, Table 4)

Holotype: BMNH 1963103W, False Bay (University of Cape Town Ecological Survey) F.B. 1007, 18 March 1950, one female: 17 mm ML (ADAM & REES 1966).

Material examined: SAIAB 205830 – female: 22 mm, 5.0 g, V, R/V Dr Fridtjof Nansen demersal survey 2000405, 28 May 2000, AN0182-034-3606, 34°18'00.0"S, 24°51'00.0"E to 34°16'48.0"S, 24°51'00.0"E, bottom trawl, 119 m.

D i a g n o s i s

Cuttlebone well calcified, unusually broad, especially posterior phragmocone and outer cone (relation of length to width ~1.4); anterior triangular; posterior spine absent; dorsal surface covered with calcareous structures, forming reticulate pattern in holotype. Inner cone distinct, broad laterally and posteriorly; together with posterior outer cone forms shallow spoon-shaped depression; limbs fused to outer cone. Outer cone exceptionally broad, surrounds inner cone. Last loculus triangular rather than trapezoid. Striae wavy, almost straight. Head with four turret-clusters dorsally above eyes, two straight transverse rows of warts between eyes, single turret-cluster under each eye. Dorsal mantle: two large prominent turrets close together on either side of dorsal midline near centre of dorsal mantle; at least four smaller turrets anterior and two posterior to large prominent turrets. Many small warts cover dorsal mantle, head and arms.

D e s c r i p t i o n

Small, known from two females, ML 17 and 22 mm (Figs 28–29). Overall habitus globose, compact, round, skin warty. Mantle broad oval, length to width ratio <1.2; antero-dorsal margin flat, "W" type; antero-ventral margin strongly emarginated in

Fig. 28. Dorsal, lateral and ventral views of the holotype of *Sepia dubia* Adam et Rees 1966 (BMNH 1963103W, female ML 17 mm). Scale bar 10 mm

Table 4. Measurements (mm), weight (g) and counts recorded for characters of the two currently known specimens of *Sepia dubia*. Values for the holotype from ADAM & REES (1966). See: Table 1 for a description of the characters

Catalogue number	BMNH 1963103W	SAIAB 205830
Sex	F	F
Maturity		V
Weight		5.0
ML	17	22
MLv	15	21
HL		12
HW		11
AMH		0.7
FL		23
FW		1.9
FIa		2.2
FIp		0
FFu		4.3
FuL		11
AL1-rt		11
AL2-rt		12
AL3-rt		12
AL4-rt		15

Catalogue number	BMNH 1963103W	SAIAB 205830
HcL		–
MHL		–
TL		25
Tcl		3.3
AS1-rt		0.6
AS2-rt		0.6
AS3-rt		0.6
AS4-rt		0.6
ASl4		–
ASl4m		–
ClS		0.3
ASC1-rt		35
ASC2-rt		50
ASC3-rt		56
ASC4-rt		42
CS#		52
CTR#		–
CES		21

Fig. 29. Dorsal (left) and ventral (right) views of *Sepia dubia* (SAIAB 205830, female ML 22 mm). Scale bar 10 mm

Fig. 30. Lateral view of *Sepia dubia* (SAIAB 205830, female ML 22 mm). Scale bar 10 mm

females, unknown in males. Fins robust but relatively narrow; ending near anterior mantle margin, (FIa 7% and 10%); no gap posteriorly between fins.

Dorsal mantle with two large prominent turrets transversely in the middle of the dorsal mantle, close to dorsal midline; at least four smaller turrets anterior and two posterior to large prominent turrets; the turrets may look like turret-clusters when squashed. Head robust, neck only slightly narrower than head; four turret-clusters dorsally above eyes (Figs 29–30); two straight transverse rows of warts between eyes; single turret-cluster under each eye. Eyes large, not protruding. Many small warts covering dorsal mantle, head and arms.

Arms subequal in length, fleshy; strong keels especially prominent in ventral (IV) arms; protective membranes thick and long: suckers biserial, pairs widely spaced, appearing uniserial when laterally squashed (Fig. 31). Arms connected by membrane; slightly more than 1/3 of arm length between pair I; extent gradually decreasing towards arms IV; no web between pair IV. Suckers on arms minute; sucker rings with no teeth (Fig. 33).

Club small; carpus plus manus with 11 rows of five suckers; dactylus with five rows of 2–5 suckers (Fig. 34); suckerless patch in photograph due to damage. Suckers minute, with 4–5 tiny blunt teeth on proximal side of sucker ring only (Fig. 32).

Upper beak (Fig. 35): rostrum blunt, relatively short, not hooked, length equal to width, rostrum angle well defined; hood long, distal tip far from crest, jaw edge straight, jaw angle <90°; lateral wall with posterior edge. Only rostrum and anterior part of hood dark.

Lower beak (Figs 36–38) characteristic: rostrum short, blunt, lacking distinct rostrum angle; hood low on crest, slightly curved, indented; crest slightly curved, not indented, not parallel to lower edge of the lateral wall (proximally further apart than distally); lateral wall with curved and rounded posterior margin. Only rostrum and anterior parts of hood and shoulders dark.

Radula homodont, with seven teeth per row (Fig. 39). Marginal plates not detected. Rhachidian teeth low, broad, triangular, fairly symmetrical. First and second laterals similar, simple, symmetrical. Heels comparatively large, broad. Marginal teeth uniformly thick, blunt, slightly curved, not indented.

Locking cartilages: funnel component bean-shaped (Fig. 40), internal margin slightly curved, groove moderately deep, without additional median (Fig. 21); mantle component simple, but prominent (Fig. 41).

Funnel organ with dorsal component well defined, bearing anterior ridge and papilla, limbs short: ventral component well defined, oval, elongated (Fig. 42).

Cuttlebone, unusual and distinctive, well calcified; dorsally covered with calcareous structures,

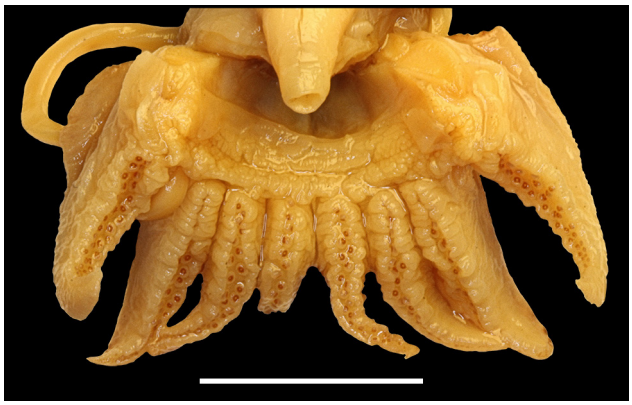
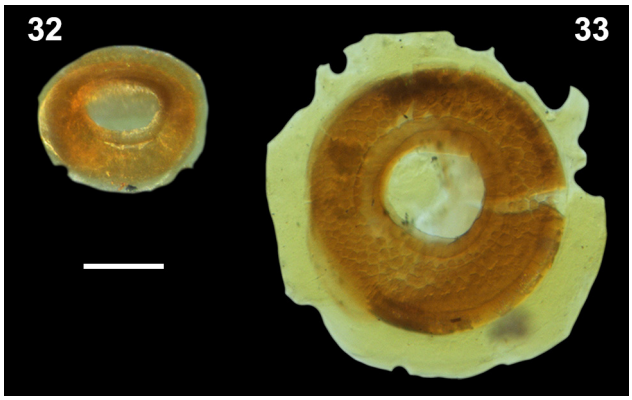


Fig. 31. Arms of *Sepia dubia* (SAIAB 205830, female ML 22 mm). Scale bar 10 mm



Figs 32–33. Sucker rings of *Sepia dubia* (SAIAB 205830, female ML 22 mm). 32 – sucker from arm III, ventral 5p from base; 33 – club sucker, middle of the manus. Scale bar 100 μm

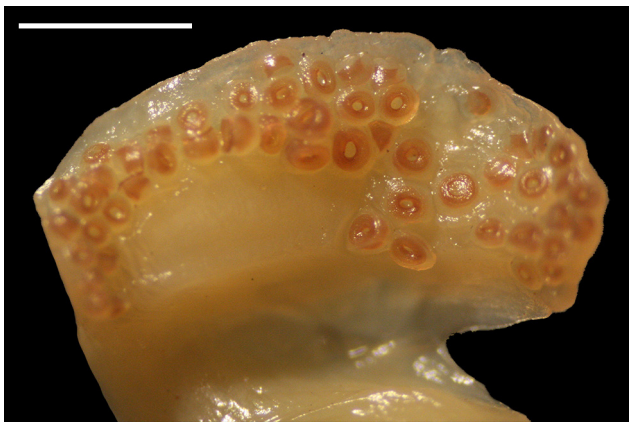
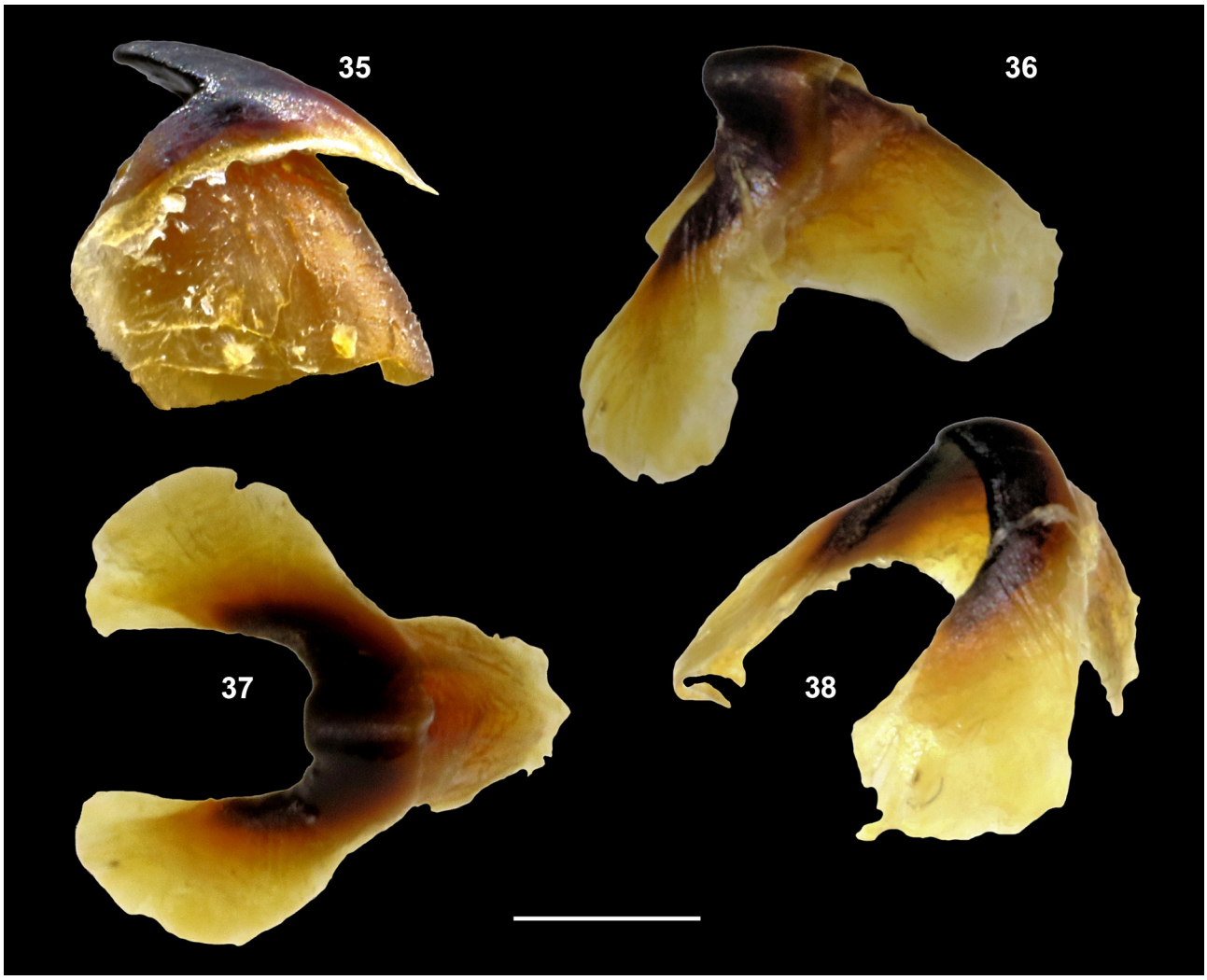


Fig. 34. Club of *Sepia dubia* (SAIAB 205830, female ML 22 mm). Bald patch resulted from the damage to the club. Scale bar 1 mm

forming reticulate pattern in holotype; very broad; posterior phragmocone and outer cone especially broad; triangular anteriorly (Figs 43 & 45); posterior spine absent (Figs 43 & 47). Inner cone distinct, broad both laterally and posteriorly; together with posterior outer cone forms shallow, spoon-shaped depression, that is not pocket-like (Figs 45 & 48);



Figs 35–38. Beaks of *Sepia dubia* (SAIAB 205830, female ML 22 mm) upper beak in profile aspect (35) and lower beak in profile (36), top (37) and oblique (38) aspects. Scale bar 5 mm

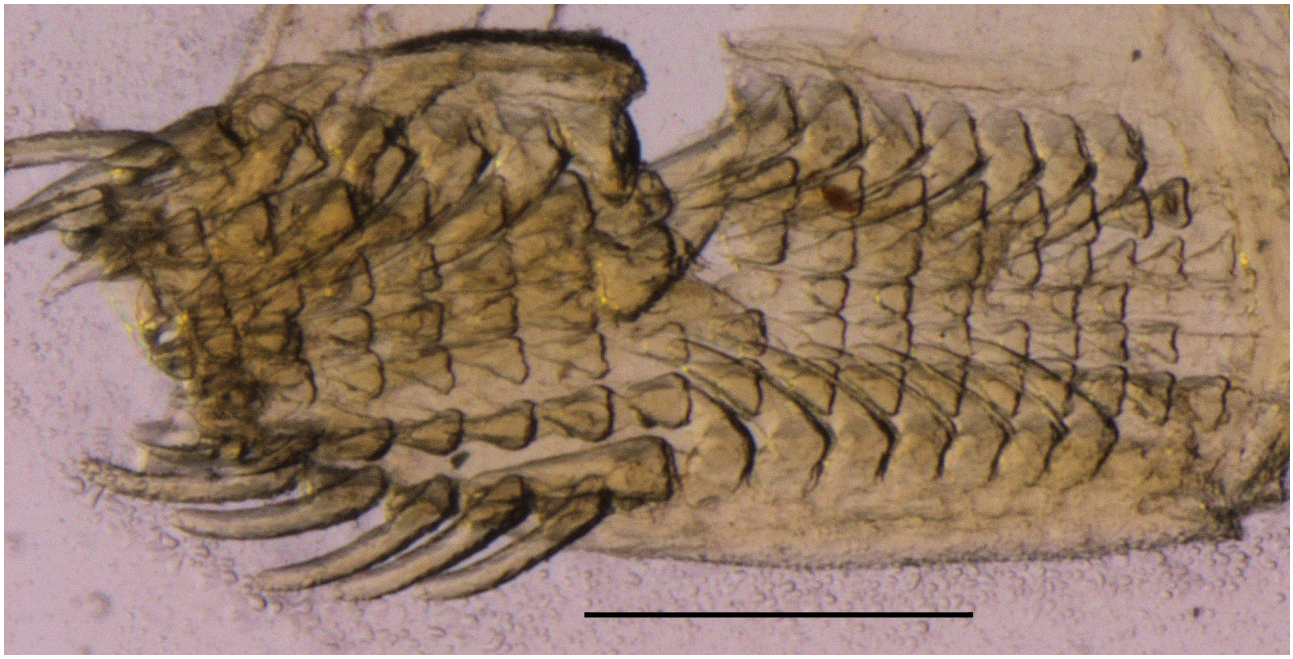


Fig. 39. Radula of *Sepia dubia* (SAIAB 205830, female ML 22 mm). Scale bar 50 μm

Figs 40–41. Funnel (40) and mantle (41) cartilages of the funnel/mantle locking mechanism of *Sepia dubia* (SAIAB 205830, female ML 22 mm)

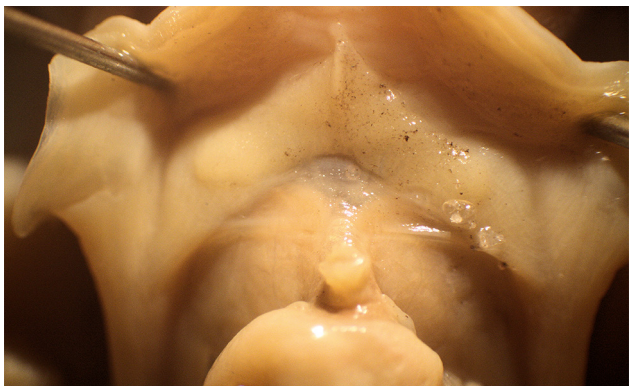


Fig. 42. Funnel organ of *Sepia dubia* (SAIAB 205830, female ML 22 mm)

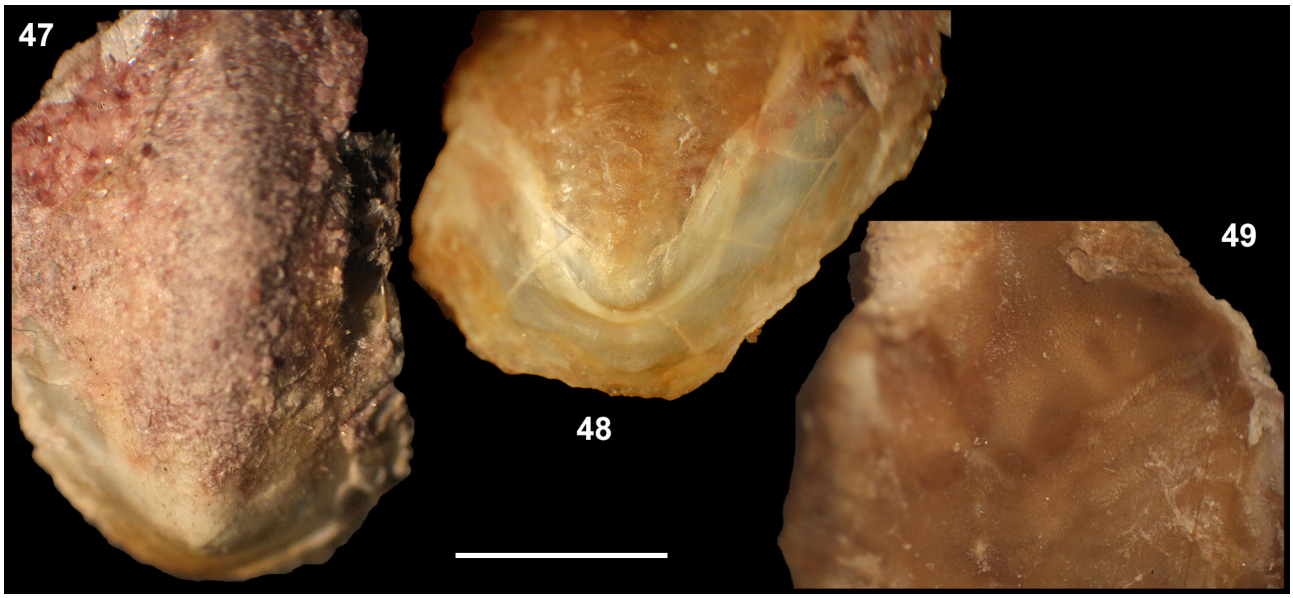
limbs fused to outer cone; surrounded by exceptionally broad outer cone. Last loculus triangular rather than trapezoid. Striae wavy, almost straight.

R e m a r k s

See: the Remarks section under *S. shazae* for differences between *S. dubia*, *S. shazae* and other small sepiids.

ROELEVELD & LILTVED (1985: p. 14) stated: "…*S. dubia* and *S. pulchra* are virtually indistinguishable at present except by the shell characters." This view is incorrect – habitus and specific characters of the bodies of these species (such as skin sculptures and position of fins in relation to anterior mantle margin) are vastly different (Figs 50–51). *Sepia pulchra* differs from both *S. dubia* and *S. shazae* in the presence of numerous large tubercles and warts covering the dorsal mantle, head and arms, and by the presence of three (not two) large, prominent tubercles above each eye.

Figs 43–46. Dorsal (43, 44) and ventral (45, 46) aspects of the two extant pieces of the cuttlebone of the *Sepia dubia* holotype (BMNH 1963103W, female ML 17 mm). Scale bar 10 mm



Figs 47–49. Three fragments of the cuttlebone of new specimen of *Sepia dubia* (SAIAB 205830, female ML 22 mm): 47 – dorsal aspect of the posterior portion; 48 – ventral aspect of posterior portion; 49 – ventral aspect of middle section of the cuttlebone showing the last loculus. Scale bar 5 mm

Fins are narrow in *S. dubia* and *S. shazae*, wider in *S. pulchra* and ending much closer to the anterior mantle marging in *S. dubia* (Fla 7% and 10%, Table 4) than in either *S. shazae* (FIa 11–22%, Table 3) or *S. pulchra* (Fla 23–25%) (Figs 50–51).

In discussing the structure of the cuttlebone among species in the *Hemisepius* group, ROELEVELD & LILTVED (1985, p. 14) state: "*Sepia dubia* has a *Hemisepius*-like shell, with the phragmocone having an inverted triangular shape and occupying little more than half the shell length, as in *Sepia (Hemisepius) typica*." and "*Sepia typica*, *S. dubia* and *S. faurei* have a *Hemisepius*-like shell with an abbreviated phragmocone, whereas that of *S. pulchra* is typically sepiid." We found that among these small sepiids, the cuttlebone of *S. dubia* is the most calcified and

Fig. 50. Dorsal view of *Sepia shazae* holotype (left, SAIAB 205824, male ML 30 mm), *Sepia pulchra* (center, SAM-MB-S001029, male ML 19 mm) and *Sepia dubia* (right, SAIAB 205830, female ML 22 mm). Scale bar 10 mm

Fig. 51. Ventral view of *Sepia shazae* holotype (left, SAIAB 205824, male ML 30 mm), *Sepia pulchra* (center, SAMMB-S001029, male ML 19 mm) and *Sepia dubia* (right, SAIAB 205830, female ML 22 mm). Scale bar 10 mm

solid. In addition it is exceptionally broad, especially across the posterior phragmocone and outer cone and relatively short resulting in a length/width ratio of ~1.4 (which may distinguish it from all other species of *Sepia*). The shape of phragmocone is also unique and does not resemble that of *S. typica* (compare our Figs 43–49 with that in ROELEVELD 1972, p. 259 Fig. 17cd). In our view each of these small sepiid species have unique cuttlebone features and there is no "*Hemisepius*-like cuttlebone".

D i s t r i b u t i o n

Currently known from only two localities, the type locality in False Bay, South Africa and from 119 m depth off the South African south coast at 34°18'00.0"S, 24°51'00.0"E (Fig. 27).

DISCUSSION

The small sepiids from southern Africa (*S. typica*, *S. robsoni*, *S. dubia*, *S. faurei* and *S. pulchra*) have been grouped as the "*Hemisepius* species complex" by KHROMOV (1998a) despite doubts expressed by earlier authors. Being a small sepiid *Sepia shazae* would also fall into the *Hemisepius*-group. However the two sepiids described here (*S. shazae* and *S. dubia*) are so different from one another that virtually the only trait that they share is their small size, and this trait alone cannot have any systematic significance. If "*Hemisepius*" were to include the six small sepiids mentioned above, it would unite under one name such contrasting characters as: normally calcified cuttlebone (*S. pulchra* and *S. dubia*) vs. not normally calcified or not calcified cuttlebone (*S. robsoni*, *S. faurei*, *S. typica*, *S. shazae*); tips of dorsal arms finger-like, devoid of suckers (*S. faurei* and *S. robsoni*) vs. presence of suckers to the end of all arms (the other four described species); skin on the mantle, head and arms almost smooth with sparse warts (*S. robsoni* and *S. typica*) vs. various structures on the skin (all the others). Thus of STEENSTRUP's (1875: p. 468) original characters separating "*Hemisepius*" from other sepiids only the presence of biserial suckers on all arms is shared among the six quite different small sepiids. Only one character separates his original species (*S. typica*) from all the others: ventro-marginal deep pores on the mantle.

STEENSTRUP (1875) erected the genus *Hemisepius* for *H. typicus* on the basis of three characters: deep pores on the ventral surface of the mantle; poorly developed cuttlebone and biserial suckers on all arms (see: ROELEVELD 1972: p. 260). ADAM & REES (1966) expanded *Hemisepius* to include their newly described taxon, *Sepia (Hemisepius) dubia*, then state (p. 144) "… if we consider *dubia* to be a *Hemisepius*,

one of the main characters of this genus, the presence of ventral pores, cannot be maintained as a generic character, and the other features of the animal seem to be related to other Sepiidae, like *S. robsoni* and *S. hieronis*. In this case only the shell of *H. typicus* and *H. dubius* permits us to separate them from all other Sepiidae and we prefer to regard *Hemisepius* as a subgenus".

Roeleveld & Liltved (1985) noted that *Sepia pulchra* shared characters with the subgenus *Hemisepius* and *Sepia* s. str. and that "… this further weakens the distinction between the subgenera *Sepia* and *Hemisepius*" (p. 14). They discussed the relationships between the five small sepiid species (*S. typica, S. robsoni, S. dubia, S. faurei* and *S. pulchra*) and note that although they share some characters, there are also some striking differences. They conclude that "… resolution of the relationships within this group of five species must await collection of further specimens of *S. robsoni, S. dubia* and *S. faurei* each of which is known only by the holotype" (p. 14–15).

With so many contrasting characters among these small sepiids, *Hemisepius* as defined by Khromov (1998a) appears to be an artificial grouping of species that is unlikely to be monophyletic.

Sepia shazae is potentially important for future ecological research on sepiids of the region and zoogeographical research on all sepiids globally. It is widespread geographically ranging from the cold Benguela System on the South African west coast to the warm temperate waters of the Agulhas Current System on the south coast. It is also found over a wide depth range from 200 to 700 m (samples collected by bottom trawl), reaching the third greatest depth recorded for any *Sepia* species in the world (Khromov 1998b, Jereb & Roper 2005). This may indicate that its cuttlebone is not physiologically functional as a buoyancy regulator, and is the subject of ongoing research (Fuchs & Lipinski, unpublished).

Relatively simple and basic research (e.g. alpha taxonomy) into the world of small sepiids is ongoing to discover and describe additional small sepiids. With the increase in available material and in the number of taxa described, it may now be opportune to research the morphological, functional and genetic interrelationships among these species of small *Sepia* occurring off South Africa and to resolve the status of "*Hemisepius*". In particular, the present description of *S. shazae* sp. nov. highlights the importance of skin structures (warts, tubercles and papillae) as a morphological character in these analyses.

Aspects of molecular ecology may be especially interesting in the case of common widespread species such as *S. shazae*. Prior to completing the research for this paper we contributed tissue samples from a number of southern African sepiids, including *Sepia shazae* (as *Sepia* sp. A and as *Sepia dubia*) to a project aimed at developing a phylogenetic tree for the family Sepiidae (see: Lupše et al. 2017, where *S. shazae* is listed as *S. dubia*). In their best tree, Lupše et al. (2017) link three small sepiid species with *Sepia hieronis* (Robson, 1924). This link is interesting and should be further explored in future research. The voucher specimens for this project are housed at the Australian Museum in Sydney and SAMC.

ACKNOWLEDGEMENTS

We would like to thank our sea-going colleagues (notably Ms Shaz du Plessis and the late Mr Barry Rose) for taking part in the collection of the material for study. We would like to thank Dr Roger Bills and Mr Nkosinathi Mazungula (SAIAB) and Mr Albé Bosman (Iziko Museum) for help with the accessioned material. We would like to thank Dr Jon Ablett and Mr Harry Taylor of The Natural History Museum London, U.K. for providing photographs of the holotype of *Sepia dubia* (copyright of these photographs rests with NHM). We would like to thank our colleagues Dr Kevin Christison for taking the photographs of *Sepia shazae* and *S. dubia* radula (Figs 19 and 39), Prof. Tomasz Linkowski and Mr Marcin Białowąs (both Sea Fisheries Institute, Poland) for an access to Nikon SMZ18 stereomicroscope, and Ms Dagmar Merkle for preparing Fig. 27.

We dedicate this paper to the memory of Ms Martina Compagno Roeleveld, professional colleague and friend of many years.

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Received: May 15th, 2018
Revised: August 25th, 2018
Accepted: September 5th, 2018
Published on-line: September 29th, 2018