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Flapjack octopods of Australia (Cephalopoda: Cirrata: Opisthoteuthidae), Part II northwestern Australia and adjacent waters

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Abstract

Herein the flapjack octopods (Opisthoteuthidae) of northwestern Australia in addition to adjacent Indonesian waters are examined. Three species are identified, all distinct from taxa recorded off southern and southeastern Australia in the preceding Part I contribution. A new species in genus *Opisthoteuthis*, *O. carnarvonensis* **sp. nov.**, is described from five specimens collected off northwestern Australia. *Opisthoteuthis* cf. *philipii* is described from off northwestern Australia (single specimen) and Indonesian waters (seven specimens). Lastly, a partial re-description is provided for *O. extensa*, which is transferred to genus *Insigniteuthis* (**comb. nov.**) and has its range extended to Java and northwestern Australia, the male of *I. extensa* is shown to be comparable to *I. dongshaensis* in enlarged sucker configuration. A key is proposed to enable the identification of Opisthoteuthidae globally.

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Introduction

The flapjack octopods are deep-sea octopods within the family Opisthoteuthidae Verrill, 1896, members of the finned octopods of sub-order Cirrata Grimpe, 1916. These mostly benthic and gelatinous animals were traditionally all allocated to the genus *Opisthoteuthis*, recently split into three genera based on differences in male enlarged suckers (Verhoeff 2024). The opisthoteuthid cirrate octopods are distinguished from the other cirrate families by a combination of external and internal features. The very short dome-like mantle with terminal fins, relative to proportionally massive eyes and thick arms, are visually distinct. Internally the presence of a branched optic nerve, and internal shell (gladius remnant) without lobe-like ends is only shared by the related Cirroctopodidae Collins & Villenueva, 2006, though these are distinguished by having proportionally massive fins, lacking male enlarged suckers, and in having a unique pallial adductor (completely dividing the pallial cavity posteriorly) (Collins & Villanueva 2006).

The waters around Australia and New Zealand, and the Pacific Ocean more broadly, host a high diversity of flapjack octopods, though this diversity remained largely undocumented until recently. The fauna around New

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Zealand comprises three species *Opisthoteuthis mero* O'Shea, 1999, *O. chathamensis* O'Shea, 1999, and *O. robsoni* O'Shea, 1999, whereas the waters around southern and southeastern Australia host four species across three genera, *Opisthoteuthis pluto* Berry, 1918, *O. kerberos* Verhoeff, 2024, *Insigniteuthis obscura* Verhoeff, 2024, and *Exsuperoteuthis persephone* (Berry, 1918).

The waters off northern Australia have received no attention regarding cirrate octopods in the scientific literature, the nearest areas receiving any such work being Indonesian waters, the remote Coral Sea, and northern Indian Ocean, but these works were limited. Hoyle (1886) described some limited cirrate material from the Coral Sea and Philippines attributable to *Grimpoteuthis* (*G. pacifica* (Hoyle, 1885) and *G. meangensis* (Hoyle, 1885)) but identified no opisthoteuthids. Chun (1903) recorded a single specimen of *Opisthoteuthis* sp. from Indonesia which was later described by Thiele (1915) as *O. extensa* Thiele, 1915, but the limited description rendered it difficult to differentiate from any other species in its genus. The next year Massy (1916) documented five *Opisthoteuthis* (designated "*Cirroteuthis grimaldii*" therein) from the Andaman Sea and Arabian Sea, but these were damaged and never illustrated or described in detail.

More recently opisthoteuthid material has been collected as part of several voyages from northwestern Australia and adjacent Indonesian waters. The fisheries vessel FV *Courageous* and research vessel RV *Soela* collected some cirrate octopods from northwestern Australia in the 1980s (though this hasn't been reported on in literature). The French–Indonesian KARUBAR 1991 expedition to waters off the Indonesian Islands of Kai, Aru, and Tanimbar collected a small number of putative *Opisthoteuthis*, which were partially worked on by the late F.G. (Eric) Hochberg, though unfortunately he never managed to publish his work (Hochberg 1996-2013, unpublished documents). Recently, additional opisthoteuthids were collected off Java as part of the 2018 SJADES (South Java Deep-Sea) biodiversity expedition (Ng & Rahayu 2021), and off northwestern Australia as part of a recent CSIRO voyage to the Gascoyne and Carnarvon Canyon Marine Parks (IN2022_V09, late-2022) (CSIRO 2023).

This contribution is the second part of a review of the Australian opisthoteuthid taxa, the first part (Verhoeff 2024) covered the southern and southeastern Australian fauna. The second part of this review herein addresses a small but significant collection of opisthoteuthids from northwestern Australia and adjacent Indonesian waters, which is revealed to have an opisthoteuthid fauna distinct from southern Australia and continuous with that of Indonesian waters and the northern Indian Ocean.

Methods

Most specimens were examined at the Tasmanian Museum and Art Gallery (TMAG) collections and research facility (Rosny Park, Tasmania), including specimens loaned from the Western Australian Museum (WAM) (Perth, Western Australia). Older material from northwestern Australia was collected by fisheries vessel FV *Courageous* and Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO) research vessel RV *Soela* in the early 1980s. More recently specimens were collected by the RV *Investigator*, Australian Marine National Facility under the CSIRO, from the Gascoyne Marine Park and Carnarvon Canyon Marine Park as part of the voyage "Valuing Australia's Gascoyne Marine Park" (IN2022_V09, Nov–Dec 2022) (CSIRO 2023). Additional material was collected as part of the Mar−Apr 2018 South Java Deep-Sea Expedition (SJADES) to the southwest of the Sunda Strait and Java, by the RV *Baruna Jaya VIII* (Ng & Rahayu 2021) (station data per Chuar *et al.* 2021), the SJADES voyage was a joint expedition by the National University of Singapore (NUS) and Lembaga Ilmu Pengetahuan Indonesia (LIPI, or Indonesian Institute of Sciences). All material was fixed in 5%–10% formalin and stored in 70%−75% ethanol. Tissue samples were generally unavailable.

Photographs of type material were provided by the Museum für Naturkunde (Zoologisches Museum der Humboldt-Universität zu Berlin or ZMB), Berlin. The Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum, National University of Singapore, provided additional photographs of non-type material.

The late Dr Frederick G. (Eric) Hochberg (1941–2023), former curator at the Santa Barbara Museum of Natural History, collected measurement and count data for seven specimens of *Opisthoteuthis* at the Muséum National d'Histoire Naturelle (MNHN), Paris, in the early 1990s, and completed line illustrations for anatomical parts of these specimens. This work was never published, but the original illustrations, data spreadsheets, and notes were generously scanned and provided by the Santa Barbara Museum of Natural History (SBMNH), Santa Barbara (USA), so that this important material could be published. Hochberg's specimens were collected during the *Karubar* expedition of late-1991 (RV *Baruna Jaya I*), a collaboration between the MNHN and Institut de Recherche pour le Développement (IRD) (formerly ORSTOM), to explore deep-sea fauna of the tropical Indo-Pacific, particularly around the Indonesian islands of Kei, Aru, and Tanimbar (Crosnier *et al.* 1997).

Collection locations of all opisthoteuthid specimens examined in this contribution are depicted in **Figure 1**.

Nomenclature, indices, photography equipment, image processing software, and abbreviations follow those used in the previous 'Part I' contribution (Verhoeff 2024) as well as earlier contributions by the author (Verhoeff &

O'Shea 2022). Beak indices and measurements are illustrated in **Figure 2**. As before, mature male specimens were designated based on presence of enlarged sucker fields, while mature females were recognized by similar size to mature males, absence of enlarged suckers, and presence of eggs in the distal oviduct or proximal oviduct indicative of spawning.

General morphological abbreviations: Acet—acetabulum, AGC—accessory gland complex, AL—arm length (arms numbered in roman numerals I to IV), CiL—cirrus length, DESF—distal enlarged sucker field, ED—eye diameter, FL—fin length, FuL—funnel length, FW—fin width, Gill LC—gill lamellae count, HW—head width, Inf—infundibulum, ML—mantle length (dorsal), MW—mantle width, PA—pallial aperture gape, PESF—proximal enlarged sucker field, SC—spermatophoric complex, SS—spermatophoric sac, SuD—sucker diameter (Inf and Acet for infundibulum and acetabulum respectively), TL—total length, WD—web depth (per sector A to E), WN—web nodule position (relative to sucker count on each arm).

Indices: ALI—arm length index (given as a multiple of ML), CLI—cirrus length index (CiL%ML), EDI—eye diameter index (ED%ML), FLI—fin length index (FL%ML), FWI—fin width index (FW%FL), FuLI—funnel length index (FuL%ML), HWI—head width index (HW%ML), MWI—mantle width index (MW%ML), PAI—pallial aperture gape index (PA%ML), SDI—sucker diameter index (SD%ML), WI—web depth index (web sector A%AL I, and web sector E%AL IV).

Other abbreviations: coll.—collector, CSIRO—Commonwealth Scientific and Industrial Research Organization (Australia), FV—fisheries vessel, L—left, NW—north-west, R—right, RV—research vessel, SE—south-east, Stn—Station, SW—south-west.

Discussion

The Opisthoteuthidae from northern Australia have never been the subject of taxonomic work, and even the adjacent waters off the Indonesian archipelago have received almost no attention other than Thiele's (1915) brief description of *O. extensa*, and the brief mention of an opisthoteuthid by Ng & Rahayu (2021).

From the present work, the opisthoteuthid taxa from northwestern Australia and adjacent Indonesian waters are distinct from those species occurring off southern Australia (Verhoeff 2024) and New Zealand (O'Shea 1999), with none of the species from off southern Australia being located in collections from northern Australia and Indonesia. Further work remains to be done on the taxonomy of opisthoteuthids across the Indian Ocean and Pacific, but this work (in combination with the Part I contribution (Verhoeff 2024)) will hopefully provide a starting point for further systematic research.

Overall, the cirrate fauna off northwestern Australia comprises three opisthoteuthid species in genera *Opisthoteuthis* and *Insigniteuthis* (*O. carnarvonensis* **sp. nov.**, *O.* cf. *philipii*, and *I. extensa*), the cirroteuthid *Cirroteuthis kirrilyae* Verhoeff & O'Shea, 2024, and an unidentified *Grimpoteuthis* sp. (family Grimpoteuthididae) collected during the IN2022_V09 cruise from northwestern Australia (specimen WAM S116650, Verhoeff personal observation). In addition, another *Grimpoteuthis* sp. has also recently been observed from the nearby Java Trench (Jamieson & Vecchione 2020). So far the genus *Exsuperoteuthis*, which is common off southern and southeastern Australia (Verhoeff 2024), hasn't been collected from off northern Australia, seemingly isolating *E. persephone* distributed off southern Australia from *E. depressa* in the northern Pacific.

Opisthoteuthis philipii seems to be rather broadly distributed, assuming the specimens from Indonesia and northwestern Australia (*O.* cf. *philipii*) are correctly attributable to it, with a range extending from the Arabian Sea (southwestern India) (Oommen 1976) and along the northeastern Indian Ocean to Indonesian waters and northwestern Australia. *Insigniteuthis extensa* comb. nov. may also have a very extensive range. The examination of specimens herein indicates that *I. extensa* and *I. dongshaensis* may be very similar, though synonymizing is decided against herein (see *I. extensa* remarks in Taxonomy Section), and some aspects of internal morphology remain uncertain (notably the lobation of the digestive gland). Examination of *I. dongshaensis* type material will be needed to resolve these issues, as well as comparison to likely conspecific specimens in the Indian Museum collections, Kolkata, India (Massy 1916). If these species do prove synonymous, *I. extansa* would have an extensive range from the South China Sea and through Indonesian waters to northwestern Australia and the Andaman Sea. Compared to the other northern Australian species, *O. carnarvonensis* sp. nov. seems to have a much more restricted distribution, only known at present from a small area off northwestern Australia, though its true range is probably somewhat greater.

It is hoped that the taxonomic key presented herein for Opisthoteuthidae will facilitate improved identifications of cirrate octopods generally (in combination with the key for all species of Cirroteuthidae and Stauroteuthidae presented in Verhoeff & O'Shea 2024). Constructing this key does reveal some longstanding problematic areas, particularly with identifications being confounded in regions where fauna remains understudied or where taxonomic confusion exists, namely the Indian Ocean, and the North Pacific. This work has made some headway into resolving the Indian Ocean fauna (clarifying *I. extensa* and *O.* cf. *philipii*), but this has been preliminary, and type material for some species (namely *O. philipii*) will need to be assessed in the future. Much more material will need to be examined (with molecular work ideally). The Opisthoteuthidae from the North Pacific are greatly confused at present (per Verhoeff 2024), and the key presented herein continues with the

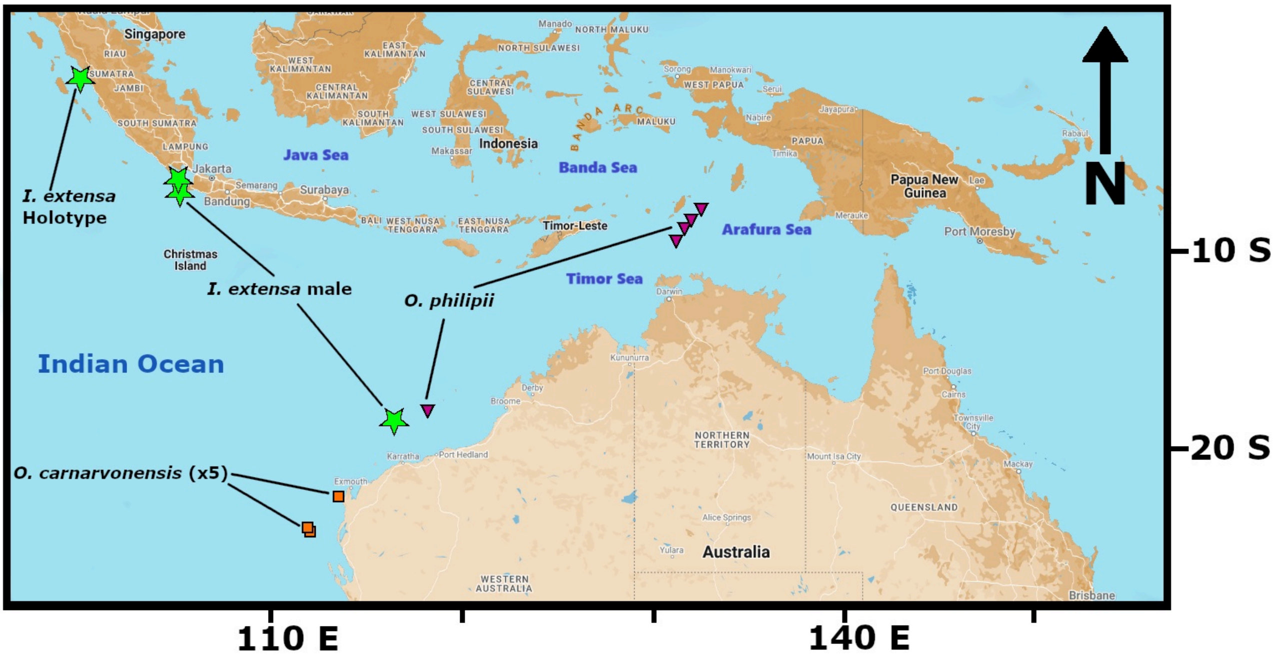

Figure 1. Localities for Australian opisthoteuthids examined during this study. Species identifications are noted. Symbols: green star—*Insigniteuthis extensa*, orange square—*O. carnarvonensis* sp. nov., purple triangle—*O.* cf. *philipii*. Base map modified from Google Maps.

assumption of some species being synonymous (*I. abatrossi* Sasaki, 1920 with *I. californiana* Berry, 1949, and *E. depressa* Ijima & Ikeda, 1895 with *E. japonica* Taki, 1962).

The descriptions of the beak forms for the Australian opisthoteuthids and other cirrates (herein, also Verhoeff & O'Shea 2022; Verhoeff & O'Shea 2024; Verhoeff 2023; Verhoeff 2024), should permit more accurate identification of cirrate taxa in predator stomach contents, and therefore the beak forms are summarized graphically in **Figure 2**. Digested beaks from marine predators have been found to be a useful means of assessing local cephalopod diversity, their relative abundance, what ecological significance different cephalopods have as prey, and the relative size and biomass of the cephalopods consumed in a region (Cherel 2020; Xavier *et al.* 2022). Such studies occasionally identify cirrate octopods, but cirrates only comprise a small percentage of the diet relative to other cephalopods and fishes (generally < 1% to 8% total cephalopod biomass consumed). Beaks from various cirrates (*Stauroteuthis gilchristi*, *Cirroteuthis* (=*Inopinoteuthis*) *magna*, *Opisthoteuthis* sp., *Grimpoteuthis* sp., and Cirrata sp. A) have been recorded from diets of Patagonian Toothfish (*Dissostichus eleginoides*) and Sleeper Sharks (*Somniosus antarcticus*) off Crozet and Kerguelen Islands in the southern Indian Ocean (Cherel & Duhamel 2004; Cherel *et al.* 2004, Table 4). Smale & Cliff (1998) recorded a single beak from a possible *Grimpoteuthis* sp. from the stomach contents of one Scalloped Hammerhead shark (*Sphyrna lewini*) (out of 433 sharks of the same species) collected off KwaZulu-Natal, South Africa.

Limited research has found cirrate beaks (as well as whole animals) in marine predator diets off Australia and the adjacent waters off New Zealand and Macquarie Island. Gales *et al.* (1993) identified beaks attributed to '*Opisthoteuthis* sp.' from diets of Australian Fur Seals off Tasmania, Goldsworthy *et al.* (2002) identified beaks from an unidentified cirrate from Patagonian Toothfish diets off Macquarie Island (Australian Antarctic Territories), and O'Shea (1999) recorded three *Opisthoteuthis mero* from Sperm Whale stomach contents from off New Zealand.

Hopefully, the more reliable identification of cirrate beaks will enable their identification in future predator dietary studies from Australia and surrounding regions. Beaks of the Australian Opisthoteuthidae and other cirrates have a large amount of variation in shape and indices (per **Figure 2**), which could allow reliable identification in future research. While it is convention to illustrate beaks of octopods in species descriptions, the calculation of beak indices for cirrate octopods has frequently been either omitted in descriptions, or given inconsistently, though sufficiently good illustrations may still permit comparison and assessment of indices.

In addition to the indices, several morphological differences are available to discriminate Australian cirrate beaks, the upper beak rostrum can be strongly hooked with a variable length (e.g., *O. pluto*, **Fig. 2 A**, or *O. carnarvonensis* sp. nov., **Fig. 2 E**), or short and relatively straight (e.g., *I. obscura*, **Fig. 2 G**), likewise the lateral walls can be short (e.g., *O. pluto*, **Fig. 2 A**) to relatively elongate (e.g., *O. kerberos*, **Fig. 2 C**), with the shape of the posterior and ventral edge of the lateral wall being

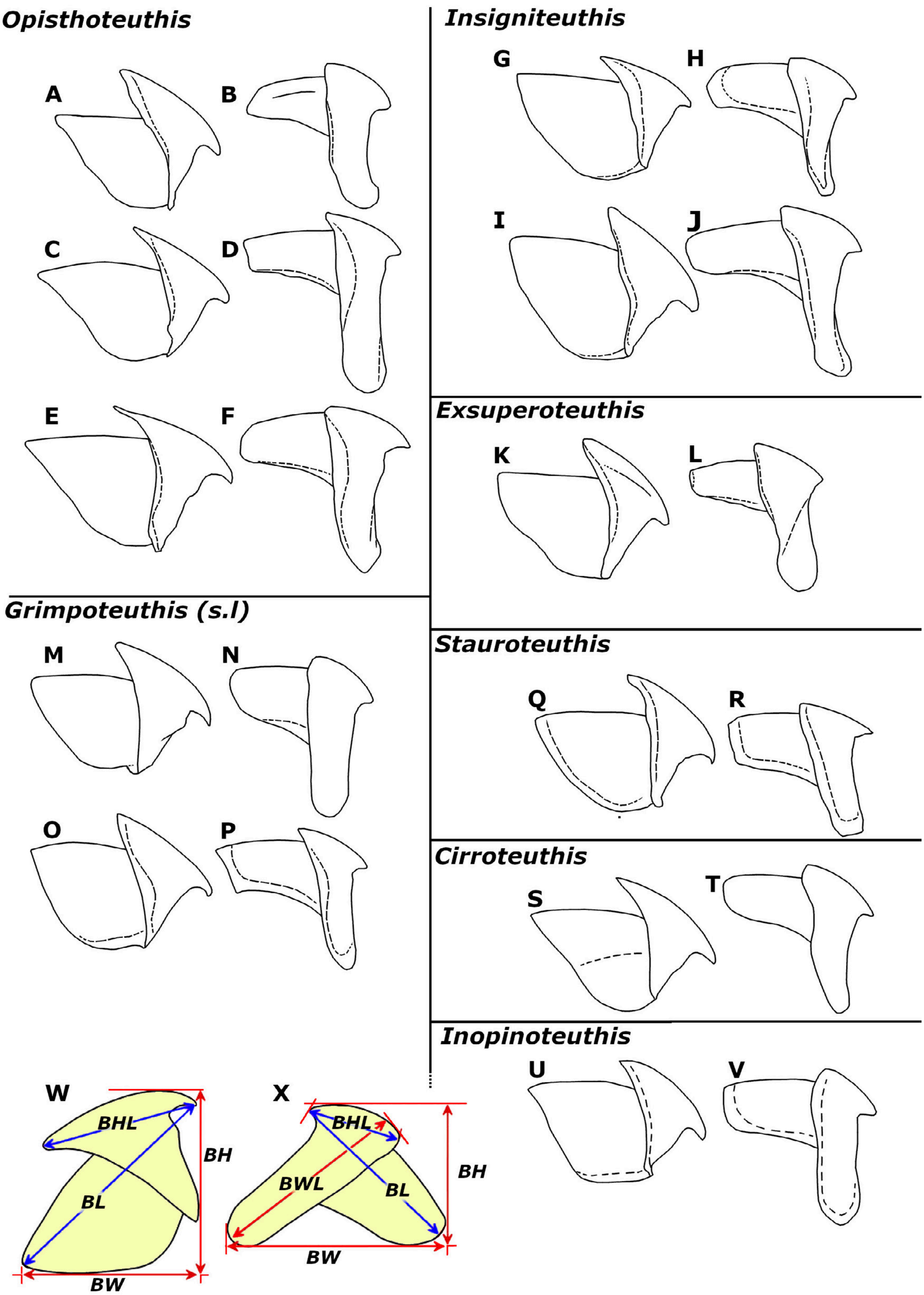

Figure 2. Beak variability amongst the Australian opisthoteuthids and comparison to other Australian cirrates. Beaks are grouped by genus. **A–F**) *Opisthoteuthis* beaks, *O. pluto* (**A**, **B**, upper and lower beaks respectively), *O. kerberos* (**C**, **D**), and *O. carnarvonensis* sp. nov. (**E**, **F**). **G–J**) *Insigniteuthis* beaks, *I. obscura* (**G**, **H**), and *I. extensa* (**I**, **J**). **K**, **L**) *Exsuperoteuthis persephone* upper and lower beaks. **M–P**) *Grimpoteuthis* (*sensu lato*) beaks, *G. greeni* (**M**, **N**), and *G. abyssicola* (**O**, **P**). **Q**, **R**) *Stauroteuthis kengrahami* upper and lower beaks. **S**, **T**) *Cirroteuthis kirrilyae* upper and lower beaks. **U**, **V**) *Inopinoteuthis ?magna* beaks (New Zealand specimen). **W**, **X**) schematic of upper and lower beaks respectively and relevant measurements used to calculate beak indices. Abbreviations/symbols: BH—beak height; BL—beak length; BHL—beak hood length; BW—beak width; BWL—beak wing length.

variably rounded, straight, or indented. Some species also display more unique features such as the distinct upper beak hood groove for *E. persephone* (**Fig. 2 K**). Relatively little distinguishes *Grimpoteuthis* beaks overall from the opisthoteuthid beaks, though the individual species (*G. greeni*, **Fig. 2 M, N**, and *G. abyssicola*, **Fig. 2 O, P**) can be distinguished by a combination of beak characters, particularly the shape of the upper beak hood and rostrum. The lower beaks for these taxa seem less variable, and could be more difficult to attribute to species, but the form of the rostrum shows some variation, as does the relative lengths and edge forms of the lateral walls and hood lateral wings, the straight and pointed rostrum of *Stauroteuthis kengrahami*'s lower beak is particularly distinct (**Fig. 2 R**), as is the blunt and non-hooked rostrum of *E. persephone*'s lower beak (**Fig. 2 L**).

One problem that may hinder the confident identification of cirrate beaks is that individual variation, ontogenetic changes, and sexual variation in beaks of cirrate octopods remain poorly known. Shallow water octopus and squid have significant differences in beak shape with ontogenetic stages (Wang & Fang 2023), and it may be expected that such differences also occur in cirrates, though the relatively long lifespan of cirrates compared to shallow water cephalopods (Collins & Villanueva 2006), may influence the extent of ontogenetic changes in beaks in as yet unknown ways.

As was mentioned in Part I (Verhoeff 2024), the Opisthoteuthidae seem to have a hotspot of diversity in the Pacific, centred around Australia, New Zealand and the northwestern Pacific, and as was seemingly apparent with the Opisthoteuthidae off southern Australia, the northwestern Australian and Indonesian taxa may also have depth stratification, possibly enabling the several species to coexist in the region without excessive competition. *Opisthoteuthis* cf. *philipii* occurs shallowest at 246–552 m, while *O. carnarvonensis* occurs deepest at 1044–1510 m, and *I. extensa* occurs at an intermediate depth of 694–1073 m. It is likely that the real bathymetric ranges are not as well separated, and are somewhat broader and overlapping. Other cirrate octopus taxa from northwestern Australian waters either overlap the bathymetric range of these taxa or occur at considerably greater depths, *Cirroteuthis kirrilyae* for example occurs at a generally greater depth (1497–2581 m) (Verhoeff & O'Shea 2024), *Grimpoteuthis meangensis* (from the Philippines) was collected from 925 m depth (Hoyle 1886), while an unidentified *Grimpoteuthis* sp. has more recently been observed near the Java trench at 5760–6957 m depth (Jamieson & Vecchione 2020).

Examination of the transitional zones where the distinct northwestern Australian and Indonesian, southern–southeastern Australian, and New Zealand opisthoteuthid faunas may be expected to overlap, may better reveal how speciation of these octopods has occurred to such a high degree in this region. One region where all three of these faunas may be expected to overlap has been poorly studied (at least for cirrates), namely the region off northeastern Australia (including the Coral Sea, New Caledonia, and the Norfolk Ridges heading south to New Zealand). Systematic and molecular work on the cirrates from this region may prove particularly informative.

Taxonomic Key

Given the updated descriptions of Australian opisthoteuthids herein, and the earlier treatments of Australian and New Zealand taxa (O'Shea 1999, Verhoeff & O'Shea 2022; Verhoeff 2024), it was possible to construct a key to all cirrates of family Opisthoteuthidae. This key is mostly of use for mature male specimens as it must rely heavily on the enlarged sucker configuration. Identification of female opisthoteuthids is more dependent on comparison to a more limited selection of local species for a given region which can then be discriminated using features such as gill lamellae, sucker counts, web nodules, digestive gland form, pigmentation, and areolar spots. Even with male *Opisthoteuthis*, some geographically separated species are morphologically rather similar, requiring examination of internal structures (AGC or intestine length). As dissection may not be practical, the geographic location is given for all opisthoteuthid species in the key so that local species can be focussed on. *Opisthoteuthis bruuni* is excluded from the key as it was described from juvenile specimens wherein the DESF was poorly developed (the partial re-description of *O. bruuni* by Pardo-Gandarillas *et al*. (2021) also didn't clarify the DESF form or the lobation of the digestive gland).

a	Fins lateral, moderately large; optic nerve as single bundle; shell wing ends lobate	**Grimpoteuthididae**
a	Fins terminal; optic nerve as multiple bundles, shell wing ends tapering to simple points	**b**
b	Fins large; shell V-shaped; mantle cavity divided posteriorly by inter-pallial septum	**Cirroctopodidae**
b	Fins small; shell U-shaped; mantle cavity with simple strap-like inter-pallial septum	**Opisthoteuthidae (1)**
1	Mature males with single enlarged sucker field spanning most of arm, on all arms; shell very broad/flattened, shoulders minimally developed; DG bilobed	***Exsuperoteuthis* (2)**
1	Mature males with PESF restricted to proximal third of arm; with or without distinct DESF, shell moderately U-shaped; DG bilobed or unilobed	**3**
2	With 30–42 enlarged suckers per arm (male); colourless/pale aborally	***E. persephone* [S Australia]**
2	With <20 enlarged suckers per arm (male); orange–brown aborally	***E. depressa* (incl. *O. japonica* as synonym) [N Pacific]**

3 DESF sucker ⌀> PESF sucker ⌀; DESF typically with 2 or 3 (< 5) greatly enlarged suckers ***Insigniteuthis* (4)**

3 DESF absent or with sucker ⌀ < PESF sucker ⌀; DESF with many similarly sized suckers (7–14) ***Opisthoteuthis* (9)**

4 DESF on all arms; DG unilobed ***I. calypso* [E Atlantic]**

4 DESF restricted to specific arm pairs; DG bilobed where known (unknown state for 2 spp.) **5**

5 DESF restricted to arm pair I (each DESF with 4 or 5 greatly enlarged suckers) ***I. albatrossi* (incl. *O. californiana* as synonym) [N Pacific]**

5 DESF restricted to arm pairs II–IV, III & IV, or just pair IV (each DESF with 2 or 3 greatly enlarged suckers) **6**

6 DESF on arm pair IV only ***I. medusoides* [SW Indian Ocean]**

6 DESF on arms II–IV or III & IV **7**

7 DESF on arms II–IV, 7 or 8 lamellae per gill ***I. obscura* [S & SE Australia]**

7 DESF restricted to arms III & IV, 6 or 7 lamellae per gill **8**

8 With multiple web nodules ***I. extensa* [NE Indian Ocean & N Australia]**

8 Without multiple web nodules ***I. dongshaensis* [NW Pacific]**

9 DG unilobed **10**

9 DG bilobed **15**

10 With multiple web nodules along ventral arm edges, DESF & areolar spots present ***O. agassizi* [W Atlantic]**

10 With single/absent web nodule on each ventral arm edge, DESF & areolar spots present/absent **11**

11 Web nodules present, DESF & areolar spots absent ***O. philipii & O.* cf. *philipii* [N & NE Indian Ocean]**

11 Web nodules absent, DESF & areolar spots present/absent) **12**

12 DESF absent, areolar spots present (AG1 or AG2 & 3 dominant) **13**

12 DESF present, areolar spots absent (AG1 dominant) **14**

13 AG1 dominant, intestine length 1.5× oesophagus ***O. robsoni* [New Zealand, SW Pacific]**

13 AG2 & 3 dominant (AG1 vestigial), intestine length 2.7× oesophagus ***O. pluto* [S Australia]**

14 Intestine approximately equal oesophagus length ***O. borealis* [N Atlantic]**

14 Intestine approximately double oesophagus length ***O. hardyi* [SW Atlantic]**

15 With multiple web nodules along ventral arm edges ***O. massyae* [E Atlantic]**

15 With single/absent nodule on each ventral arm edge **16**

16 DESF not developed (DESF sucker ⌀ = mid-arm sucker ⌀), intestine 2× oesophagus length, web nodules absent ***O. mero* [New Zealand, SW Pacific]**

16 DESF developed (DESF sucker ⌀ > mid-arm sucker ⌀), intestine ≤1.5× oesophagus length, nodules present/absent **17**

17 Web nodules absent, AGC dominated by AG1, with DESF of 6-11 enlarged suckers over suckers 17–30 ***O. chathamensis* [New Zealand, SW Pacific] & *O.* cf. *chathamensis* [Macquarie Island]**

17 Web nodules present **18**

18 AGC dominated by AG1 (double size combined AG2 & 3), DESF over suckers 28–38 ***O. carnarvonensis* [NW Australia]**

18 AGC dominated by combined AG2 & 3 (equal or exceeding AG1 dimensions) **19**

19 DESF 9–10 suckers (position suckers 22-31 – 31-39), AG1 equal to combined AG2 & 3 dimensions ***O. grimaldii* [E Atlantic]**

19 DESF 7–9 suckers (positioned suckers 22–31), AG1 half size of combined AG 2 & 3 ***O. kerberos* [SE Australia]**

Taxonomy

Classification

Phylum **Mollusca** Linnaeus, 1758

Class **Cephalopoda** Cuvier, 1797

Order **Octopoda** Leach, 1817

Suborder **Cirrata** Grimpe, 1916

Superfamily **Opisthoteuthoidea** Verrill, 1896 (*fide* Verhoeff 2023)

Family **Opisthoteuthidae** Verrill, 1896

Genus ***Opisthoteuthis*** Verrill, 1883

Opisthoteuthis carnarvonensis sp. nov.

(Figures 3 & 4, Tables 1 & 2)

ZooBank LSID: urn:lsid:zoobank.org:act:6E4A0901-5404-4B0C-9037-C351824C932B

Type specimen lodged at the Western Australian Museum, Perth (WAM S116628).

Diagnosis: Opisthoteuthid with 70–78 suckers per arm of adult, a DESF of 6–10 enlarged suckers on all arms of males, located between the ~28–38th sucker, DESF sucker ⌀ < PESF sucker ⌀, and arms with web nodules; with dark brown−red aboral pigmentation and areolar spots on head and along arms. Internally with digestive gland bilobed, 7 or 8 lamellae per gill, AGC2 and 3 com-

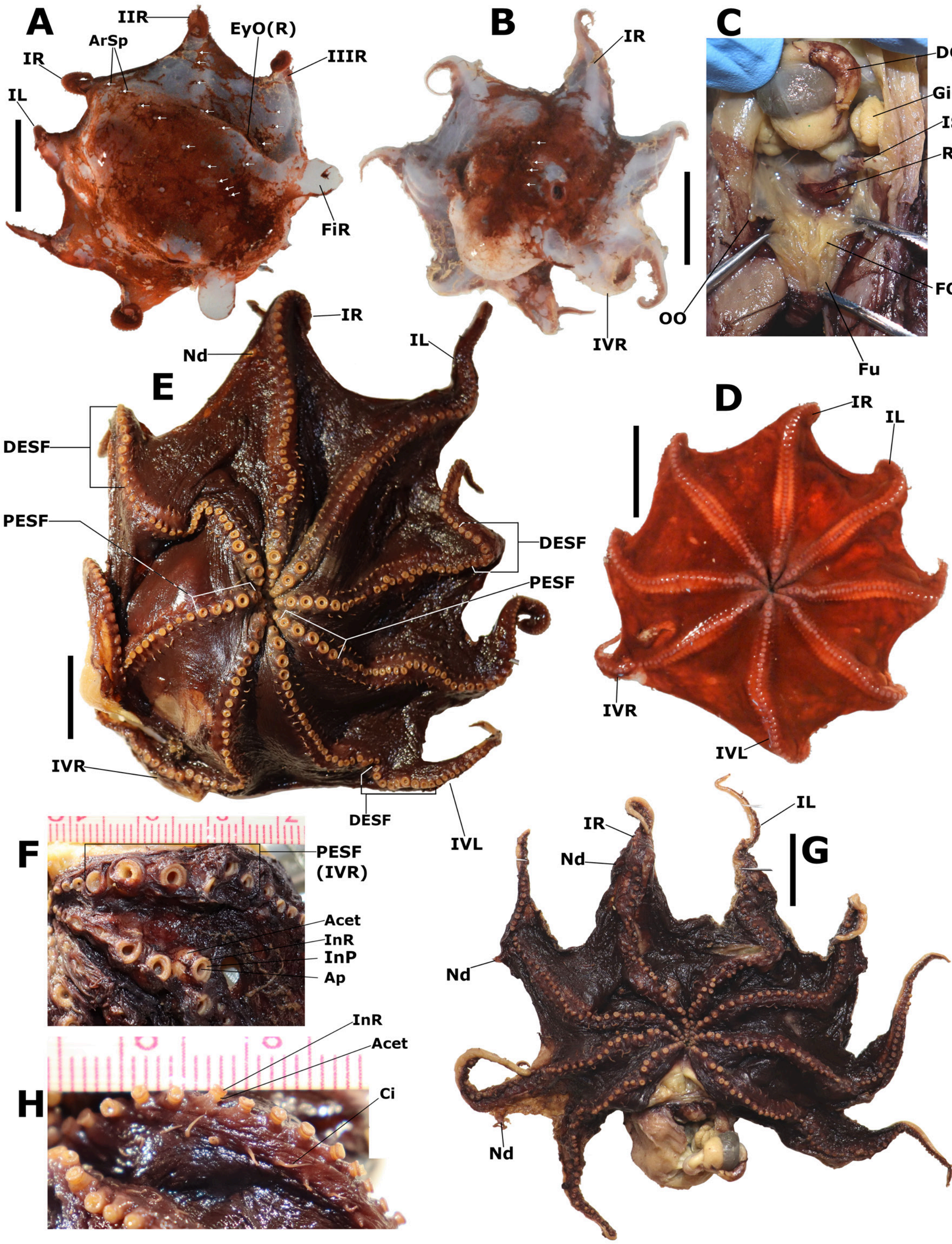

Figure 3. *Opisthoteuthis carnarvonensis* sp. nov., whole aspects, arm detail and funnel organ. **A, B**) aboral aspects of fresh specimens, male holotype (WAM S116628) and female paratype (WAM S116713) respectively. **C**) funnel organ and mantle cavity detail (female, WAM S116713). **D, E**) oral aspect of mature male depicting enlarged sucker fields in fresh condition (**D**) and preserved (**E**) (WAM S116628). **F**) close-up aspect of male PESF (WAM S116714). **G**) oral aspect of female arms and webbing (WAM S116713). **H**) close-up of mid-arm suckers on female (WAM S116713). Abbreviations/symbols: Acet—acetabulum; Ap—sucker aperture; ArSp—areolar spots (marked with white arrows); Ci—cirri; DESF—distal enlarged sucker field; DO—distal oviduct; EyO(R)—eye opening (right side); FiR—fin (right side); FO—funnel organ; Fu—funnel; Gi-R—right side gill; InR—infundibular ring; InP—infundibular pad; ISe—interpallial septum (pallial adductor); I–IV R/L—arm I–IV right/left; Nd—nodule; OO—olfactory organ; PESF—proximal enlarged sucker field. Scale bars = 50.0 mm (**A, B, D**), 20.0 mm (**E, G**), 10.0 mm (**C**), image ruler in mm marks (**F, H**). Photography (**A**, **B**, **D**) copyright Western Australian Museum (taken by WAM/CSIRO staff onboard RV *Investigator*), used with permission.

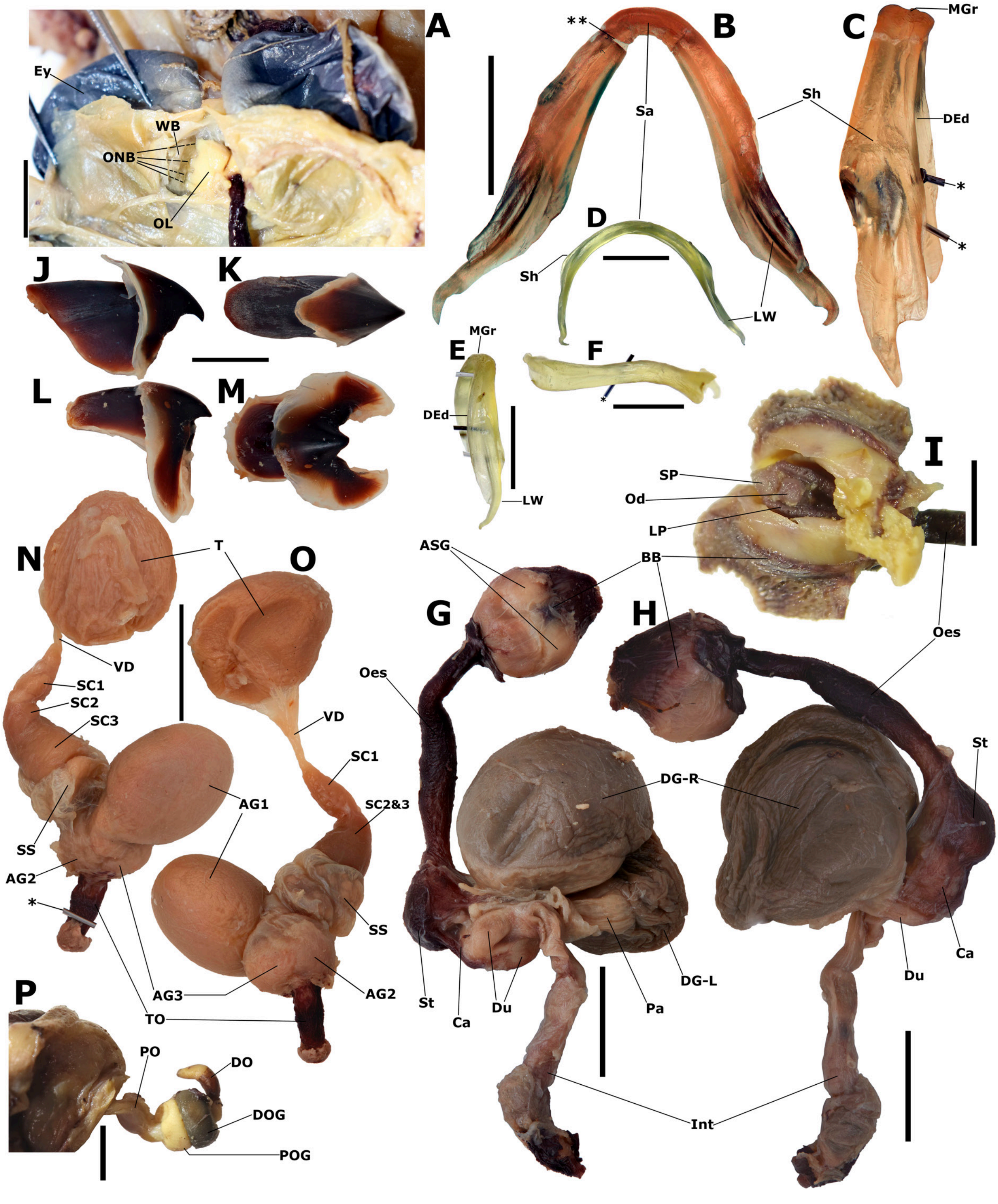

Figure 4. Internal morphology of *Opisthoteuthis carnarvonensis* sp. nov. **A**) left optic lobe and retinal nerve branching pattern (WAM S116714). **B**, **C**) internal shell of male (WAM S116714), dorsal (**B**) and lateral (**C**) aspects. **D–F**) internal shell of female (WAM S116681). **G**, **H**) right and left aspects of the digestive system (male WAM S116714), buccal bulb viewed ventrally (**G**) or lateral (**H**). **I**) buccal mass internal detail, showing odontophore (buccal bulb opened dorsally with beaks removed; WAM S116714). **J–M**) beaks (male WAM S116714), upper beak lateral and dorsal aspects (**J**, **K**), and lower beak lateral and ventral aspects (**L**, **M**). **N**, **O**) male reproductive system (WAM S116714). **P**) female reproductive system, partially dissected free (WAM S116713). Abbreviations/symbols: *—props for photography; **— broken sections of shell; AG1–3—accessory gland part 1–3; ASG—anterior salivary glands; BB—buccal bulb; Ca—caecum; DEd—dorsal edge (of shell); DG—digestive gland (DG-R & -L are right and left lobes); DO—distal oviduct; DOG—distal oviducal gland; Int—intestine; LP—labial palps; LW—lateral wing of shell; MGr—median groove of shell; Od—odontophore; Oes—oesophagus; OL—optic lobe; ONB—optic nerve bundle; Pa—pancreas; PO—proximal oviduct; POG—proximal oviducal gland; Sa—saddle; SC1–3 —spermatophoric complex part 1–3; Sh—shoulder; SP—salivary papilla; SS—spermatophore sac (Needham's sac); St—stomach; T—testis; TO—terminal organ; VD—vas deferens; WB—white body. Scale bars = 10.0 mm (**A–H, N–P**), 5.0 mm (**I–M**).

ID	WAM S116628 Holotype	WAM S116714	WAM S116713	WAM S116681	WAM S116694
Sex	male	male	female	female	male
TL	~150	~190	~140	~130	NA
ML	37	~40	34	28.5	32.8
MW	30.3	35	30.7	28	30.5
HW	48	54	36	44.6	39
ED	23.2–23.5	30–32	17.5	23.1R	22.2–23.3
FL (L/R)	24/19*	29/28	14.3*/19.1	20L	17.5/17.8
FW (L/R)	12/10	13.5/12	8.4*/9.0	~10L	10.8/10.3
FuL	20.0	23	15.1 (FO ~5mm)	~16 distorted	14.3
PA	12.3	14	9.8	~13 distorted	10.5
Gill LC (L/R)	7L	7/7	7L	7L	8/8
AL I (L/R)	106/107	142/134*	103/110	82*/102	92 R
AL II (L/R)	108/110	140/143	100/96*	105/83*	95 R
AL III (L/R)	107/114	140/142	116/119	96*/97*	98 R
AL IV (L/R)	110/114	131/132	112/115	85*/99	96 R
SC I (L/R)	66/68	70/65	35*/68	5–7 suckers remain at arm bases.	69/70
SC II (L/R)	73/74	75/75	39*/64*		58*/68
SC III (L/R)	75/78	~59*/73	65/65		67/71
SC IV (L/R)	77/75	~49*/67	74/67		53*/66
SuD (Normal)	Smallest mid-arm suckers 1.5–1.7 acet/inf	Smallest mid-arm suckers 2.35 acet, 2.3 inf (~20–30th)	1.6 acet/inf (5–7th largest, 1.35–1.6 acet; 1.23 acet by 9th)	1.6 acet/inf (6th) (5–7 largest)	Smallest mid-arm suckers 1.2-1.35 acet/inf (~24th)
PESF position L/R (largest)	5–7 (6 largest), I 5–8 (6–7 largest), II–IV	5–9/8 (6–7), I 5–9/8 (6/5–7), II 5–8/9 (6–7/8), III 5/4–8 (5–7/6), IV	NA	NA	5–8 (6/5–7), I 5–9 (6–7/8), II 5–9 (6–7), III & IV
PESF size	3.5 acet, 3.2 inf others: 3.3–3.5 acet, 2.9–3.1 inf	5.3 acet, 4.2 inf others: 5.1–5.2 acet, 3.7–4.1 inf	NA	NA	2.9 acet, 2.5 inf (6th, IIR) others: 2.6–2.7 acet, 2.3 inf
DESF position L/R (largest)	30–36/31–37 (34–36 largest), I 31–37 (32–35 largest), II 30–37 (33–35 largest), III 30–37 (33–36 largest), IV	30/31–35 (32–34) 28–35/33 (29–32/32) NA* / ~30–36** (30**) NA* / ~27–35** (28–30**)	NA	NA	31/30–38 (34/34–37) 31–37/30–36 (32–35) 29/30–38/36 (32–35) 30–38 (33/32–35)
DESF size	2.65 acet, 2.3 inf others: 2.4 acet, 2.0 inf	3.35 acet, 2.9 inf (30th, IIIR) others: 3.0 acet, 2.6 inf	NA	NA	1.75 acet, 1.6 inf (34–35th, IIR) others: 1.6 acet, 1.4 inf
CiL	2.1 (16–17th, IIIR) (others 1.6–2.0)	2.2 (others 1.5)	2.9 (22–23rd, II L) (others 2.3–2.7)	Cirri damaged	2.0 (others 1.5–1.8)
Ci start sucker position	2nd & 3th	2–4	2–4	3 & 4	2 & 3
WD A	60	100	42*	*	53
WD B L/R	56/	84/85	44/42	*	56 R
WD C L/R	55/	45*/84	50/45	*	51 R
WD D L/R	59/	55*/80	55/ NA*	*	51 R
WD E	56	76*	45	*	52*
WN I II III IV	30–31 29–30 28–29 29–30	30–31 R 29–30 R 29–30 R 27–28 or 29 R	31–33 29–30 29–30 27–29	~33 IR estimated Other nodules destroyed.	30–31 IR 29–30 IIR 27–28 IIIR ? IVR*
Notes	Areolar spots: Arm I, 9 or 10 spots; Arm II, 6 or 7 spots; Arms III & IV, each 4+	Arm I thickness 17.5 mm; Arm II & III thickness 14–15 mm.	Areolar spots: Arm I, 6+ spots (4 on head).		

Table 1. *Opisthoteuthis carnarvonensis* sp. nov. specimen measurements, counts, and other notes. Measurements in mm. Sucker counts include countable but missing sucker positions (i.e., missing sucker still apparent by a distinct scar, or flanking cirri), PESF and DESF note ranges L/R if the sucker position differs on the left or right arm, *denotes damage (including missing and uncountable suckers), **denotes where the largest DESF position is likely inaccurate due to several suckers from the DESF region being missing.

bined only half AG1 greatest dimensions, and with intestine approximately equal to oesophagus in length.

Description: Mantle short, posteriorly rounded and dome-like, width slightly less than length (MWI 82%–93% males, 90%–98% females); head wider than mantle and exceeding ML (HWI 119%–135% males, 106%–157%

Indices	WAM S116628 Holotype	WAM S116714	WAM S116713	WAM S116681	WAM S116694
MWI	81.9%	87.5%	90.3%	98.2%	93.0%
HWI	129.7%	135%	105.9%	156.5%	118.9%
FuLI	54.1%	57.5%	44.4%	56.1%	43.6%
FLI (L/R)	64.9% (L)	72.5 / 70%	56.2% (R)	70.2% (L)	53.4 / 54.3%
FWI (L/R)	50% (L)	46.6 / 42.9%	47.1% (R)	50% (L)	61.7 / 57.9%
EDI	63.5%	71.4 – 80 %	51.5%	81.1%	67.8%
PAI	33.2%	35%	28.8%	45.6%	32.0%
Arm formula	IV>II>III>I / IV=III>II>I	I>II=III>IV / II>III>I*>IV	IV>III>I>II / III>IV=I>II*	II>III*>IV*>I* / I>IV>III*>II*	III>IV>II>I (R)
Dorsal ALI	2.9× ML	3.6× ML	3.2× ML	3.6× ML	2.8× ML
Ventral ALI	3.1× ML	3.3× ML	3.4× ML	3.5× ML	2.9× ML
SDI	Male mid-Arm 4.1%–4.6%	Male mid-Arm 5.9% acet (5.8 Inf)	Female largest sucker 4.7% acet/Inf	Female largest sucker 5.6% acet/Inf	Male mid-Arm 3.7%–4.1%
SDI PESF	9.5% acet (8.6% Inf)	13.3 acet (10.5% Inf)	NA	NA	8.8% acet (7.6% Inf)
SDI DESF	7.2% acet (6.2% Inf)	8.4% acet (7.3% Inf)	NA	NA	5.3% acet (4.9% Inf)
CLI	5.7%	5.5%	8.5%	NA*	6.1%
Web formula	A>D>B=E>C	A>B>C>D>E*	D>C>E>B>A	NA*	B>A>E*>C=D (R)
WI A	56.1%	70.4%	42.7% (B)	NA*	57.6%
WI E	49.1%	60.6% (D)	39.1%	NA*	54.2%

Table 2. *Opisthoteuthis carnarvonensis* sp. nov. indices and formulas. *arm I damaged (Dorsal ALI using longer arm II, WI A is relative to longer arm II).

females) (see **Fig 3 A, B**). Fins sub-terminally placed, relatively small (FLI 53%–72% males, 56%–70% females), posterior fin edges near-straight, anterior edges rounded, distally rounded, widest midway along length (FWI 47%–62%), with slight constriction proximally (**Fig 3 A**). Eyes very large, ~⅔ head width, size variable due to shrinkage or damage (EDI 52%–81%), openings small and constricted. Funnel relatively long, tapering (FuLI 44%–58%). Funnel organ (examined on female **WAM S116713**), V-shaped, limbs thin distally (as they converge), broad and thickened proximally (**Fig 3 C**), occupying ~33% FuL. Pallial aperture gape small (PAI 29%–35% [not counting large value on S116681 due to damage]), enclosed around funnel. Olfactory papillae small, ovoid. Pallial adductor a narrow strap or band, attached to right hand side of distal reproductive tract (oviducal gland or AGC).

Gills: half-orange, with 7 (rarely 8) primary lamellae per gill on material examined.

Optic nerves: Pass through each white body as four distinct bundles (**Fig 4 A**), optic lobes ~rectangular, each white body relatively small (~7.8 mm long, ~14% HW; **WAM S116714**), kidney-shaped, pigmented brown.

Internal shell: Dissected from male (**Fig 4 B, C**), and female (**Fig 4 D–F**) (shell from male distorted and strongly arched due to shrinkage, with indices and wing angle not calculated); shell U-shaped, saddle outer (posterior) face slightly concave (i.e., with a groove), basal shelf absent, broad (SSI 80%, but probably less originally due to distortion to shell), saddle over a third of shell height in antero-posterior axis (SHI 37%); saddle shoulders moderately developed, with concave outer faces; wings diverge at ~45–47° relative to antero-posterior axis, wings terminate with sharp point, with small lobe apparent on dorsal edge (especially on the male specimen, less on the female; see **Fig 4 C, E**); shell translucent, amber coloured.

Arms and webbing: Arms thick, relatively long, dorsal arm pair of males being slightly more robust (thicker) than the other arms (17.5 mm arm I thickness, vs. 14–15 mm on arms II and III; **WAM S116714**). Arms without consistent formula, ~equal in length, perhaps slightly longer in females (dorsal ALI 2.8–3.6× ML males, 3.2–3.6× ML females; ventral ALI 2.9–3.3× ML males, 3.4–3.5× ML females).

Web simple, deep (see **Fig 3 D, E, G**), web formula variable (in part due to distortion), but generally with dorsal sector 'A' deeper (formula A>B>C>D>E on one specimen only), and with webs shallower on single female specimen with relatively intact webbing, WI A ~56%–70% males (43% on female), WI E 49%–61% males (39% female). Web attached to ventral arm edge with a web nodule (see **Fig 3 E, G**), at level of suckers 30–33 on dorsal arms or 27–30 on ventral arms (approximately at level of DESF of males). Webs attach ~10+ suckers distal to the nodule on dorsal arm edges.

Suckers and cirri: Maximum sucker counts 71–78 on males (counts ~60–70 on most arms due to damage), maximum sucker count 74 on single female specimen with relatively intact arms. Suckers sexually dimorphic, males with proximal and distal enlarged sucker fields.

Males with first 3 or 4 suckers small and increasing in size, followed by abrupt increase in sucker ⌀, marking the proximal enlarged sucker field (PESF) (see **Fig 3 E–F**), comprising 3–5 suckers, from the 5th (rarely 4th) – 7th, 8th or 9th sucker, and with central suckers in each PESF generally largest (~6th–7th or 8th suckers). PESF suckers with acetabular bases large, swollen (PESF SDI 8.8%–13.3%), infundibular diameter smaller than acetabular (PESF infundibular ⌀~80–90% acetabular ⌀), infundibular ring and pad narrow but well defined, with radiating striations and large acetabular aperture (see **Fig 3 F**).

Sucker diameter reduces following PESF, mid-arm 'normal' suckers on males with SDI 3.7%–5.9%, with acetabular and infundibular diameters similar. Distal enlarged sucker field (DESF) present on all arms of males, but relatively subtle in terms of sucker enlargement, and less well developed on arm pair I compared to arms II–IV. DESF comprises ~6–10 suckers, between approximately the 28th–38th suckers, and with the central 3 or 4 suckers slightly larger than flanking suckers (DESF SDI 5.3%–8.4%) (**Fig 3 E**), DESF suckers with acetabular bases slightly swollen (infundibular ⌀~84–90% acetabular ⌀). Distal to DESF the suckers continue to arm tips with minute size.

Females with the first 4 or 5 suckers small and increasing in size, the following ~5 suckers out to the 9th are larger, 5th–7th suckers largest (SDI 4.7%–5.6%), decreasing subtly thereafter and remaining similar in size out to web junction, then decreasing in size more rapidly and continuing to arm tips with minute size. Larger suckers of female (WAM S116713) with acetabular and infundibular diameters comparable, acetabulum rounded, small, infundibular ring thick compared to infundibular pad and aperture, extending well above acetabulum (see **Fig 3 H**); the proximal sucker acetabulae were somewhat elevated on fleshy lumps (1.7 mm wide) (**Fig 3 H**), possibly a preservation artefact from shrinkage of the skin around the suckers.

Sucker spacing relatively compact, on males the distal and proximal enlarged suckers have bases touching, whereas mid-arm suckers have more spacing (~0.5–1.0 sucker ⌀ between adjacent suckers) (see **Fig 3 E**), on females the proximal larger suckers are more compact with bases contacting, with mid-arm suckers again with greater spacing (**Fig 3 G, H**).

Cirri commence between the 2nd–4th suckers as minute buds, length increasing to maximum in proximal third of arm length, similar over mid-arm and gradually reducing in length to arm tips. Maximum cirrus length less in males versus females (CLI 5.5%–6.1% males or 0.9–1.5× mid-arm sucker ⌀; 8.5% female or 1.8× mid-arm sucker ⌀).

Digestive system: Dissected from male specimen (see **Fig 4 G, H**); buccal bulb large (dimensions equal to combined stomach and caecum); anterior salivary glands possibly present, partly imbedded, posterior salivary glands absent; odontophore small, lacking radula, flanking labial palps (lacking palatine teeth) and salivary papillae well-developed (see **Fig 4 I**). Upper beak (**Fig 4 J, K**) tall (height 68% beak length, 83% width), hood deep (hood length 67% beak length); rostrum long, sharp, strongly deflected down, each jaw cutting edge with single low tooth, hood crest rounded (convex); lateral walls near parallel, with subtle longitudinal groove on each lateral face, dorsal edge of lateral walls slightly rounded (near-straight), posterior edges relatively flat with slight indentation, crest rounded at postero-dorsal apex. Lower beak (**Fig 4 L, M**) relatively tall (height 69% width), with short hood (hood length 54% beak length), rostrum pointed and sharp, slightly hooked; hood wings elongate (wing length 100% beak length) with weak diagonal flexure each side.

Oesophagus narrow near buccal bulb (proximal third), thereafter slightly expanded as simple crop (without diverticula); stomach simple, muscular; caecum smaller than stomach (~75% its greatest dimensions), simple; digestive gland bilobed, pancreas well defined, paler in colour relative to bulk of digestive gland; hepatic ducts short, somewhat thick (compared to observed on other opisthoteuthids); intestine relatively short, ~1.4× oesophagus length; ink sac and anal flaps absent. Digestive system with dark purplish membrane over buccal bulb (except ventro-posterior parts around salivary glands), oesophagus, stomach, and caecum (though less strongly on latter two), as well as the rectum where it projected into the mantle cavity; intestine and hepatic ducts lacking strong pigmentation.

Male reproductive system: Illustrated **Figure 4 N, O**; testis ovoid, vas deferens narrow, short; spermatophoric complex with three parts (SC 1–3) (though division between SC 2 and 3 rather indistinct); spermatophoric sac (Needham's sac) large, folded, slightly shorter than SC but exceeding its width, containing visible spermatophores; accessory gland complex dominated by AG1, AG2 and AG3 fused closely together (ovoid, with faint medial seam visible between the two parts), conjoined AG2 and AG3 width only ~50% AG1 greatest dimensions; terminal organ elongate and cylindrical, length ~equal to width of conjoined AG2 and AG3, with expanded distal end, terminal organ darkly pigmented.

Female reproductive system: Partly dissected from female (**WAM S116713**), per **Figure 4 P**; ovary large, occupying body posterior half; proximal oviduct elongate, with at least two sequential oocytes in specimen examined (largest oocyte with length 9.4 mm, more oocytes may have been present in the proximal oviduct but this was not fully dissected free); oviducal gland large, longitudinally striated, two parted, each part rounded, the proximal beige coloured, the distal dark brown and larger in length and width (proximal oviducal gland ~86% width of distal gland); distal oviduct longer than oviducal gland (~1.4× oviducal gland length), medially expanded.

Colouration: Per **Figure 3 A, B**; aboral surfaces, head, and body with orange-brown pigmentation on freshly captured specimens, abraded away in places (e.g., on fins) to reveal unpigmented tissue. Pigmentation becomes darker and more brownish in ethanol preserved specimens. Areolar spots distinct and numerous (particularly well preserved on **WAM S116628**) (see **Fig 3 A**), each arm with one proportionally larger spot (~2.2 mm ⌀) near arm base, with smaller spots extending anteriorly and posteriorly, each arm I with 9 or 10 spots, 3 or 4 posterior to the larger spot, extending over the central head between the eyes (stopping just anterior to fin bases), and 5 or 6 extending more distally along the arms to at least the junction of the webbing. Each arm II with ~7 spots (starting above each eye). Spots associated with arms III and IV less certain (due to skin abrasion) but each had at least 4 spots, starting near ventral eye edges and fin bases. Spots comprised circular patches of pale unpigmented tissue, surrounded by a darker pigmented ring. Oral surfaces with dark red-orange pigmentation in freshly captured specimens, sucker infundibular rings and cirri contrasting with paler colouration (see **Fig 3 D**). In ethanol preserved specimens the webbing and arm faces shifted in colour to a darker brown or maroon, with the suckers and cirri contrasting with pale beige (**Fig 3 E–H**).

Material examined.

Holotype.

WAM S116628, male (ML 37 mm), 180 km NW of Bernier Island, 23°50'17.5" S, 111°44'27.1" E, 1510 m, RV *Investigator*, IN2022_V09 Station 048, 16.xii.2022.

Paratypes.

WAM S116714, male (ML 40 mm), off Northwest Cape, 22°22'5.99" S, 113°32'4.92" E, 1075 m, RV *Investigator*, IN2022_V09 Station 005, 24.xi.2022 [dissected]. WAM S116713, female (ML 34 mm), 180 km NW of Bernier Island, 23°50'17.5" S, 111°44'27.1" E, 1510 m, RV *Investigator*, IN2022_V09 Station 048, 16.xii.2022. WAM S116681, female (ML ~27 mm), 150 km NW of Bernier Island, 23°59'46.02" S, 111°58'3.36" E, 1044 m, RV *Investigator*, IN2022_V09 Station 047, 14.xii.2022 [badly damaged, parts of viscera missing, arms partially stripped of suckers]. WAM S116694, male (ML 33 mm), 180 km NW of Bernier Island, 23°50'17.5" S, 111°44'27.1" E, 1510 m, RV *Investigator*, IN2022_V09 Station 048, 16.xii.2022.

Distribution: Presently only known from the type locality, northwestern Australia, off North West Cape (Gascoyne Commonwealth Marine Reserve) and outer shelf off Carnarvon (Carnarvon Canyon Commonwealth Marine Reserve), bathymetric range 1044–1510 (**Fig 1**).

Etymology: Specific epithet '*carnarvonensis*' is in reference to the Carnarvon Canyon Marine Park, from where the type material was collected, the Latin adjectival suffix '-ensis' (=originating in) added to form an adjective.

Proposed vernacular name: Carnarvon flapjack octopus.

Remarks: When considering the other Australian *Opisthoteuthis* (excluding members of *Insigniteuthis* and *Exsuperoteuthis*), *O. carnarvonensis* sp. nov. can be readily distinguished from most taxa either given its bilobed digestive gland (distinguishing it from *O. pluto*, *O.* cf. *philipii*, and *O. robsoni*), or the DESF configuration. The large number (6–10) of DESF suckers with diameter < PESF suckers, distinguishes the species from *O. pluto*, *O.* cf. *philipii*, *O. mero* and *O. robsoni* which all lack a distinct DESF.

The species is morphologically close to *O. kerberos*, known from off southeastern Australia, and *O. chathamensis* from off New Zealand and Macquarie Island (Verhoeff 2024).

The most obvious difference between *O. carnarvonensis* and *O. kerberos* relates to the male reproductive system, with the former having the AGC dominated by AG1 (~double combined AG2 and 3 greatest dimensions), versus the latter having AG1 considerably smaller than the combined AG2 and 3. The AGC was examined in mature males of both species, the difference not being due to immaturity. The two species share similar arm sucker counts, web nodule positions, and similar intestine length (1.4× vs. 1.2× oesophagus length), but O. *carnarvonensis* has a more distal DESF spanning from suckers 28–38 (29–37 largest), vs. 22–31 (25–28 largest). In addition, *O. kerberos* occurs at a greater bathymetric range (2000 m) compared to *O. carnarvonensis*.

Comparison is also needed with the New Zealand taxa *O. mero* and *O. chathamensis*, as both these species have a bilobed digestive gland. As mentioned, *O. mero* is more easily separable given the lack of a distinct DESF (suckers in DESF region being comparable to mid-arm sucker dimensions) and differences in AGC (AG1 equal in size to AG2 and 3) and intestine length (double oesophagus length). *Opisthoteuthis chathamensis* is closer in morphology to *O. carnarvonensis*, which also has an AGC dominated by AG1 (exceeding combined AG2 and 3 dimensions per O'Shea 1999, fig 14d) and a similar intestine length (1.5× oesophagus length per O'Shea 1999, fig 14g), however the species can be separated given that *O. chathamensis* lacks web nodules, has substantially lower sucker counts overall (maximum count 46–55 per arm), and has a DESF spanning from suckers 19–21 to 24–28, much more proximal than in *O. carnarvonensis.*

Opisthoteuthis cf. *philipii* Oommen, 1976

(Figure 5 & 6, Tables 3 & 4)

Type statement: see remarks section.

Diagnosis: Opisthoteuthid with ~80–104 suckers per arm of adult, PESF with 4 or 5 enlarged suckers on males, DESF absent (suckers on mid arm and near web-

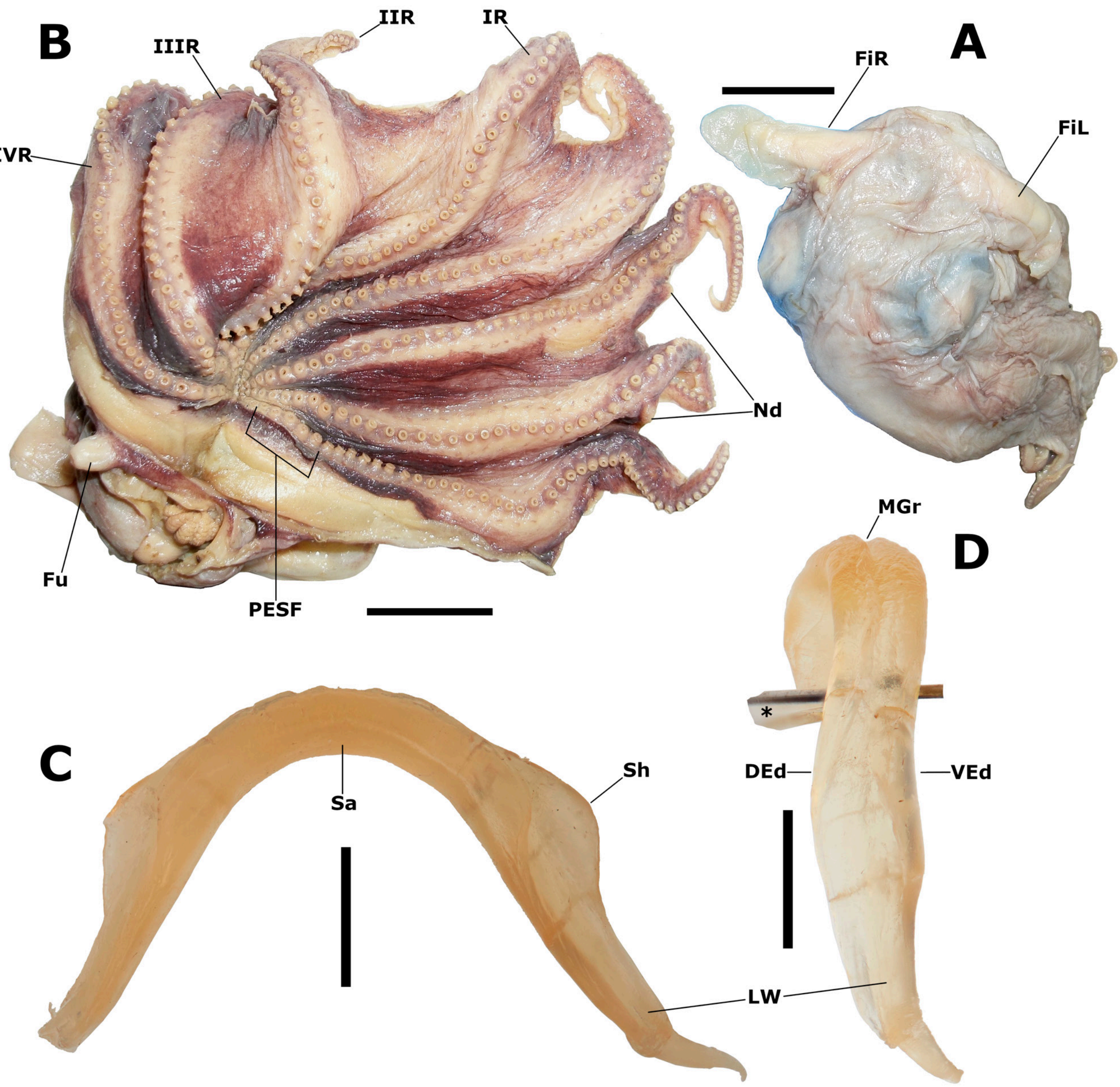

Figure 5. Putative *Opisthoteuthis* cf. *philipii* from northwestern Australia (WAM S35958). **A**) dorsal aspect showing fin form and relative size of eyes. **B**) oral aspect of arms, webbing, and suckers. **C**, **D**) internal shell dorsal (**C**) and lateral (**D**) aspects. Abbreviations/symbols: DEd—shell dorsal edge; FiL/R—fin left/right; Fu—funnel; I–IVR—arms I–IV right; LW—lateral wing (of shell); MGr—median groove (of shell saddle); Nd—web nodule; PESF—proximal enlarged sucker field; Sa—saddle (of shell); Sh—shoulder (of shell); VEd—shell ventral edge. Scale Bars: 20.0 mm (**A**, **B**), 5.0 mm (**C**, **D**).

bing attachment similarly sized), dorsal arms not more robust, and with arms each with single nodule. Pigmentation reddish-brown aborally, and maroon orally on webbing; areolar spots absent. Internally with digestive gland bilobed, 8 (rarely 7 or 9) lamellae per gill, AGC2 and 3 combined and slightly larger than AG1, with intestine ~1.5× oesophagus in length.

Description: Mantle short, posteriorly rounded, mantle width and length comparable, somewhat narrower in males (MWI 89%–111% female, 87%–108% male) (see body and fin form; **Fig 5 A** and **Fig 6 A**). Head much wider than mantle (HWI 131%–155% females, 117%–178% males). Fins sub-terminal, relatively small (FLI 81%–109% females, 69%–94% males), fin width approximately greatest near base (FWI 33%–63% female, 37%–52% males), posterior edge relatively straight, anterior edge convex, tapering to acutely rounded distal end. Eyes very large, comprising 66% head width, proportionally larger in males (EDI 71%–79% female, 60%–81% males). Funnel relatively long, tapering (FuLI 54%–62% females, 43%–66% males), distal ~20%–46% of the funnel free (not attached dorsally). Funnel organ V-shaped, proximal ends of limbs thickened and fleshy (**Fig 6 B**). Pallial aperture gape small (PAI 28%–33% females, 16%–30% males), enclosed tightly around funnel. Olfactory papillae large, rounded

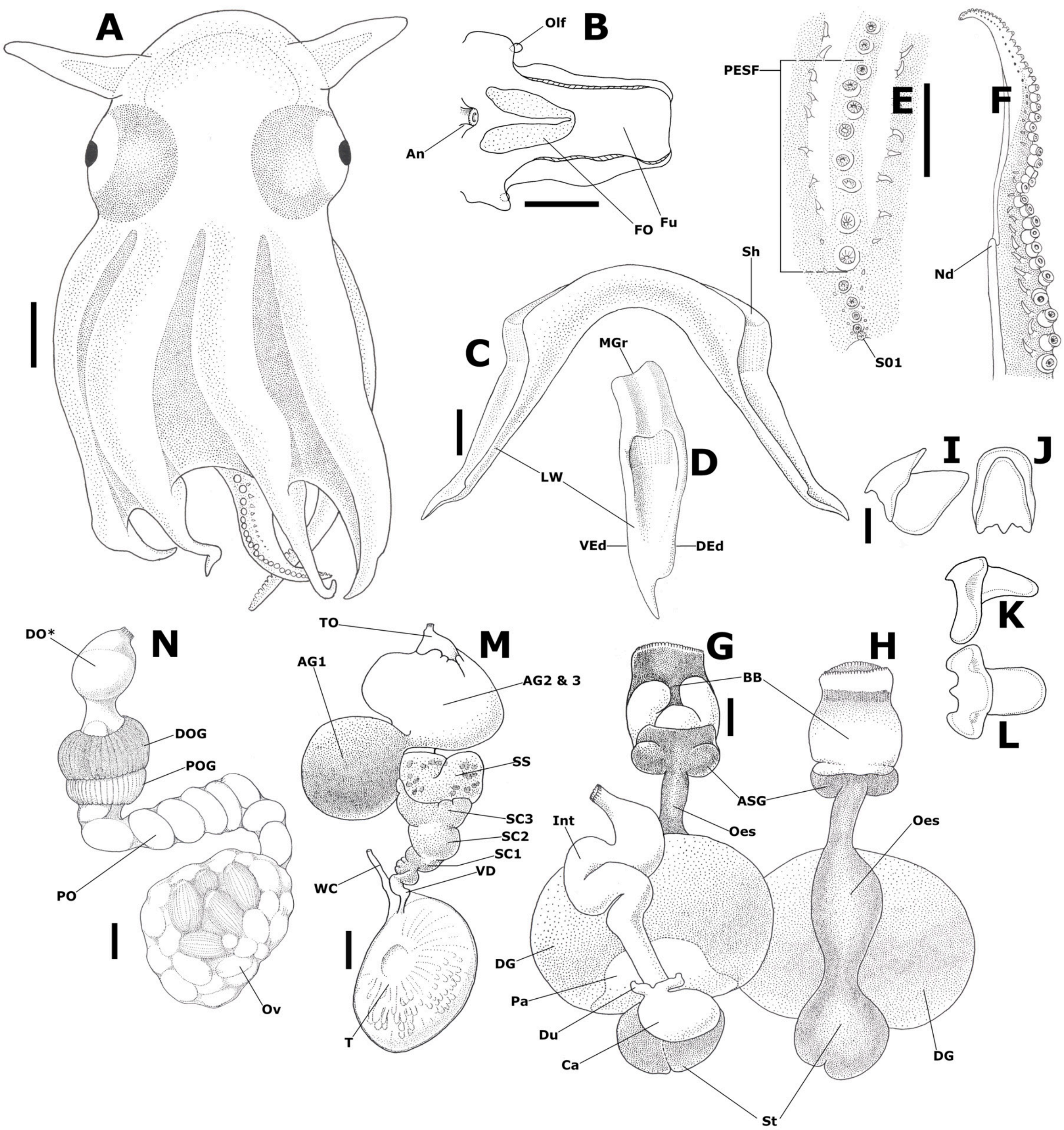

Figure 6. Previously unpublished illustrations of *Opisthoteuthis* cf. *philipii* by the late F. G. (Eric) Hochberg, from MNHN specimens collected off Tanimbar. Original line illustrations provided by the SBMNH (used with permission). **A**) Dorsal aspect (specimen uncertain, MNHN). **B**) Funnel organ (specimen uncertain, MNHN). **C**, **D**) dorsal and lateral aspects of internal shell (specimen uncertain, MNHN). **E**) proximal enlarged sucker field (MNHN male specimen). **F**) distal arm suckers and web nodule (MNHN 2043B). **G**, **H**) ventral and dorsal aspects of the digestive system (MNHN 2043A, ML 45 mm). **I**, **J**) upper beak lateral and anterior aspects. **K**, **L**) lower beak lateral and ventral aspects. **M**) male reproductive system (MNHN 2048). **N**) female reproductive system with egg ready to be spawned in distal oviduct (*) and others in proximal oviduct (MNHN 2043A, ML 45 mm). Abbreviations/symbols: ASG—anterior salivary glands; AG1–3—accessory gland part 1–3; An—anus; BB—buccal bulb; Ca—caecum; DEd—dorsal edge; DG—digestive gland; DO—distal oviduct; DOG—distal oviducal gland; Du—hepatic duct; Int—intestine; LW—lateral wing (of shell); MGr—medial groove (of shell); Nd—web nodule; Oes—oesophagus; Ov—ovary sac; PESF—proximal enlarged sucker field; PO—proximal oviduct; POG—proximal oviducal gland; S01—1st sucker; SC1–3 —spermatophoric complex part 1–3; Sh—shoulder; SS—spermatophore sac (Needham's sac); St—stomach; T—testis; TO—terminal organ; VD—vas deferens; VEd—ventral edge; WC—water canal (coelomic duct). Scale bars = 10.0 mm (**A, B**, **E**, **F**), 5.0 mm (**C, D**, **G–N**).

(see **Fig 6 B**). Pallial adductor reduced to a narrow strap or band (alike other Opisthoteuthidae).

Gills: Half-orange, generally with 8 lamellae per gill (sometimes 7 or 9; one specimen with 8 left gill & 7 on right gill, another had 9 lamellae on both gills).

Optic nerve: Not examined on material available.

Internal shell: Illustrated from two specimens (**Fig 5 C**, **D**; **Fig 6 C**, **D**); broadly U-shaped, saddle relatively deep (SHI 28%–38%) and broad (SSI 73%–79%), outer (posterior) face concave, i.e., with distinct groove, basal shelf absent; saddle shoulders well developed, with concave outer face below saddle prominences; shell lateral wings diverge from saddle mid-point by 42–45°, wings

ID	WAM S35958	MNHN 2065†	MNHN 2048†	MNHN 2059†	SBMNH 143067A†	MNHN 2043A†	MNHN 2043B†	SBMNH 143067B†
State	Male Sub-mature	Male Mature	Male Mature	Male Mature	Male Sub-mature	Female Mature	Female Mature	Female Mature
TL	~150	NA	NA	NA	NA	NA	NA	NA
ML	35	83.2	60	53	37	45	48	43
MW	31	72.2	57	55	40	50	42.5	43
HW	41	97.8	96	75	66	69.8	63.0	63
ED (L/R)	21.6/21.0	51.3	43.2	35.8	30	32.5	34.1	34.0
FL (L/R)	24/25	69.8	53.5	50	32	49	39.1	35.0
FW (L/R)	12.5/12.0	33.5	23.5	18.5	14.5	16	24.5	18.3
FuL	16.0	46.4 (13 free)	32 (14 free)	23 (7 free)	24.6 (10 free)	28 (13 free)	26 (5 free)	25 (8 free)
PA	7.0	13.4	14.3	16	9	14.8	13.6	13.4
Gill LC (L/R)	8/7	8	9	8	8	8	8	8
AL I (L/R)	128/122	345	220	222	148	178	184	182
AL II (L/R)	122/120	300	215	213	158	174+	172	171
AL III (L/R)	108*/120	300	245	220	155	198	170	165
AL IV (L/R)	110*/116	315	235	218	157	205	160	165
SC I (L/R)	70/68	94	98	86+	90	74	83	92
SC II (L/R)	76/70	90	98	87	87	90	83	91
SC III (L/R)	52*/68	99	102	90	87	89	84	96
SC IV (L/R)	52*/70	103	104	94	96	94	87	99
SuD (normal)	1.6 ^{acet} (10th, IIL) Mid-distal arm	5.1	2.5	2.3	2.0	2.3	2.3	2.3
PESF position	5th–9th (6th–8$^{th\ largest}$)	Not recorded	Not recorded	Not recorded	Not recorded	NA	NA	NA
SuD (PESF)	2.4 ^{acet}, 2.0 ^{inf} (6th IIL)	9.8 ^{Acet}, 7.5 ^{Inf}	6.1 ^{Acet}, 3.9 ^{Inf}	5.6 ^{Acet}, 4.0 ^{Inf}	3.6 ^{Acet}, 2.5 ^{Inf}	NA	NA	NA
DESF position	NA	NA	NA	NA	NA	NA	NA	NA
SuD DESF	NA	NA	NA	NA	NA	NA	NA	NA
CiL	2.3 (18th–19th) (others 1.9)	2.6	3.6	2.2	2.4	3.2	2.6	2.7
Ci start	2nd–4th	Not recorded	Not recorded	Not recorded	Not recorded	Not recorded	Not recorded	Not recorded
WD A	76	215	105	120	84+	68	103	110
WD B (L/R)	76–78	185	110	105	94	90	95	105
WD C (L/R)	76	170	115	100	95	90	90	110
WD D (L/R)	66–74	135	105	90+	90	90	88	90
WD E	64	130	100	100	65	75	68	75
WN (sucker position & arm)	32, IL 31–32 IIL 29–30 IIIL 29–30 IVL	Present	Present	Present	Present	Present	Present	Present
Areolar spots	NA	NA	NA	NA	NA	NA	NA	NA
Notes		1344.6 g wet weight	504.3 g wet weight	373.3 g wet weight	204.6 g wet weight	Distal oviduct egg 9.3 x 6.4 Ovarian egg 8.0 x 5.0	Ovarian egg 8.8 x 5.5	Ovarian egg 8.6 x 4.5

Table 3. *Opisthoteuthis* cf. *philipii* specimen measurements, counts, and notes. Measurements in mm. † = specimen data from unpublished Hochberg datasets provided by SBMNH.

tapering to simple outwardly flared points; shell translucent and yellow or amber colour.

Arms and webbing: Arms relatively long, thick, approximately equal in length with no consistent arm formula but approximately I>II>III>IV on some specimens (dorsal ALI 3.7–4.2× ML, ventral ALI 3.3–4.6× ML). Dorsal arms approximately equal in thickness to other arms (WAM S35958 with arm I and II thicknesses 13.3–13.5 mm). Webs simple, deep (see **Fig 5 B**), web formula variable, approximately A>B>C>D>E, but often subequal, medial depth of sector A ~48%–62% arm I length, sector E medial depth ~37%–55% arm IV length. Each web sector attached to ventral arm edge with a single web nodule (see **Fig 5 B**; **Fig 6 F**), on one specimen (WAM S35958) web nodule was at level of sucker 31–32 on dorsal arms or 29–30 on ventral arms (position not recorded on MNHN specimens by Hochberg). Web sectors attach to the dorsal arm edges 5–10 suckers more distally.

Suckers and cirri: Sucker counts variable, maximum counts 94–104 on mature males (76–96 sub-mature males), 87–99 on mature females. Suckers sexually dimorphic, males with only the proximal enlarged sucker fields (PESF), distal enlarged sucker field (DESF) absent (suckers similarly sized across mid- and distal-arm). Males with proximal 3 or 4 suckers very small and increasing in size; an abrupt size increase (less pronounced in sub-mature males) marks the PESF of 4 or 5 suckers, from the 4th or 5th–7th or 9th sucker, and with central 2 or 3 suckers largest (see **Fig 5 B**; **Fig 6 E**); proximal enlarged suckers with acetabular bases large, swollen (PESF SDI 10.2%–11.8% mature males, 6.9%–9.7% in sub-mature males), infundibular diameter

Indices	WAM S35958	MNHN 2065†	MNHN 2048†	MNHN 2059†	SBMNH 143067A†	MNHN 2043A†	MNHN 2043B†	SBMNH 143067B†
MWI	89%	87%	95%	104%	108%	111%	89%	100%
HWI	117%	118%	160%	142%	178%	155%	131%	147%
FuLI	46%	56%	53%	43%	66%	62%	54%	58%
FLI (L/R)	69% / 71%	84%	89%	94%	86%	109%	81%	81%
FWI (L/R)	52% / 48%	48%	44%	37%	45%	33%	63%	52%
EDI	62% / 60%	62%	72%	68%	81%	72%	71%	79%
PAI	20%	16%	24%	30%	24%	33%	28%	31%
Arm formula (L/R)	I>II>IV>III / I>II=III>IV	I>IV>II=III	III>IV>I>II	I>III>IV>II	II>IV>III>I	IV>III>I>II	I>II>III>IV	I>II>III=IV
Dorsal ALI	3.7× ML	4.1× ML	3.7× ML	4.2× ML	4.0× ML	4.0× ML	3.8× ML	4.2× ML
Ventral ALI	3.3× ML	3.8× ML	3.9× ML	4.1× ML	4.2× ML	4.6× ML	3.3× ML	3.8× ML
SDI (mid-arm)	4.6%	6.1%	4.2%	4.3%	5.4%	5.1%	4.8%	5.3%
SDI PESF	6.9%	11.8%	10.2%	10.6%	9.7%	NA	NA	NA
SDI DESF	NA	NA	NA	NA	NA	NA	NA	NA
CLI	6.3%	3.1%	6.0%	4.2%	6.5%	7.1%	5.4%	6.3%
Web formula	A=B=C>D>E / B>A=C>D>E	A>B>C>D>E	C>B>A=D>E	A>B>C=E>D*	C>B>D>A*>E	B=C=D>E>A	A>B>C>D>E	A=C>B>D>E
WI A	59%	62	48%	54%	64% **	38%*	56%	60%
WI E	55%	41%	43%	46%	41%	37%	43%	45%

Table 4. *Opisthoteuthis* cf. *philipii* indices. † = specimen data from unpublished Hochberg datasets provided by SBMNH, * = Damage, ** = Web B as Web A damaged.

less than acetabular, infundibular pad with radiating striations, large aperture. Suckers reduce in diameter following PESF, mid-arm 'normal' suckers with SDI 4.2%–6.1% on males (infundibular and acetabular diameters comparable), imbedded into arm with aperture ~flush with skin; DESF absent, instead suckers remain at comparable size out to web attachment position (see **Fig 5 B**; **Fig 6 F**), suckers then reduce in size rapidly distal to webbing, continuing to arm tips with minute size. Females without enlarged suckers, largest ~mid-arm suckers with SDI 4.8%–5.3%.

Cirri commence between suckers 2–4 as minute buds (on WAM S35958), or between 1st and 2nd sucker per Hochberg's illustration (**Fig 6 E**); reaching greatest length by ~33% arm length (CLI 5.4%–7.1% female, 3.1%–6.5% male), diminishing in size rapidly distal to webbing and continuing to arm tips with minute size.

Digestive system: Dissected and illustrated (by Hochberg) from a mature female (**Fig 6 G**, **H**); buccal bulb large, ~equal to combined stomach and caecum dimensions, anterior salivary glands present (partially intra-bulbar), posterior salivary glands absent, radula absent (other buccal mass structures not described). Upper beak (**Fig 6 I**, **J**) tall (height 73% beak length, or 85% width), hood moderately deep (hood length 72% beak length); rostrum blunt, deflected down, jaw cutting edge irregular (slightly dentate), hood crest rounded; lateral walls near-parallel (without longitudinal grooves/ flexures), dorsal edge of lateral walls slightly curved, posterior edges relatively flat – convex, crest rounded at postero-dorsal apex. Lower beak (**Fig 6 K**, **L**) tall (height 69% width), hood short (hood length 49% beak length), crest rounded, wings elongate (wing length 97% beak length) with weak diagonal flexures; rostrum small, blunt tipped. Oesophagus narrow in proximal third, before becoming swollen as a simple crop (without diverticula) (see **Fig 6 H**); stomach, rounded, muscular, with weak constriction partially dividing it; caecum small (~50% stomach dimensions), non spiral; digestive gland unilobed, hepatic ducts short; intestine short, approximately 1.5× oesophagus length, narrow, slightly expanded in distal third towards rectum, distal half looped into an S-shape. Blackish purple pigmented membrane covers digestive tract from posterior face of buccal bulb and over oesophagus and stomach, remainder of gut with minimal pigmentation.

Male reproductive system: Illustrated per **Figure 6 M**; testis ovoid, vas deferens thin, short; spermatophoric complex three parted (SC 1–3); spermatophoric sac (Needham's sac) large, folded, filled with small ovoid spermatophores, similar to spermatophoric complex in size; accessory gland complex (AGC) exceeds previous glandular structures in overall dimensions, dominated by AG2 and AG3, fused closely together (the seam separating this wasn't examined on material available), AG1 more proximal, rounded, well separated (diameter ~70% greatest dimension of combined AG2 and AG3); terminal organ projecting medially from conjoined AG2 and AG3, short and conical.

Female reproductive system: Illustrated per **Figure 6 N**; ovary unremarkable (with ovarian oocytes up to 8.8 × 5.5 mm, with ~10 or 11 longitudinal follicular folds); proximal oviduct elongate and containing up to eight sequential oocytes (oocytes 8.4–9.0 mm × 4.6–5.0 mm, with smooth chorion); oviducal gland large, two parted, each rounded and longitudinally striate, the proximal lighter coloured than distal, distal part slightly larger in length and width (proximal oviducal gland ~85% width of the distal); distal oviduct longer than oviducal gland (oviducal gland ~66%, distal oviduct length). Mature egg in distal oviduct with dark brown coloured hard capsule (9.3 mm × 6.4 mm).

Colouration: On WAM specimen (WAM S35958), aboral pigmented skin was mostly abraded away to reveal pale cream coloured flesh, areas of remaining skin aborally with a maroon–reddish colouration. Hochberg described preserved MNHN specimens as having a “burnt sienna” (reddish-brown) aboral pigmentation on mantle, webs, arms and fins, with the arm tips being redder. Oral surfaces of webbing on WAM specimen reddish-brown or maroon proximally, paler distally, and with arm aboral surfaces lighter than adjacent webbing (**Fig 5 A**, **B**); suckers with a light beige colouration. Hochberg described MNHN material as being similarly pigmented, red to reddish-brown. Areolar spots not observed on WAM specimen and were described as absent by Hochberg on MNHN material.

Material examined.

WAM S35958, male (ML 35 mm), SW of Imperieuse Reef, Rowley Shoals, WA, 18°05′S, 118°08′E, 440–442 m, prawn trawl, FV *Courageous*, Station 026, 22.viii.1983 [coll. P. Berry & N. Sinclair, fisheries observers]. MNHN 2059, male (ML 53 mm), off Tanimbar Island, Indonesia, 07°46′S, 132°31′E, 443–468 m, *RV Baruna Jaya I*, KARUBAR Station CP40, 28.x.1991. MNHN 2048, male (ML 60 mm), off Tanimbar Island, Indonesia, 08°16′S, 131°59′E, 549–552 m, *RV Baruna Jaya I*, KARUBAR Station CP56, 31.x.1991. MNHN 2065, male (ML 83 mm), off Tanimbar Island, Indonesia, 09°23′S, 131°09′E, 246–275 m, *RV Baruna Jaya I*, KARUBAR Station CP84, 4.xi.1991. MNHN 2043, 2 females (ML 45, 48 mm), off Tanimbar Island, Indonesia, 08°16′S, 131°59′E, 549–552 m, *RV Baruna Jaya I*, KARUBAR Station CP56, 31.x.1991. SBMNH 143067, 1 female (ML 43 mm) & 1 male (ML 37 mm), off Tanimbar Island, Indonesia, 08°46′S, 131°36′E, 451–452 m, *RV Baruna Jaya I*, KARUBAR Stn CP75, 3.xi.1991 [donated to SBMNH by the MNHN].

Distribution: Material examined herein indicates distribution off northern and northwestern Australia, extending into Indonesian waters (off Tanimbar Island), bathymetric range 246–552 m (**Figure 1**). Type material for *O. philipii* was collected from off Alleppey, at the southern end of India, 275–365 m depth (Oommen 1976), and if the northern Australian and Indonesian material is conspecific, this species would have an extensive range along the northeastern Indian Ocean shelf into Indonesian and northern Australian waters.

Remarks: Oommen (1976) described *O. philipii* Oommen, 1976 from three specimens collected by the RV *Varuna* in 1973 (type location off Alleppey, southwest of India, Arabian Sea). The type series *Opisthoteuthis philipii* had 92–97 suckers per arm, with “1st to 4th sucker from mouth opening comparatively small, 5th to 11th usually largest [i.e., the PESF] and then gradually diminishes in size towards the distal end of arms”.

The absence of a DESF, sucker counts, and gill lamellae counts (8 primary lamellae per gill) of *O. philipii* type material from off India were all consistent with Australian and Indonesian material examined herein (provisionally attributed to *O.* cf. *philipii*), the bathymetric ranges were also similar (275–365 m for type *O. philipii* vs. 246–552 m for *O.* cf. *philipii*).

Unfortunately, Oommen (1976) failed to describe the form of the male accessory gland complex, or the form of the digestive gland. To complicate matters, the *O. philipii* type material lodged at the Integrated Fisheries Project Marine Research Laboratory (IFLC), Cochin, India, was apparently lost c.2000 when collections were relocated to the Central Institute of Fisheries Nautical and Engineering Training (CIFNET), Kochi, India (Sajikumar, K.K. – personal communications, March 2024). Fortunately, more material has been recently collected from near the *O. philipii* type location, with this material seeming to have a unilobed digestive gland (Sajikumar, K.K. – personal communications, March 2024).

Several of the specimens here attributed to *O.* cf. *philipii* from Indonesia were examined by the late Frederick “Eric” Hochberg (material collected during the French–Indonesian KARUBAR 1991 expedition to waters off the Indonesian Islands of Kai, Aru, and Tanimbar (Crosnier *et al.* 1997)). These specimens were stored in the MNHN, Paris, with a pair also donated to the SBMNH. Eric’s manuscript drafts, datasets, and line illustrations (1996–2013) indicated that he was planning on attributing this material to *Cirroteuthis meangensis* Hoyle, 1885, which he was to redescribe as "*Opisthoteuthis meangensis*". Eric retired from the SBMNH in 2013, in part due to illness, and ultimately passed away in May 2023. Subsequent work has reinforced the placement of *Cirroteuthis meangensis* in the genus *Grimpoteuthis* (Grimpoteuthididae) (Verhoeff & O’Shea 2022), however the KARUBAR material that Eric worked on was *Opisthoteuthis* and generally consistent with *O. philipii* (the poor original description of *C. meangensis* likely causing confusion at the time). Following the passing of Eric, the fate of his datasets and illustrations on the Indonesian *Opisthoteuthis* was left to an uncertain fate. However, the SBMNH generously made available Hochberg’s files for posthumous publication. The specimen collected off northwestern Australia (**WAM S35958**) also seems to be the same species that Eric was working on.

Attribution of this species to *O. extensa* (also from Indonesia) is decided against herein. This is largely due to the *O. extensa* holotype having a series of web nodules along the ventral arm edge, a feature seen on further specimens with DESF characteristic of genus *Insigniteuthis* (discussed in later species entry).

Opisthoteuthis cf. *philipii* from Indonesia and northwestern Australia can be compared to other *Opisthoteuthis* from around Australia (and the broader Indian and Pacific Ocean) that lack a DESF and have a unilobed digestive gland. Only two species have these traits; *O.*

robsoni from off New Zealand, and *O. pluto* from the Great Australian Bight (southern Australia).

Opisthoteuthis pluto is known with certainty from the Great Australian Bight and at a similar bathymetric range to *O.* cf. *philipii*, this taxon differs in its reproductive system rather strongly, *O. pluto* having an extremely reduced AG1 (see Verhoeff 2024), but can also be differentiated with greater intestine length (~2.7× oesophagus length for *O. pluto*, vs. 1.5× for *O.* cf. *philipii*), lower sucker counts (80–85 vs. 87–104 for mature *O.* cf. *philipii*, though lower and overlapping on sub-mature specimens), presence of areolar spots (vs. absence on *O.* cf. *philipii*), and possibly by absence of web nodules (vs. presence on *O.* cf. *philipii*).

Opisthoteuthis robsoni is known from off New Zealand, and occurs at much greater bathymetric range than *O.* cf. *philipii* (~1600 m vs. 246–552 m), but has a similar sucker count range to *O.* cf. *philipii* (73–89), similar intestine length (1.5× oesophagus length), and similar accessory gland complex (AG1 being similar in size to combined AG2 and 3). Differences between these species are more subtle (and may be biased by preservation differences making areolar spots or web nodules more or less apparent), but include the presence of areolar spots (*O. robsoni* with dorsal arms each with 7 spots, extending posteriorly over the head) and absence of web nodules on *O. robsoni* (O'Shea 1999).

The fecundity, diet, and parasites of *O.* cf. *philipii* from Indonesia was commented on by Eric Hochberg. The larger mature female (**MNHN 2043B**) had a total of 42 mature oocytes in the reproductive tract: 20 mature oocytes in the ovary sac (with length > 7 mm, with follicular folds), 5 smaller oocytes in the ovary sac (minute oocytes not counted), 15 oocytes in proximal oviduct, 1 in distal oviducal gland (with partially deposited capsule), and 1 in the distal oviduct (encased) (Hochberg 1996–2013). Overall this is indicative of continuous spawning, a single very prolonged spawning period occupying most of the lifespan with eggs being spawned one at a time, as reported for other opisthoteuthids (Villanueva 1992; Collins & Vallanueva 2006). Regarding diet, the crop and intestine of one specimen (**MNHN 2043A**) contained microcrustaceans and polychaete setae (Hochberg 1996–2013). This was also consistent with other opisthoteuthids, Villanueva & Guerra (1991) studied the diets of *O. calypso* and *O. massyae* (designated *O. agassizii* and *O. vossi* in the paper) across 292 specimens and found consistent diet of small epibenthic and suprabenthic crustaceans (mostly amphipods, isopods, and mysidacea) and polychaetes. Golikov *et al.* (2020) similarly found that *O. borealis* predated mostly upon small polynoid polychaetes along with smaller amounts of copepods, isopods and other small crustaceans.

The Indonesian *O.* cf. *philipii* specimens examined by Hochberg also had numerous small white cysts of an unidentified sporozoan parasite imbedded under the skin of the dorsal mantle and mantle cavity (Hochberg 1996–2013), a form of parasitism not previously reported for cirrates.

Genus *Insigniteuthis* Verhoeff 2024

Type species: *Insigniteuthis obscura* Verhoeff, 2024.

Diagnosis: Opisthoteuthids with DESF variably on arms I–IV and comprised of a small number (~2–5) of greatly enlarged suckers (diameter > PESF suckers); digestive gland bilobed or unilobed (from Verhoeff 2024).

Species allocated: *Insigniteuthis obscura* (type species), *I. calypso* Villanueva et al., 2002, *I. dongshaensis,* and *I. extensa* **comb. nov**. Tentatively allocated are *I. albatrossi* (including synonymised *O. californiana*) and *I. medusoides* Thiele *in* Chun, 1915.

Remarks: The four species assigned to this genus more confidently (*Insigniteuthis obscura*, *I. calypso*, *I. dongshaensis,* and *I. extensa*) all have a DESF with 2 or 3 massively enlarged suckers on arms I–IV, II–IV, or III and IV.

Other species assigned more tentatively share the DESF having few enlarged suckers (exceeding diameter of PESF suckers), but differ substantially from the more confidently assigned species or are poorly known. *Insigniteuthis medusoides* cannot be confidently allocated using its original description (Thiele *in* Chun 1915), but O'Shea (1999, pp. 25, 28) reported additional material in the South African Museum (SAM S3052) as having 1 or 2 massively enlarged suckers per DESF on arm pair IV only. *Opisthoteuthis bruuni* (Voss, 1982) may belong in this genus or to *Opisthoteuthis*, but the DESF form on mature specimens has yet to be described.

Insigniteuthis albatrossi (including the synonymized *O. californiana*) is unique in having the DESF restricted to arm pair I, and in having somewhat more suckers per DESF (4 or 5 greatly enlarged vs. 2 or 3). Genetic data also seems to indicate a closer relationship between "*O. californiana*" and *Exsuperoteuthis depressa* (see Verhoeff 2023), but molecular analyses are compromised by the lack of comparable CO1 sequencing data for *Insigniteuthis* and *Exsuperoteuthis* species (no CO1 sequences are available for *I. obscura*, *I. dongshaensis*, *I. extensa* and *E. persephone* for example), and indeed for many cirrate species more generally.

Insigniteuthis extensa (Thiele *in* Chun, 1915) comb. nov.

(Figure 7–9, Tables 5 & 6)

Synonymy.

Opisthoteuthis n. sp.—Chun 1903, p. 538

Opisthoteuthis extensa—Thiele *in* Chun, 1915, p. 135, Plate XCIV & XCV

Opisthoteuthis (Teuthidiscus) extensa—Roberts, 1932, p. 173

Grimpoteuthis sp.—Ng & Rahayu 2021, fig 10 E

Type specimen lodged (by Thiele 1915) at the Museum für Naturkunde, Berlin (ZMB Moll. 110010).

Diagnosis: Opisthoteuthid with up to 80 suckers per arm of adult, males with DESF of 4 enlarged suckers (with 2 or 3 greatly enlarged per DESF) on arms III and IV only, DESF sucker diameters considerably exceeding maximum diameter of PESF suckers; with multiple web nodules (5–11) along ventral edge of each arm (more on dorsal arms). Internally with 6 or 7 lamellae per gill and AG1 dominating AGC (approximately equal to size of combined AGC2 and AG3).

Description: Mantle short and rounded posteriorly, width and length comparable (MWI 73%–100% male, 135% female); head wider than mantle (HWI 113%–171% in males, 173% female) (see male **Fig 7 A**; female holotype badly damaged, **Fig 9 A**). Fins sub-terminally placed on mantle, relatively small, especially on female (FLI 64%–82% male, ~58% female); fins with slight basal constriction, greatest width halfway along fin length, distally rounded (FWI 22%–56% male, ~67% female). Eyes large (EDI 60%–71% male, uncertain female), openings small. Funnel relatively long, tapering (FuLI 55% male, 88% female), approximately half funnel length free. Funnel organ indistinct on male specimen (WAM S113334) but V-shaped for female holotype (per Thiele 1915). Pallial aperture too damaged to assess gape on male (WAM S113334) or could not be assessed (ZRC.MOL.30073), aperture small and enclosing tightly around funnel on female holotype (though not measured); olfactory papillae small, ovoid; pallial adductor reduced to a narrow strap or band (per earlier species descriptions).

Gills: half-orange form, with 7 lamellae per gill on male, and 6 per gill on female holotype.

Optic nerve: On male specimen (WAM S113334), optic nerve penetrates through each white body as three optic nerve bundles, white body kidney-shaped and brown coloured (**Fig 8 A**). Female holotype in poor condition, but a separated eye seems to have three optic nerve bundles entering the back of the eye (**Fig 9 G**).

Internal shell: Dissected from male specimen (**Fig 8 B–D**). With broad U-shape, saddle relatively deep or elongate (SHI 37%) and broad (SSI 83%), outer (posterior) face concave (with strong groove), basal shelf absent. Saddle shoulders well developed, with large concave outer face below each saddle prominence. Wings diverge from saddle mid-point at 41–43°, outer faces non-parallel, wings tapering to simple point (without any lobe), ends flared laterally. Shell translucent and pale-yellow coloured.

Arms and webbing: arms approximately sub-equal, thick and imbedded in webbing (see **Fig 7 B–E**); in males ventral arms slightly longer (formula ~IV>III>II>I, dorsal arm lengths 2.9–3.2× ML, ventral arm lengths 3.1–3.5× ML), female holotype with dorsal arms slightly longer (formula ~I>II>III=IV, dorsal arms 4.8× ML, ventral arms 4.2× ML). Web deep, simple, sub-equal (no consistent formula, but with ventral sector shorter), males with web A medial depth ~52%–60% arm I length, web E medial depth ~49% arm IV length (web depths uncertain for female holotype). With multiple web nodules along each ventral arm edge, centred around distal attachment point of webbing to arm edge, number of web nodules greatest on dorsal arms, less on ventral arms. Males with dorsal arms (pair I) having ~11 nodules each (see **Fig 7 F, G**), between suckers 33–49 on smaller male (ZRC.MOL.30073), 37–52 on larger male (WAM S113334); nodule placement slightly more proximal (suckers 30–50) on remaining arm pairs, and nodule counts lower, arms II with 9 or 10 nodules each, arms III and IV with 8 or 9 nodules each. Female holotype also with multiple web nodules (**Fig 9 B, C**), but with exact nodule counts and sucker positions uncertain (approximately 8 or 9 nodules countable on dorsal arms, probably more, ~6 countable on ventral arms).

Suckers and cirri: Maximum sucker counts up to 80 (missing suckers and arms tips often give counts per arm ~70). Suckers sexually dimorphic, males with proximal and distal enlarged sucker fields (PESF and DESF) (depicted **Fig 7 B–E, H, I**).

Males with proximal four suckers very small, followed by abrupt sucker enlargement of PESF, spanning from suckers 5 to 7–10 (thus 3–6 suckers per PESF), the central 2 or 3 suckers of each PESF largest. Largest PESF suckers with acetabulae swollen, globular, partially elevated above arm tissue, with bases touching (maximum PESF SDI 10.4%–13.8%), infundibular ring and pad narrow, encircling large aperture (largest PESF suckers with infundibular ⌀ ~55%–62% acetabular ⌀) (see **Fig 7 B, D, H**). Following mid-arm 'normal' suckers reduced in size (SDI 3.6%–4.7%, suckers 12–30), with spacing increasing to approximately 1–1.5 sucker ⌀ between adjacent suckers mid-arm (see **Fig 7 B, F**).

DESF restricted to arms III and IV, comprising 4 suckers, within suckers 34–40 (slightly more distal within this range on larger males); each DESF with 2 or 3 grossly enlarged suckers; typically central two suckers of each field enormously enlarged, and with flanking two suckers with subtle enlargement (see **Fig 7 B–D, I**), but on one specimen which couldn't be properly assessed (ZRC.MOL.30072) all four suckers of DESF had great enlargement, though less on the most proximal sucker (**Fig 7 E**); DESF suckers frequently detached (**Fig 7 C**); largest DESF SDI 17%–24%, almost double PESF sucker ⌀. Largest DESF suckers approximately conical in form (acetabula greatly swollen, but with base truncated to a flattened face); infundibular structures of largest DESF suckers proportionally smaller, infundibular ⌀ 41%–56% acetabular ⌀, infundibular ring and pad poorly differentiated and forming narrow ring around large aperture. Distal to the DESF, or on arms I and II without the DESF, suckers have small size (⌀ less than mid-arm

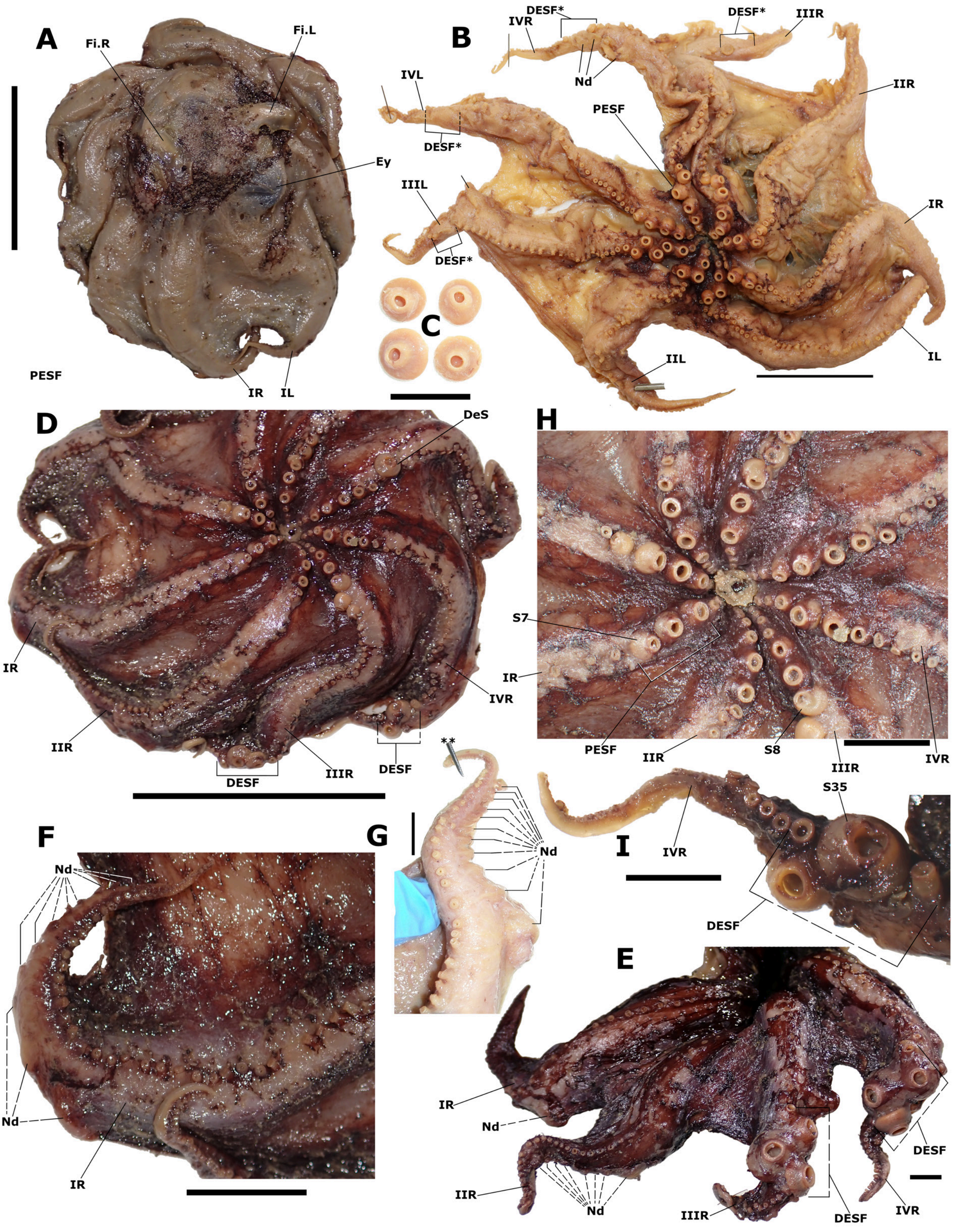

Figure 7. Body and arm detail of *Insigniteuthis extensa* comb. nov. (male specimens). **A**) dorsal aspect of whole animal (ZRC.MOL.30073). **B, D, E**) oral aspects of arms and webbing, depicting enlarged sucker fields; damaged specimen from north-western Australia (**B**, WAM S113334) with closeup (**C**) of several detached DESF suckers from the same specimen, good condition specimen from Sunda Strait, Indonesia (**D**, ZRC.MOL.30073), damaged specimen from Sunda Strait (**E**, ZRC.MOL.30072). **F**, **G**) distal aspects of dorsal arms with multiple web nodules (**F**, ZRC.MOL.30073; **G**, WAM S113334). **H**) closeup of PESF (ZRC.MOL.30073). **I**) closeup of DESF on arm IVR (ZRC.MOL.30073), DESF also depicted by **D**, **E**. Abbreviations/symbols: **—props used to pin down structures in photography; DESF—distal enlarged sucker field (*—denotes DESF with enlarged suckers detached); DeS—detached suckers (from DESF); Fi.L/R—fin left/right; I–IVL/R—arm I–IV left/right; Nd—web nodules; PESF—proximal enlarged sucker field. Scale bars = 50.0 mm (**A**, **B**, **D**), 20.0 mm (**C**), 10.0 mm (**E–H**), 5.0 mm (**I**).

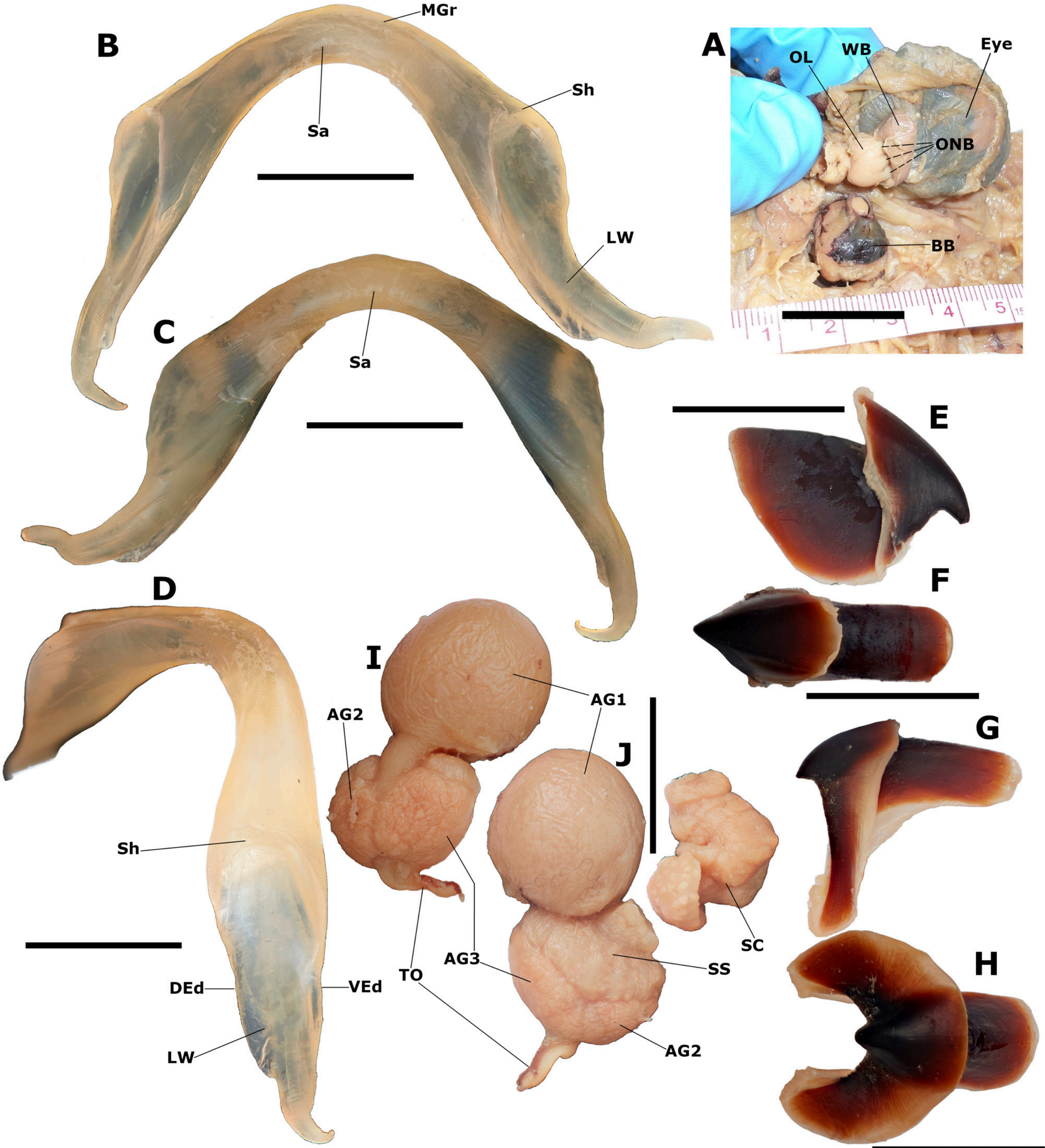

Figure 8. Internal morphology of *Insigniteuthis extensa* comb. nov. (male, WAM S113334). **A**) left-side optic nerve branching pattern through white body. **B–D**) internal shell with dorsal (**B**), ventral (**C**), and lateral (**D**) aspects. **E**, **F**) lateral and dorsal aspects of upper beak. **G**, **H**) lateral and ventral aspects of lower beak. **I**, **J**) left and right aspects of the male reproductive system (AGC and part of SC, testis and vas deferens missing due to damage). Abbreviations/symbols: AG1–3—accessory gland part 1–3; BB—buccal bulb; DEd—dorsal edge (of shell); LW—lateral wing of shell; MGr—medial groove of shell saddle; OL—optic lobe; ONB—optic nerve bundle; Sa—saddle; SC—spermatophoric complex; Sh—shoulder (of shell); SS—spermatophore sac (Needham's sac); TO—terminal organ; VEd—ventral edge (of shell); WB—white body. Scale bars = 20.0 mm (**A**), 10.0 mm (**B–J**).

suckers) and continue to arm tips with minute size and compact spacing (see **Fig 7 F, G, I**).

Female (holotype) with suckers reaching largest size by approximately 5th sucker (per Thiele 1915) and remaining similarly sized until distal arm, maximum sucker ⌀ calculated to be 1.2 mm (SDI 4.6%), sucker spacing mid-arm 1–2 sucker ⌀, becoming smaller and more compacted towards arm tips (**Fig 9 B, C**).

On males cirri commence between suckers 2–5 suckers as minute buds, increasing to maximum length by mid-arm and slowly decreasing in length towards arm tips; cirri short and often retracted into small "pockets"

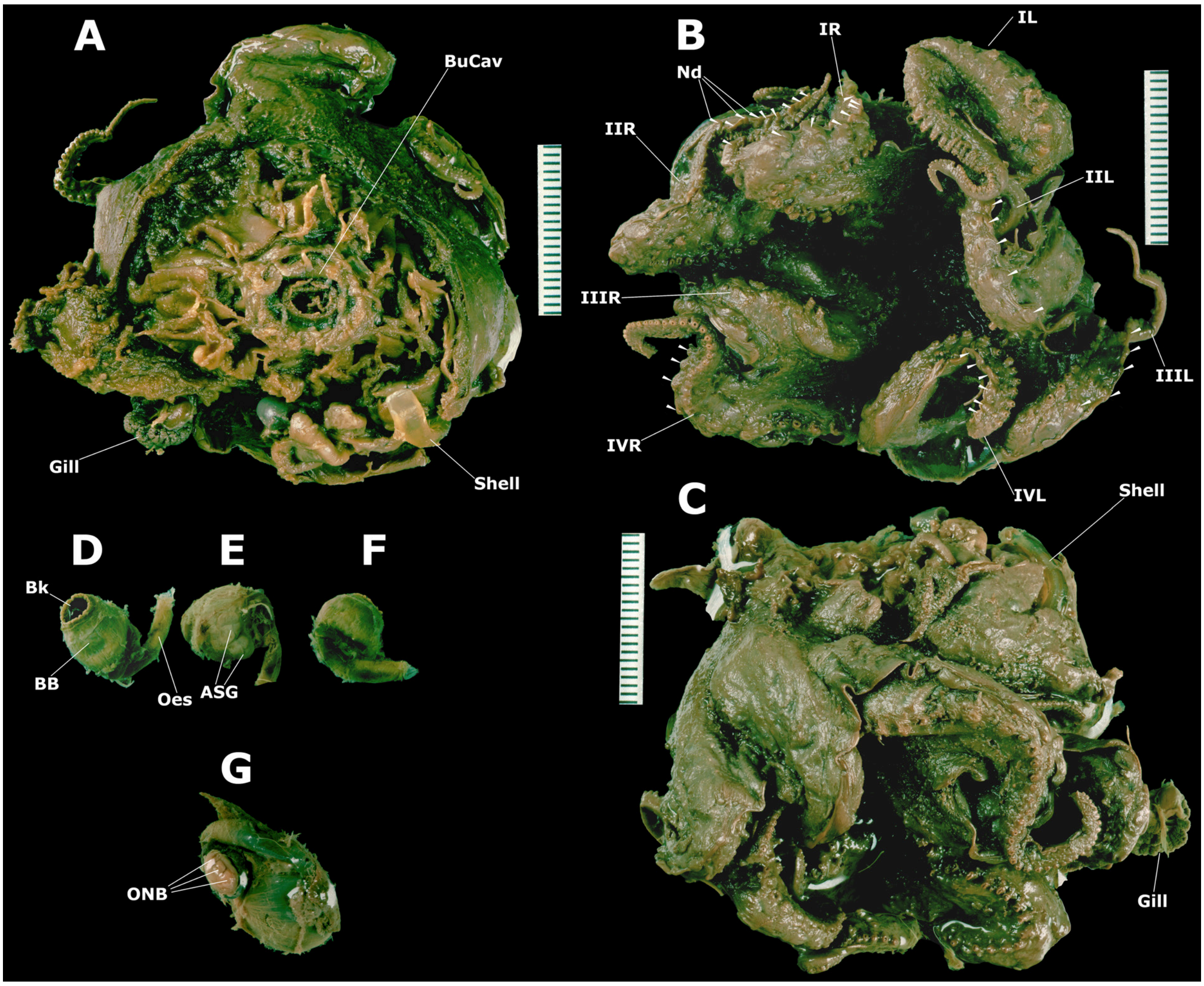

Figure 9. Female holotype of *Insigniteuthis extensa* comb. nov. (ZMB 110010). **A**) dorsal image depicting the heavily dissected state of the head and mantle (most viscera removed). **B**) oral aspect of specimen, depicting multiple web nodules along ventral arm edges (white arrows, noted as 'Nd', mark web nodule positions). **C**) lateral aspect of the specimen, better depicting the broadly U-shaped internal shell. **D–F**) different aspects of the buccal bulb, still containing the beaks. **G**) separated eye with cut optic nerve bundles. Abbreviations/symbols: ASG—anterior salivary glands; Bk—beaks; BB—buccal bulb; BuCav—buccal bulb cavity (space from where buccal bulb was removed); I–IVL/R—arms I–IV left or right; Nd—web nodules; Oes—oesophagus; ONB—optic nerve bundles. Scale bars = image rulers (in mm marks).

(greatest CLI 5.4%–6.2%). On the female holotype cirri also commence between suckers 2 and 3 (from Thiele's 1915 illustration) with CLI estimated at 4.2%.

Digestive tract: Largely missing on specimens examined (beaks examined from male, WAM S113334), buccal bulb and part of oesophagus remaining (remainder missing). Upper beak (**Fig 8 E, F**) moderately tall (height 73.5% beak length; height 90.5% beak width), hood somewhat deep (hood length 68.0% beak length). Rostrum deflected down (not strongly) and blunt tipped, jaw cutting edge irregular (near straight), hood with rounded (convex) crest. Lateral walls near-parallel (without apparent grooves or flexures), dorsal crest of lateral walls gently convex, posterior edges convex, posterodorsal apex of crest rounded (without any posterior indentation). Lower Beak (**Fig 8 G, H**) moderately tall (height 60.0% width), hood short (hood length 50.6% beak length) with crest rounded, wings elongate (wing length 101.6% beak length) with weak diagonal flexures. Rostrum small, straight, and blunt tipped. Buccal bulb large and with anterior salivary gland pair on posteroventral face (see **Fig 8 A**, **Fig 9 D–F**), radula absent, posterior salivary glands absent, length of oesophagus unremarkable, without any crop diverticula. Remainder of digestive system unknown.

Male reproductive system: Fragmentary in material examined (WAM S113334), but AGC in good condition (**Fig 8 I, J**). Testis large, rounded, vas deferens and spermatophoric complex parts damaged or destroyed (the remains of the three spermatophoric complex parts seem to be present). Spermatophore sac (Needham's sac) large, attached to proximal face of AG2 and AG3. Accessory gland complex dominated by AG1 (rounded, separated from other accessory glands), AG2 and AG3 closely associated as a rounded mass (with greatest dimensions ~equal to AG1). Terminal organ originating

ID	WAM S113334	ZRC.MOL.30073	ZMB Moll. 110010 Holotype **
Sex	Male	Male	Female (immature?)
TL	NA	NA	NA
ML	~55* (damaged)	28	~26
MW	~40	~28	35
HW	62	48	45
ED	33 (eye opening ~7.0)	20	NA
FL (L/R)	45/41	20/18	15
FW (L/R)	10/14	9/10	10
FuL	30	NA	23
PA	NA*	NA	NA
GLC (L/R)	7/7	NA	6/6
AL I (L/R)	178/163	81 R	125
AL II (L/R)	168/166	83 R	115
AL III (L/R)	170/177	85 R	110
AL IV (L/R)	192/185	86 R	110
SC I (L/R)	80*/58*	63* R	~70–80
SC II (L/R)	70*/72*	64* R	
SC III (L/R)	71*/58*	59* (10+ missing) R	
SC IV (L/R)	63*/65*	59* (10+missing) R	
SuD (Normal)	Smallest mid-arm suckers 2.0–2.6 $^{\text{acet}}$, 1.8–2.0 $^{\text{Inf}}$ (~16–24$^{\text{th}}$)	Smallest mid-arm suckers 1.0–1.3 $^{\text{acet/Inf}}$ (12–30$^{\text{th}}$, III & IVR)	1.2 $^{\text{acet}}$, 1.0 $^{\text{Inf}}$ (mid-arm, 15–20$^{\text{th}}$, IL)
PESF position L/R	5–9/8 (6–8/7 $^{\text{largest}}$) 5–9 (6–8 $^{\text{largest}}$) 5–10 (6–8 $^{\text{largest}}$) 5–9 (7–8 $^{\text{largest}}$)	5–7 (5–6 $^{\text{largest}}$) R 5–8 (6–7 $^{\text{largest}}$) R 6–10 (8–9 $^{\text{largest}}$) R 5–9 (6–7 $^{\text{largest}}$) R	NA
SuD (PESF)	7.6 $^{\text{acet}}$, 4.2 $^{\text{Inf}}$ (others 7.0 $^{\text{acet}}$)	3.7 $^{\text{acet}}$, 2.1 $^{\text{Inf}}$ (8$^{\text{th}}$, IIIR) (others 2.9–3.4 $^{\text{acet}}$, 1.8–2.0 $^{\text{Inf}}$)	NA
DESF position L/R	NA, I NA, II 35/36–38/39 (36/37–37/38 $^{\text{largest}}$), III 37/36–40/39 (38/37–39/38 $^{\text{largest}}$), IV	NA, I NA, II 34–37 (35–36 $^{\text{largest}}$), IIIR 34–37 (35–36 $^{\text{largest}}$), IVR	NA
SuD (DESF)	13.0 $^{\text{acet}}$, 5.3 $^{\text{Inf}}$ (sucker detached) (others 11.8 $^{\text{acet}}$, 5.1 $^{\text{Inf}}$) Flanking DESF sucker ⌀ 5.0 $^{\text{acet}}$	5.0 $^{\text{acet}}$, 2.8 $^{\text{Inf}}$ (35$^{\text{th}}$, IVR) 4.8 $^{\text{acet}}$, 2.4 $^{\text{Inf}}$ (36$^{\text{th}}$, IIIR)	NA
CiL	3.4 (15–16$^{\text{th}}$, IVL) (others 1.3–2.0); many retracted into "pockets"	~1.5 (mid arm) Many damaged or retracted	0.8–1.1
Ci start sucker position	2$^{\text{nd}}$ & 3$^{\text{rd}}$ sucker	3–5$^{\text{th}}$ sucker	2$^{\text{nd}}$ & 3$^{\text{rd}}$
WD A	106	~42	NA
WD B (L/R)	100*R/50*L	~52 R	NA
WD C (L/R)	106*R/95	~52 R	NA
WD D (L/R)	106*R/95L	~50 R	NA
WD E	35	~42	NA
WN (L/R) I II III IV	11 nodules, 37–52$^{\text{th}}$ / 8 nodules* 10 nodules, 33–50$^{\text{th}}$ / 8 nodules*, 32–47$^{\text{th}}$ 9 nodules, 32–47$^{\text{th}}$ / 10 nodules, 31–50$^{\text{th}}$ 8* nodules, 30–44$^{\text{th}}$ / 9 nodules, 31–48$^{\text{th}}$	11 nodules, R (33–49$^{\text{th}}$) ~9 nodules, R ? (>5) nodules, R ? (>5) nodules, R	~8 nodules, R ~9 nodules, R ~6 nodules, L ~6 nodules, L
Other notes			Distal oviduct 9 mm long

Table 5. *Insigniteuthis extensa* comb. nov., measurements (in mm) and counts. *Denotes damage (including missing and uncountable, suckers), sucker counts include countable but missing sucker positions (i.e., sucker scars, or flanking cirri positions). PESF and DESF positions are sucker ranges, listed L/R if the sucker positions differ on the left or right arm. **Data from Thiele in Chun 1915, calculated from Thiele's (1915) Plates XCIV & XCV, or calculated from photos of the specimen.

between AG2 and AG3, elongate and narrow (length slightly less than half the greatest dimensions of combined AG2 and AG3).

Female reproductive system: unknown, Thiele (1915) described a 9 mm long distal oviduct projecting into the mantle cavity, but nothing else besides.

Colouration: mantle, head, and aboral arms/webbing, with remnants of a dark maroon–brown pigmentation, though mostly abraded away (**Fig 7 A**). Oral surfaces of webbing and arms with dark maroon pigmentation overall (with more red or purple tinge in places) (**Fig 7 B, D, E**); suckers contrasting with paler, yellowish to beige colouration. Areolar spots: possibly present, with 1 or 2 visible proximally on some arms, but very uncertain due to skin abrasion.

Material examined.

Holotype.

O. extensa, ZMB Holotype Moll. 110010, female, Mentawei Basin, off Sumatra (eastern Indian Ocean),

Indices	WAM S113334	ZRC.MOL.30073	ZMB Moll. 110010 Holotype *
MWI	~73% (64.5% of HW)	~100% (58.3% of HW)	135% (77.8% of HW)
HWI	113%	171%	173%
FuLI	54.5%	NA	88%
FLI (L/R)	81.8% / 74.5%	71.4% / 64.3%	58%
FWI (L/R)	22.2% / 34.1%	45.0% / 55.6%	67%
EDI	60%	71.4%	NA
PAI	NA	NA	NA
Arm formula	IV>I>III>II / IV>III>II>I	IV>III>II>I (R)	I>II>III=IV
Dorsal ALI	2.9–3.2× ML	2.9× ML	4.8× ML
Ventral ALI	3.4–3.5× ML	3.1× ML	4.2× ML
SDI	3.6%–4.7% (mid-arm)	3.6%–4.6% (mid-arm)	4.6%
SDI PESF	12.7%–13.8%	10.4%–13.2%	NA
SDI DESF**	21.5%–23.6%	17.1%–17.9%	NA
CLI	6.2% (smaller cirri 2.4%)	5.4%	4.2%
Web formula	A=C=D>B>E *	B=C>>D>A=E	NA
WI A	60% arm I	~52%	NA
WI E	18% arm IV*	~49%	NA

Table 6. *Insigniteuthis extensa* comb. nov. indices and formulas. *SDI values for PESF and DESF only include the size range for the largest suckers, and do not include the flanking suckers with only slight enlargement (even though these are counted within the enlarged fields).

0°57.5′S, 99°51.1′E, 768 m, SS *Valdivia*, Station 189, 30.i.1899 [photography and measurements provided].

Other material.

WAM S113334, male, 160 nautical miles NW of Port Hedland, Western Australia, 18°42′S, 116°21–23′E, 694–704 m, Engel Trawl, RV *Soela*, Cruise SO 2/82, Station 23, 5.iv.1982 (coll. L. Marsh). ZRC.MOL.30072, male, SW of Djungkulon Peninsula, Sunda Strait, 6°50.185–50.923′S, 105°10.353–10.776′E, 876–937 m, RV *Baruna Jaya VIII*, SJADES, Station CP25, 27.iii.2018 [photography and measurements provided]. ZRC.MOL.30073, male, 35 km west of Krakatoa Island, Sunda Strait, 6°10.758–11.587′S, 105°05.589–05.735′E, 1060–1073 m, RV *Baruna Jaya VIII*, SJADES, Station CP18, 26.iii.2018 [photography and measurements provided].

Distribution: Type specimen was from the Mentawei Basin, off Sumatra (eastern Indian Ocean), 768 m depth. Additional material herein was from south west of the Type location, south of the Sunda Strait off Java (876–1073 m depth), and from off Port Hedland, northwestern Australia (694–704 m). Additional material, matching the male specimens herein, was reported by Massy (1916) from the Arabian Sea (northern Indian Ocean) (see remarks). Overall, this species may be found widely around the northern Indian Ocean, from off northwestern Australia, Indonesia, and to the Arabian Sea. The species distribution may be expanded further north into the South China Sea if it proves conspecific with *I. dongshaensis*.

Etymology: Thiele *in* Chun (1915) did not define etymology, but the specific epithet '*extensa*' is a singular feminine of the Latin adjective *extensus* (derived from verb *extendo*), referring to something stretched out or extended, possibly in reference to the extensive webbing.

Remarks: The male specimens herein are very distinctive in possessing a DESF only on arms III and IV, with each distal sucker field containing ~2 or 3 massively enlarged suckers (greatly exceeded PESF sucker diameters), and in having multiple web nodules on each ventral arm edge. Such a DESF configuration is shared with *I. dongshaensis*, but the web nodules are not. The capture locations of two of these specimens (ZRC.MOL.30072 and 30073), collected during the recent 2018 SJADES expedition (Ng & Rahayu 2021), is of note given the relative proximity to the type locality of *O. extensa*. Only a partial dataset of measurements and counts could be obtained for one of the SJADES specimens (ZRC.MOL.30073), and more work remains to be done on this material.

In addition to locality of capture, the allocation of these SJADES specimens to *O. extensa*, and allocation of this species to genus *Insigniteuthis*, was also supported by the unusual web nodule configuration, and re-examination of the holotype. The identity of *O. extensa* (known only from its female holotype, which is in poor condition) has been difficult to determine for a long time, and from Thiele's (1915) description it could not be differentiated from other Australian and Indo-Pacific opisthoteuthids. Re-examination of the *O. extensa* holotype revealed multiple web nodules along the ventral arm edges (see **Fig 9**), and mid-arm suckers with increased spacing, and relatively minute mid-arm suckers compared to *O. carnarvonensis* sp. nov. and *O.* cf. *philipii*. These features were shared with the male specimens from northwestern Australia and the Sunda Strait (ZRC.MOL.30072, 30073, and WAM S113334), linking the female holotype to these male specimens and their distinctive enlarged sucker morphology. The DESF form means that *O. extensa* should also be allocated to genus *Insigniteuthis* given the male enlarged sucker configuration (as *I. extensa* **comb. nov.**).

Additional specimens of this taxa are very much needed, and important morphological states (digestive gland and intestine length) remain unknown. The DESF configuration is consistent with *I. dongshaensis* as mentioned (Lu 2010), and though this species reportedly lacks multiple web nodules, these structures may have been overlooked. Synonymy is not proposed herein as *I. dongshaensis* type material could not be examined to confirm the presence or absence of web nodule, but if they do prove synonymous the species would have a significantly extended distribution.

Massy (1916) documented five opisthoteuthids (designated "*Cirroteuthis grimaldii*" therein) from the Andaman Sea and Arabian Sea stored in the Indian Museum, Kolkata, with the male specimens of this collection seemingly being attributable to two species. Some specimens had only a PESF and may be attributable to *O.* cf. *philipii*, Massy (1916) described these as follows: *"[having] three or four [suckers] next the mouth are very minute, and are suddenly succeeded by very large ones until about the seventh or eighth sucker, after which they become much smaller and continue gradually diminishing in size until the tip is reached".* One of the other specimens (M 8127/1 from the Arabian Sea) seems attributable to *Insigniteuthis extensa*, with Massy (1916) describing it as having *"enormously enlarged suckers on the ventral arms at the edge of umbrella. One of the arms is mutilated and only shows one large sucker, the other has five".* However, material from the Indian Museum was not tracked down and Massy's brief descriptive notes leave some ambiguity.

Examination of the *I. extensa* holotype revealed extensive dissection, with the entire viscera cut away, and buccal bulb separated out. In the description of the species by Thiel (1915), the specimen was described as relatively intact, with the mantle cavity opened to count gill lamellae and determine sex, but no other dissection was indicated, and the specimen was certainly not described as damaged or mangled. The extent of dissection implies that someone else conducted extensive work on the specimen, including of the digestive system, but it is unclear who this was.

Given the limited original description of the holotype, and details such as the multiple web nodules not being later noticed (the type material not being examined?), different authors have suggested affinities or synonymies regarding *I. extensa*. Berry (1918, p. 289) compared the species to his newly described *O. pluto*, noting "Superficially at least, *O. extensa* seems nearer to the form now described [*O. pluto*] than do any of the other species, so much in fact that it is not impossible that it may prove conspecific when better known", however, Berry did note the difference in gill lamellae counts (6 vs. 8 per gill). Hochberg *et al.* (2014) make a statement that *O. extensa* "Appears to be similar to *Grimpoteuthis meangensis*..." (p. 251) and that *G. meangensis* is distributed "Philippines and Sumatra (as synonym ***extensa*** Thiele, 1915)" (p. 258), this seemingly stems from the allocation by Hochberg (1996–2013, unpublished manuscript) of *G. meangensis* to *Opisthoteuthis* and a synonymy in that work for *O. extensa*, which is not supported from examination of the *G. meangensis* holotype (Verhoeff & O'Shea 2022). While the current description is sufficient to discard comparison of *I. extensa* to *O. pluto* or *G. meangensis*, there is still a need to critically assess its relationship with *I. dongshaensis*.

Disclosures

Conflicts of Interest: The author declares no conflict of interest.

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