




REDESCRIPTION OF *TERETOCTOPUS* *ALCOCKI* ROBSON, 1932 (CEPHALOPODA: ENTEROCTOPODIDAE), AND COMMENTS ON THE NOMENCLATURE OF “INKLESS OCTOPUS” GENERA

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ABSTRACT: Two species have been attributed to the genus *Teretoctopus* Robson, 1929: *T. indicus* Robson, 1929, the type species of the genus, and *T. alcocki* Robson, 1932. Of the four original *T. alcocki* syntypes, we relocate and redescribe the remains of two of them, and designate one of them the lectotype. Of three original *T. indicus* syntypes, it is probable that one is lost permanently, but the whereabouts of two of them remains unknown. What we can discern from remaining *T. alcocki* type material, augmented with descriptions of these specimens by Anne Massy and Guy Robson, is compared with what is known of the type species of this genus, *T. indicus*. A rediagnosis of the genus *Teretoctopus* is proffered, and relationships between this genus and others historically referred to as “inkless octopuses” are evaluated. While *Teretoctopus* has nomenclatural priority over *Vulcanoctopus* González et Guerra, 1998 and *Muusoctopus* Gleadall, 2004, for which it is possibly the senior synonym, and shares many characters and states with *Ameloctopus* Norman, 1992, further taxonomic resolution of relationships among these genera must await description and molecular analyses of accurately identified *Teretoctopus* specimens from the Gulf of Oman and northern Arabian Sea.

KEYWORDS: lectotype; taxonomy; *Atlantoctopus*; *Benthoctopus*; *Teretoctopus*; Octopoda

INTRODUCTION

Whenever GUY COBURN ROBSON, a former Deputy Keeper of the Zoology Department of the (now) Natural History Museum, London, had doubts regarding the identity of an octopus specimen, a species, or relationships among them, he volunteered these freely in his writing. His proclivity to do so rendered his texts rich in commentary. As a case in point, he declared an increased difficulty with upholding a distinction among three very poorly described genera (*Atlantoctopus* Grimpe, 1921, *Bathypolypus* Grimpe,

1921, and *Benthoctopus* Grimpe, 1921) of “inkless octopuses” (sensu GLEADALL et al. 2010) in a series of publications (ROBSON 1924a, 1924b, 1927, 1929a, 1929b) that ultimately led to his regarding *Atlantoctopus* to be a junior synonym of *Benthoctopus* (ROBSON 1932: 51, 249). His insights are particularly valuable today as we continue to grapple with taxonomic problems with these genera caused by Grimpe’s taxonomic approach, Robson’s untimely mental deterioration (O’SHEA et al. 2025) that cur-



tailed any further contributions to resolving the taxonomy of these octopuses, and the at-times contentious interpretations of relationships among these genera presented by a gamut of subsequent authors.

ROBSON (1928, 1929a) contributed two genera (*Grimpella* Robson, 1928 and *Teretoctopus* Robson, 1929) to this complex of inkless octopuses. His *Teretoctopus* was proposed to accommodate *T. indicus* Robson, 1929 in a brief note (ROBSON 1929a) wherein a new classification of octopuses was presented, followed by a generic diagnosis several years later, along with descriptions of *T. indicus* and a second species, *T. alcocki* Robson, 1932 (ROBSON 1932). ROBSON recognised these two species to share a novel combination of characters then unknown for any other genus, including a distinct funnel organ. He also volunteered “unwilling as I am to create new generic groups, I seem to have no other course open in this instance” (ROBSON 1932: 249).

Excepting the radula of one *T. alcocki* syntype figured by ADAM (1939: 106), no syntype of either *Teretoctopus* species has been subsequently reported on. Because other genera have been described without critical reference to this genus, at least eight names (*Atlantoctopus*, *Bathypolypus*, *Benthoctopus*, *Grimpella*, *Teretoctopus*, *Ameloctopus* Norman, 1992, *Vulcanoctopus* González et Guerra, 1998 (in GONZÁLEZ et al. 1998), and *Muusoctopus* Gleadall, 2004) are potentially available to accommodate taxa with two rows of suckers but which lack an ink sac. Of these, species referred

to *Muusoctopus* were referred to by GLEADALL et al. (2010) as “inkless octopuses”.

Of the eight specimens historically assigned to one of either species of *Teretoctopus*, seven were referred to as syntypes. The type species of the genus (*T. indicus*) was founded on three small males from collections of the (then) Indian Museum that MASSY (1916) attributed to *Polypus pricei* Berry, 1913, collected from the Gulf of Oman to (more questionably) Andaman and Arabian seas and Bay of Bengal. *Teretoctopus alcocki* Robson, 1932 was based on four specimens from this same collection, two of which MASSY (1916) referred to *O. januarii* Hoyle, 1885, and two of three specimens that GOODRICH (1896: 19) referred to “?*O. januarii*”. The eighth specimen, collected off the “Pearl grounds” (Mannar, Sri Lanka), referred to “?*O. pricei* (Berry)” by WINCKWORTH (1926) and *T. indicus* by ROBSON (1929a), had no type status.

We redescribe and designate a lectotype for *T. alcocki*, augment this with redescription of a (now) paralectotype radula illustrated by ADAM (1939), and separately describe the third of three specimens that GOODRICH (loc. cit.) referred to “?*O. januarii*”. We then compare our redescription of this species with what is known for *T. indicus*, for which we have been unable to locate any type material, and evaluate relationships between these two species, and between *Teretoctopus* and other genera in a greater “inkless-octopus” complex.

MATERIALS AND METHODS

Institutional abbreviations. MNHN – Muséum national d’Histoire naturelle, Paris, France; NMI – National Museum of Ireland, Dublin, Ireland (NMINH); NHM – Natural History Museum, London, United Kingdom (UK); OUMNH – Oxford University Museum of Natural History (ZC, zoological collection), London, UK; RBINS – Royal Belgian Institute of Natural Sciences, Brussels, Belgium; RIMS – Royal Indian Marine Survey Ship; and ZSI – Zoological Survey of India.

Morphological abbreviations. Excepting less-conventional (by modern standards) counts and measurements of octopuses reported by MASSY (1916) and ROBSON (1932), those used herein are based on standards detailed by ROPER & VOSS (1983), excepting arm sucker counts, which are reported for the entire arm. For completeness, frequently used abbreviations in the text and tables (and how they are measured) are (alphabetically): AL – arm length, herein denoted 1 [dorsolateral] to 4 [ventrolateral], measured from the beaks to arm tip); ASC – whole arm sucker count; ASn – normal [not abruptly en-

larged] arm sucker diameter; CaL – calamus length, measured from the distal-most sucker to its distal tip (CaLI – calamus length as a percentage of ligula length); EO – diameter of the opening of the eye; FFL – free funnel length (measured from the anterior opening to its point of dorsal attachment to the head); FuL – funnel length: measured from the anterior funnel opening to the posterior border along the ventral midline; GiL – gill length along the antero-posterior axis; GiLC – gill lamellae count, inner/outer demi-branch; HcL – hectocotylus length (length of modified portion of arm measured from distal-most sucker to arm tip); HcLI – hectocotylus length as a percentage of hectocotylised arm length; HcAL – hectocotylised arm length [3R]; HW – head width (greatest width of head at the level of the eyes); LAL – longest arm length (measured from the beaks to its arm tip); LL – ligula length (measured from distal-most sucker to tip of arm); ML – dorsal mantle length (measured from the midpoint between the eyes to the posterior end of the mantle); MW – mantle width (greatest dorsal straight-line width of the mantle); OAI –

length of hectocotyliised arm [3R] as a percentage of the opposite [3L] arm length; TL – total length of the body (measured from the tip of the mantle to the outstretched arm tips, along the antero-posterior axis); WD – web depth (measured from the beaks to web margin at the mid-point between adjacent arms); WDI – web depth as a percentage of longest arm length; WF – web formula (relative depth of web sectors, conventionally labelled A [between dorsolateral arm pair] to E [between ventrolateral arm pair]). “I” following an abbreviation denotes an index (as a percentage of ML, unless otherwise stipulated) and R or L denotes right or left.

Search strategy. Searches of MNHN, NHM, OUMNH, and RBINS collections for *Teretocopus* types were performed by the authors, the ZSI in Kolkata by AMIT MUKHOPADHYAY, NMI by PAOLO VISCARDI, and the Colombo Museum, Sri Lanka, by LANKANI SOMARATHNA. RBINS collections yielded a largely intact male in poor condition, and a slide mount of the radula of a second male. OUMNH collections yielded one specimen attributed by GOODRICH (1896) to “?O. januarii” from an original syntype collection locality.

After confirming the provenance of the largely intact RBINS syntype (Appendix) we designate it the lectotype of *Teretocopus alcocki*. Our description of it is necessarily separated into accounts of MASSY (1916) and ROBSON (1932), because descriptions were based upon multiple, not-necessarily conspecific specimens in different states of preservation, each of which reported different characters and their states. This is followed by our redescription of type material, a critical comparison of the lectotype and OUMNH specimen, and a comparison with what is known for *T. indicus*. We conclude with an evaluation of the status of each species and of the genus. Our synonymies are limited to instances in which type material has been examined.

Image stacking

Stacked photo reconstructions were prepared using a Canon EOS 6D Mark II equipped with either a Canon MP-E 65 mm (lectotype) or 100 mm objective (lectotype and OUMNH specimens). One system (65 mm objective) was fixed on a Cognisys StackShot Macro Rail guided by Helicon Remote software; 30

images were stacked using Zerene Stacker Software. The second system (100 mm objective) involved manual focusing and photo-stacking of four (lectotype) and five (OUMNH specimen) images using open-source software Picolay (www.picolay.de); specimens were blot dried using tissue paper; flash highlights were removed and minor cosmetic corrections were made using the open-source software Paint.net.

Radula reconstruction

An image of the paralectotype radula was reconstructed using an automated Leica DM5500B microscope with motorized Z-focus. Views were captured with a Leica DFC450C (5 Megapixel CCD sensor) digital microscope camera, using Z-Stack acquisition with the multifocus module of Leica Application Suite (LAS: Z-range 565 μm ; Z-Step 15 μm ; steps 39; with depth of focus determined after visualisation directly through the microscope). LAS software v.4.12.0 was used to fuse different images, and to recombine multiple views using the reconstruction multifocus module. Stitching of isolated stacked views was achieved using Affinity Photo version 1.10.5.

Station Map

RIMS “Investigator” station coordinates were sourced from ANON (1914), and converted from the original degrees, minutes, seconds (Fig. 1, Table 1) into decimal degrees for mapping purposes.

Family placement

The Enterocropodidae Strugnell, Norman, Vecchione, Guzik et Alcock, 2014 was originally differentiated from the Bathypolypodidae Robson, 1929 and Octopodidae d’Orbigny, 1839 on molecular grounds. No recognised morphological criteria consistently differentiate these taxa. Accordingly, without molecular data, our attribution of *Teretocopus* to the Enterocropodidae is provisional, and based on its greater overall similarity to taxa historically attributed to *Benthocopus*, *Vulcanocopus*, and *Muusocopus* than to those of *Amelocopus*, *Bathypolypus*, or *Grimpella* (not necessarily related genera that share the basic character combination “two rows of suckers along the arms and no ink sac”).

Table 1. Recorded (not necessarily correct) coordinates (degrees, minutes, seconds) of *Teretocopus* type material: sourced GOODRICH (1896), ANON (1914), ROBSON (1932). IM – Indian Museum, L – lectotype, P – paralectotype, S – syntype; NR – not reported; “?” – denotes uncertainty

Specimen(s)	Investigator stn	Location	Coordinates	Depth (m)
<i>T. indicus</i> S IM 8129–8131	366	Arabian Sea	24°45'N, 63°50'15"E	995
<i>T. alcocki</i>				
L IM 1341	297	Gulf of Oman	25°11'30"N, 57°15'E	1,260–1,280
P IM 350	NR	?Andaman Sea	NR	496
P IM 3348	343	Gulf of Oman	?23°46'15"N, 58°31'50"E	1,114
P IM 347	NR	?Bay of Bengal	?20°17'30"N, 88°30'E	353

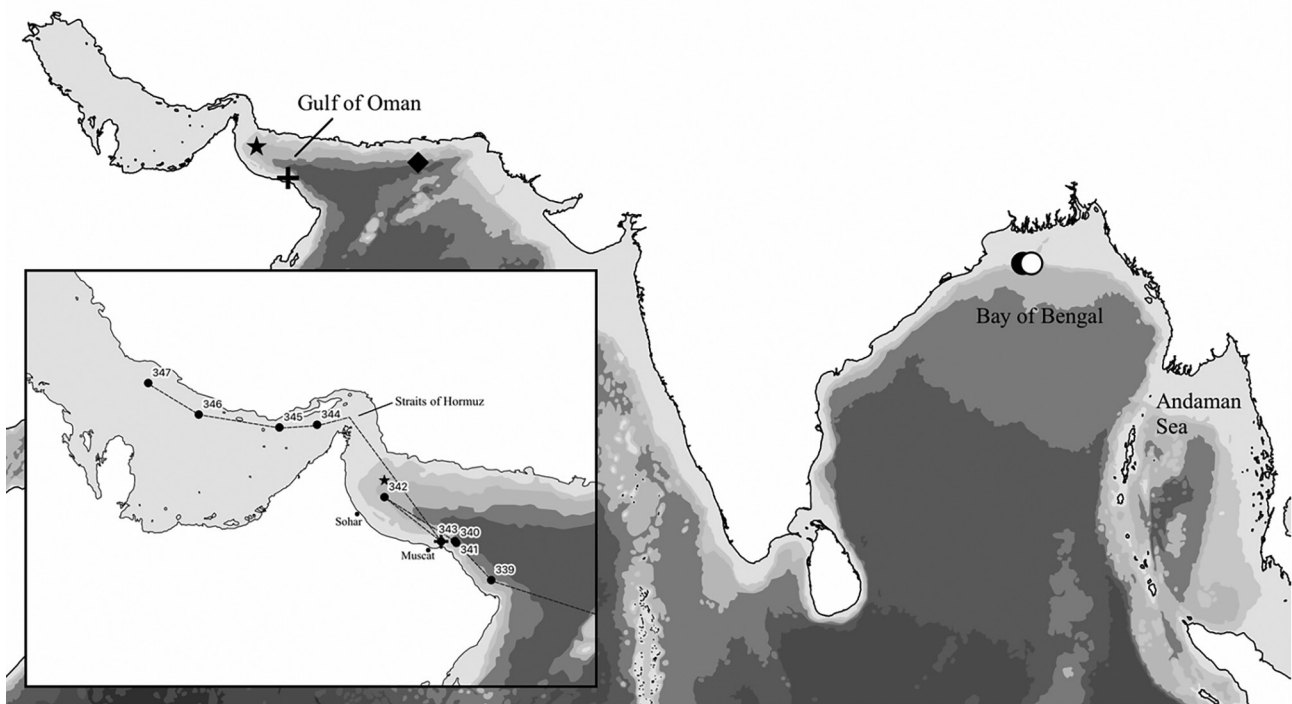


Fig. 1. Type localities, *Teretoctopus indicus* (closed rhombus) and *T. alcocki* (cross – lectotype, and large open and closed circles – in Bay of Bengal). For coordinates (latitudes, longitudes), please see Table 1. Inset: RIMS “Investigator” survey path from stations 339–347, with anomalous U-turn from station 342 off Sohar to 343 off Muscat, before a course correction to sample at station 344 within the Strait of Hormuz (closed circle), but more likely in a location depicted by a closed star. Bathymetric contours (light to dark grey): 200, 500, 1,000, 2,000, 10,000 m

RESULTS

SYSTEMATICS

Order Octopoda Leach, 1817

Suborder Incirrata Grimpe, 1916

Superfamily Octopodoidea d’Orbigny, 1839

Family Enteroctopodidae Struignell, Norman, Vecchione, Guzik et Allcock, 2014

Genus *Teretoctopus* Robson, 1929

Type species by original designation, *T. indicus* Robson, 1929: 608.

Diagnosis. Body smooth; suckers in two rows; ink sac absent; funnel organ reduced, quadripartite; crop with or without anterior diverticulum; radula with lateral cusps on rachidian; posterior salivary gland length < 20% mantle length.

Teretoctopus alcocki Robson, 1932

Figs 1–10, 12–15, Tables 2–4

Teretoctopus alcocki Robson, 1932 – ROBSON (1932: 252–253, pl. III (fig. 3), text fig. 47); ADAM (1939: 105–106, text fig. 25).

?[sic.]*Octopus januarii* Hoyle, 1885 – GOODRICH (1896: 19).

Polypus januarii (Hoyle, 1885) – MASSY (1916; partim [specimens 1341/1, 3348/1], 199–200).

Etymology. Though not explicitly stated, this species was most certainly named after Alfred William Alcock, the dual surgeon/naturalist aboard RIMS “Investigator” from 1888 to 1902.

Type material examined. RBINS (I.G. – Inventaire générale (general inventory); INV – Recent Invertebrate) I.G. 11917/INV.190100, lectotype (designated herein), ♂, mantle length (ML) c. 49.8 mm, 25°11'30"N, 57°15'E (Gulf of Oman), 1,260–1,280 m (689–700 fath), 13 April 1902, bottom temperature 6.7 °C, soft green mud, Agassiz trawl, RIMS “Investigator” Stn 297 (formerly IM 1341/1). IM 350/1 paralectotype, ML unknown, radula mount (in RBINS collections), ?Andaman Sea, 496 m (271 fath), date not recorded (datNR).

Additional material examined. OUMNH.ZC.1979, ♂, ML 40.0 mm, 8570/1, ?Andaman Sea, 496 m (271 fath), datNR.

Distribution. Gulf of Oman (lectotype), ?Andaman Sea (OUMNH specimen and IM 350/1 paralectotype), to Arabian Sea and (questionably) Bay of Bengal (paralectotypes), 353–1,280 m (Fig. 1).

Description

Type material according to [MASSY \(1916\)](#) (Table 2)

Mantle round; tissues very soft; eyes “enormous”. Colour “pinkish”. Arm pairs I or II the longest, slightly thicker than arm pair IV; arm length 3.0–4.8¹ times ventral ML². Suckers small, prominent, widely spaced, none abruptly enlarged in male. Web 25–33%³ arm length; sector E deepest, sectors A–D subequal. Mantle opens just below eye. Funnel fused to head, its aperture opening ~33% the distance between its base and the “margin” of web sector E.

Table 2. Measurements (mm) of *Teretocotopus alcocki* Robson, 1932 type material in [MASSY \(1916\)](#) (as *Polypus januarii* (Hoyle))

	Specimen S1341/1	Specimen S3348/1
End of body to mantle margin	37	42
End of body to eye	54	60
Eye to umbrella	40	70
Breadth of body	30	40
Breadth of head	18#	26#
AL1R/L	140/*	182/185
AL2R/L	136/124	201/168
AL3R/L	65/114	201/172
AL4R/L	117/122	192/180
Hectocotylus	13	–
ASn	1.5	3

* damage, – not relevant (female).

Type material according to [ROBSON \(1932\)](#) (Table 3)

Mantle elongate-ovoid; head narrow; eyes large (~10% total body area), prominent. Dorsal arm pair I the “largest” (?longest), 76–79% TL. Suckers small (ASIn 5.0–6.6%), none abruptly enlarged, with moderately thick-walled acetabulum. Web depth 29–34% of longest arm; sector A deepest; web formula unknown. Mantle aperture type ?B–C (sensu [ROBSON \(1925: 1334, text fig. 1\)](#)). Funnel cylindrical, rather broad, with quadripartite funnel organ: patches in specimens 1341/1 and 3348/1 subcircular, small, bead-like; patches larger and more oblong in 347/1, and larger still (represented by scars only) in 350/1.

¹ Calculated using [MASSY's \(1916\)](#) measurements for specimens 1341 and 3348.

² We assume that this is [MASSY's \(1916\)](#) “end of body to mantle margin”. Because ventral ML is invariably shorter than dorsal ML, a direct comparison of relative arm lengths described for taxa following standards of [ROPER & VOSS \(1983\)](#) must be made with caution.

³ [MASSY \(1916\)](#) does not specify how she calculated this percentage (if relative to longest or adjacent arm).

Hectocotylised arm 53–59% of longest arm length; ligula long, narrow, 12–16% arm length, with copulatory groove constricted just above calamus, with clear laminae; sides of ligula form acute angle with calamus, enfolding its base; calamus (from figure) ~24% LL.

Table 3. Measurements (mm) and indices of type material of *Teretocotopus alcocki* Robson, 1932

	Specimens 347/1, 350/1, 1341/1, 3348/1
MWI	63–55
HWI	51–46
WDI	34–29
WF	A (deepest)
Mantle aperture	?B–C
ALI (TL)	Arms I: 76–79
GiLC	10 or 11
GiL (%ML)	38–40
HcLI	12–16
HcAL/LAL	38–40
ASIn	4.4–3.5

Note: Indices (denoted by “I”) or ratios (denoted by “/”) are percentages; HcAL/LAL is hectocotylised arm length/longest arm length.

Lectotype (Figs 2–7, Table 4)

Mantle distorted, damaged; previously dissected; viscera incomplete. Mantle skin parchment-like, with impression of fabric (both preservation artefacts); brachial and nuchal constrictions well developed (Figs 2, 3). Points of mantle attachment to head damaged. Head narrow, (now, an artefact) almost free of brachial crown, attached to mantle by oesophagus and fragmentary mantle tissue. Funnel (now, an artefact) almost entirely free of ventral head surface; funnel aperture not constricted; funnel organ comprising four elliptical (1.4–1.5 mm length) pads (Fig. 6).

Arm widths at level where web vestiges attach to arm bases: 1R (7.0 mm), 2R (7.0 mm), 3R (6.5 mm), 4R (6.0 mm). Arms 235–289% ML, 75.4–61.3% TL, formula 1 > 2 > 4 > 3. Web obliterated. Intact arms with 140–154 suckers; suckers uncrowded, none abruptly enlarged, biserial to tips, with acetabulum wider than infundibulum; greatest diameter 4–4.2% ML, slightly smaller on arm pairs 1 and 2 than 3 and 4.

Gills distorted, almost filling pallial chamber: left, ~17 × 11 mm; right, ~25 × 11 mm (Fig. 7). Epithelium connecting ventral renal surfaces with inner mantle surfaces unapparent. Left gill with basal 4 lamellae regularly disposed, thereafter chaotic (gill distortion precludes precise differentiation of demi-branches or counting of lamellae); with ~22 lamellae in total, with terminal 2 or 3 lamellae gradually reducing in size.



Ligula long, narrow, 17.6% arm length; with ~15–17 transverse rugae (basal 9 apparent; distal 6–8 largely obliterated, inferred by remnants of scalloped margins or raised ridges) (Figs 4, 5). Copulatory groove constricted immediately distal to calamus;

sides of ligula form acute angle with calamus, enfolding its base; calamus ~30.8% LL. Hectocotylied arm ~149% ML, 38.7% TL, 70.5% opposite arm length, 51.4% longest arm length; with 39 suckers.



Figs 2–7. *Teretoctopus alcocki*, lectotype, ♂, ML c. 49.8 mm, RBINS I.G. 11917/INV.190100 (formerly IM 1341/1): 2 – dorsal view, entire specimen, tissue (blot) dried, MNHN post-postage, before examination; 3 – dorsal view, entire specimen, immersed in water, RBINS, pre-postage; 4, 5 – oral and lateral view of hectocotylus, respectively; 6 – quadripartite funnel organ (with outline stippled for clarity); 7 – mantle cavity and apparent viscera: a – anus; cr – crop; br – branchial heart; f – funnel; g – gill; sg – spermatophoric complex; st – stomach; t – testis; to – terminal organ; v – arm vein. Absolute measurements for characters are detailed in Table 4 and descriptive text



Digestive gland missing. Remnants of alimentary canal unremarkable. Caecum (8.2 × 11 mm) pouch-like, with two hepatic ducts. Stomach (9.2 × 8.6 mm) muscular. Crop without apparent diverticulum; residual contents include fish scales; posterior oesophagus thick-walled. Posterior salivary glands broadly heart-shaped, 6.6 × 5.3 mm (13.3% ML). Buccal bulb (distance between beaks and where oesophagus enters arm crown) ~12.5 mm (~25% ML). Anal flaps absent.

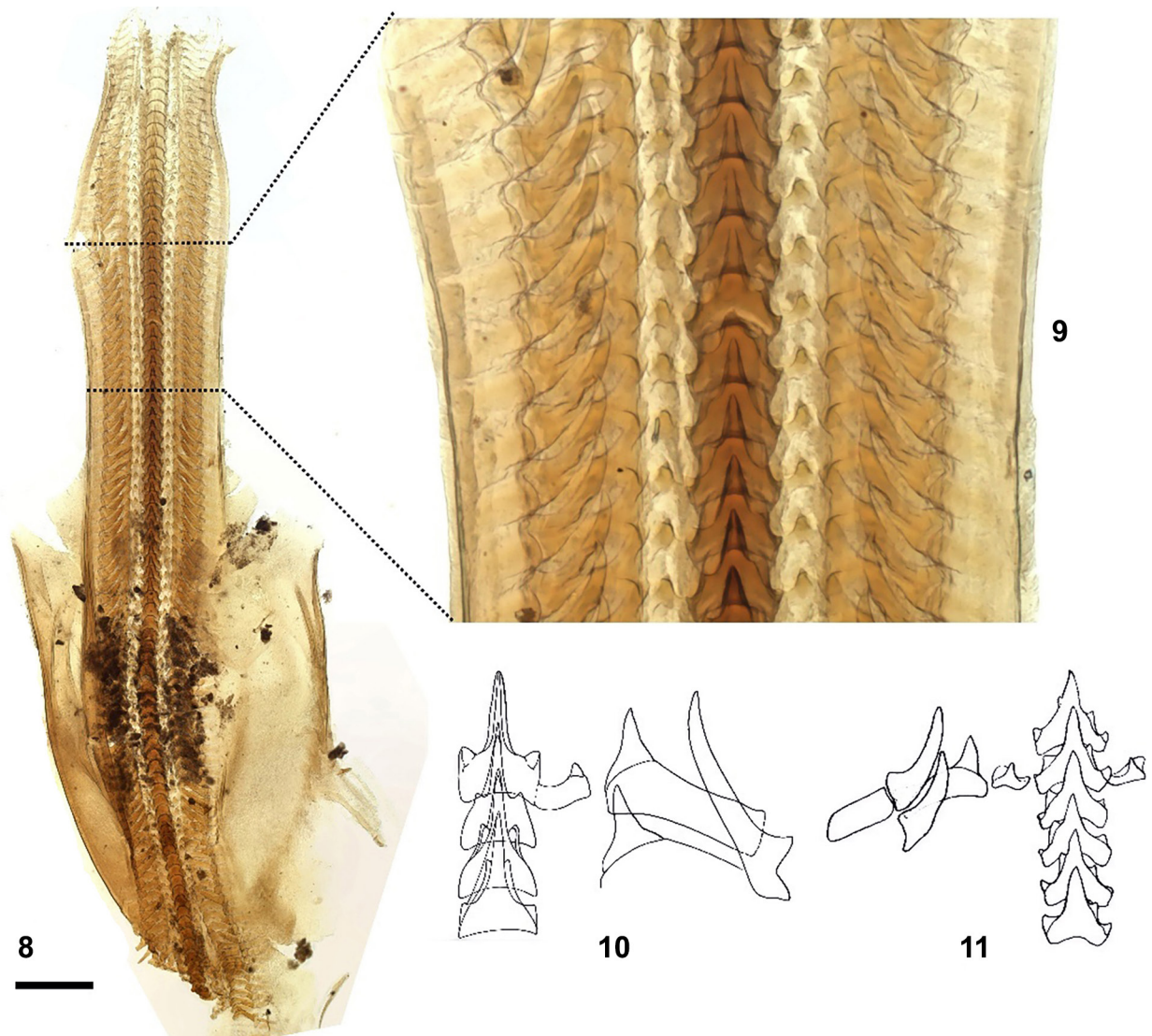
Paralectotype 350/1 (Figs 8–10)

Radula ribbon with ~85 visible transverse rows of teeth, with 7 teeth per row, without consistent seriation (seriation repeats from rows 6 to 9 or more). Rachidian tooth damaged from rows 50–61, and worn from rows 62–85; consistently with strong basal cusp either side of medial cusp, inconsistently with single asymmetrically disposed lateral cusp on one side of medial cusp from transverse rows 1–11, and single lateral cusp either side thereafter. Laterals 1–3 and marginal blocks unremarkable.

Table 4. Measurements (mm) of *Teretoctopus alcocki* Robson, 1932 lectotype (1341/1) and OUMNH non-type (8570/1) of GOODRICH (1896): * – damage; + – plus more; – – no data

Raw	1341/1	Index		8570/1	Index	
TL	191			175		
ML	49.8			40.0		
MW	26.1	MWI	52.4	29.5	MWI	73.8
HdL	15.6	HdLI	31.3	16.5	HdLI	41.3
HdW	17.4	HdWI	34.9	25.5	HdWI	63.8
EO	3.5	EOI	7.0	1.5	EOI	3.8
AL1R/L	144	ALI1	289.1	130/117*	ALI1	325/*
AL2R/L	131	ALI2	263.1	126/130	ALI2	315/325
AL3R/L	74/105	ALI3	148.6/210.8	78/115	ALI3	195/287.5
AL4R/L	117	ALI4	234.9	126/115	ALI4	315/287.5
		AL (%ML)	~211–289		AL (%ML)	~719–812
		AL (%TL)	~55–75		AL (%TL)	~66–74
		AF	1.2.4.3		AF	1 = 2.3 = 4
OAI		OAI	70.5		OAI	67.8
WDA	–	WDIA	–	43	WDIA	33.1
WDBR/L	–	WDIB	–	41/36	WDIB	31.5/27.7
WDCR/L	–	WDIC	–	42/45	WDIC	32.3/34.6
WDDR/L	–	WDID	–	35/38	WDID	26.9/29.2
WDE	–	WDIE	–	26	WDIE	20.0
		WF	–		WF	A = B = C.D.E
ASC1R	146			70+*		
ASC2R	140			104+*		
ASC3R/L	39/			55		
ASC4L	154			~167/158		
		ASC1–4	140–154		ASC1–4	158–167
ASn1R	2.0	ASI1R	4.0	2.5	ASI1R	6.3
ASn2R	2.0	ASI2R	4.0	2.5	ASI2R	6.3
ASn3R/L	2.1	ASI3R/L	4.2	2.2/2.3	ASI3R/L	5.5/5.8
ASn4R	2.1	ASI4R	4.2	2.2	ASI4R	5.5
FuL	13.9	FuLI	27.9	16.0	FuLI	40.0
FFL	–	FFLI	–	6.5	FFLI	16.3
PA	–	PAI	–	20.6	PAI	51.5
		HcAL/LAL	51.4		HcAL/LAL	60.0
CaL	4.0	CaLI	30.8	5.0	CaLI	45.0
LL	13.0	LLI	17.6	11.1	LLI	14.2
GiLC	?11/11			–		

HcAL/LAL is hectocotylied arm length/longest arm length.



Figs 8–11. *Teretotopus alcocki*, paralectotype (formerly IM 350/1), ♂, ML unknown: 8 – entire radula, dashed lines indicate where ADAM (1939) may have illustrated the radula (9 – inset) from this preparation (between transverse rows 20 and 31); 10 – *T. alcocki* radula, redrawn from ADAM (1939, text fig. 25); 11 – *T. indicus* radula, redrawn from ROBSON (1932: text fig. 46). Scale bar 1 mm (for 8); no scales were presented for figures in ROBSON (1932) or ADAM (1939)

OUMNH specimen (Figs 12–15, Table 4)

Mantle spherical, soft, smooth; nuchal constriction stronger than brachial constriction (Fig. 12); skin with numerous minute red chromatophores. Points of ventral mantle attachment to head ventrolateral to eye. Head narrower than mantle. Funnel with distal 40% free; funnel aperture not constricted.

Arm widths at points of web attachment: 1R (7.5 mm), 2R (7.1 mm), 3R (6.2 mm), 4R (6.2 mm); web extends dorsally and ventrally as narrow riblet along arms to distal 30%. Arms 287–325% ML, 65.7–74.3% TL, formula 1 = 2 > 3 = 4. Deepest web sector (C) 34.6% longest arm, 39.1% shortest non-hectocotylised arm; shallowest web sector (E) 20% longest arm, 22.6% shortest non-hectocotylised arm. Intact arms with 158–167 uncrowded suckers,

none abruptly enlarged, biserial to tips, with acetabulum wider than infundibulum; greatest diameter 5.5–6.3% ML, slightly larger on arm pairs 1 and 2 than 3 and 4.

Digestive gland, gills, and reproductive system missing. Posterior salivary glands asymmetrical: broadly triangular, 7.0 × 7.0 mm (17.5% ML), almost circular, 6.1 × 6 mm (15.3% ML). Buccal bulb intact; length cannot be reliably estimated. Viscera largely destroyed; no vestige of ink sac apparent; anal flaps absent. Funnel organ quadripartite (Figs 14, 15), with central two pads (3.2 × 1.1 mm) more prominent than lateral two pads (5.1 × 1.8 mm).

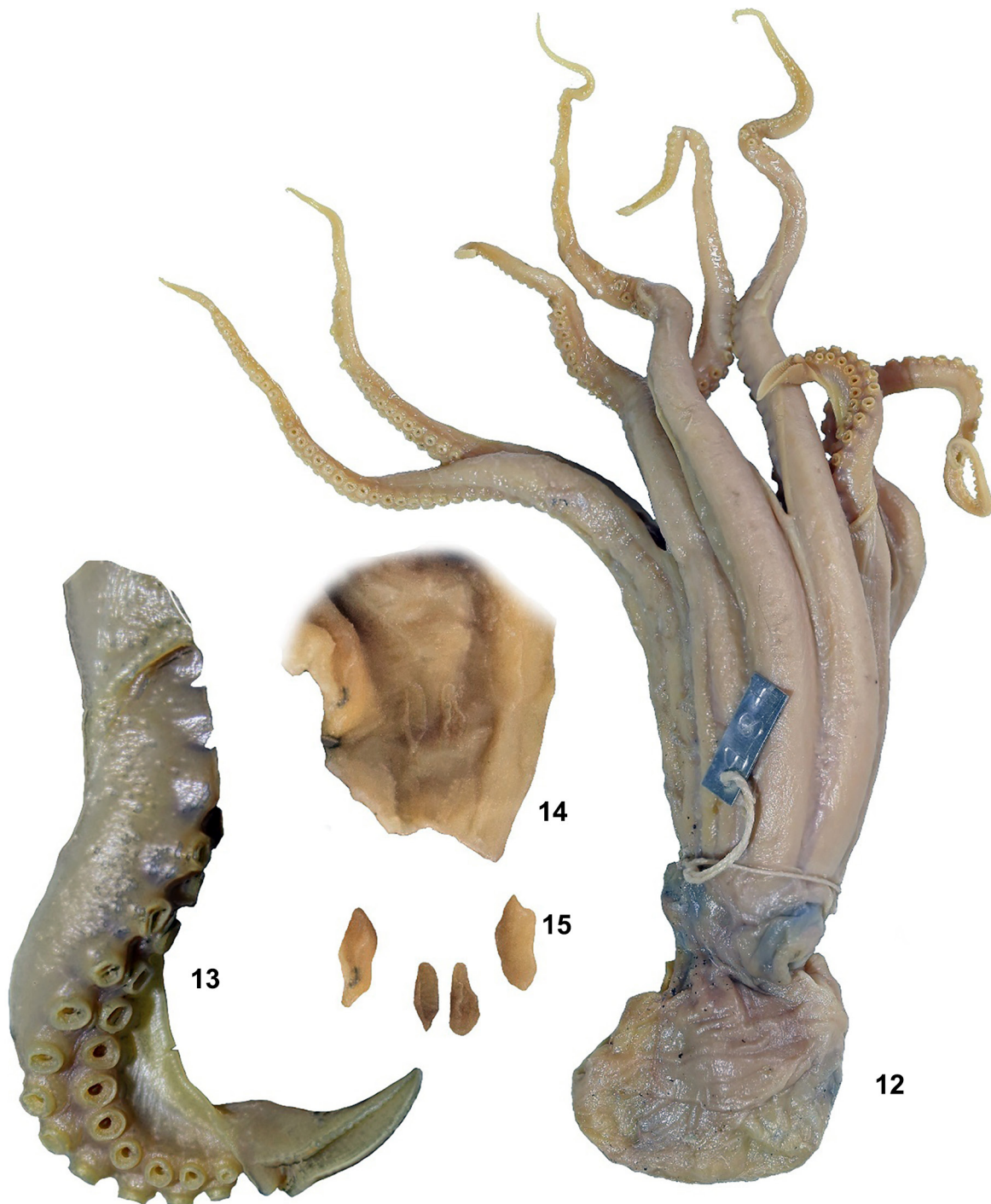
Ligula long, narrow, 14.2% arm length (Fig. 13); with ~16 transverse rugae, more clearly defined basally. Copulatory groove wide, well developed; sides of ligula form acute angle with calamus, enfolding its

base; calamus ~45.0% LL. Hectocotylied arm 195% ML, 44.6% TL, 67.8% opposite arm length, 60.0% longest arm length; with 55 suckers.

Remarks

While our redescription of the lectotype proffers novel information, the specimen's poor condition and incompleteness limit what can be discerned from it;

to extract its beaks, radula, and vestiges of the male reproductive and alimentary systems would destroy what limited structural integrity remains (micro-CT data for this specimen [images not presented, but available on reasonable request] revealed no characters of value). If the lectotype and OUMNH specimens are conspecific, enough information is provided to re-identify this species from specimens collected



Figs 12–15. *Teretotopus alcocki*, OUMNH ZC.1979, ♂, ML 40.0 mm: 12 – whole animal, dorsal; 13 – terminal portion of third right hectocotylied arm; 14 – quadripartite funnel organ (central two limbs obvious; lateral limbs less obvious); 15 – funnel organ (same image as 14, with funnel tissue digitally erased). Absolute measurements for characters are detailed in [Table 4](#) and descriptive text



from or proximal to “syntype” (= paralectotype) localities. However, with regard to these, problems are apparent for three of them.

While GOODRICH (1896) cites a collection depth of 193 fathoms and coordinates 20°17'30"N, 88°30'E for Bay of Bengal specimen 347/1, the closest station to this (14) cited by ALCOCK (1902) and ANON (1914) is ~40 nautical miles (nm) away (20°17'30"N, 88°51'E). A “? position” remark adjacent to coordinates for “Investigator” stn 343 in ANON (1914) also suggests uncertainty regarding coordinate accuracy for specimen 3348/1. Our plot of the “Investigator” course from stns 338–346 (Fig. 1, inset) reveals an anomalous U-turn from stn 342 off Sohar to stn 343 off Muscat (near stns 340 and 341), followed by an approximate 250 nm reversal and steam north within 24 h through the Gulf of Oman, then west and through the Strait of Hormuz to sample at stn 344. While possible, it is more plausible that station 343 (609 fath, 1,113 m) was made near but north of stn 342, and within the Gulf of Oman, because depths within the Strait of Hormuz are far shallower.

Paralectotype 350/1 was purportedly collected from the Andaman Sea in 271 fathoms (GOODRICH 1896), but neither ALCOCK (1902) nor ANON (1914) report any Andaman Sea, Bay of Bengal, or Arabian Sea station prior to 1895 (to “Investigator” stn 182) from this depth. Because GOODRICH’s account of cephalopods from (then) Calcutta Museum collections was read to the Linnean Society on 18 December 1895 (GOODRICH 1896) and was based on collections received by a Professor RAY LANCASTER “last year” (i.e., 1894), those specimens available to GOODRICH must have been collected earlier in or prior to 1894. Stations from similar depths, or a range including 271 fath collected between 1884 and the end of 1894 include Andaman Sea stns II⁴ (272 fath), 7 (267 fath), and 13 (265 fath) (Fig. 1); Bay of Bengal stns 6 (272 fath), 129 (270 fath), 130 (258–281 fath), and 172 (200–350 fath); and Arabian Sea stn 151 (142–400 fath). Only for the herein-designated lectotype (from “Investigator” stn 297) are the coordinates unambiguous.

The metal tag and string tied around the body of the OUMNH specimen are identical to those of the herein-designated lectotype, except that the former tag has “48 B” crudely scratched into it, whereas the latter has “M ” punched into it. The OUMNH specimen was likely retained by or gifted to GOODRICH and accessioned into Oxford collections on 13 January 1896 following his report on this collection (GOODRICH 1896). The (new name) Indian Museum loan made out to ROBSON (27 November 1928) re-

fers to only one male (M350/1) from this Andaman Sea station.

ROBSON (1932) described the hectocotylus of both males (350/1, 1341/1); specimens 347/1 and 3348/1 were female (GOODRICH 1896, MASSY 1916, respectively). Because MASSY’s (1916) “end of body to eye” and ROBSON’s (1932) ML measurements are broadly comparable, we estimate the ML of the lectotype (1341/1) to have been ~54 mm when ROBSON (1932) examined it, and that of 3348/1 to have been ~60 mm. As the lectotype bears no resemblance to the specimen figured by ROBSON (1932: pl. III, fig. 3) for which the caption cites “type”, we surmise (given no hectocotylus is visible) that the figured specimen was the now missing 3348/1.

Although the digestive gland of the lectotype is missing, no traces of anal flaps or an ink duct remain, indicating that an ink sac was absent. We also describe the posterior salivary glands to be “vestigial” relative to ML following O’SHEA (1999, table 2, p. 9). While we cannot precisely measure the buccal bulb length, nor determine its outline using micro-CT imagery, it is (at most) of moderate length (~25%) relative to the mantle according to O’SHEA (1999: table 2, p. 9). Accordingly, the buccal bulb is of “normal size” for an octopus species, but the posterior salivary glands are, as described by ROBSON (1932), “vestigial” relative to ML for this specimen. They are “small” for the OUMNH specimen.

Two characters/states ROBSON (1932) considered remarkable for this species and genus were the quadripartite funnel organ, which ROBSON (1932) noted was almost identical for Gulf of Oman specimens 1341/1 and 3348/1, but which differed from that of the “?Andaman Sea” (350/1) and Bay of Bengal (347/1) specimens, which he maintained were also unlike, and gill size (ROBSON 1932: 252). ROBSON (1932) described the absolute size of the funnel organ as decreasing with increased ML, and he ROBSON (1932: 241) also commented that “I ought to remark that in none of these specimens ... is the funnel-organ well preserved. It may be therefore open to question whether the very peculiar quadripartite form seen in Nos. 347, 3348 and 1341 is not purely accidental”. Although gill length is seldom reported in descriptions of octopus taxa, values reported for *Muusoctopus longibrachus akambeii* Gleadall, Guerrero-Kommritz, Hochberg et Laptikhovskiy, 2010 (24–43% ML) include and exceed those ROBSON (1932) reported for *Teretoctopus*, rendering them equally remarkable in relative length, and this character state of dubious taxonomic value (should *M. longibrachus akambeii* be correctly attributed to this genus).

ROBSON (1932: 240) referred to specimen 350/1 (a paralectotype, for which only the radula remains) as so mangled that it could not be properly described, and that it was only possibly referable to *T. alcocki*.

⁴ The first three “Investigator” stations (I–III) were identified by Roman numerals, and thereafter, numbering recommenced at 1 (Arabic numerals).

Because the OUMNH specimen collected with it is similar in many respects to the lectotype, and likely to be conspecific, specimen 350/1 was more probably conspecific also. Accordingly, the radula described by ADAM (1939), reimaged herein (Figs 12–14), is most plausibly conspecific.

The descriptions of this species from accounts of MASSY (1916) and ROBSON (1932) differ in details such as mantle shape (whether elongate-ovoid or round) and which web sector (A or E) is deepest. GOODRICH (1896) provided no description. The OUMNH specimen (ZC.1979) is in better condition than the lectotype (RBINS I.G. 11917/INV.190100), and shares with it a quadripartite funnel organ, similar hectocotylus, and minimum and maximum arm sucker counts (lectotype 140–154; OUMNH specimen 158–167), but differs most notably (and disconcertingly) in having more (55 vs 39) suckers on the hectocotylised arm. With only two intact specimens at our disposal we cannot appraise the significance of this latter difference, although it is more than one of us (SO) would regard as “normal” variation within a species.

Teretoptopus indicus Robson, 1929

Fig. 11; Tables 5, 6

Teretoptopus indica ROBSON 1929a: 608.

Teretoptopus indicus Robson, 1929 – ROBSON (1932: 249–251, pl III (fig. 2), text fig. 46).

Polypus pricei Berry, 1913 – MASSY (1916; partim, specimens 8129–8131/1, 209–210)

Type locality. Arabian Sea, 24°45'N, 63°50'15"E, 995 m (544 fath), Agassiz trawl, 10 April 1906, bottom temperature 8.9 °C, “brown mud”, RIMS “Investigator” stn 366.

Etymology. Though not explicitly stated, likely from Ancient Greek *ινδικός* (*indikós*), meaning from *Ἰνδία* (India).

Description

According to MASSY (1916) (Table 5)

Animal delicate, transparent. Body soft, elongate; eyes large, prominent. Arm length ~2.5 times “body length⁵”, with small, prominent suckers placed “rather far apart”, with none particularly enlarged. Web depth ~33% arm length, sector E slightly shallower,

⁵ Because MASSY's (1916) “body length to eye” measurements exceed those of her “body length to mantle margin”, and she described the mantle as opening “just below the eye”, we deduce that her “body length to eye” was measured from the tip of the mantle to at least the mid-point of the eyes, or perhaps included the entire orbit. MASSY (1907: 379) describes measuring arm length from the “mouth”, which we assume to mean beaks, or their base near the buccal lips.

continuing little along the arms. Mantle opens “just below the eye”, funnel aperture “unusually broad”, and funnel organ (two specimens) with four pads: the median pads very small, oblong, widely spaced, and flanked by a single lateral pad (in the smallest individual, median pads 1.5 mm, separated by 3 mm). Hectocotylus with “small” terminal organ, with faint transverse rows in largest specimen, with “moderately defined” sperm canal. Body perfectly smooth, pale-buff, with minute yellow-brown chromatophores interspersed with a few larger ones. Alternating longitudinal rows of conspicuous large, light-coloured chromatophores extend along arms where skin has

Table 5. Measurements (mm) of *Teretoptopus indicus* Robson, 1929 type material in MASSY (1916) (as *Polypus pricei* Berry)

	Specimen 129/1	Specimen 131/1
End of body to mantle margin	26	20
End of body to eye	34	27
Breadth of body	20	13
Breadth of head	14	10
AL1R/L	70/70	54/48
AL2R/L	64/72	53/49
AL3R/L	41/70	30/*
AL4R/L	71/68	47/47
Hectocotylus	2.5	1.75
FuL	14	12
ASn	1.0	0.75
ED	7	5

* – damage.

abraded.

According to ROBSON (1932) (Fig. 11, Table 6)

Mantle elongate-ovoid; head distinct, very narrow; eyes large, prominent; skin smooth; mantle aperture wide (B–C). Arm lengths approximate-

Table 6. Measurements (mm) and indices *Teretoptopus indicus* Robson, 1929 syntypes in ROBSON (1932)

	Specimen 129/1	Specimen 131/1
ML	31	25
MWI		60–48
HWI		40–37
WDI		40–35
WF		?A = B = C = D.E
Mantle aperture		B–C
ALI		71–69
GiLC		10 or 11
HcLI		6.3–5.5
FuL	14	12
ASIn		4.4–3.5

Note: Indices (denoted by “I”) are percentages.



ly subequal. Web very deep (WDI 35–40), formula ?A = B = C = D.E, extending little along arms, fragile. Suckers small, widely spaced, prominent. Hectocotylied arm 59–66% longest arm length; hectocotylied portion 5.5–6.3%⁶ its length; ligula flat, with few faint lamellae; calamus ~33% LL. Gills long, well developed, with 10 or 11 lamellae per demibranch; inner demibranch reduced. Radula with moderately developed cusps, with main cusp long relative to base width; first lateral with prominent cusp, wide; second lateral with long base and submarginal cusp; third lateral slender, with small base. Crop small, with diverticulum; posterior salivary glands “singularly small”; stomach “exceedingly muscular”; intestine slender, with little local dilatation. Ink sac absent.

Remarks

All syntype material of this species was sourced to collections of the Indian Museum (subsequently named the Kolkata Museum), which, until the outbreak of World War II, had been based in Calcutta. In May of 1942, these collections, along with those of the Zoological Society of India (ZSI), were moved to Varanasi into temporary accommodation at Kaiser Castle on the banks of Varuna River (CHOPRA 1946). A flood in 1943 (see Appendix for a more complete account) destroyed many of these wet-collection specimens. When we attempted to loan this material, it could not be located; we were also informed that it was most likely lost during this flood. To be sure, we extended our search of this material to other candidate collections, in the event this material had not been (as presumed) returned to the IM (given we had relocated specimens of *T. alcocki* that should also have been there).

We suspect that only one of the original three *T. indicus* syntypes was lost in this flood, for two of them were neither dispatched to ADAM in Brussels nor returned to India, because correspondence from ROBSON to ADAM (23 December 1932) indicates that ROBSON could not locate them in December 1932.

DISCUSSION

GENERIC DIAGNOSIS

A direct comparison of *T. indicus* and *T. alcocki* is hindered by our inability to locate any *T. indicus* syntype, and the inconsistent nature of characters and their states, and measurements referred to and used by MASSY (1916) and ROBSON (1932). Descriptions for these two species are also based on specimens in

Moreover, between 1927 and 1937 no record exists of any loan of cephalopods from the British Museum (Natural History) having been returned to any museum that may accidentally have included these two specimens (pers. obsv.).

We note that in the second to last sentence of his description of *T. indicus*, ROBSON (1932: 251) commented (with reference to the length and form of the hectocotylus) that “the latter seem to be undeveloped in all our specimens of *calmani*, but even so it is very unlike that of the smallest *alcocki*”. From this we surmise that ROBSON may have intended to call *T. indicus* “*T. calmani*”, after the then Keeper of Zoology at the British Museum (Natural History), WILLIAM THOMAS CALMAN (1871–1952). However, no specimens identified as *T. calmani* have been located in NHM collections either.

It is possible that metal tags tied around the missing *T. indicus* types have been removed before being photographed for ROBSON’s memoir, and not replaced. If so, these two specimens may still exist, unlabelled in some collection, so it is premature to refer to either of them (or all syntype material of *T. indicus*, the type species of this genus) as being “lost”.

We exclude the Pearl Banks “*O. pricei* (Berry)” record of WINCKWORTH (1926) from our synonymy because insufficient information is reported for it, and we have been unable to locate the specimen. ROBSON appears not to have examined it either, and it has no type status. While this specimen has not been located in Colombo Museum collections (SOMARATHNA pers. com.), it is possible that WINCKWORTH retained it, for RBINS correspondence (28 September 1938) reveals that he donated his entire Indian Ocean cephalopod collection, including unspecified material from the Pearl Banks, to ADAM. Unfortunately, no specimen labelled “*O. pricei* (Berry)” of WINCKWORTH (1926) has been located in RBINS collections to date. Nevertheless, it is premature to refer to this specimen as lost. The hectocotylied portion of the arm illustrated by MASSY (1916: pl. XXIII, fig. 7) appears to be from an immature specimen.

very different states of preservation. From what we can glean from historical texts and images, and from our own examination of *T. alcocki* material, little differentiates these two species. Their radulae are similar, most notably in having a rachidian tooth with a narrow base and few lateral cusps, although the teeth in *T. alcocki* (ADAM 1939: 106, text fig. 25) are slightly shorter and stouter than those of *T. indicus* (ROBSON 1932: 250, text fig. 46). Our stacked photo-

⁶ It is unknown if points of measurement are comparable with the HcLI index of ROPER & VOSS (1983).

micrograph of this preparation is consistent with the illustration of ADAM (1939), which we believe was based on teeth closer to the base of the ribbon than its cutting edge. One noteworthy difference between species descriptions regards the crop diverticulum, which is absent in *T. alcocki*, but present in *T. indicus*. However, O'SHEA (1999: 201) described a diverticulum to be present or absent within a single species referred to "*Benthooctopus*", so it may be an unsuitable character upon which to differentiate species. By necessity, our generic rediagnosis is based largely on what we can discern from the more mature *T. alcocki* lectotype and OUMNH specimens.

THIELE (1935) reconfigured ROBSON'S (1932) diagnosis of *Teretooctopus* to "integument smooth; arms short with 2 rows of suckers and broad velar membrane; funnel organ quadripartite; radula normal; crop distinctly developed; posterior salivary glands weak". VOSS (1988) amended this to "crop with diverticulum; radula with lateral cusps on rachidian; skin smooth; funnel organ III" and, anomalously, with "posterior salivary glands large" (VOSS 1988: 270) and contrarily "reduced" (VOSS loc. cit.: 262). In accordance with O'SHEA (1999: 9, table 2), for the *T. alcocki* lectotype, these glands are "vestigial" to "small", ranging 13.3–17.5% ML. Our revised diagnosis for this genus incorporates this variability in the size of these glands and in crop diverticulum expression.

Molecular studies consistently reveal relationships between *Muusoctopus* and *Vulcanooctopus* to be far closer than GLEADALL (2004) surmised, for the group to be paraphyletic, and for there to be no molecular support to retain these two genera as distinct (JORGENSEN et al. 2010, IBÁÑEZ et al. 2016, 2018, 2020, SANCHEZ et al. 2018, STRUGNELL et al. 2009, 2011). Unfortunately, STRUGNELL et al. (2009), VOIGHT (2012), and SANCHEZ et al. (2018) (by exclusion of *Vulcanooctopus* from their phylogeny) regarded *Vulcanooctopus* to be a junior synonym of *Muusoctopus*, when the former has indisputable nomenclatural priority. GLEADALL (2013: 109) acknowledged as much. We recognise *Vulcanooctopus* to be the senior synonym of the two, and for it to be the more appropriate of these two names to use for most taxa in GLEADALL'S inkless-octopus complex.

While ROBSON (1932) was uncertain if the quadripartite funnel organ of *Teretooctopus* was real or an artefact, it is well preserved in the OUMNH specimen. This organ in the *T. alcocki* lectotype and *Amelooctopus* (NORMAN 1992: fig 1e–g) are for all intents and purposes identical, and they are otherwise very similar in the OUMNH specimen to that of *V. normani* (Massy, 1907) (new comb.) (ALLCOCK et al. 2006: 377–379, fig. 3C), and to a lesser extent, *Bathypolypus bairdii* Verrill, 1873 and *Bathypolypus pugniger* Muus,

2002 (MUUS 2002: 208, fig. 18). The other character state that ROBSON (1932) considered remarkable for *Teretooctopus*, relative gill length, is also not unique to this genus. Therefore, because no single character or state described for *Teretooctopus* is unique to this genus, the better-preserved OUMNH *T. alcocki* looks very much like other species formerly attributed to *Muusoctopus* or *Benthooctopus*, and *Teretooctopus* has nomenclatural priority over *Vulcanooctopus*, *Teretooctopus* may prove to be the most appropriate name to apply to species in this complex of three genera. While we lean towards this course of action, we stress that no such synonymy should be made until molecular data for *T. indicus* or *T. alcocki* from specimens collected from or proximal to the type locality (consistent with redescription herein) is procured. For this reason, we describe these specimens in as much detail as possible to facilitate reidentification of this taxon.

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Conflict of interest. The authors declare no conflict of interest.

Ethical approval. No animal testing was performed during this study (materials referred to herein have been accessioned into museum collections).



Sampling and field studies. The study is based on historical museum preserved specimens, for which we can only assume that any (if appropriate) permit was used during specimen collection.

Data availability. All data generated or analysed during this study are included in this published ar-

ticle. Micro-CT scans of the *Teretoctopus alcocki* lectotype are available on reasonable request.

Author contribution. All authors contributed to the writing of this manuscript, and/or information presented in it, and to extensive searches of collections, and archived information.

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APPENDIX

Until the outbreak of World War II, the Kolkata Museum (formerly the Indian Museum) collections were based in Calcutta. However, for security, these collections were moved in May of 1942, along with the Zoological Society of India (ZSI) collections, to Varanasi into temporary accommodation at Kaiser Castle on the banks of Varuna River (CHOPRA 1946). As the designated repository for the seven syntypes (ROBSON 1932: 249, 251) we requested their loan to redescribe them to stabilise the concepts of the genus and two species. However, none could be located (MUKHOPADHYAY pers. comm.) and their whereabouts was unknown. It was speculated that they had been lost during the 1943 Varuna Flood (CHOPRA 1946), or that they may not have been returned to the ZSI after having been previously loaned. To eliminate the latter possibility, obvious starting points to locate them were the collections of the NHM (because of Robson's association) and Royal Belgian Institute of Natural Sciences (RBINS) in Brussels (because of William Adam's association). Search efforts were also extended to collections of the National Museum of Ireland (NMI), the former base of Annie Massy, Oxford University Museum of Natural History (OUMNH) because of Goodrich's association, and Muséum national d'Histoire naturelle (MNHN), because of Louis Joubin's association.

Thorough searches located no *Teretocopus* specimens in collections of the MNHN (SO), NHM (JDA), or NMI (VISCARDI pers. comm.), but the collections of the OUMNH yielded a specimen referred by GOODRICH (1896) to “?*O. januarii*” that had not been examined by ROBSON, and those of the RBINS yielded a single *T. alcocki* syntype and a slide-mounted radula of another. The RBINS archives also yielded correspondence between ROBSON and ADAM dated 25 Jan 1933 confirming that ROBSON had forwarded the four *T. alcocki* and one of three *T. indicus* syntypes (for two syntypes could not be located) to ADAM, and an exchange between ADAM and BAINI PRASHAD, the ZSI director on 24 August 1938 that not only indicated that these specimens had been returned from Brussels to India, but that following their return, duplicate specimens had been returned to ADAM as “retribution de détermination” for accessioning into the RBINS collections. This correspondence confirms that the specimen of *T. alcocki* in RBINS collections is an original syntype (that we designate to be the lectotype), that it was donated to this repository, and that all other syntypes of this species (excepting what is now a paralectotype radula) had been returned to India in the late 1930s.