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Flapjack octopods of Australia (Cephalopoda: Cirrata: Opisthoteuthidae), Part I Southern Australia

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Abstract

The flapjack octopods, genus *Opisthoteuthis* (Opisthoteuthidae) are globally distributed deep-sea finned octopods. The *Opisthoteuthis* fauna of many regions remains poorly understood, and members of this genus from Australian waters have been little studied. Herein, Australian *Opisthoteuthis* from southern and southeastern Australia, including Macquarie Island, were assessed using museum specimens, with comparisons made to other species traditionally allocated to this genus. Based on configuration of male enlarged suckers it is proposed that the genus be split into three genera, including the two new genera *Insigniteuthis* **gen. nov.** and *Exsuperoteuthis* **gen. nov.**, and the genus *Opisthoteuthis* '*sensu stricto*' be restricted to species sharing a similar pattern of male enlarged suckers with the type species *O. agassizii*. Redescriptions are provided for the two *Opisthoteuthis* previously known from Australian waters, *O. pluto* and *E. persephone* **comb. nov**. Two new species are described, *O. kerberos* **sp. nov.** from five specimens collected at 2 km depth off southeastern Australia, significantly deeper in bathymetric range than the other Australian taxa, and *I. obscura* **sp. nov.** from southeastern Australia and the Great Australian Bight. Description is also provided for a species from Macquarie Island, Australian Antarctic Territories, that may be comparable to the New Zealand *O. chathamensis*.

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Introduction

The genus *Opisthoteuthis* Verrill, 1883 is the most speciose of the suborder Cirrata Grimpe, 1916, with ~20 species recognized at the time of writing (MolluscaBase eds. 2024). These animals are the most benthic of the cirrates, and while comprising deep-sea megafauna, several *Opisthoteuthis* have the shallowest bathymetric ranges of the cirrates (less than 200 m depth). Their abundance, relatively shallow bathymetric range, easy collection in trawling gear, and demonstrated ability to be kept alive in captivity (Pereyra 1965, Hunt 1999), has also permitted this genus to be the best understood in terms of ecology (aspects all thoroughly reviewed by Collins & Villanueva 2006).

Opisthoteuthis is currently recognized as the only genus within the family Opisthoteuthidae Verrill, 1896 (MolluscaBase eds. 2024), with both this family and family Cirroctopodidae Collins & Villanueva, 2006 united by the presence of multiple optic nerve bundles passing through the white body each side of the head as well

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as the internal shell 'wings' terminating in simple spikes (i.e., without any lobe-like expansions) (Collins & Villanueva 2006). These features are in distinct contrast to the Grimpoteuthididae which have single optic nerve bundles and shells with distinctly lobate shell 'wings' (with complex and variable spike-like projections). All three of these families are united by both morphological and molecular features as the superfamily Opisthoteuthoidea (per Verhoeff 2023a). Opisthoteuthidae is distinct within this superfamily in having a far greater degree of sexual dimorphism, with the males having remarkably enlarged suckers (more than double or triple the 'normal' sucker size) in distinct regions of the arms. Presumably these enlarged suckers have some role in mating or competition (Collins & Villanueva 2006).

Yet, while significant strides have been made in the taxonomy of this genus, including recent revisions of the taxa from the Atlantic (Villanueva *et al.* 2002), New Zealand waters (O'Shea 1999), South China Sea (Lu 2010), and southeastern Pacific (Pardo-Gandarillas *et al.* 2021), there are still many problematic species. For example, certain taxa in the North Pacific may be synonymous (per Young & Vecchione 2003), namely *Opisthoteuthis albatrossi* Sasaki, 1920 and *O. californiana* Berry, 1949, as well as *O. depressa* Ijima & Ikeda, 1895 and *O. japonica* Taki, 1962. Meanwhile, other species are difficult to distinguish due to inadequate original descriptions. Moreover, the great variability within the genus, particularly in digestive gland form, placement and extent of enlarged male suckers, and differences in the male accessory reproductive glands have prompted researchers to propose splitting the genus (O'Shea 1999).

Samuel Stillman Berry (1918) conducted what remains the only work reviewing the Australian *Opisthoteuthis* fauna. From material collected by the F.I.S *Endeavour* during 1909–1914 off the Great Australian Bight and southeastern Australia, Berry recognized two species of *Opisthoteuthis* from southern Australia, *O. pluto* Berry, 1918 and *O. persephone* Berry, 1918. Since the description of these two species, very little work has been done on them, either morphologically or ecologically, except for a study on *O. persephone* spermatozoa (Healy 1993), a brief comparison by Lu (2010) (without redescription), description of beaks by Lu & Ickeringill (2002), and observation of an *Opisthoteuthis* (misidentified as *Grimpoteuthis* sp.) off southwestern Australia (Hood Canyon, 1109 m depth) by remotely operated vehicle (Trotter *et al.* 2022, fig. 10C).

The present research is a continuation of a larger review of the Australian Cirrata by the author and colleagues, with earlier works in this series revising families Grimpoteuthididae and Cirroteuthidae (Verhoeff & O'Shea 2022, Verhoeff 2022, Verhoeff 2023b). The aim of this research is to review the Opisthoteuthidae from Australia, redescribing taxa and describing new species as needed. This is to be completed in two parts, Part I herein looking at the southern Australian and Macquarie Island species, and Part II (in preparation) will look at a smaller grouping of differing species from off northern and northwestern Australia and provide an overall key.

Methods

Opisthoteuthis material was examined at the Tasmanian Museum & Art Gallery (TMAG) collections facility (Rosny Park, Tasmania), supplemented by material loaned from the South Australian Museum (SAM) (Adelaide, South Australia), the Western Australian Museum (WAM) (Perth, Western Australia), and the Melbourne Museum or Museums Victoria (MV; formerly National Museum of Victoria, NMV) (Melbourne, Victoria). This material was collected by both research vessels (RV *Soela*, FRV *Southern Surveyor*, and FRV *Kapala*) and commercial fisheries vessels (FV *Comet*, FV *Longva III*, FV *Margaret Philippa*, FV *Austral Leader*, and FV *Saxon Progress*). Data and photography were also provided for *Opisthoteuthis* specimens stored at the Australian Museum (AM), Sydney, and the Smithsonian National Museum of Natural History, Washington DC (NMNH; former US National Museum, USNM). The localities for specimens examined in this contribution are shown in **Figure 1**.

All material was likely fixed in formalin, and some were possibly frozen (especially those from fishing vessels) and stored in 70%−75% ethanol.

Standard teuthological nomenclature, meristics, and indices are used. Dissection of the digestive system and reproductive systems was conducted for representative specimens of different species by opening the mantle with a ventral longitudinal incision (sometimes extending dorsally when the internal shell was removed, and/or if the optic lobes were examined). Mature male specimens were designated based on presence of distinct enlarged suckers. Mature female specimens were recognized by similar size to mature males, absence of enlarged suckers, and presence of an encased egg in the distal oviduct indicative of spawning. Encased eggs in the distal oviduct were examined in some specimens by making an incision along the distal oviduct and carefully removing the egg.

Terminology for the male reproductive system follows that previously used in Verhoeff & O'Shea (2022). The designations of accessory gland parts 1–3 (AG1–3) is derived from Ebersbach (1915) (translated as Verhoeff 2023c) who demonstrated the internal connections between these glands in *Grimpoteuthis* Robson, 1932 and *Stauroteuthis* Verrill, 1879, and in turn this is consistent with the structures shown by Meyer (1906; fig. 8, p. 228) for *O. depressa*, though Meyer designated accessory gland (AG) 2 and 3 as a two-parted AG2 (and didn't designate AG3).

Photography of smaller parts used a stacking camera macro-imaging setup (100 mm or 65 mm lens). Passport

linear actuator software (Visionary Digital), Capture One (Phase One), and Zerene Stacker (Zerene Systems) were the software used.

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 or I).

Other abbreviations: coll.—collector, CSIRO—Commonwealth Scientific and Industrial Research Organization (Australia), FV—fisheries vessel, FRV—fisheries research vessel, NW—north-west, RV—research vessel, SE—south-east, Stn—Station, SW—south-west, SSW—south-south-west, TFDA—Tasmanian Fisheries Development Authority.

Discussion

Specimens attributable to Opisthoteuthidae have been frequently collected around Australia over the last century, but despite this, very little work has been done on their morphology and ecology. The original descriptions of *O. pluto* and *O. persephone* lacked detail of most internal organ systems and did not clearly describe the enlarged suckers of male specimens, essentially meaning that other than geographical location, very little clearly separated these species from others in the genus. Lu's (2010) research clarified some defining features of these species (though the specific identity of *O. pluto* was confused with the then undescribed *I. obscura*), notably the bilobed digestive gland and pattern of enlarged sucker fields was noted, but this work did not compare type material and did not illustrate or describe these structures (i.e., there was no formal redescription). Other researchers may have been attempting redescription of Australian Opisthoteuthidae, e.g., the late Gilbert Voss, loaned at least seven *Opisthoteuthis* from the Melbourne Museum in 1983 (including some of the *E. persephone* examined herein), but didn't publish anything before his passing in 1989 (Chris Rowley & Chung-Chen Lu—personal communication). It became apparent early in this research project that additional opisthoteuthid taxa were present off southern Australia, further complicating issues with local species identification. In order to stabilize the local taxonomy, and provide a framework for further research, the present work redescribes Berry's Australian Opisthoteuthidae, describes two additional taxa from southern Australia, and allocates several of these species to new genera to better represent the morphological diversity of the species traditionally placed in the genus *Opisthoteuthis* (the only genus generally recognized in the family). The description of some species herein was admittedly limited by the number of specimens available, particularly for *O. pluto*, however material examined (including type material) was sufficient to match suspected species, and thus allow description of new taxa. As will be covered in the following Part II contribution (Verhoeff in preparation), the waters off northern and northwestern Australia host a completely different opisthoteuthid fauna that extend northwards in distribution into Indonesian waters and the northern Indian Ocean.

Overall, four opisthoteuthid taxa covered in this contribution seem confined to the outer shelf and continental slope of southern and southeastern Australia, with this fauna apparently separated from the three species of the New Zealand continental shelf, i.e., Zealandia (as documented by O'Shea 1999) and *vice versa*. These southern Australian and New Zealand opisthoteuthid faunas are in-turn separated from the northern and northwestern Pacific which hosts its own collection of species (approximately four[1]), with the tropical latitudes of northern Australia and Indonesia also hosting their own distinct species covered in Part II (Verhoeff in preparation). These regionalized opisthoteuthid faunal groupings in the Pacific are rather different from the Atlantic, where *I. calypso* comb. nov. (Villanueva et al., 2002), *O. massyae* (Grimpe, 1920), and *O. grimaldii* (Joubin, 1903) have enormous latitudinal ranges along the eastern Atlantic off northwestern Europe down to southern Africa (Villanueva et al. 2002), easily encompassing the latitudinal ranges of all the separated faunal groupings in the Pacific and Indian oceans. This may in-part be due to the higher biodiversity of Opisthoteuthidae in the Pacific and Indian ocean compared to the Atlantic (approximately 13 species vs. 6) and competition between taxa, and in part due to the greater age and geological complexity of the Indo-Pacific region. These biodiversity trends mirror coastal and mid-water cephalopods, which have significantly greater biodiversity in the Pacific and Indo-Pacific compared to the Atlantic (Rosa et al. 2019, Otjacques et al. 2023). Bathymetric stratification may also permit the relatively high biodiversity of opisthoteuthids, off southern Australia *O. pluto* and *E. persephone* were sympatric in bathymetric ranges (250–820 m and 274–595 m respectively), while *I. obscura* (900–1300 m) and *O. kerberos* (1923–1962 m)

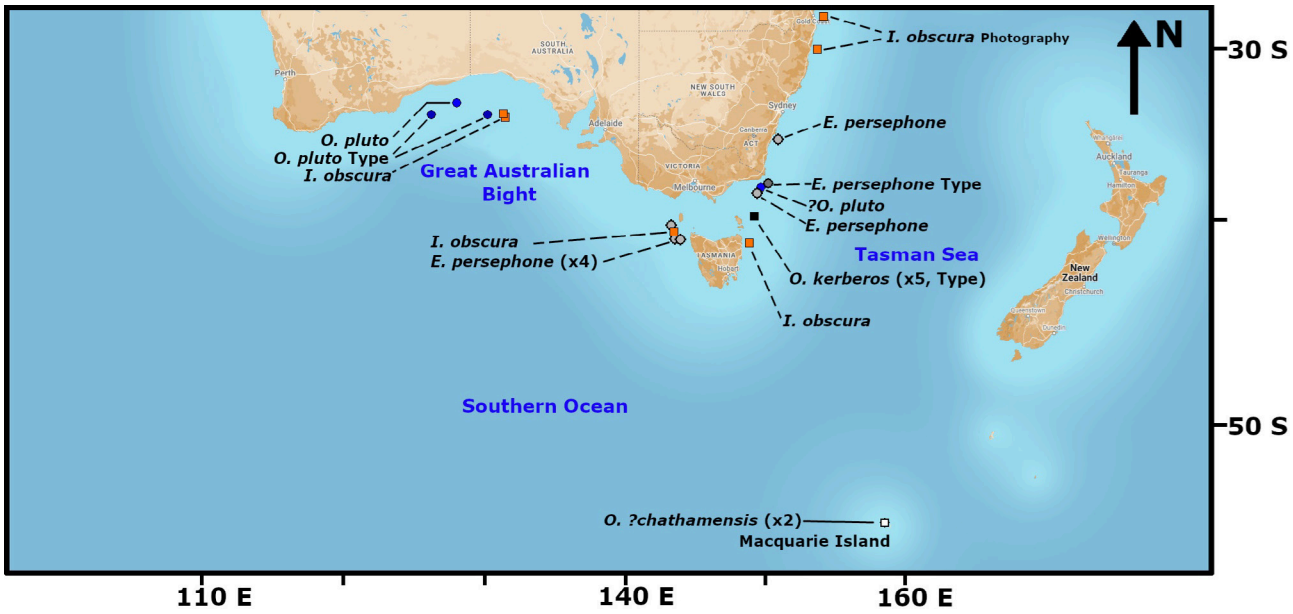

Figure 1. Localities for southern Australian opisthoteuthids examined during this study. Species identifications are noted, including type material (holotype, paratype, and other type series material) and specimens confirmed from photography (noted "photography"). Symbols: orange square—*Insigniteuthis obscura* sp. nov., grey circle—*Exsuperoteuthis persephone*, black square—*Opisthoteuthis kerberos* sp. nov., blue circle—*O. pluto*, white square—*O. ?chathamensis*. Base map modified from Google Maps.

were separated out at increasing depth ranges. Cirrate octopods in the northeastern Atlantic also display depth vs. abundance stratification (though this was for cirrates overall, rather than just the Opisthoteuthidae), with some taxa having broad bathymetric ranges and others being bathymetrically restricted (Collins et al. 2001).

As part of the literature assessment for species comparisons herein, a tabulation of species morphological traits across the Opisthoteuthidae was completed (per **Table 1**), though for the moment *O. extensa* Thiele, 1915 and *O. medusoides* Thiele, 1915 are excluded from this table (their morphology will be discussed in greater detail in Part II of this contribution, Verhoeff in preparation). The opisthoteuthids from the North Pacific are greatly confused at present, and even molecular work is hampered by possible sequence species identification issues. In addition to species being assigned to new genera (per taxonomy section), some species pairs were assumed to be synonymous, male *I. abatrossi* comb. nov. (as described by Sasaki 1929 and Kondakov 1941) is near identical to male *I. californiana* comb. nov. (as described by Berry 1955 and Taki 1963), and sympatric in distribution, though details of the male reproductive system have never been adequately described. Likewise, male *E. depressa* comb. nov. (as described by Sasaki 1929) and *E. japonica* comb. nov. (as described by Taki 1963) are again sympatric and extremely similar. While these species are considered synonymous herein based on the males, this is not necessarily the case with female specimens (which may have been confused), and formal synonymizing of these species will require detailed study of the North Pacific opisthoteuthids. Obtaining molecular data from mature males and females of these North Pacific species will also greatly assist resolving the taxonomy (and likely synonymy) of these taxa.

The generic identification of *O. bruuni* (Voss, 1982) is still somewhat uncertain (relative to the new genera proposed herein) but is herein tentatively allocated to *Insigniteuthis* gen. nov. (see later taxonomy section). This species was described by Voss (1982) from the southeastern Pacific and was recently re-described (Pardo-Gandarillas et al. 2021), but this recent work failed to clarify the main points left unanswered by the original description, i.e., the bilobed/unilobed state of the digestive gland, the relative size of DESF suckers in mature males, and configuration of the accessory gland complex in mature specimens. The two or three enlarged suckers of the DESF (as illustrated by Voss 1982) are consistent with *Insigniteuthis*, but these suckers were no larger than the PESF suckers, however Voss's specimens were immature, and it is likely that the DESF suckers would increase substantially in size with maturity (though this still needs confirmation). Examination of immature specimens of *E. persephone* (specimen MV F164064 B) herein indicate that the enlarged suckers distally are very poorly developed on young specimens, with the proximal enlarged suckers apparently developing earlier (the relative growth rates of PESF vs. DESF on opisthoteuthids have yet to be investigated). An undescribed opisthoteuthid has long been recognized from the northeastern Pacific, and molecular work strongly indicated that this species is conspecific with *I. bruuni* (Verhoeff 2023a). Examination of magnetic resonance imaging data for a putative *I. bruuni* female specimen

from California (Dr Alexander Ziegler personal communication), confirms that *I. bruuni* has a unilobed digestive gland.

Interestingly, **Table 1** makes it apparent that several geographically well separated species are morphologically surprisingly similar. *Opisthoteuthis borealis* Collins, 2005 and *O. hardyi* Villanueva et al., 2002 are similar in all aspects examined except for intestine length yet are well separated geographically; *O. grimaldii* and *O. kerberos* sp. nov., are also remarkably similar (AG1 being proportionally smaller in the latter), though could hardly be more distantly separated geographically. Comparable molecular data for these similar species pairs are not available, but it is expected that these similarities are simply convergence given the greatly separated distributions and subtle morphological differences. Lastly, *I. calypso* and *I. bruuni* are surprisingly similar (molecular data indicates that these species are clearly distinct, as would be expected given their widely separated distribution (Verhoeff 2023a)), differing only clearly in the AGC. The DESF of *I. bruuni* resembles *I. calypso* (2 or 3 enlarged suckers per DESF on all arms), but in the former these were still smaller than PESF suckers (Voss 1982), but since this was on sub-mature males the DESF suckers were likely not at full size as explained earlier.

The splitting of *Opisthoteuthis* into three genera herein (*Opisthoteuthis*, *Insigniteuthis* gen. nov., and *Exsuperoteuthis* gen. nov.) is largely based on the configuration of enlarged sucker fields in mature males. The great enlargement of suckers seen in this family is immediately distinctive and unique in the Cirrata, and while some members of *Grimpoteuthis* have slightly larger overall sucker proportions in males vs. females (Collins & Villanueva 2006; Verhoeff & O'Shea 2022) the enlargement in these species is very subtle and distributed across all the suckers. Cirrates lack the classical hectocotylus seen in incirrate octopods, a modified arm with a spermatophore groove and tipped with a calamus and ligula, the whole functioning as an intromittent organ to insert a spermatophore into the females' mantle cavity. How cirrates mate is still a mystery, however the great sucker enlargement in male opisthoteuthidae is reminiscent of some sepioline squids, for example *Amutatiola macroventosa* Lu & Okutani, 2022 in which the males lack the hectocotylus seen in related genera but possess greatly enlarged suckers (Lu & Okutani 2022), that presumably have some equivalent role. The enlarged suckers in male opisthoteuthids, especially the few greatly enlarged distal suckers in *Insigniteuthis*, may have a role in transferring spermatophores directly into the female's mantle cavity (but this needs confirmation). Species of opisthoteuthids (outside Australian waters), *O. massyae* and *I. calypso* have been subject to detailed reproductive study, which revealed them to be continuous spawners, maturing at an early phase in the life cycle (before most somatic growth) and with females undergoing continuous egg production and intermittent spawning of small numbers of eggs (1 or 2) over a long period lasting several years with no seasonality (Villanueva 1992). The same reproductive strategy likely occurs in *I. albatrossi* comb. nov. (reported as *O. californiana*) (Laptikhovsky 1999), and *O. hardyi* (Collins et al. 2010) given the size-frequency distribution of oocytes in the reproductive tract. While continuous spawning hasn't been confirmed as directly in the other cirrate families, the presence of single large eggs in the distal reproductive tract, and single spawned eggs, implies that continuous spawning and a multi-year spawning period is common of the cirrates in general (Ziegler et al. 2021). Very few if any spawned cirrate eggs have been collected in Australian waters (collections of deep-water corals and sponges examined by the author over the last several years failed to reveal any), excepting an egg casing collected in the Great Australian Bight (35.814°S, 131.632°E, 4618−4750 m) (MV F220375), this casing is more consistent with *Grimpoteuthis* egg casings than opisthoteuthids (per Ziegler et al. 2021) and its estimated length of 20.0 mm is consistent with the 18 mm ovarian eggs reported for *G. abyssicola* O'Shea, 1999 which is known from southeastern Australia at somewhat shallower depths (2821–3180 m) (O'Shea 1999, Verhoeff & O'Shea 2022). It is unknown what spawning substrate is used by Opisthoteuthidae in general, with grimpoteuthidids often spawning on octocorals, but captive opisthoteuthids have attached eggs to tank surfaces (Ziegler et al. 2021). Given the general lack of opisthoteuthid eggs collected, they may attach eggs to less frequently sampled rocky substrates.

Relatively little research has been conducted on the ecological significance of Australian *Opisthoteuthis*. Given that they are large and relatively abundant benthic animals, it may be presumed they are significant prey items, and some work supports this assumption. Australian fur seals (*Arctocephalus pusillus doriferus* Wood Jones, 1925) from colonies around Tasmania preyed heavily on cephalopods, mostly squid *Nototodarus gouldi* (McCoy, 1888) and *Sepioteuthis australis* Quoy & Gaimard, 1832, but cirrates (*Opisthoteuthis* sp., likely *O. pluto* or *E. persephone*) occurred in 4.2% of samples (Gales *et al.* 1993). This implies that these *Opisthoteuthis* may occur at relatively shallow depths < 200 m (the approximate dive limit of fur seals). The Sperm Whale (*Physeter macrocephalus* Linnaeus, 1758) also feeds heavily on deep-sea squid, and O'Shea (1999) reported that three specimens of *O. mero* (1 male and 2 females, ML 46–55 mm) were recovered from the stomach contents of Sperm Whales off New Zealand. This benthic species occurs at 360–1000 m, suggesting that Sperm Whales occasionally prey on large benthic cirrates. However, cirrates only make up a small dietary component for these predators compared to squids (Clarke & MacLeod 1982). It remains to be seen if other cetaceans such as beaked whales, and deep-sea sharks also predate on cirrates.

Table 1. Comparison of selected morphological states and values for opisthoteuthid taxa. Data is sourced from original descriptions or re-descriptions, as well as specimens examined herein. As detailed later, some species names (in parentheses) are considered synonyms. DESF is broken into types 1–3, per taxonomy section: 1. *Opisthoteuthis* (with DESF either present or absent entirely), 2. *Insigniteuthis* (with DESF variably on different arms pairs), and 3. *Exsuperoteuthis*. Intestine length (relative to oesophagus) is frequently based on original description illustrations (rather than stated values), and likewise the designations of AGC parts is often from re-interpretation of original description figures. *For *I. dongshaensis* the original description illustrates AG1 as larger than the combined AG2 and 3 (though AG1 was confused with part of the seminal vesical complex in that paper); **The original description of *I. bruuni* mentions a single nodule being present (though this is counter to the re-description by Pardo-Gandarillas et al. 2021). ***Estimated from Sasaki (1929) textfig. 3, but possibly an underestimate of true intestine length.

Species	DESF Type	DESF count	Digestive gland	Intestine length	Accessory gland complex
O. agassizii	1. Present	8–12	Unilobed	1.5	AG2&3>AG1
O. philipii	1. Absent	NA	?	?	?
O. robsoni	1. Absent	NA	Unilobed	1.5	AG1>AG2&3
O. pluto	1. Absent	NA	Unilobed	2.7	AG2&3>>AG1
O. borealis	1. Present	9–15	Unilobed	1.2	AG1>AG2&3
O. hardyi	1. Present	9–13	Unilobed	2.0	AG1>AG2&3
O. massyae	1. Present	9–11	Bilobed	1.2~	AG2&3>AG1
O. mero	1. Absent/slight	NA	Bilobed	2.0~	AG2&3=AG1
O. chathamensis	1. Present	6-8	Bilobed	1.5	AG1>AG2&3
O. grimaldii	1. Present	9–10	Bilobed	1.2~	AG2&3=AG1
O. kerberos	1. Present	7–9	Bilobed	1.2	AG2&3>AG1
I. albatrossi (californiana)	2. Arms I	5-7	Bilobed	1.5~***	?
I. dongshaensis	2. Arms III, IV	3–4	Bilobed	1.0~	AG1>AG2&3*
I. obscura	2. Arms II-IV	3–5	Bilobed	1.6	AG1>AG2&3
I. bruuni	2. Arms I-IV	2–3	Unilobed	1.3~	AG1>AG2&3
I. calypso	2. Arms I-IV	2–3	Unilobed	1.0~	AG1>>AG2&3
E. depressa (japonica)	3.	15–20	Bilobed	2.0~	AG2&3>AG1
E. persephone	3.	30–40	Bilobed	2.2	AG1>AG2&3
References: *O. pluto*, *O. kerberos*, *I. obscura*, & *E. persephone* (data herein); *O. philipii* (Oommen 1976); *O. robsoni*, *O. mero*, & *O. chathamensis* (O'Shea 1999); *O. agassizii*, *O. hardyi*, *O. massyae*, *O. grimaldii* & *I. calypso* (Villanueva et al. 2002, Collins et al. 2010); *O. borealis* (Collins 2005, Golikov et al. 2020); *I. albatrossi/californiana* (Sasaki 1929, Berry 1955, Kondakov 1941, Taki 1963); *I. dongshaensis* (Lu 2010); *I. bruuni* (Voss 1982, herein); *E. depressa/japonica* (Meyer 1906, Taki 1963).					

[1]Four species: *I. dongshaensis*, *I. albatrossi=californiana*, *E. depressa=japonica*, & *I.* sp.=*bruuni*(?).

Taxonomy

Phylum **Mollusca** Linnaeus, 1758

Class **Cephalopoda** Cuvier, 1797

Order **Octopoda** Leach, 1817

Suborder **Cirrata** Grimpe, 1916

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

Family **Opisthoteuthidae** Verrill, 1896

Type genus: *Opisthoteuthis* Verrill, 1883.

Diagnosis: Cirrates with body antero-posteriorly compressed, gelatinous. Fins small to long, sub-terminally placed. Shell broadly U-shaped, lateral wings 'flaring' (non-parallel), lateral wings tapering to fine points (without distinct lobe). Optic nerves passing through white body in 2–4 bundles. Males with enlarged sucker fields, always with a proximal enlarged sucker field, and with or without a distal arm enlarged sucker field with variable arm placement and coverage. Cirri short. Web nodules present or absent, webs deep and simple. Digestive gland usually bilobed, rarely unilobed. Radula, posterior salivary glands, and palatine teeth absent. Anterior salivary glands present though often imbedded within buccal bulb (per Meyer 1906). Gills short, 'half-orange'. (Modified from Collins & Villanueva 2006; Lu 2010).

Three genera (*Opisthoteuthis*, *Insigniteuthis* **gen. nov.**, and *Exsuperoteuthis* **gen. nov.**).

Description: Per diagnosis.

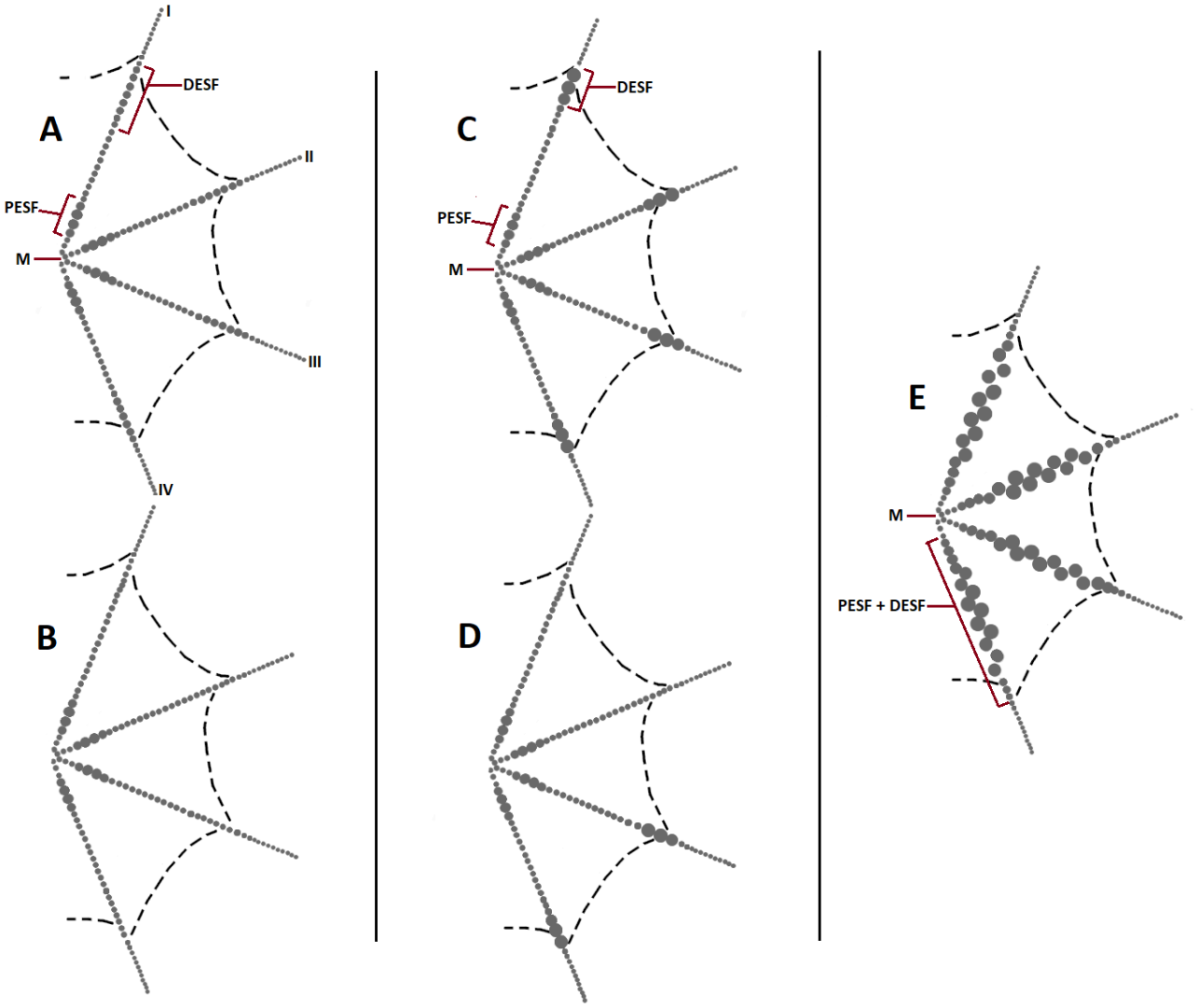

Figure 2. Schematized illustrations of male enlarged sucker configurations for genus proposals within Opisthoteuthidae. **A, B**) Genus *Opisthoteuthis* '*sensu stricto*', characterized by the DESF reduced to a large number of suckers with diameter ≤ diameter of PESF suckers (**A**), and sometimes reduced to being absent entirely (**B**). **C, D**) Genus *Insigniteuthis* gen. nov., characterized by DESF's comprising a very small number of greatly enlarged suckers (diameter > PESF sucker diameter), the DESF may be on all arms (**C**), or variably restricted to a smaller number of arms (**D**). **E**) Genus *Exsuperoteuthis* gen. nov. characterized by a combined PESF and DESF spanning the proximal to distal arm. Diagrams are oral views of arms I – IV for one side, the dashed lines demarcating the web margins. Abbreviations: M = mouth, PESF = proximal enlarged sucker field, DESF = distal enlarged sucker field.

Taxonomic remarks: Opisthoteuthids, while being united as a group by the configuration of optic nerves, shell form, and presence of distinctly enlarged suckers (not comparable to the very subtle enlargement seen in males of some grimpoteuthidids), display a high degree of morphological variation, especially in the patterns of male sucker enlargement. Different authors have attempted to split *Opisthoteuthis* into different groups. Berry (1918) proposed the subgenus *Teuthidiscus* Berry, 1918, though the grounds for its creation were erroneous. More recently, O'Shea (1999) split *Opisthoteuthis* into three informal 'groups', but these have generally not been used by later authors.

Looking at the specimens analyzed here, in addition to all *Opisthoteuthis* described in literature, the configuration of enlarged suckers in males falls into three distinct groups, which are proposed herein to represent genera:

1. Genus *Opisthoteuthis* Verrill, 1883: species with a proximal enlarged sucker field (PESF) but with the distal enlarged sucker field (DESF) not developed or reduced to a large number (~10+) of suckers with only subtle enlargement (diameter < those of PESF). The type species of *Opisthoteuthis*, O. *agassizii* Verrill, 1883, has this enlarged sucker configuration, and the genus is thus restricted.
2. Genus *Insigniteuthis* **gen. nov.**: species with a DESF comprising a small number (2–5) of greatly enlarged suckers (diameter > those of

PESF).

3. Genus *Exsuperoteuthis* **gen. nov.**: species with a single series of greatly enlarged suckers covering the whole central arm region, essentially a merging of both PESF & DESF.

The enlarged sucker configurations of these three genus divisions are depicted in **Figure 2**, the breakdown of species into genera and type taxa are given in the following taxonomic descriptions herein. Other morphological differences, e.g., digestive gland bilobed vs. unilobed, relative intestine vs. oesophagus length, configuration of male accessory glands, and presence or absence of web nodules, are useful for identifying some of the genera, but are not as consistent.

Unfortunately, present molecular datasets on *Opisthoteuthis* don't help much in elucidating the interrelatedness of *Opisthoteuthis* taxa. Piertney *et al.'s* (2003) analysis using 16S data indicated some sub-clades, but subsequent analyses with greater species coverage lacked good bootstrap support for clades within *Opisthoteuthis* and were inconsistent or not well resolved in clade structure (Pardo-Gandarillas *et al.* 2021, Ziegler & Sagorny 2021). While COI seems to offer better support values for clades within *Opisthoteuthis* (Verhoeff 2023a) it is compromised by far less species coverage. Furthermore, the identification of some sequences is suspect, as it is unclear if sequences came from male specimens which are more reliably identified. Overall, until the molecular situation improves the new genus divisions of *Opisthoteuthis* are proposed purely on morphological grounds.

Genus *Opisthoteuthis* Verrill, 1883

Type species: *Opisthoteuthis agassizii* Verrill, 1883

Diagnosis: Opisthoteuthids with DESF generally on all arms (though sometimes reduced on dorsal arm pair) and comprised of a large number (7–14) of suckers with moderate enlargement (diameter ≤ PESF), with the DESF reduced or absent entirely in some taxa (see **Figure 2**). Digestive gland bilobed or unilobed.

Species allocated: *Opisthoteuthis agassizii*, *O. borealis*, *O. chathamensis* O'Shea, 1999, *O. grimaldii*, *O. hardyi*, *O. kerberos* **sp. nov.**, *O. massyae* (incl. synonymized *O. vossi* Sánchez & Guerra, 1989), *O. mero* O'Shea, 1999, *O. pluto*, *O. philippi* Oommen, 1976, and *O. robsoni* O'Shea, 1999.

Etymology: Derived from the prefix 'opistho-', itself from the Ancient Greek '*opisthen*' (ὄπῐσθεν) meaning 'behind' or 'backwards', and the Greek '*teuthis*' (τευθίς) meaning 'a squid' (or cephalopod more generally in modern teuthological usage). Verrill (1883, pp. 113 & 114) doesn't explain his etymology, but his emphasis on the funnel projecting "backwards beneath the posterior end [of the body]", and the "posterior position of the siphon" as "the most remarkable characteristic of this species" (the only known member of the genus at the time), makes it likely that 'opistho-' was referring to the posteriorly projecting funnel (opisthoteuthids, including Verrill's specimen, are sometimes preserved in a disk-like posture, with the mantle and head appearing as a dome, surrounded by arms/webbing, the funnel thus projecting 'backwards').

Remarks: This genus incorporates both O'Shea's (1999) 'Type 3' group of *Opisthoteuthis* and part of 'Type 1', excluding *O. depressa* and *O. persephone* (now moved to *Exsuperoteuthis*), and *O. extensa* (moved to *Insigniteuthis* (per Part II, Verhoeff in preparation)).

This genus can also be broken down into a group with a unilobed digestive gland (which notably includes the type species *O. agassizii* along with *O. borealis*, *O. hardyi*, *O. philipii*, *O. pluto*, and *O. robsoni*) with the DESF reduced or absent (unilobed nature of *O. philippi* per Part II, Verhoeff in preparation), and another with the digestive gland bilobed (*O. chathamensis*, *O. grimaldii*, *O. kerberos* sp. nov., *O. massyae*, and *O. mero*) all with the DESF reduced only.

Opisthoteuthis kerberos sp. nov.

(Figures 3–5, Tables 2 & 3)

ZooBank LSID: urn:lsid:zoobank.org:act:87799554-8122-426D-AB2E-80BA4B6423DD

Type specimen lodged at the Tasmanian Museum and Art Gallery (TMAG E46511), see materials examined.

Diagnosis: *Opisthoteuthis* with 70–80 suckers per arm of adult, a DESF of 7–9 enlarged suckers on all arms of males with these suckers being smaller in diameter than PESF suckers, and arms with web nodules; with dark brown−maroon aboral pigmentation. Internally with digestive gland bilobed, 7 or 8 lamellae per gill, AG2 and 3 combined and larger than AG1, and with intestine approximately equal to oesophagus in length.

Description: Mantle short and posteriorly rounded, mantle width and length comparable (MWI 70%–103%) (see **Fig 3 A–C**). Head considerably wider than mantle (MW ~ 65%–80% HW), its width generally exceeding the mantle length, head wider in males (HWI 108%–125% in females, 147%–152% in males). Fins sub-terminally placed, relatively small, proportionally longer in males (FLI 53%–62% females, 69%–87% males). Fin width approximately greatest basally (FWI 31%–60%), tapering to pointed ends. Eyes very large, easily accounting for ⅔ of the head width, proportionally larger in males (EDI 50%–57% female, 67%–74% males), but with small and constricted openings. Funnel relatively long and tapering, proportionally longer in males (FuLI 49%–57% females, 62% males), the distal ~70% of the funnel being free (not attached dorsally). Funnel organ examined on male specimen (**E46507**), V-shaped, limbs thickened proximally, tapering where they converge distally (**Fig 4 A**). Pallial aperture gape small (PAI 35%–52%), enclosed around funnel. Olfactory papillae small, ovoid, either

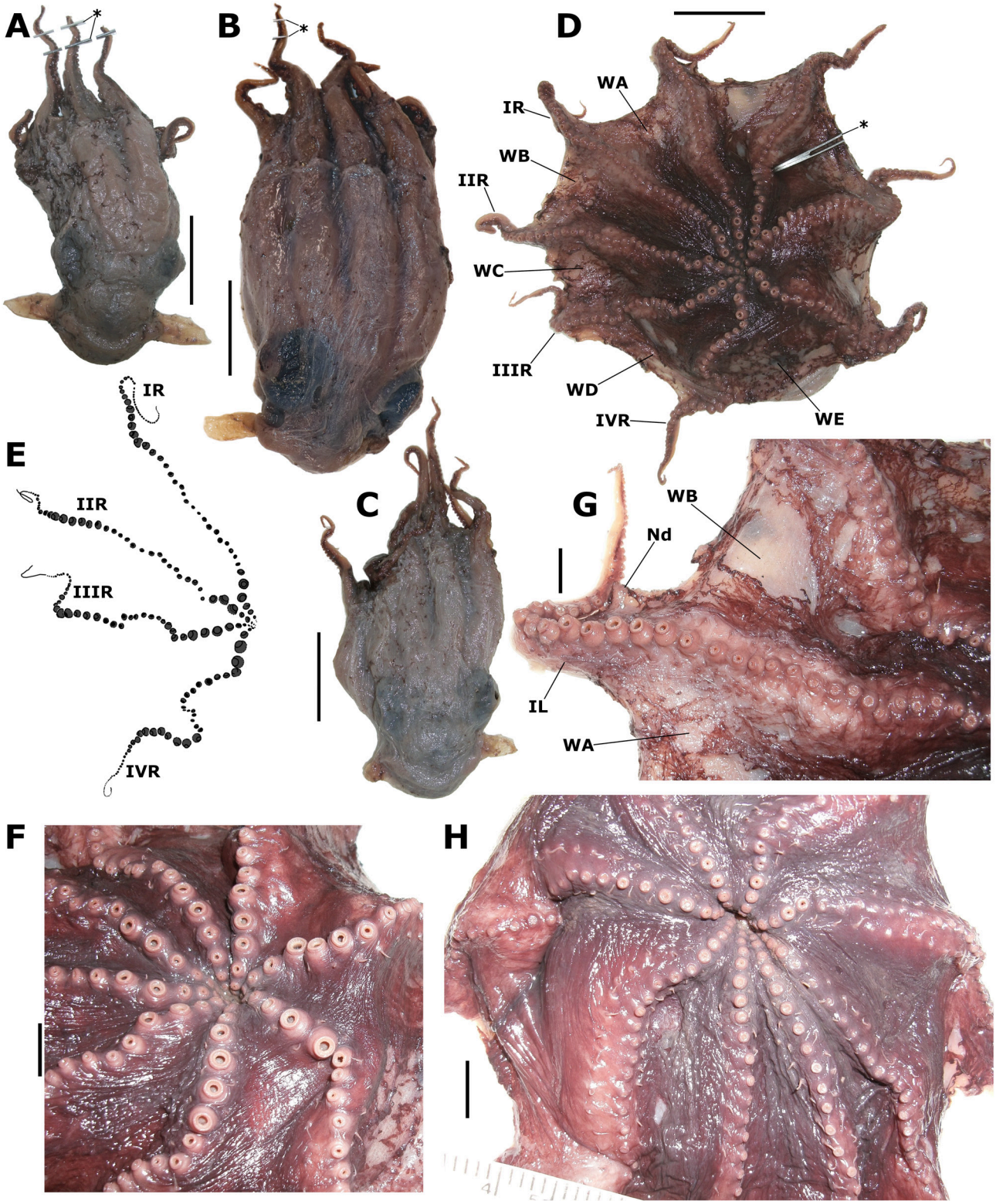

Figure 3. Whole aspects and arm detail of *Opisthoteuthis kerberos* sp. nov. **A–C**) dorsal aspects of whole animals, **A**) female E46508, **B**) male E46511 (Holotype), **C**) female E46506. **D**) oral view of arms and webbing of male (E46507). **E**) Schematic of the relative male sucker enlargement along the right-side arms (derived from E46507). **F**) closeup of proximal enlarged suckers on male (E46507). **G**) closeup of distal enlarged suckers and web nodule on male (arm IL, E46507). **H**) proximal and medial suckers of female (E46506). Abbreviations/symbols: *—prop used to pin down structures in photography; IR/L—arm I right/left, IIR—arm II right; IIIR—arm III right; IVR—arm IV right; Nd—nodule; WA–E—web sector A–E. Scale bars = 50.0 mm (**A–D**), 10.0 mm (**F–H**).

side of funnel immediately within pallial opening. Pallial adductor reduced to a narrow strap or band, attached at the anterior right edge of the oviducal gland or male AGC.

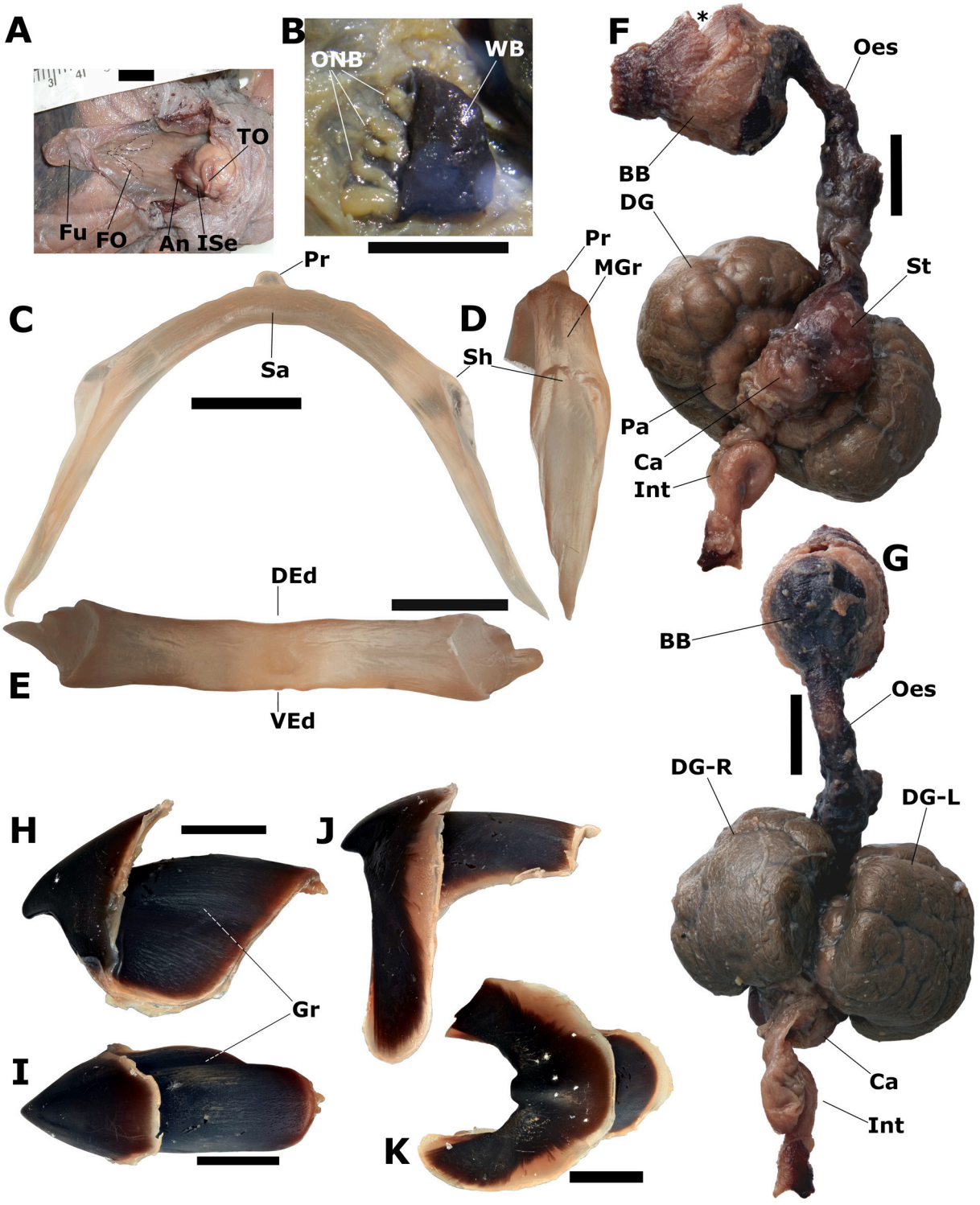

Figure 4. Internal morphology of *Opisthoteuthis kerberos* sp. nov. **A**) funnel organ form with outline dashed (male, E46507). **B**) right-side optic nerve branching pattern through white body (male, E46507). **C–E**) internal shell (male, E46507) with dorsal (**C**), lateral (**D**), and posterior (end-on) (**E**) aspects. **F**, **G**) dorsal and ventral aspects of the digestive system (male, E46507), in '**F**' the buccal bulb is positioned laterally with dorsal edge at top, in '**G**' the posterior face of the buccal bulb is shown with ventral edge at top. **H–K**) beaks (male, E46507) with upper beak lateral and dorsal aspects (**H**, **I**), and lower beak lateral and ventral aspects (**J**, **K**). Abbreviations/symbols: *—cuts to remove beak; An—anus; BB—buccal bulb; Ca—caecum; DEd—dorsal edge; DG—digestive gland (DG-R & -L are right and left lobes); Fu—funnel; FO—funnel organ; Gr—groove of upper beak lateral walls; Int—intestine; ISe—Interpallial septum; Oes—oesophagus; ONB—optic nerve bundle; Pa—pancreas; Pr—prominence; Sa—saddle; Sh—shoulder; St—stomach; TO—terminal organ; VEd—ventral edge; WB—white body. Scale bars = 10.0 mm (**A–G**), 5.0 mm (**H–K**).

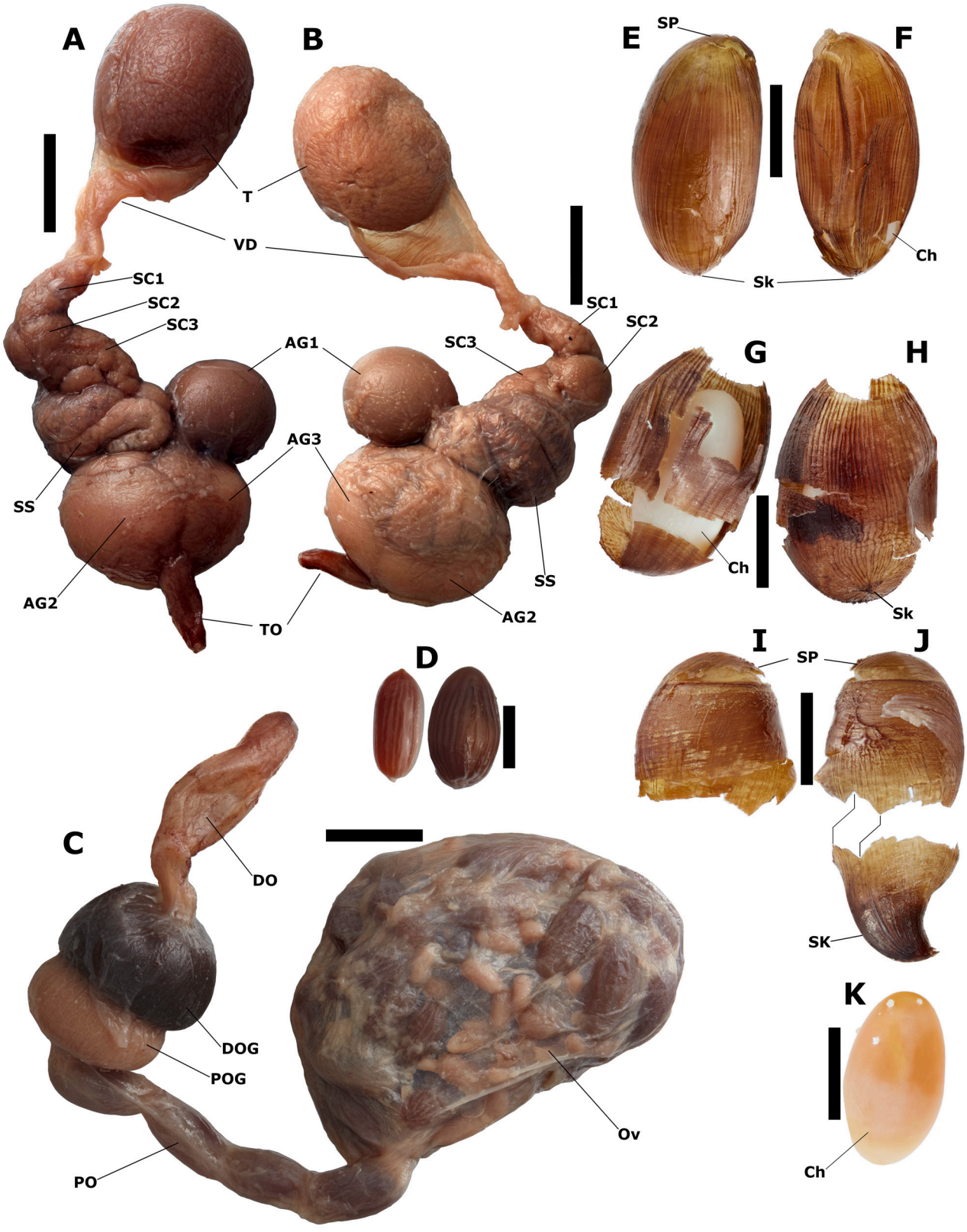

Figure 5. Reproductive systems of *Opisthoteuthis kerberos* sp. nov. **A**, **B**) male reproductive system (E46507). **C**) female reproductive system (E46506). **D**) two ovarian eggs of different form (E46506). **E–K**) encased eggs from distal oviduct of specimen E46506 (**E**, **F**), E46509 (**G**, **H**), and E46508 (**I**, **J**) with the casing broken and egg chorion removed (**K**). Abbreviations: AG1–3—accessory gland part 1–3; Ch—chorion; DO—distal oviduct; DOG—distal oviducal gland; Ov—ovary sac; PO—proximal oviduct; POG—proximal oviducal gland; SC1–3 —spermatophoric complex part 1–3; Sk—stalk; SP—smooth patch (or cap); SS—spermatophore sac (Needham's sac); T—testis; TO—terminal organ; VD—vas deferens. Scale bars = 5.0 mm (**A**, **B**, **D–K**), 10.0 mm (**C**).

Gills: half-orange with 7 or 8 primary lamellae per gill, distal lamellae share a common base, proximal and distalmost lamellae somewhat smaller.

Optic nerve: passes through white body as three distinct bundles, immediately after leaving the white body each bundle branches into two which then undergo fine branching into the back of the eyeball (right side white body exposed on male specimen **E46507**) (**Fig 4 B**). Each white body was relatively small (~11 mm long or ~12% HW), kidney-shaped, and with a dark purple colouration.

Internal shell: dissected from male specimen **E46507** (**Fig 4 C–E**). Broad U-shape, saddle relatively deep (SHI 38%) and broad (SSI 73%), outer (posterior) face slightly concave, i.e., with a groove, basal shelf absent. On the shell dissected, a small process was located medially on the saddle posterior face, this was absent on other shells (from palpitation through skin). Saddle shoulders moderately developed, with concave outer face below saddle prominences. Wings diverge from saddle midpoint at 41–42° (relative to antero-posterior axis), outer faces non-parallel, wings tapering to simple points (without any lobe). Shell translucent and amber-coloured.

Arms and webbing: arms thick and relatively long, the dorsal arm pair of males being slightly more robust (thicker) than the other arms (thickness measured in proximal arm half). Arms are approximately equal in length with no consistent arm formula (though the ventral arms are often slightly shorter) and are slightly longer in males (female dorsal ALI 2.3–2.9× ML, male dorsal ALI 3.3–3.5× ML).

Web simple and deep (**Fig 3 D**), web formula variable but approximately A>B>C>D>E, medial depth of sector A ~48%–60% arm I length, sector E medial depth ~36%–46% arm IV length. Web attached to ventral arm edge with a web nodule (though only discernible on some arms given the thick and somewhat damaged webbing edges) (see **Fig 3 G**), at level of sucker 28–32 on dorsal arms or 26–29 on ventral arms (approximately at level of DESF of males). Webs attach to the arms 4 or 5 suckers further along the distal arm edge from the nodule.

Suckers and cirri: maximum sucker counts 72–76 on females (counts slightly lower on ventral arms) and 78–79 on males (highest count on arms II and III). Suckers sexually dimorphic, males with proximal and distal enlarged sucker fields (depicted **Fig 3 D**, schematized **Fig 3 E**).

In males the first four suckers are small and increasing in size (the 4th somewhat abruptly so), followed by PESF (see **Fig 3 F**), comprising 4 or 5 suckers, from the 5th to 9th, and with central 2 or 3 largest (~6th to 8th suckers). Proximal enlarged sucker with acetabular bases large (PESF SDI 10.3%–11.6%), globular and risen above arm, infundibular diameter smaller than acetabular, infundibular ring with radiating striations and large acetabular aperture.

Suckers reduce in diameter following PESF, mid-arm 'normal' suckers with SDI 5.0%–5.5%. DESF present on all arms of males, comprising ~7 to 9 suckers, from approximately the 22nd to 31st sucker, and with the 25th to 28th largest (DESF SDI 8.8%–9.5%) (**Fig 3 G**).

Females with the first 4 or 5 suckers small and increasing in size, and while lacking a distinct PESF, the following 3 or 4 suckers (5th–8th) are still the largest, SDI 4.4%–5.0%, though the acetabular bases are not greatly elevated above the arm (see **Fig 3 H**). The following suckers slowly decrease in size, before decreasing in size more rapidly distal to the webbing.

Cirri commence between suckers 2−5 as minute buds, attaining their greatest length approximately between ⅓ and ½ arm length, gradually reducing in length to the arm tips. Maximum cirrus length slightly greater in males (CLI 4.0%–5.0% females, 5.5%–7.2% males), the cirrus length comparable to diameter of mid-arm suckers.

Digestive system: examined in male specimen (**Fig 4 F, G**). Buccal bulb very large (overall size slightly exceeding combined stomach/caecum dimensions). No salivary glands (anterior or posterior) apparent externally on the buccal bulb or oesophagus, but anterior salivary glands within the buccal bulb were likely present (given the somewhat swollen form of the bulb's postero-ventral end). Odontophore a small fleshy lump, lacking radula or chitinous lining. Labial palps (lacking palatine teeth) and salivary papillae well-developed. Upper beak (**Fig 4 H, I**) tall (height 69% beak length, or 89% width), hood moderately deep (hood length 63% beak length); rostrum blunt and deflected down slightly, jaw cutting edge smooth (without teeth), hood crest rounded (convex); lateral walls near-parallel and with a faint longitudinal groove on each lateral face, dorsal edge of lateral walls strongly rounded (convex), their posterior edges gently indented (concave), crest rounded at postero-dorsal apex. Lower beak (**Fig 4 J, K**) tall (height 63% width), with relatively short hood (hood length 54% beak length), and elongate wings (wing length 114% beak length) with only weak diagonal flexure; rostrum small and blunt tipped, hood crest rounded. Oesophagus narrow in proximal third, slightly expanded towards the stomach as a simple crop (without diverticula); stomach simple, muscular, without demarcations; caecum smaller than stomach (~¾ its greatest dimensions), poorly developed, lacking spiral coiling; digestive gland bilobed, each lobe with multiple smaller and irregular lobes, greenish; pancreas large, sharply defined, paler in colour relative to digestive gland; hepatic ducts short; intestine with distinct coil, overall length (if straightened) slightly greater than oesophagus length (~1.2× its length); ink sac and anal flaps absent. Digestive system with dark purplish membrane over buccal bulb, oesophagus, and stomach,

as well as the rectum where it projected into the mantle cavity, caecum and intestine lacking strong pigmentation.

Male reproductive system: illustrated in **Figure 5 A, B**; testis ovoid; vas deferens thin, relatively short; spermatophoric complex with three parts (SC1–3); spermatophoric sac (Needham's sac) large, folded, similar to spermatophoric complex in size, located between SC3 and the accessory gland complex (AGC); AGC exceeds other glandular structures in overall dimensions, dominated by AG2 and 3, both similarly sized and fused closely together (as a single ovoid structure with a faint medial seam visible between the two parts), AG1 more proximal, rounded, well separated (diameter approximately half the greatest dimension of the combined AG2 and 3); terminal organ projecting medially from conjoined AG2 and 3, relatively thin, elongate (length about ½ the width of combined AG2 and 3).

Female reproductive system: illustrated in **Figure 5 C**; all three females examined were mature with encased eggs in the distal oviduct ready to be spawned (see below). The reproductive system (dissected from **E46506**) was typical of *Opisthoteuthis*, ovary large, occupying posterior half of body (immature oocytes up to 10.0 mm long, **Fig 5 D**); proximal oviduct elongate, with four sequential oocytes in specimen examined; oviducal gland large, two parted, each part well rounded, proximal beige coloured, distal dark purple-brown and slightly larger in length and width (proximal oviducal gland ~90% the width of the distal), both parts longitudinally striate; distal oviduct slightly longer than oviducal gland, medially expanded.

Encased eggs were dissected from the distal oviducts of three specimens. Egg № 1 (from **TMAG E46506**) (**Fig 5 E, F**), with casing ovoid, 13.2 mm long × 6.8 mm wide (L:W = 1.94), with prominent longitudinal ridges along the full length of the casing (roughly 60−70), ridges fading out into a small 'smooth patch' antipodal to a casing 'stalk' (probably not homologous with stalk of other cephalopod eggs), casing 'stalk' located where longitudinal ridges converge; casing brown with a yellow-green hue; chorion whitish, length and width significantly less than that of casing, leaving just over 20% of the casing length hollow, causing part of the casing to indent. Egg № 2 (from **TMAG E46509**) (**Fig 5 G, H**), resembled egg № 1 in shape, ornamantation, and colour, but the casing was badly broken, making it impossible to accurately assess dimensions (~12 mm long, but likely greater), casing again with prominent longitudinal ridges and a small 'stalk' at one pole, but with opposite pole of casing missing as a circular break; chorion ovoid, whitish, 10.5 mm long × 5.2 mm wide, again giving much free space between the chorion and casing. Egg № 3 (from **TMAG E46508**) (**Fig 5 I, J**), different from eggs № 1 and № 2; casing broken in two around midway, with the original dimensions of the casing estimated at 14.4 mm long × 7.5 mm wide (L:W = 1.92), ~ovoid with a very large and hook-shaped 'stalk' comprising over 25% of the casing length, casing antipodal to the 'stalk' with a distinct and dark circular ridge surrounding the pole, seemingly demarcating a weak point where parts of the casing were separating (designated a cap, width ~70% of casing width); casing with longitudinal ridges commencing at the 'stalk' and running along the long axis, becoming fine and more numerous around casing midpoint, before being interrupted approaching the cap by more irregular sculpting (patches of dimples and ridges); the cap surface was rough with some fine parallel ridges; casing brown with a greenish-yellow tinge, 'stalk' darker. Chorion from egg № 3 ovoid, whitish (**Fig 5 K**), substantially smaller than egg casing, 9.6 mm long × 5.4 mm wide, leaving a large amount of space within the casing.

Colouration: per **Figure 3 A–D**, aboral surfaces, head, and body largely unpigmented due to skin being abraded, with traces of a more extensive dark brown−maroon-coloured skin. Presence or absence of areolar spots not confirmed due to skin damage. Oral surfaces with maroon pigmentation, sucker infundibular rings and cirri contrasting with paler beige colour.

Material examined.

Holotype.

TMAG E46511, male (ML 58 mm), east of Flinders Island, SE Australia, 39°48'6"−50'11" S, 149°5'56"−6'15" E, 1923−1962 m, FRV *Southern Surveyor*, SS01/00, Stn 261 (recorded 260 but likely 261), 29.iv.2000.

Paratypes.

TMAG E46507, male (ML 60 mm), from same trawl as Holotype. TMAG E46506, female (ML 56 mm), from same trawl as Holotype. TMAG E46508, female (ML 60 mm), from same trawl as Holotype. TMAG E46509, female (ML 63 mm), from same trawl as Holotype.

Distribution: Southeastern Australia, 1923−1962 m (**Fig 1**).

Etymology: A specific epithet was decided upon that related to the mythological Pluto and Persephone (the other local *Opisthoteuthis* being named after these characters), thus *'kerberos'* was used, the Greek spelling of three-headed dog guarding Pluto's underworld.

Proposed vernacular name: Kerberos' flapjack octopus.

Remarks: The presence of a DESF on all arms, and the reduced size of the DESF suckers relative to the proximal, clearly distinguish this species from *Exsuperoteuthis persephone* comb. nov. with enlarged suckers over the mid-arm, as does the darker overall colouration compared to *E. persephone*. The species is distinguished from *O. pluto* by its bilobed digestive gland (vs. unilobed) and its prominent DESF suckers (vs. absent DESF on *O. pluto* males). The form of the DESF also readily distinguishes this species from *Insigniteuthis obscura* sp.

Table 2. *Opisthoteuthis kerberos* sp. nov. specimen measurements, counts, and notes. Measurements in mm.

ID	TMAG E46506	E46508	E46509	E46507	E46511 Holotype
Sex	Female	Female	Female	Male	Male
TL	~227	~204	NA	~253	~257
ML	56	60	63	60	58
MW	~56	52	44	59	~60
HW	70	72	68	88	88
ED	32	~26−30	34	39−40	43
FL (L/R)	22/30	32/32	36/39	52/50	46/40
FW (L/R)	12/18	15/15	16/13	~16 (base)	16/16
FuL	32 (22 free)	31	31 (22 free)	37	36
PA	25−26	21	20−22	28	30
Gill LC (L/R)	8/8	8/8	7/7	7/8	7/7
AL I (L/R)	160/162	122*/122*	142/138	200/196	200/176*
AL II (L/R)	146/146	144/141	144/142	198/192	198/190
AL III (L/R)	134/148	142/140	132/148	206/200	188/200
AL IV (L/R)	146/151	138/132	128/140	194/188	186/186
SC I (L/R)	71/71	52*/53*	72/69	72/74	70/44*
SC II (L/R)	70/74	73/70	69/71	77/75	76/72
SC III (L/R)	73/76	75/61	65/67	79/76	71/78
SC IV (L/R)	61/69	68/69	50/58	77/79	72/68
SuD (Normal)	2.5–2.7 ^{Acet} (5^{th}–7^{th} sucker)	3.0 ^{Acet} (6^{th}–8^{th})	2.8 ^{Acet} (5^{th}–8^{th}, IIR)	2.3–2.7 ^{Inf}, 3.0–3.3 ^{Acet}	2.6 ^{Inf}, 3.2 ^{Acet} (~15^{th}, I & IIL)
PESF position	NA	NA	NA	5-8 or 9 (6-7 or 8 ^{largest})	5–8 (6-7 ^{largest}) I 5–8 (6-7 ^{largest}) II 5–9 (7-8 ^{largest}) III 5–8 (5-7 ^{largest}) IV
PESF size	NA	NA	NA	4.1−4.2 ^{Inf}, 6.0−6.2 ^{Acet} (7^{th}, IL & IVL)	5.3–5.7 ^{Inf}, 6.4–6.7 ^{acet} (7^{th}, IIIR)
DESF position	NA	NA	NA	24-31 (26-28 ^{largest}) I 23-29 (26-28 ^{largest}) II 23-29 (25-28 ^{largest}) III 22-30 (26 ^{largest}) IV	24-30 (27-28 ^{largest}) I 22-30 (25-28 ^{largest}) II 24-31 (25-28 ^{largest}) III 23-28 (25-27 ^{largest}) IV
DESF size	NA	NA	NA	3.3−5 ^{Inf}, 5.0−5.3 ^{Acet}	3.9–4.0 ^{Inf}, 5.5 ^{Acet} (27^{th}, IL)
CiL	2.6, 2.7	3.0	2.5	3.0−3.3	4.1−4.3
Ci start sucker position	3–5	3–5	4–5	3–5	2–4
WD A	92	78	68	106	120
WD B (L/R)	72/84	70/64	70/62	108/110	122/110
WD C (L/R)	64/70	70/54	70/62	102/104	110/108
WD D (L/R)	52/58	64/54	74/68	84/92	100/80
WD E	60	64	62	70	70
WN I II III IV	29 (R arms), 27 28 28-29	31-32 28-30 25-26 27	28–29 (Damaged on several arms)	30 (IL) (Damaged on most arms)	28 IR, 26 IIL 26 IIIL 26 IV
Notes				5–6 cm am tip free of webbing.	

				Arm I R thickness 28 mm, Arms II & III thickness 24 & 22 mm.	

Table 3. *Opisthoteuthis kerberos* sp. nov. indices and formulas. *Arm I damaged (Dorsal ALI using longer arm II, WI A is relative to longer arm II).

Indices	TMAG E46506	E46508	E46509	E46507	E46511 Holotype
MWI	100%	87%	70%	98%	103%
HWI	125%	120%	108%	147%	152%
FuLI	57%	52%	49%	62%	62%
FLI (L/R)	39%/54%	53%	57%/62%	87%/83%	79%/69%
FWI (L/R)	55%/60%	47%	44%/33%	31%/32%	35%/40%
EDI	57%	50%	54%	67%	74%
PAI	46%	35%	35%	47%	52%
Arm formula	I>II=IV>III/ I>IV>III>II	*II>III>IV/ *II>III>IV	II>I>III>IV/ III>II>IV>I	III>I>II>IV/ III>I>II>IV	I>II>III>IV/ *III>II>IV
Dorsal ALI	2.9× ML	*2.4× ML	2.3× ML	3.3× ML	3.5× ML
Ventral ALI	2.7× ML	2.3× ML	2.2× ML	3.2× ML	3.2× ML
SDI	4.8%	5.0%	4.4%	5.0%–5.5%	5.5%
SDI PESF	NA	NA	NA	10.3%	11.6%
SDI DESF	NA	NA	NA	8.8%	9.5%
CLI	4.8%	5.0%	4.0%	5.5%	7.2%
Web formula	A>B>C>E>D	A>B=C>D=E/ A>B=E>C=D	D>B=C>A>E/ A=D>B=C=E	B>A>C>D>E/ B>A>C>D>E	B>A>C>D>E/ A>B>C>D>E
WI A	57%	*54%	48%	53%	60%
WI E	40%	46%	44%	36%	38%

nov. with its DESF on arms II–IV, and 2 or 3 massively enlarged suckers per DESF. The bathymetric range of *O. kerberos* sp. nov. (1923–1962 m) is also significantly greater than other Australian opisthoteuthids, however, since all material was collected from a single station the species' true bathymetric range is likely much greater.

The possibility was apparent that this species may be comparable to a New Zealand *Opisthoteuthis* with bilobed digestive gland. *O. mero* is abundant around New Zealand from 360–1000 m depth, whereas *O. chathamensis* is more restricted in distribution to north-eastern New Zealand and the Chatham Islands from 900–1438 m depth (O'Shea 1999), both again at shallower depths compared to *O. kerberos* sp. nov. *O. mero* is not comparable to *O. kerberos* sp. nov., as it lacks a DESF (the suckers 'gradually and slightly decreasing' from the PESF to the web intersect), has a considerably longer intestine (2× oesophagus length), and has an AGC with larger AG1 (equal in size to combined AG2 and 3; per O'Shea 1999, fig. 10F) rather than the combined AG2 and 3 dominating the AGC. *O. chathamensis* is closer in morphology to *O. kerberos* sp. nov. but differs in having the male AGC dominated by AG1 (AG1 significantly larger than the combined AG2 and 3; per O'Shea 1999, fig. 14D) and in lacking web nodules, and though it shares a similar DESF on all arms, *O. chathamensis* sucker counts are considerably less, especially for males (maximum sucker counts 46–49 and 55 for males and females respectively, vs. 72–78 suckers for *O. kerberos* sp. nov.), with the DESF occurring somewhat more proximally. The spawned egg casing of *O. chathamensis* is also smaller at 8.3 mm length with irregular sculpting (O'Shea 1999, fig. 14F), vs. 12–14 mm length with consistent longitudinal sculpting (but variability of egg casings in *Opisthoteuthis* is poorly known).

Opisthoteuthis ?chathamensis O'Shea 1999

(Figure 6, Table 4)

Type specimen lodged at National Institute of Water and Atmospheric Research (NIWA), Auckland (H-664).

Diagnosis: See description.

Description: Mantle short, posteriorly rounded, width comparable to length (MWI 85%–92%), head wider than mantle and slightly greater than ML (HWI 106%–113%). Fins lateral to sub-terminally placed, small (FLI 28%–52%), without basal constriction (FWI 39%–65%), pointed distally (see **Fig 6 A, B**). Eyes large (EDI 27%–50%). Funnel long, tapering (FuLI 37%–52%), distal ~60% free, funnel organ not examined. Pallial aperture gape small (PAI ~25%). Olfactory organs small, ovoid. Pallial adductor reduced to a narrow strap or band, attached to right side of either the oviducal gland or AGC in females and males respectively. Optic nerve configuration not examined.

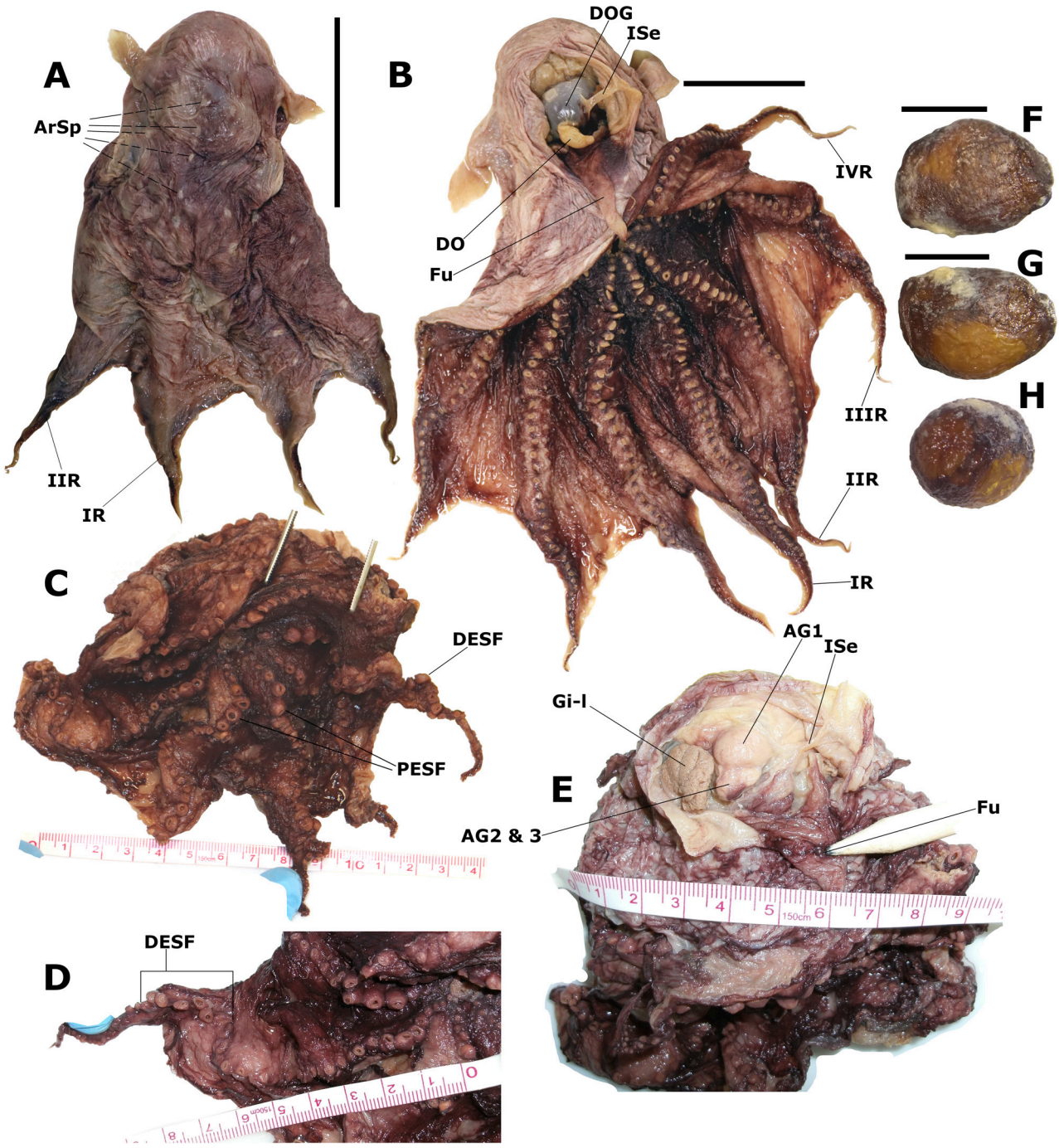

Figure 6. *Opisthoteuthis ?chathamensis* from Macquarie Island, aspects of whole animal and details of arms, webbing, and eggs. **A, B**) dorsal and ventral aspects of female specimen (TMAG E21381). **C–E**) male specimen (MV F164029) in poor condition, with oral aspect of enlarged suckers (**C**), closeup of DESF (**D**), and pallial cavity depicting accessory gland complex (**E**). **F–H**) encased egg removed from distal oviduct of female (TMAG E21381), with two aspects rotated along long axis (**F**, **G**) and distal end (**H**). Abbreviations/symbols: IL, IIL, IIIL & IVL—arms I–IV left; AG1—accessory gland 1; AG2 & 3—combined 2nd and 3rd accessory glands; ArSp—Areolar spots; DESF—distal enlarged sucker field; DO—distal oviduct; DOG—distal oviducal gland; Fu—funnel; Gi-l—left gill; ISe—interpallial septum; PESF—proximal enlarged sucker field. Scale bars = 100 mm (**A**), 50.0 mm (**B**), 5.0 mm (**F**, **G**), ruler in image with mm marks (**C–E**).

Gills: half-orange with 6 or 7 lamellae per gill.

Arms and webbing: arms thick and long, approximately equal in length and without a consistent arm formula, dorsal and ventral arms approximately 2.4–2.5× ML. Web deep (depicted in **Fig 6 B**), without consistent formula but with ventral web sector 'E' shallower (deepest web sectors medially with depth 54%–69% arm I lengths, ventral web depth 46% arm IV length). Web sectors attach slightly more proximally on ventral arm edges, though web nodules could not be located.

Suckers and cirri: sucker counts to 67 or 68 on both specimens examined. Suckers sexually dimorphic, males with proximal and distal enlarged sucker fields (see **Fig 6 B** female, **Fig 6 C, D** male). Male with first four suckers small, increasing in size. Following PESF with 5–7 enlarged suckers, from the 5th or 6th to 9th or 11th sucker, with central 4 or 5 suckers largest. Proximal enlarged suckers with acetabular bases somewhat globular and elevated above arm (PESF SDI 9.3%), with infundibular ring and pad smaller in diameter. Suckers reduce in diameter mid-arm (following PESF), becoming more sunken into arm, with SDI 4.7%. DESF present on all arms of male, comprising 8–11 enlarged suckers, from approximately the 20th or 24th to 28th or 33rd sucker, with the central 6 to 8 suckers largest.

Female with proximal 4 suckers very small and increasing in size, thereafter suckers are somewhat larger, largest within proximal third (SDI 5.2% at 6th sucker IR; 4.7% by 11th sucker). Sucker size slowly decreasing, then decreasing more rapidly distal to the webbing (after ~30 suckers).

Cirri commence between suckers 1–3, reaching greatest length over mid-arm (CLI 4.7%–5.2%), and gradually decreasing in length in the distal third of the arm.

Internal structures including shell, optic nerves, and digestive system not examined in detail.

Male reproductive system: observed *in situ* (**Fig 6 E**), AGC and terminal organ exposed within mantle cavity. Large and rounded AG1 dominates AGC (located posteriorly), slightly anterior are the smaller and conjoined AG2 and 3 (overall dimensions only ~⅔ greatest dimension of AG1) from which protrudes a very short and broad-based terminal organ (terminal organ pigmented maroon, rest of AGC unpigmented).

Female reproductive system: observed *in situ* (**Fig 6 B**), ovary occupying distal third of mantle; oviducal glands large, two-parted, each part rounded, distal oviducal gland darkly pigmented; distal oviduct beige-coloured, similar to oviducal gland in length. Encased egg dissected from distal oviduct (**Fig 6 F–H**), length 9.3 mm, width 6.4 mm; egg case sculpting irregular, with short stalk at one end, colour brown.

Colouration: head, mantle, and aboral surfaces with a light reddish-purple, areas around eyes and the distal parts of the fins are somewhat paler. Funnel proximally with a darker pigmentation. Oral surfaces of web a similar colour but much darker in pigmentation, especially on the webbing, suckers and cirri with a contrastingly pale beige colour. Areolar spots: observed on female specimen (**Fig 6 A**). Arm I each with 8 or 9 spots (starting on the dorsal mantle between the fin bases and eyes), 7 along each arm II (starting with 2 spots above each eyes), 7 along arm III, and 4 along arm IV. Areolar spots ~4 mm across, comprising a whitish ring with a translucent 'window' in the centre.

Material examined.

TMAG E21381, female (ML 85 mm), Macquarie Island, FV *Austral Leader*[1]

MV F164029, male (ML 60 mm), Macquarie Island, FV *Austral Leader*, 28.xii.1995 (collector S. Lake).

[1] The collection data with the single TMAG specimen is uncertain, the specimen was originally one of several Antarctic/sub-Antarctic cephalopods collected by the RV *Austral Leader*, with the various labels (written on sheets of paper) stored separately from the jars, several labels noted "AL23 shot 8" closer to East Antarctica, while other labels noted "Macquarie Island".

Remarks: A small number of *Opisthoteuthis* have been collected by fisheries vessels from around Macquarie Island (Australian Antarctic Territories). These specimens have not been previously described. Steve O'Shea briefly assessed one specimen (MV F164029) in 1998 and noted its similarity to New Zealand taxa (writing "aff. *chathamensis* O'Shea, 98" on a specimen label).

The two specimens examined, both mature individuals, have a superficial similarity to *O. kerberos* sp. nov., and *O. chathamensis*, and all have similar configuration of enlarged suckers. However, the Macquarie Island specimens (compared to *O. kerberos* sp. nov.) have lower sucker counts (67 or 68 vs. 72–79), lower gill lamellae counts (6 or 7 vs. 7 or 8), male AGC dominated by AG1 (vs. dominated by combined AG2 and 3), and a rough or irregular egg case sculpting (vs. longitudinally striate).

The New Zealand *O. mero* lacks the DESF, but otherwise has similar sucker counts (up to 70) to the Macquarie Island specimens but has an AGC with AG1 similar in size to the combined AG2 and 3 (O'Shea 1999, fig. 10F), considerably smaller than observed on the Macquarie Island male (**Fig 6 E**). *O. chathamensis* is much closer in morphology to the Macquarie Island specimens, this species has somewhat fewer suckers (≤55 per arm) but shares the DESF configuration of the Macquarie Island specimens, also has AG1 significantly larger than the combined AG2 and 3 (the latter being ~⅔ the greatest dimension of AG1) (O'Shea 1999, fig. 14D), and has a rough or irregular egg case sculpting. Lastly, the aboral pigmentation and prominent series of areolar spots (especially on the Macquarie Island female) are very similar to that depicted for *O. chathamensis* (O'Shea 1999, fig. 13A).

Overall, these Macquarie Island specimens are generally consistent with *O. chathamensis*, though differing in arm sucker count, and until more specimens are examined they are designated herein *O. ?chathamensis* in agreement with O'Shea's interpretation. The sub-Antarctic islands of the Australian Antarctic Territories, including Macquarie Island, are largely unstudied in terms of cirrate octopods, but Nesis (1987, p. 288) noted that undescribed *Opisthoteuthis* were collected from bathyal depths of the Kerguelen and Crozet Islands in the south-

Table 4. *Opisthoteuthis ?chathamensis* measurements, counts, and indices (all measurements in mm). *Arm damaged, DESF likely commencing at an earlier sucker.

ID	TMAG E21381	MV F164029	Indices	TMAG E21381	MV F164029
Sex	Female	Male	MWI	92%	85%
TL	~275	...	HWI	106% (101% across eye openings)	113%
ML	85	60	FuLI	52.4%	36.7%
MW	78	51	FLI (L/R)	52.4%/39.4%	28.3%
HW	~90 (85.6 eye openings)	68	FWI (L/R)	38.9%/49.3%	64.7%
ED	~23 (shrunken)	30 (opening ~10)	EDI	27.1%	50.0%
FL (L/R)	44.5/33.5	17 R	PAI	25.3%	25.0%
FW (L/R)	17.3/16.5	11 R	Arm formula (L/R)	II>IV>I>III / IV>I>II=III	III>I>IV>II* / IV>III>II>I*
FuL	44.5	22	Dorsal ALI	2.4× ML	2.5× ML (longest arm)
PA	21.5	~15	Ventral ALI	2.5× ML	
Gill LC (L/R)	6L	7L	SDI	5.2% (6th sucker, IR) (4.7%, 11th sucker)	4.7%
AL I (L/R)	207/198	140/92*	SDI PESF	NA	9.3%
AL II (L/R)	217/196	110*/100*	SDI DESF	NA	8.3%
AL III (L/R)	198/196	150/120	CLI	6.5%	5.0%
AL IV (L/R)	210/212	130/123	Web formula	B>C>A=D>E / A>C>B>D>E	C>D>A>B=E
SC I (L/R)	67/66	60/33*	WI A	57.9% (of arm I) (web B deeper at 69.1%)	46.4% (arm I) (web C deeper at 53.6%)
SC II (L/R)	61/63	49/52	WI E	46.2% (of arm IV)	46.2%
SC III (L/R)	56*/68	67/40			
SC IV (L/R)	62/66	63/52			
SuD (normal)	4.4 ^{Acet} (6th, IR) (4.0 by 11th)	~2.7–2.8 ^{Acet} (mid arm)			
PESF position	NA	5–10/5–10 (6–9 ^{largest}) I 5–9/5–11 (6–9/6-10 ^{largest}) II 5–10/5–10 (6–9/5–9 ^{largest}) III 5–9/6–9 (5–8/6–9 ^{largest}) IV			
SuD (PESF)	NA	5.6 ^{Acet} (7th or 8th, IIR) (5.2 ^{Acet} other arms)			
DESF position	NA	24–31/28*–33 (24–33 ^{largest}) I 22–32/22–31 (23–28 ^{largest}) II 22–31/20–28 (22–28 ^{largest}) III 21–28/21–30 (22–28 ^{largest}) IV			
SuD (DESF)	NA	4.9 or 5.0 ^{Acet} (4th enlarged sucker, IIR)			
CiL	5.1–5.5 (13th–15th suckers, dorsal arms); Maximum length by ~sucker 8 or 9.	2.0–3.0			
Cirrus start sucker position	1 & 2	1–3			
WD A	120	65			
WD B (L / R)	143/110	60R			
WD C (L / R)	135/114	75R			
WD D (L / R)	120/107	70R			
WD E	98	60			

Web nodules	NA	NA			
Areolar spots	8 or 9 for arm I 7 for arm II 7 for arm III 4 (or more) for arm IV	Not observed, mantle damaged, skin abraded & contracted.			
Notes		Digestive gland bilobed, mantle partly stripped away.			

ern Indian Ocean. Future study should focus on describing the opisthoteuthid taxa from these sub-Antarctic Islands.

Opisthoteuthis pluto Berry, 1918

(Figures 7–9, Tables 5 & 6)

Type specimen lodged (by Berry 1918) at the Australian Museum, Sydney (AM E3638), lost.

Synonymy.

Opisthoteuthis (Teuthidiscus) pluto—Berry, 1918; Robson 1932

Diagnosis: Opisthoteuthid with 80–85 suckers per arm of adult, DESF absent, web nodules absent; with brown−maroon aboral pigmentation, and series of at least 6–8 small areolar spots along dorsal arms, starting on the head for arm pair I. Internally with digestive gland unilobed, 7 or 8 lamellae per gill, with AG1 vestigial (combined AG2 and 3 dominating AGC), and with intestine approximately 2.7× oesophagus length.

Description: Mantle short, rounded, especially short on juvenile, width greater than length (MWI 112%–116% male, ~150% female, 108% juvenile) (see **Figs 7 A**; see **Fig 8 A, E** for type material). Head wider than mantle (HWI 144%–154% male, ~176% female, 172% juvenile). Fins sub-terminally placed, small (FLI 60%–70% male, ~48% female, fins inverted on juvenile), fin width approximately greatest basally (FWI 50%–74% male & female), tapering to rounded end. Eyes large, obscured in gelatinous tissue (EDI ~44%–46% male, ~57% female, ~115% juvenile), openings small, constricted. Funnel relatively long and tapering (FuLI 56%–63% male, ~50% female, ~71% juvenile), free funnel length depending on shrinkage (either not free or up to 38% funnel length free). Funnel organ poorly preserved, a pair of faint marks possibly forming a V-shape (Berry 1918, fig. 64, illustrated funnel organ as two pads converging distally on male specimen USNM 815830). Pallial aperture gape small (PAI 33% male, 46% juvenile), enclosed around funnel. Olfactory papillae small, ovoid. Pallial adductor reduced to a narrow strap, attached at anterior right edge of male AGC.

Gills: half-orange, with 8 lamellae per gill (7 lamellae on juvenile).

Optic nerve: from optic lobe, optic nerves pass through each white body as four bundles, each undergoing fine branching into the back of the eyeball (**Fig 9 A**). White bodies relatively small, kidney-shaped, dark purple-coloured.

Internal shell: illustrated per **Figure 9 B–D** (male SAM D19762); broadly U-shaped, saddle relatively deep (SHI 34%) and broad (SSI 68%), outer (posterior) face concave (groove, see **Fig 9 D**), basal shelf absent. Saddle shoulders well developed, with concave outer face below saddle prominences. Wings diverge from saddle mid-point by 42–46°, outer faces non-parallel, wings tapering to simple point that are flared laterally relative to the wings. Shell translucent and amber-coloured. Berry (1918) illustrated the shell from his large male specimen (USNM 815830; see **Fig 9 L**), this shell was similar, SHI 33%, SSI 62%, saddle with distinct posterior groove, shoulders well developed, wings diverging 47–50°, wing ends pointed.

Arms and webbing: arms relatively long (compared to short ML), approximately equal in length, but with arm pair IV slightly longer on specimens (dorsal ALI 3.2–4.2× ML, ventral ALI 3.1–4.7× ML). Web simple (**Fig 7 B**), web formula variable, approximately A>B>C>D>E (though generally subequal), medial depth of sector A ~54–66% arm I length, sector E medial depth ~41%–63% arm IV length (similar male, female, and juvenile). Web sectors attached to ventral arm edges more proximally, no web nodules were apparent (though possibly obscured in gelatinous tissue?), on one specimen (SAM D19762) webs attached along ventral arm edges at level of sucker ~45 (arm I) or ~43 (arm IV), and along dorsal edges at sucker ~60 (arm I) or ~53 (arm IV).

Suckers and cirri: sucker count to 80–85 per arm (both male and female), juvenile with up to 69 suckers per arm. Males with only a proximal enlarged sucker fields (PESF) and with distal enlarged sucker field (DESF) absent (depicted **Fig 7 B, C**; male type material **Fig 8 B–D**). Males with proximal 3 suckers very small and increasing in size. An abrupt size increase marks the PESF of 6 or 7 suckers, from the 4th to 9th or 10th sucker, and with central 3 or 4 largest. PESF suckers with acetabular bases large (SDI 10%–15%), globular, though generally imbedded into gelatinous arm tissue (making measurement difficult), infundibular diameter smaller than acetabular, infundibular ring and pad with radiating striations and large aperture. Suckers reduce in diameter slowly following PESF (SDI still 8% by ~13th sucker on SAM D19762), before decreasing to ~6–7% over much of the central arm (from ~16th to 30th sucker), before sucker size decreases more rapidly distal to the webbing.

Female paratype (see **Fig 8 F, G**) with first three suckers minute, before increasing in diameter, and with 5th to

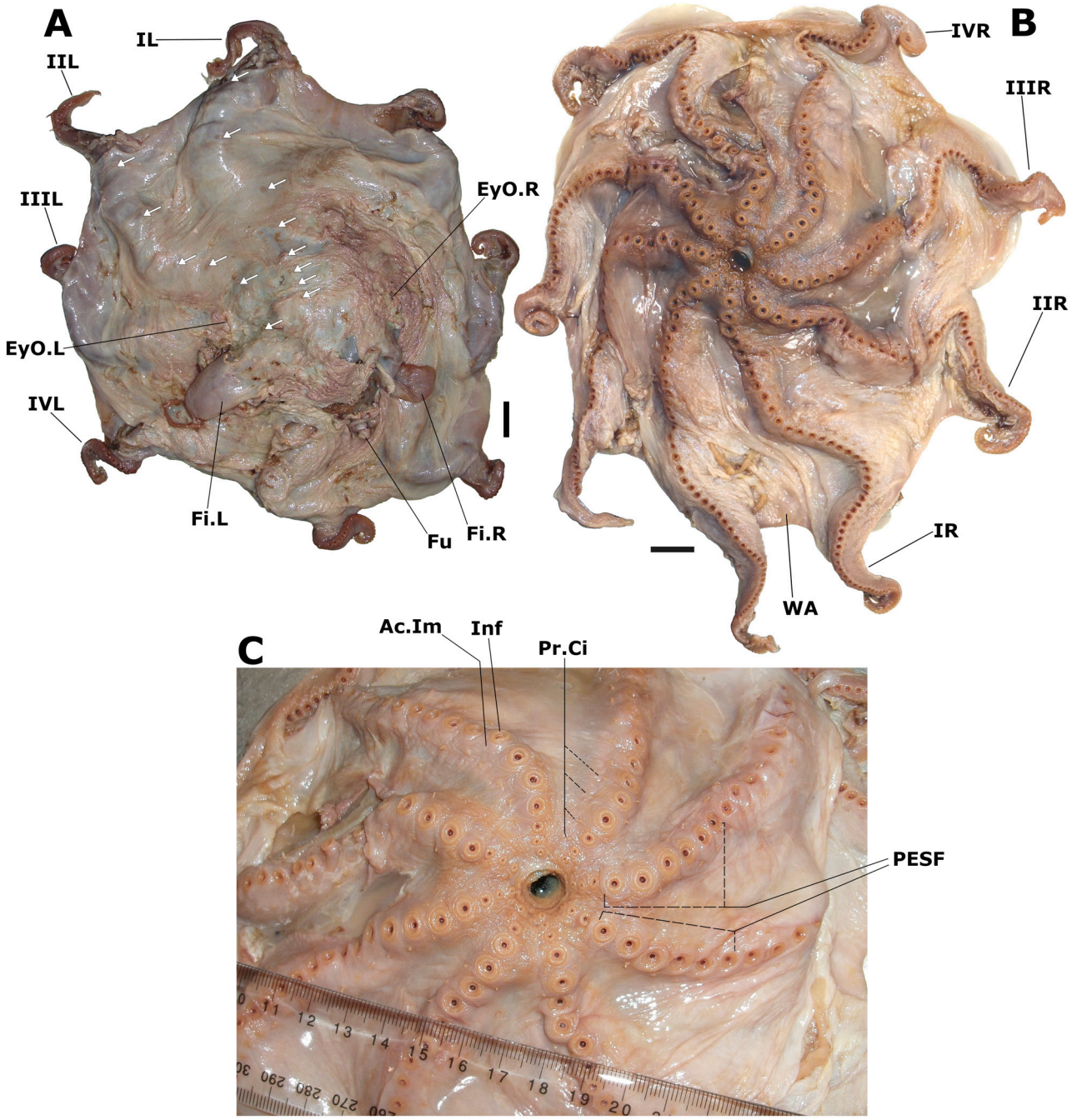

Figure 7. *Opisthoteuthis pluto* aspects of whole animal and details of arms and webbing (male, SAM D19762). **A, B**) aboral and oral aspect respectively, white arrows mark positions of areolar spots along arms I and II. **C**) close-up of male proximal enlarged sucker field and proximal-most cirri, sucker acetabula are generally imbedded in arm tissue. Abbreviations/symbols: Ac.Im—Acetabulum (imbedded); Ci—cirrus; EyO.L/R—eye opening left/right; Fi.Iv—fin (inverted); Fi.L/R—fin left/right; Fu—funnel; Inf—infundibular ring of sucker; I–IVL/R—arm I–IV left/right; PESF—proximal enlarged sucker field; Pr.Ci—proximal-most cirri; WA—web sector 'A'. Scale bars = 20.0 mm (**A, B**), image ruler in mm (**C**).

7th largest, though smaller than in male PESF (SDI ~8.3%), mid-arm suckers with SDI ~5%. Juvenile with largest suckers over proximal to mid-arm (SDI ~5.7%).

Cirri commence between suckers 2 and 3 as minute buds (**Fig 7 C**) (between 1st to 3rd suckers on juvenile), reach greatest length in proximal ⅓–½ arm length (maximum CLI 3.9%), before reducing to arm tip.

Digestive system: digestive tract dissected from mature male, see **Figure 9 E, F**. Buccal bulb very large, exceeding combined stomach/caecum maximum dimensions; anterior salivary glands visible at postero-ventral face of buccal bulb, partially intra-bulbar; posterior salivary glands absent; odontophore present, lacking radula; labial palps lacking palatine teeth; salivary papilla well-developed. Upper beak (**Fig 9 G, H**) moderately tall (height 70% beak length, or 79% width), hood deep

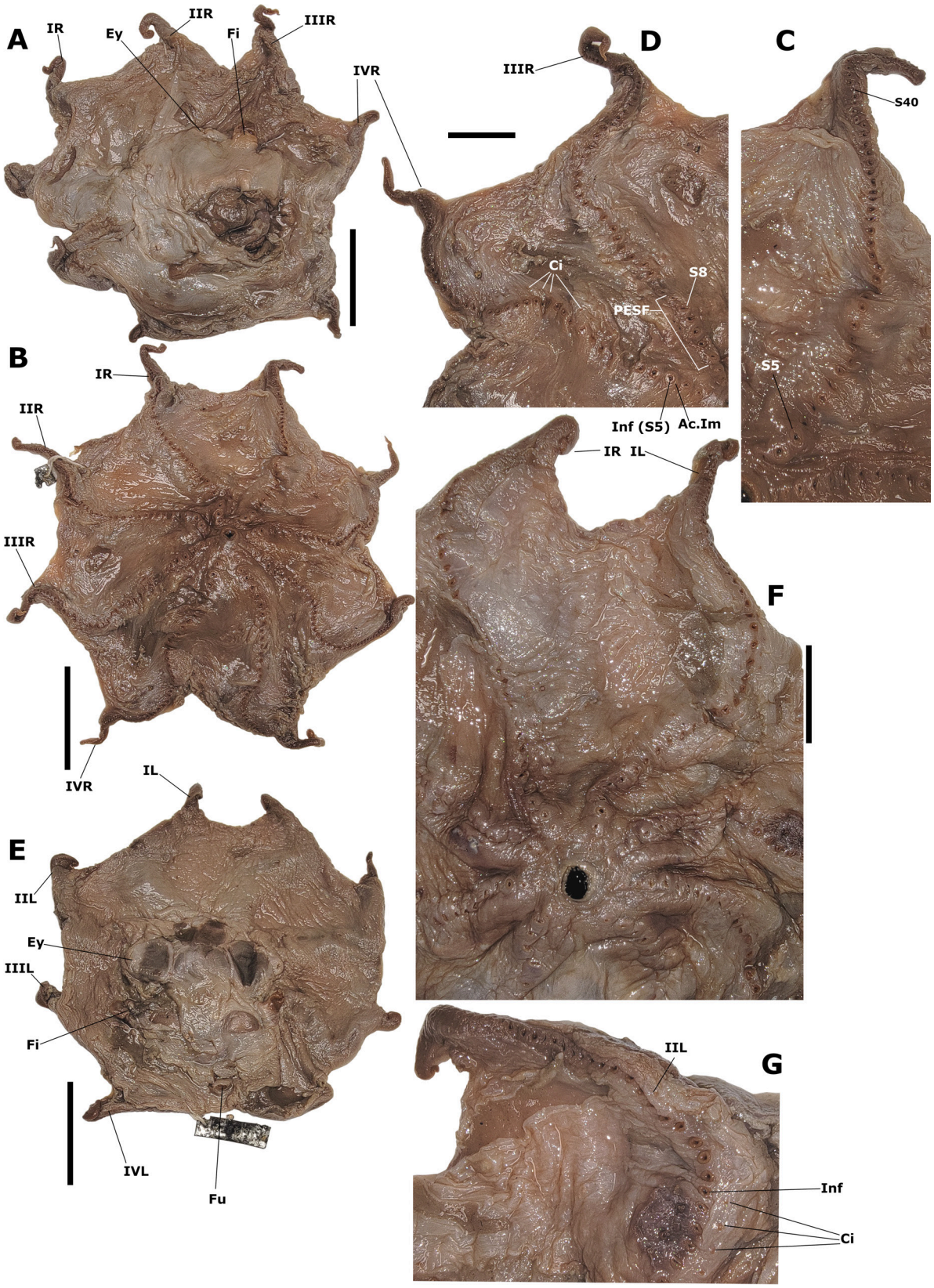

Figure 8. *Opisthoteuthis pluto* paratype and type series material. **A–D**) type series male specimen (USNM 815830), aboral aspect (**A**), oral aspect (**B**), closeup of PESF and distal suckers of arm IL (**C**) and arms IIIR & IVR (**D**). **E–G**) female paratype specimen (USNM 815718), aboral aspect, close-up of proximal suckers and distal suckers for arms IL/R (**F**), and arm IIL (**G**). Photography by Michael Vecchione, Smithsonian Museum National History, used with permission. Abbreviations/symbols: Ac.Im—Acetabulum (imbedded); Ci—cirrus; EyO—eye opening left/right; Fi—fin; Fu—funnel; Inf—infundibular ring of sucker; I–IVL/R—arm I–IV left/right; PESF—proximal enlarged sucker field. Scale bars = 50.0 mm (**A**, **B**, **E**), 20.0 mm (**D**, **F**).

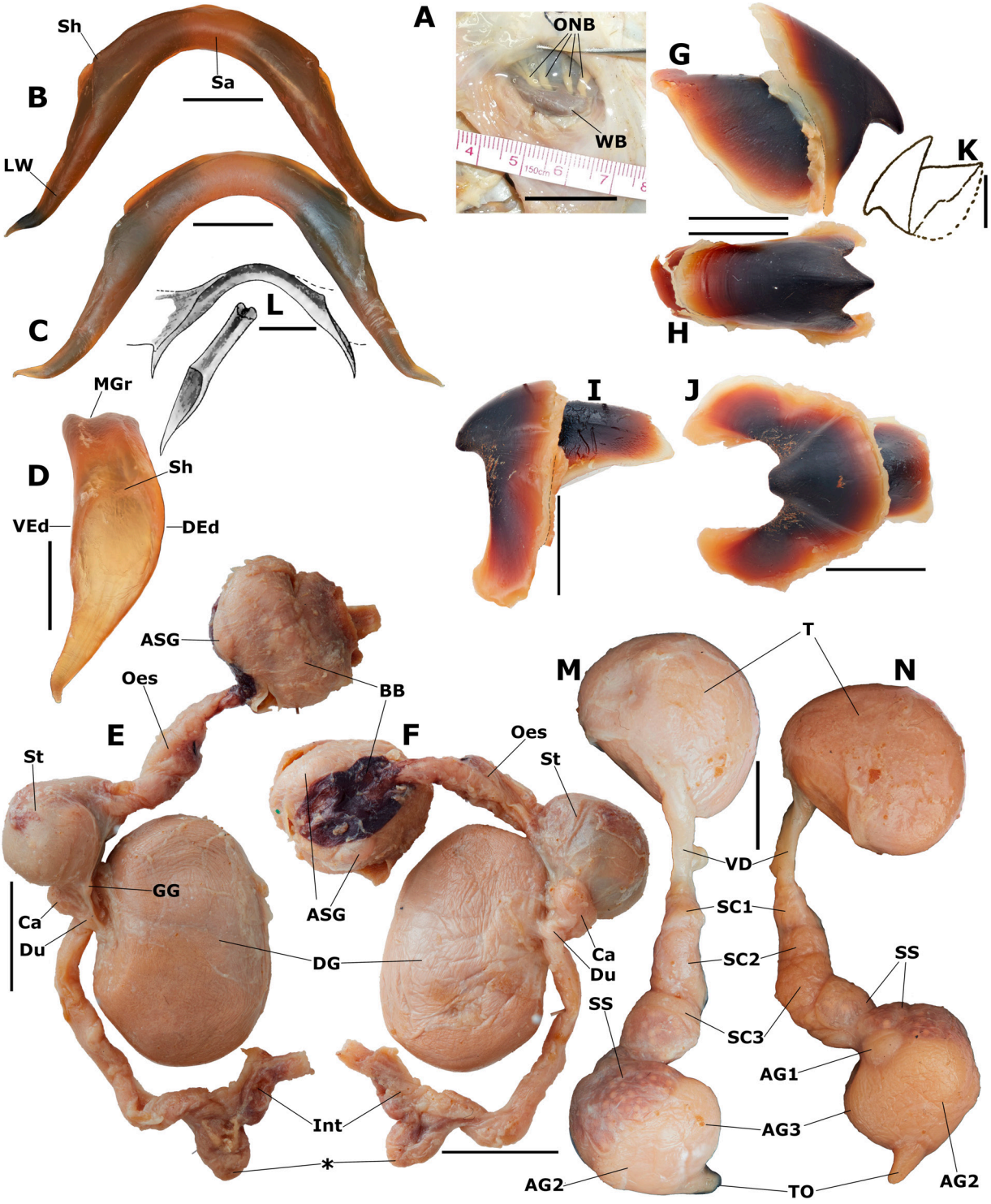

Figure 9. Internal morphology of *Opisthoteuthis pluto* (male SAM D19762). **A**) left-side white body and retinal nerve branching. **B–D**) internal shell depicting dorsal (**B**), ventral (**C**), and lateral (**D**) aspects. **E**, **F**) digestive system depicting dorsal and ventral aspects left and right respectively (digestive gland viewed dorso-ventrally with other structures moved to the side, buccal bulb viewed laterally and ventrally in **E** & **F** respectively). **G–J**) beaks illustrating upper beak lateral (**G**) and dorsal (**H**) aspects, and lower beak lateral (**I**) and ventral (**J**) aspects. **K, L**) comparison to beak and shell from type material (as illustrated by Berry 1918), upper break (**K**) from type-series material (modified from Berry 1918, fig. 65), and internal shell dorsal and lateral aspects (**L**) (modified from Berry 1918, Plate 82, fig. 7, 8). **M, N**) male reproductive system rotated aspects. Abbreviations/symbols: *—Bend in intestine; AG1–3—accessory gland part 1–3; ASG—anterior salivary glands; BB—buccal bulb; Ca—caecum; DEd—dorsal edge; DG—digestive gland; Du—hepatic duct; Int—intestine; LW—lateral wing (of shell); MGr—medial groove (of shell); Oes—oesophagus; ONB—optic nerve bundle; Sa—saddle; 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; WB—white body. Scale bars = 20.0 mm (**A**, **E**, **F**); 10.0 mm (**B–D, G–J, M, N**).

(hood length 77% beak length); rostrum blunt and strongly deflected down, jaw cutting edge smooth (without teeth), hood crest rounded (convex); lateral walls near-parallel (without longitudinal grooves/flexures), dorsal edge of lateral walls near-straight, posterior edges near-flat to slightly convex, crest rounded at postero-dorsal apex. Berry (1918) fig. 65 illustrated beaks from type-series specimen, the upper beak (**Fig 9 K**) being similar in shape to that herein (height ~76 length, height 98% width, hood length 80% beak length). Lower beak (**Fig 9 I, J**) tall (height 68% width), hood relatively short (hood length 53% beak length) with rounded crest, elongate wings (wing length 105% beak length) with weak diagonal flexures; rostrum small, blunt-tipped. Oesophagus narrow in proximal third, distal two thirds (towards stomach) with moderate swelling as a simple crop (without diverticula) (see **Fig 9 E, F**). Stomach large, rounded, muscular; caecum small (just under ½ stomach greatest dimensions), non-spiral; digestive gland unilobed, hepatic ducts short; intestine very long, ~2.7× length of oesophagus, relatively narrow, slightly expanded in distal third towards rectum, the distal half of the intestine looped into an S-shape.

Male reproductive system: illustrated per **Figure 9 M, N**; testis rounded; vas deferens short (< length of spermatophoric complex); spermatophoric complex three-parted, SC1 smaller, SC3 largest; spermatophoric sac (Needham's sac) large, partly overlapping SC3 and posterior face of accessory gland complex, with numerous small and rounded spermatophores visible internally; AGC dominated by distal AG2 and 3, closely attached as a single rounded mass (with division between the two glandular structures still just apparent), the more proximal (posteriorly located) AG1 is very small (only ~30% of combined AG2 and 3 width in maximum dimension and imbedded at their proximal base); terminal organ short, conical, projecting from between AG 2 and 3, length ~⅓ combined AG2 and 3 maximum width.

Female reproductive system: unknown.

Colouration: pigmented skin generally abraded to reveal pale cream-coloured flesh both on body surfaces and the aboral webbing, areas of remaining skin aborally with a light brown–maroon pigmentation, darker on the fin edges (this same pigmentation was present on type material) (**Fig 7 A**). Oral surfaces of webbing with light-brown pigmentation (limited pigmentation distally, darker proximally), suckers and cirri with a beige-brown colouration, contrasting against the adjacent arm tissue (**Fig 7 B, C**). Areolar spots: present (visible in **Fig 7 A**), small (diameter 2–3 mm), arm I and II with 8 and 6 spots respectively (first two or three starting on the head between the eyes, just anterior to the fins), arms III and IV with 3 and 2 spots, though more were likely originally present towards the arm tips where the skin was more damaged (arm II–IV spot series starting just anterior to fin base for arm II, or below fin base for III & IV). Berry (1918) also states that the series of areolar spots commences for dorsal arms between the eyes, with spots for other arms commencing near fin bases.

Material examined.

SAM D19762, male (ML 57 mm), 194 km SW of Eucla, Great Australian Bight, 33°19'S, 128°02'W, 250 m, trawl, FV *Comet*, 13.i.1989. TMAG E45562, juvenile male (ML 23 mm), 78 km SSW of Mallacoota, 38°12'35"–37"S, 149°36'23"–34'33"E, 382–435 m, FRV *Southern Surveyor*, SS01/00, Stn 183, 21.iv.2000.

Material not examined directly (photography and measurements provided).

Paratype. USNM 815718 [Berry registration No. S.S. 465], female, RV *Endeavour* Stn E3629, south of Eucla, Great Australian Bight (WA), 34°S, 126°10'E, 366 m (200 fathoms), i.1917. USNM 815830 [Berry registration No. S.S. 468], male, RV *Endeavour* Stn E3632, south of Eucla, Great Australian Bight (WA), 34°S, 130°10'E, 274 m (150 fathoms), i.1917.

Distribution: Type series all from the central Great Australian Bight (southern Australia) between 126°10′E–130°10′E, along the outer edge of the shelf/upper slope, depth of type series 274–823 m (150–450 fathoms), the holotype being from 129°28′E and 350–450 fathoms specifically (Berry 1918; table 28). SAM specimen was from the same approximate location, and at slightly shallower depth (250 m), while the juvenile was collected off southeastern Victoria (382–435 m depth). Overall, likely distributed around the southern and southeastern Australian continental slope at ~250–820 m.

Etymology: Specific epithet after the mythological *Pluto*, the ruler of the Ancient Greek underworld, supposedly due to the dark pigmentation having a connection to the darkness of the underworld.

Proposed vernacular name: Pluto's flapjack octopus.

Remarks: Berry (1918) makes no reference to enlarged suckers fields in his description of *O. pluto*, even though his description was based both on mature male and female specimens, however, Berry (1918, p. 285) does note that the suckers are "...moderate in size, the 5th to 7th from the mouth usually the largest, thence rapidly diminishing in size proximally and more gradually distally to the extremity of the arm...", consistent with the presence of a PESF and the lack of a DESF. Photography of the female paratype (USNM 815718) and the large male type-series specimen (USNM 815830), that were used in Berry's description, confirm that *O. pluto* only has a PESF, with Berry's material also comparable in gill lamellae counts, upper beak form, shell form, and areolar spots to a unique male specimen from the SAM (D19762), which in addition has a unilobed digestive gland and unique accessory gland complex. Berry (1918) deposited his holotype at the Australian Museum (AM E3638; Berry registration number S.S.B 464), but during

Table 5. *Opisthoteuthis pluto* measurements and counts (all measurements in mm).

ID	SAM D19762	USNM 815830 [S.S. 468]	USNM 815718 Paratype [S.S. 465]	TMAG E45562
State	Mature male	Mature male	Female	Juvenile male
TL	~270			
ML	~57	~50 (from photography)	~42 (from photography)	~22.7
MW	~66	55 (~57 from photography)	75 (~63 from photography)	24.6
HW	88 (eye openings)	70 (72 from photography)	75 (74 from photography)	39 (28 $^{\text{eye openings}}$)
ED (L/R)	~25 (sunken)	~23 (from photography)	~24 (from photography)	~26
FL (L/R)	38/40	30	20	NA*
FW (L/R)	28/26	15	10	NA*
FuL	36 (none free)	28	21	16 mm (6 free)
PA	19			~10.5
Gill LC (L/R)	8/8	8	8	7/7
AL I (L/R)	240/229	160/160	145/145	76/74
AL II (L/R)	215/244	155/155	140/150	76/76
AL III (L/R)	220/241	145/170	145/140	84/82
AL IV (L/R)	258/270	160/160	130/115*	89/84
SC I (L/R)	81/81	80–85 (arm not specified)	~80	60/62
SC II (L/R)	73/79			57/59
SC III (L/R)	82/82			62/59
SC IV (L/R)	78/83			63/69
SuD (normal)	4.6 $^{\text{Acet}}$, 4.2 $^{\text{Inf}}$ (13$^{\text{th}}$, IL); 4.0 $^{\text{Acet}}$, 3.8 $^{\text{Inf}}$ (~25$^{\text{th}}$–30$^{\text{th}}$, IIL); mid-arm.	2.6–3.0 (15$^{\text{th}}$/16$^{\text{th}}$ suckers) (from photography)	3.5 $^{\text{Inf}}$ (5$^{\text{th}}$, IR) Mid-arm suckers ~1.7–2.0 (from photography)	1.2 or 1.3
PESF position	4–10 (5–8 $^{\text{largest}}$) I 4–10 (5–7 $^{\text{largest}}$) II 4–9 (5–7 $^{\text{largest}}$) III 4–9 (5–7 $^{\text{largest}}$) IV	~4–9 (5–8 largest)	NA	NA
SuD (PESF)	7.4 $^{\text{Acet}}$, 5.7 $^{\text{Inf}}$ (5$^{\text{th}}$, IL); 8.4 $^{\text{Acet}}$, 5.5 $^{\text{Inf}}$ (6$^{\text{th}}$, IIL)	4.0 $^{\text{Inf}}$ (5$^{\text{th}}$, IR) (~4.5–5.0 $^{\text{Acet}}$ per photography)		NA
DESF position	NA			NA
SuD DESF	NA			NA
CiL	2.2 (most cirri somewhat retracted)	Not measured (mostly retracted)	Not measured (mostly retracted)	1.3–1.4 (mid-arm)
Ci start sucker position	2 & 3	2 & 3 (from photography)	2 & 3 (from photography)	1–3
WD A	130	105	95	46
WD B (L/R)	124/128			46/42
WD C (L/R)	120/124	95	100	42/42
WD D (L/R)	120/122			50/46
WD E	110	100	80	46
WN (sucker position & arm)	Uncertain: ~60$^{\text{th}}$ dorsal edge, ~45$^{\text{th}}$ ventral edge (arm IR); 53$^{\text{rd}}$ dorsal, 43$^{\text{rd}}$ ventral (arm IVL).			dorsally attached ~5 suckers distal
Areolar spots	8, Arm I 6, Arm II 3, Arm III 2, Arm IV	Present	Present	Uncertain
Notes				20 suckers distal to web.

WWII this specimen was lost, likely during a period when material stored offsite as a wartime safety measure was neglected, with many specimens drying out or being otherwise destroyed (Rudman 1983). Luckily, the

Table 6. *Opisthoteuthis pluto* indices (all measurements in mm).

Indices	SAM D19762	USNM 815830 [S.S. 468]	USNM 815718 Paratype [S.S. 465]	TMAG E45562
MWI	115.8%	~112%	~150%	108.4%
HWI	154.4%	~144%	~176%	171.8%
FuLI	63.2%	~56%	~50%	70.5%
FLI (L/R)	66.7% / 70.2%	~60%	~48%	*
FWI (L/R)	73.7% / 65.0%	~50%	~50%	*
EDI	~43.9%	~46%	~57%	114.5%
PAI	33.3%	NA	NA	46.3%
Arm formula (L/R)	IV>I>III>II / IV>II>III>I	I=II>III>IV / III>IV=I>II	I=III>II>IV / II>I>III>IV*	IV>III>II=I / IV>III>II>I
Dorsal ALI	4.2× ML	3.2× ML	3.5× ML	3.3× ML
Ventral ALI	4.7× ML	3.2× ML	3.1× ML	3.9× ML
SDI (mid-arm)	8.1% (13th); 7.0% (~25th–30th sucker)	~6.0%	~5.0%	5.7%
SDI PESF	13.0%–14.7%	~10.0%	~8.3%	NA
SDI DESF	NA	NA	NA	NA
CLI	3.9%	NA (not measured)	NA (not measured)	5.9%
Web formula	A>B>C=D>E / A>B>C>D>E	A>E>C (other sectors not measured)	C>A>E (other sectors not measured)	D>A=B=E>C / A=D=E>B=C
WI A	54.2%	~65.6%	~65.5%	60.5%
WI E	40.7%	~62.5%	~61.5%	51.7%

paratype specimen, and some other type-series specimens were accessioned into the USNM upon Berry's death in 1984, allowing comparison to type material to be made.

The main specimen examined for this species herein, SAM D19762, was originally suspected to be a new species, as it lacked a DESF, and had a unilobed digestive gland, differing clearly from Lu's (2010) diagnosis of *O. pluto* (bilobed digestive gland with greatly enlarged DESF suckers on arms II–IV). However, the SAM specimen is morphologically comparable to Berry's type material as mentioned, and furthermore matches the type locality (all from the Great Australian Bight over a similar bathymetric range). Lu's specimens were not from the type locality, and are herein attributed to a new species, in a new genus (*Insigniteuthis obscura* sp. nov. described later). The juvenile *Opisthoteuthis* (TMAG E45562) was tentatively assigned to *O. pluto* given its depth of capture (comparable to *O. pluto* specimens) and its high gill lamellae count (7) despite its very small size (presumably with more lamellae as an adult).

While the number of *O. pluto* specimens assessed herein was not ideal, they were sufficient to establish the distinct features of this species, describe its internal organ systems, and enable recognition of other taxa. Hopefully future research can assess a greater collection of this species to better establish morphometric variation and range.

With regards to *Opisthoteuthis* taxa in the Pacific and Indian Oceans, *O. pluto* is superficially like both *O. robsoni* and *O. philipii* (per Part II, Verhoeff in preparation), as all three have a unilobed digestive gland and share an absent DESF on mature males. The disjunct distributions of these three species are also notable, but do not necessarily mean that the species are distinct. Instead, there are further distinctions in both the morphology and bathymetric range between *O. pluto* and these other two taxa. *O. robsoni* from New Zealand waters occurs at a far greater depth than the other New Zealand taxa (*O. mero* and *O. chathamensis*) at depths of 1600 m (O'Shea 1999), whereas the specimens of *O. pluto* were collected from 250–823 m depth. Morphologically, *O. pluto* has a much longer intestine than *O. robsoni* (2.7× oesophagus length vs. 1.5×), and in *O. robsoni* the AGC of the male is dominated by the proximal AG1 (equal in size to the combined distal AG2 and 3) (see O'Shea 1999, fig. 18E), whereas in *O. pluto* AG1 is reduced to the point of being vestigial. Most other states and counts including absence of web nodules, arm sucker counts, number of PESF suckers, and gill lamellae counts are all comparable between *O. pluto* and *O. robsoni*. Relative to *O. philipii*, the Australian species is again distinguished by intestine length and the male AGC, in *O. philipii* AG1 dominates the AGC (per Part II, Verhoeff in preparation).

While *O. pluto* is unlikely to be confused with *E. persephone* comb. nov., the pigmentation of *E. persephone* is distinct, being more 'bluish' or 'slate-grey' on the oral surfaces of the arms and webbing (vs. more reddish or

maroon in *O. pluto*) and is also readily distinguished by the enlargement of suckers in the male along the whole arm length (combined PESF & DESF), bilobed digestive gland, far broader shell without well-developed shoulders, and reduced gill lamellae count.

O'Hara *et al.* (2020) reported the collection of six '*O. pluto*' down to a depth of 2692 m (eastern and southeastern Australia), however these records are problematic for several reasons. Out of the putative *Opisthoteuthis* collected on the RV *Investigator* voyage IN2017_V03, only one from station 22 was from 2692–2760 m depth. This same specimen (MV F245704) was recently illustrated by Ziegler & Sagorny (2023) using photos of it in fresh condition and preserved state. However, it is evident from the lateral fin placement, large paddle-like fins with basal constriction, distinct web nodules, and long cirri (>2× sucker diameter) (per photography provided by Chris Rowley, Museums Victoria), that this specimen is not attributable to *O. pluto* or even to the family Opisthoteuthidae, and it is potentially attributable to *Grimpoteuthis greeni* (Grimpoteuthididae). The other '*Opisthoteuthis*' from IN2017_V03 were collected over a depth range of 999–1257 m and from photographs of the freshly collected animals, these are attributable to *Insigniteuthis obscura* gen. et sp. nov. (described later) due to the small number of greatly enlarged DESF suckers (at least on MV F245722) and the single large areolar spot near the base of each arm.

Genus *Exsuperoteuthis* gen. nov.

ZooBank LSID:
urn:lsid:zoobank.org:act:47DA4214-C508-4529-9DEC-F098F6B1FEE3

Type species: *Exsuperoteuthis persephone* (Berry, 1918), here designated.

Diagnosis: Opisthoteuthids with PESF and DESF combined into a single row of greatly enlarged suckers, covering at least two thirds of the arm length, on all arms (see **Fig 2**). Digestive gland bilobed.

Species allocated: *E. depressa* **comb. nov.** (including *O. japonica* as synonym) and *E. persephone* **comb. nov.**

Etymology: From the Latin *exsupero*, meaning to surpass or exceed, in reference to the far greater number of enlarged suckers on the males compared to other members of Opisthoteuthidae.

Remarks: This genus seems to be restricted to the northern and southwestern Pacific. The two species allocated were placed within O'Shea's (1999) 'Type 1' *Opisthoteuthis*.

Exsuperoteuthis persephone comb. nov. (Berry, 1918)

(Figure 10–12, Table 7 & 8)

Type specimen lodged (by Berry 1918) at the Australian Museum, Sydney (AM C.148253).

Synonymy.

Opisthoteuthis (Teuthidiscus) persephone—Berry, 1918; Robson 1932

Diagnosis: Opisthoteuthid with ~80–90 suckers per arm of adult, males with combined PESF and DESF, of 30–40 enlarged suckers, over proximal, mid, and distal regions of all arms; web nodules absent; with pale, colourless aboral surfaces and distinct greyish blue-purple oral surfaces, and series of at least 7–12 small areolar spots along dorsal arms, starting on the head. Internally with digestive gland bilobed, 6 (and rarely 7) lamellae per gill, with AG1 dominating AGC (greater in size than combined AG2 and 3), and with intestine approximately 2.2× oesophagus length.

Description: Mantle short, dome-like, posteriorly rounded, width equal or exceeding length (MWI 105%–139% male, 113%–116% female), head much wider than mantle (HWI 124%–179% male, 154%–157% female) (**Fig 10 A, B, J**). Fins sub-terminal on mantle, small, though proportionally large relative to the very short mantle (FLI 65%–76% male, 36%–46% female), fin width greatest near base, with minimal/no basal constriction (FWI 38%–64% male, 60%–66% female), rounded fin edges distally. Fins were inverted/retracted into the thick and gelatinous mantle tissue on two specimens. Eyes very large, but heavily imbedded in head tissue and difficult to measure accurately (EDI 60%–75% male, 54%–70% female), opening small, constricted shut, openings often shifted closer to the top of the head (due to shrinkage). Funnel relatively long, tapering, often only with short length exposed beyond pallial aperture (FuLI 64%–72% male, 54%–66% female), between half and a third funnel length free. Funnel organ V-shaped, proximal end of limbs thickened, thinning out where they connect medially (almost appearing separated) (**Fig 11 A**), funnel organ length ~40% the funnel length, similar to funnel organ illustrated by Berry (1918, fig. 66). Pallial aperture small, enclosed around funnel (PAI 29%–54% in males, females in same range). Olfactory papillae small, ovoid. Pallial adductor, a narrow and delicate strap (15 mm long × 2 mm wide on TMAG E46505) connecting ventral mantle to the viscera, attaching to the right side of the oviducal gland or AGC.

Gills: half-orange form, compact (gill length ~90% width, gill greatest width 26%–27% ML), generally with 6 lamellae per gill, rarely 7 (one male with 7 lamellae on both gills, another male with 7 lamellae on left gill and 6 on right; Berry (1918) also noted a specimen with 6 lamellae on one gill and 7 on another).

Optic nerve configuration: each optic lobe large and ovoid (**Fig 11 B**), with optic nerves present as four bundles penetrating each white body (examined on male specimen). White bodies relatively small, approximately 'kidney-shaped', dark purple-brown, well separated.

Internal shell: examined on male, **Figure 11 C–E** (compared to type material shell illustration, **Figure 11 F**).

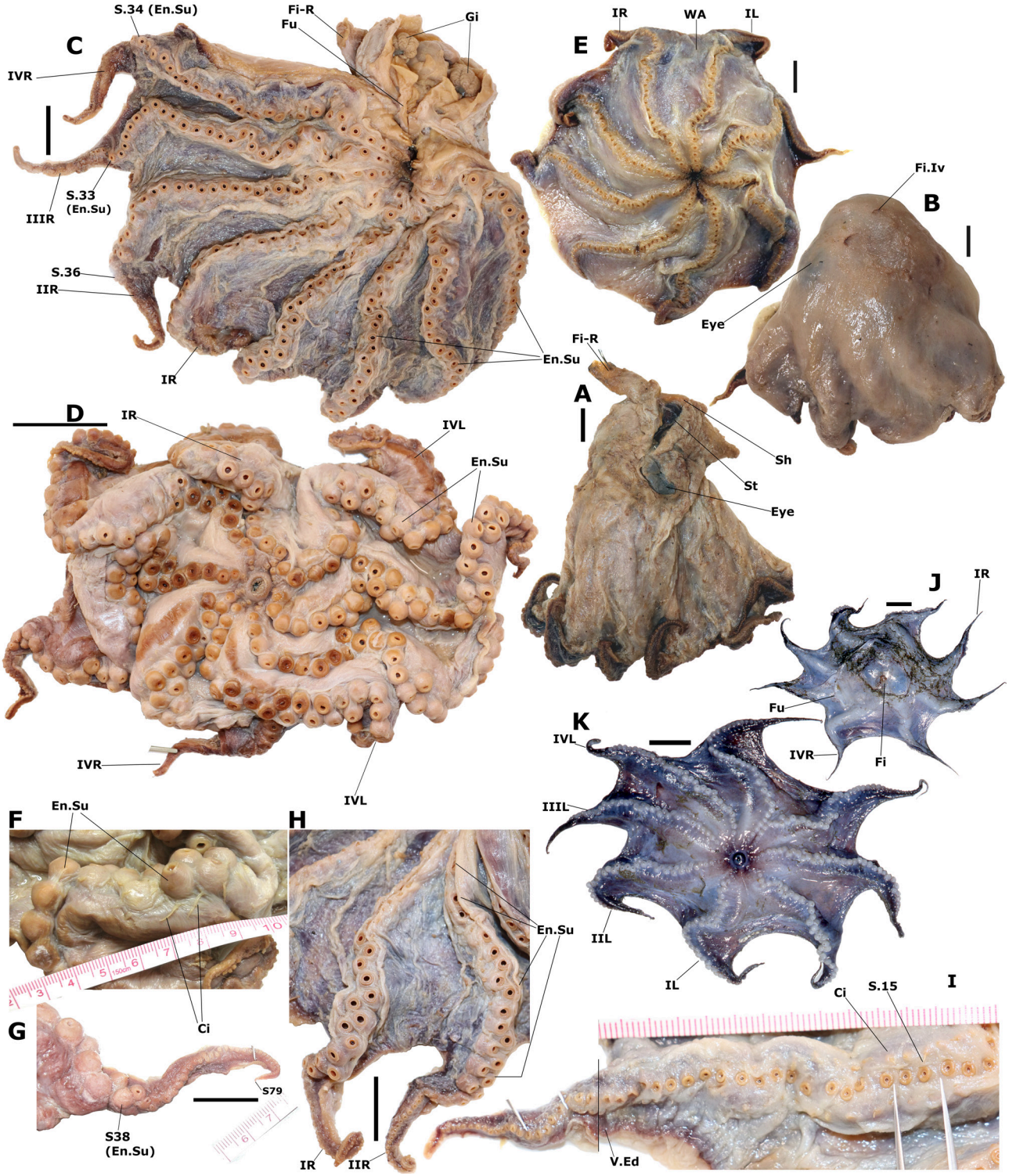

Figure 10. *Exsuperoteuthis persephone* aspects of whole animal and details of arms and webbing. **A**, **B**) Dorsal aspects of male (**A**) (MV F51086), and female (**B**) (TMAG E46505) specimens. **C, D**) oral aspects of male specimens, with less tissue shrinkage (**C**: MV F164064), and a greater degree of tissue shrinkage (**D**: WAM S113335). **E**) oral aspect of a mature female (TMAG E46505). **F–H**) close-up aspects of male enlarged suckers, mid-arm enlarged suckers relative to the longest cirri (**F**: arm IIIR, WAM S113335), and distal transition from enlarged suckers to distal minute suckers (**G**: arm IIIR, WAM S113335) (**H**: MV F51086). **I**) close-up aspect of mid-arm and distal suckers and cirri of female (TMAG E46505). **J, K**) aboral and oral views of a fresh *E. persephone* specimen (AM C.392646) collected off Sydney by the FRV *Kapala* in May 1971 (Photographer: Unknown, Copyright: Australian Museum). Abbreviations/symbols: Ci—cirrus; En.Su—enlarged suckers; Fi.Iv—fin (inverted); Fi-L/R—fin left/right; Fu—funnel; Inf—infundibular ring of sucker; I–IVL/R—arm I–IV left/right; Le-R/L—lens of eye (R/L), actual eye itself collapsed; S38/79—38th and 79th sucker; Sh—internal shell; St—stomach; V.Ed—ventral arm edge; WA—web sector 'A'. Scale bars = 20.0 mm (**A–C**, **E**, **G, H**), 50.0 mm (**D, J, K**), image ruler in mm marks (**F**, **I**).

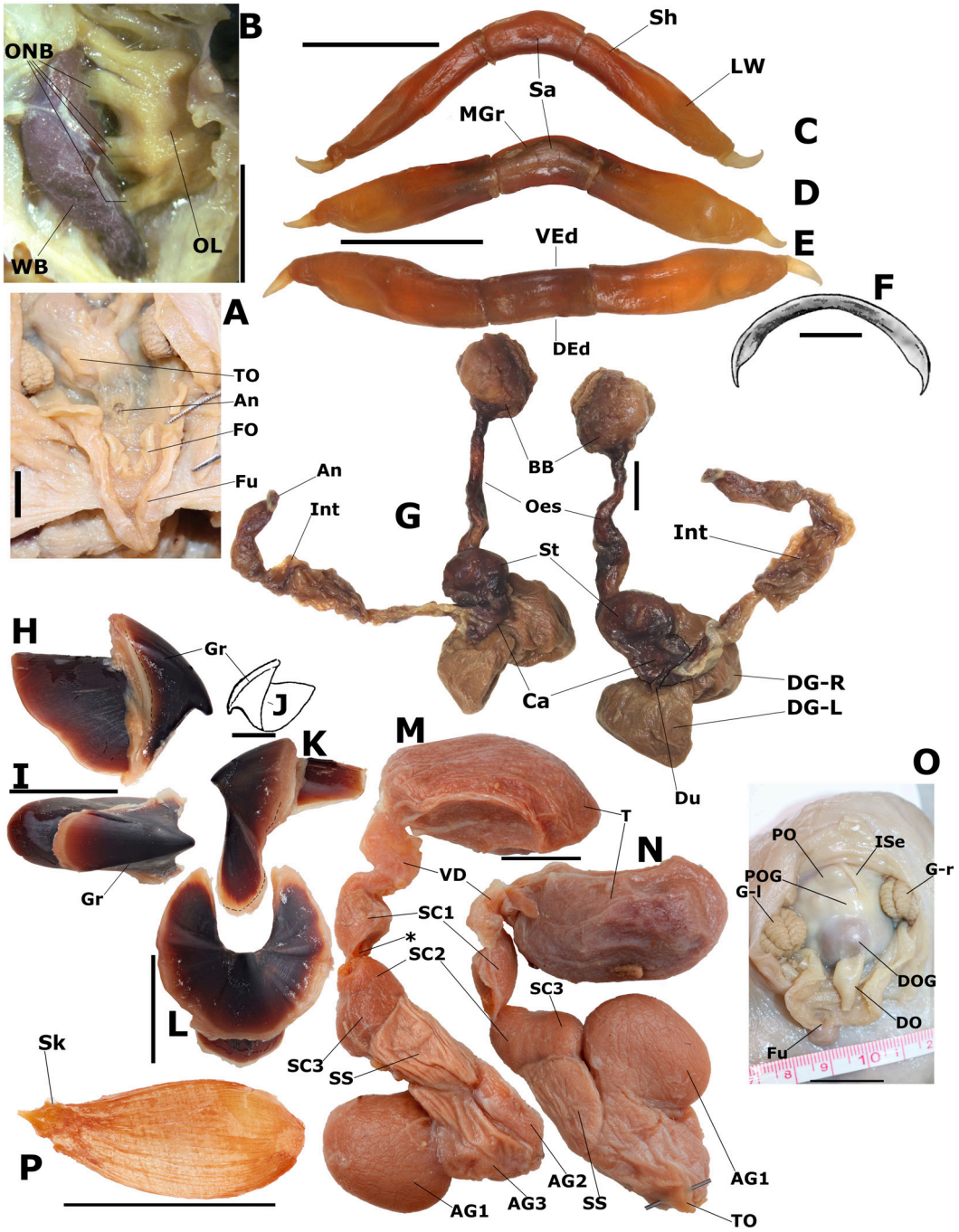

Figure 11. Internal morphology of *Exsuperoteuthis persephone*. **A**) Funnel organ and adjacent structures (male, MV F51086). **B**) Left-side optic nerve branching pattern through white body (male, WAM S113335). **C–E**) internal shell (male, WAM S113335) with dorsal (**C**), antero-posterior (**D**), and posterior (end-on) (**E**). **F**) internal shell from type series female (modified from Berry 1918, Plate 82 fig. 10) **G**) two dorsal aspects of the digestive system (structures moved to show lateral aspects in the two images, e.g., in the right-hand image the buccal bulb is positioned laterally with dorsal edge at left (male, WAM S113335). **H**,**I**) upper beak (male, WAM S113335), lateral and dorsal aspects. **J**) upper beak from female type material (modified from Berry 1918, fig. 67). **K, L**) lower beak (male, WAM S113335) lateral and ventral aspects (**K**, **L**). **M, N**) male reproductive system (WAM S113335), right and left lateral aspects. **O**) female reproductive system *in situ* (TMAG E46505). **P**) encased egg dissected from distal oviduct (TMAG E46505). Abbreviations/symbols: *—cut between SC1 & SC2; An—anus; AG1–3—accessory gland part 1–3; BB—buccal bulb; Ca—caecum; DEd—dorsal edge; DG—digestive gland (DG-R & -L are right and left lobes); DO—distal oviduct; DOG—distal oviducal gland; FO—funnel organ; Fu—funnel; G-r/l—Gill-right/left; Gr—groove (of flexure) of beak hood; Int—intestine; ISe—Interpallial septum; LW—lateral wing of shell; MGr—medial groove of shell saddle; Oes—oesophagus; OL—optic lobe; ONB—optic nerve bundle; PO—proximal oviduct; POG—proximal oviducal gland; Sa—saddle; SC1–3—spermatophoric complex part 1–3; Sh—shoulder (of shell); Sk—stalk; SS—spermatophore sac (Needham's sac); St—stomach; T—testis; TO—terminal organ; VD—vas deferens; VEd—ventral edge; WB—white body. Scale bars = 10.0 mm (**A**, **B**, **F–I**, **K**, **L–N**, **P**), 20.0 mm (**C–E**,**O**), 5.0 mm (**J**).

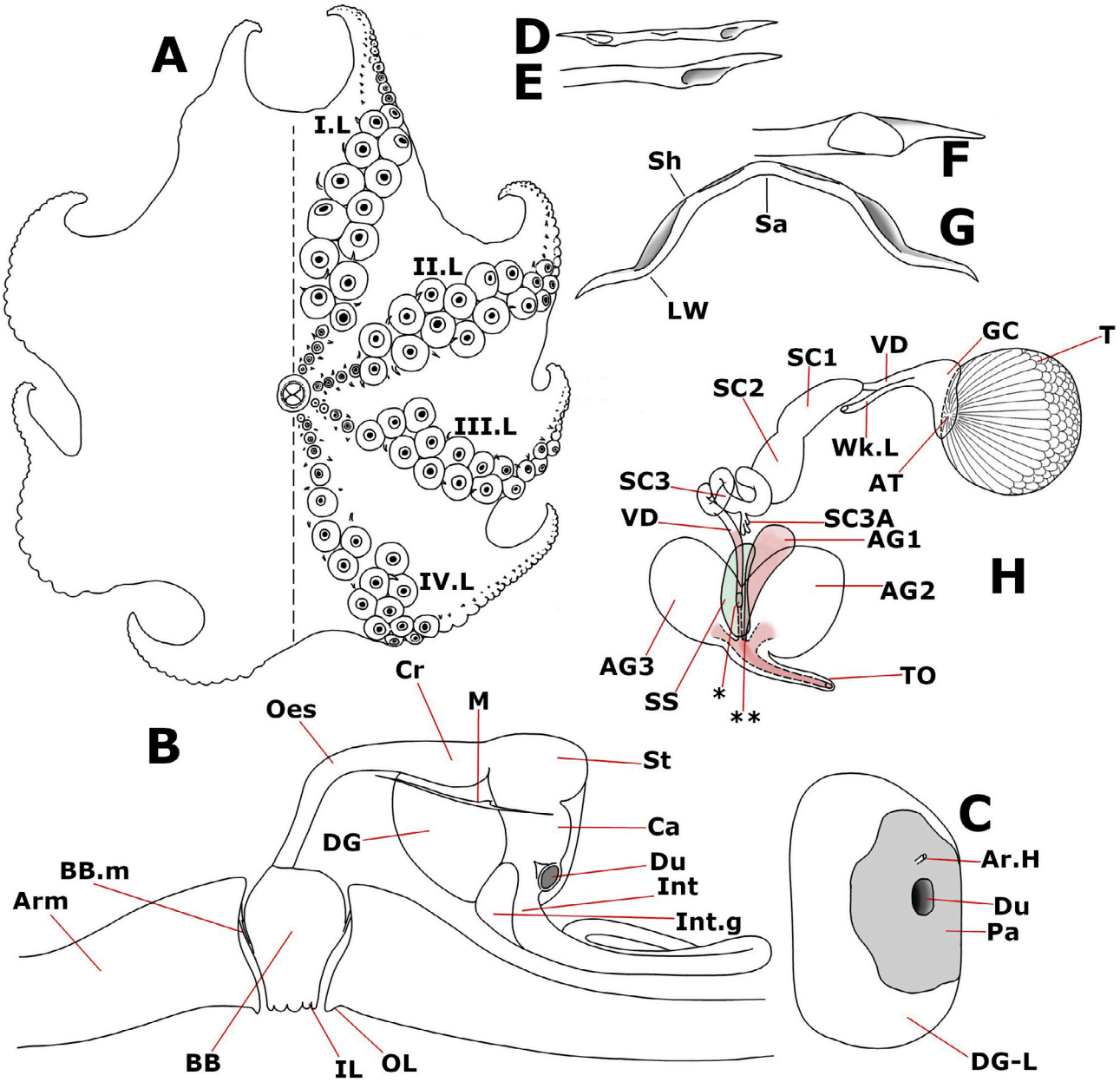

Figure 12. Comparative illustrations of *Exsuperoteuthis depressa* (redrawn from literature). **A**) Oral aspect of male specimen showing enlarged suckers (from Sasaki 1929, textfig. 4). **B**) lateral schematic of digestive system of male *O. depressa* (left DG lobe cut-away) (from Meyer 1906, Plate 12, fig. 9). **C**) inner-side view of left DG lobe (from Meyer 1906, Plate 12, fig. 11). **D**, **E**) internal shell from the *O. depressa* Holotype (female), posterior (end-on) aspects with '**E**' a close-up (from Sasaki 1929, Plate 7, fig. 9). **F**, **G**) Internal shell of a mature male, dorsal aspect (**F**) and a posterior (end-on) close-up of one side of the shell (**G**) (from Sasaki 1929, Plate 7, fig. 8). **H**) Male reproductive system (from Meyer 1906, textfig. 8). Abbreviations/symbols (original wording of some structures differ in original sources and this is noted in parentheses): AG1/2/3—accessory gland 1–3 (AG2 and 3 originally both labelled AG2); Ar.H—Arteria hepatogastrica; AT—aperture of testis; BB—buccal bulb; BB.m—buccal bulb attachment muscles; Ca—caecum (2nd or spiral stomach); Cr—crop (dilation of oesophagus); DG—digestive gland (liver), Du—hepatic duct (liver duct); GC—gonad cavity; Int—intestine (3rd stomach); I/II/III/IV.L—Arms I–IV left; Int.g—glandular wall of intestine; LW—lateral wing of shell; M—membrane (organ of unknown importance); Oes—oesophagus; Pa—pancreas; SC1–3—spermatophoric complex parts 1–3 (vesicula seminalis 1–3); Sa—saddle of shell; SC3A—SC3 appendage; Sh—shoulder of shell; SS—spermatophoric sac (Needham's sac); St—stomach (muscular or chewing stomach); T—testis; TO—terminal organ (penis); VD—vas deferens; Wk.L—left water canal.

With a very gently arching U-shape (far broader than other opisthoteuthids examined herein), amber-coloured, semi-translucent; saddle outer (posterior) face with strong groove, inner (anterior) face convex, saddle very shallow relative to the broadly-flared lateral wings (SHI ~50%); lateral shoulders poorly developed, relatively flush with saddle–lateral wing outer face (SSI 48%); lateral wings very strongly flared (angle 57°–58° from saddle mid-point along antero-posterior line) with gentle concave indentations lateral to each saddle

shoulder, wings gently expanding and medially wider than saddle; wings distally tapering to short spike-like tips, flared out. Berry (1918) illustrated the internal shell from a female specimen (USNM 816320, station E5722) (**Fig 11 F**), Berry noted that compared to *O. pluto* the shell of *O. persephone* was shallower and broader (wing angle ~56° from mid-point), and with less pronounced and abrupt muscle insertion points (shoulders), in agreement with material examined herein.

Arms and webbing: arms thick, heavily imbedded in webbing and gelatinous tissue (see **Fig 10 C–E, J, K**), elongate but variable in length (due to mantle/head shrinkage), no consistent arm formula but ventral arms III & IV longer than the dorsal arms I & II (on all but one specimen), dorsal arm length 3.8–5.9× ML males, 2.9–3.2× ML females, ventral arms 4.2–5.2× ML males, 3.1–3.3× ML females. Dorsal arms not more robust compared to other arms (mid-arm thickness 21 mm (IL), 22.6 mm (IL), 21 mm (IIIL) on male MV F51086) (also confirmed by Lu 2010). Webs deep, simple, subequal (no consistent formula), web A medial depth 38%–54% arm I length males, 64%–66% females; web E medial depth 39%–51% arm IV length males, 61%–70% females. Web nodules not apparent, web edges thick, fleshy, web edges run close to arm tips and attach slightly more distal on the dorsal arm edges (~45–55th sucker).

Suckers and cirri: maximum sucker count to 78–90 (similar on males and females, arm tip damage often gives counts ~70 on several arms), female holotype with up to 78 suckers on arms I & II per Berry (1918, p. 291).

Suckers sexually dimorphic, males with single enlarged sucker field on all arms (**Fig 10 C, D** (preserved); **Fig 10 K** (fresh condition); **Fig 10 F–H** (close-up aspects of enlarged suckers)), covering majority of the arm, essentially as a combined PESF and DESF. Proximal 3 or 4 suckers very small, 4th or 5th abruptly larger and steadily increasing in size, maximum size of enlarged suckers reached approximately at the 12th to 16th sucker, remaining at comparable size over most of the central arm and out to the distal quarter. The distribution of largest enlarged suckers within the combined field varies subtly between specimens, on some the largest suckers are more distal (towards the 29th–34th sucker) whereas the largest is closer to the 15th or 16th on others, and a slight reduction in enlarged sucker diameter is sometimes just perceivable between these regions[1], though for a given specimen the largest suckers proximally and distally along the combined field are within 1 or 2 mm diameter. Maximum diameter of enlarged suckers 14.3%–18.6% ML (immature male F164064 B, without clear enlarged field, largest suckers ~8%–9% ML), infundibular ring of enlarged suckers ~44%–74% acetabular ⌀. Enlarged suckers crowded, bases touching, appearing as biserial row in distal half of enlarged sucker fields (see **Fig 10 D, H**) (biserial pattern inconsistent across arms). Enlarged suckers with acetabular bases swollen and globose (well evident in **Fig 10 F, G**), variably exposed given shrinkage of arm tissue. Infundibular structures with ring thick, pad relatively narrow, aperture large. In distal ~quarter of the arm, near webbing attachment, enlarged suckers are still near maximum size at 29th to 34th sucker as mentioned, before reducing in size, most distal enlarged sucker number 35th–45th (last 3 or 4 intermediate in size with following small suckers, **Fig 10 G**; or the drop in size distally is more abrupt[2]), followed by ~40 to 50 small suckers extending out to the arm tips with minute size.

Females with the first 3 suckers very small, increasing in size, 4th notably larger with maximum sucker dimensions reached approximately between the 10th to 20th sucker and remaining similar over most of the arm (SDI mid-arm 6.0–6.4% ML), before decreasing in the distal arm. Female suckers generally more imbedded into and with infundibular disk flush with the arm surface, the acetabular and infundibular diameter being comparable (**Fig 10 E, I**).

Cirri commence between 1st and 2nd suckers (rarely 2nd and 3rd on some arms of some specimens) as minute buds, slowly increasing in length, reaching greatest length at approximately 18th to 20th sucker, remaining similar in length over central arm. Cirri frequently retracted into pockets, especially on specimens where flabby skin tissue has minimal shrinkage. Longest cirri 7.1%–15.2% ML males (0.5–1.1× mid-arm, enlarged sucker ⌀), 5.5%–5.9% ML females (0.9–1.0× mid-arm sucker ⌀). Cirri lengths reduce on distal third of arms, continuing to arm tips.

Digestive system: dissected from male specimen (**Fig 11 G**). Buccal bulb large (equalling combined stomach/caecum dimensions); no salivary glands (anterior or posterior) apparent externally on the buccal bulb or oesophagus; odontophore present, radula absent; labial palps (lacking palatine teeth) and salivary papillae well-developed. Upper beak tall (height 73% beak length, or 85% width), hood deep (hood length 68% beak length), with distinctive lateral groove each side running up to hood crest (see **Fig 11 H, I**), hood crest rounded (convex); rostrum blunt, deflected down, jaw cutting edge smooth; lateral walls near-parallel, their posterior edges convex (with small indentation midway along the edge), postero-dorsal apex (crest) rounded. Berry (1918, fig. 67) (**Fig 11 J**) illustrated the upper beak matching that herein (USNM 816320, from station E5722), including the distinctive lateral groove or "angle" along the sides of the hood. Lower beak tall (height 60% width), with relatively short hood (hood length 57% beak length), and elongate wings (wing length 116% beak length) with strong diagonal flexures each side (**Fig 11 K, L**); rostrum small and blunt-tipped (non-hooked), hood crest rounded. Oesophagus with swelling in proximal two thirds towards the stomach, representing a simple crop without diverticula (**Fig 11 G**); stomach simple, muscular, rounded; caecum smaller than stomach

(greatest dimensions ~70% that of stomach), simple, non-spiral; digestive gland bilobed, two short ducts connecting to caecum; intestine very long, approximately 2.2× length of oesophagus and crop, in distal half intestine makes a single loop before terminating at anus. Digestive system with dark purplish membrane over buccal bulb, oesophagus, stomach, and rectum where it projects into the mantle cavity; caecum, and intestine without strong pigmentation.

Male reproductive system: illustrated per **Figure 11 M, N**; testis ovoid; vas deferens short; spermatophoric gland complex three-parted, more proximal SC1 separated, more distal SC2 and 3 thicker and well joined to each other; spermatophoric sac (Needham's sac) large, positioned between SC3 and accessory gland complex; AGC dominated by posteriorly positioned AG1, rounded, greatest dimension exceeding combined AG2 and 3 (latter's greatest dimension 75% of the former); terminal organ short, triangular, flush with combined AG2 and 3 (though more projecting in other male specimens).

Female reproductive system: observed *in situ* (**Fig 11 O**); ovary large, occupying posterior part of body; proximal oviduct elongate, containing multiple oocytes; oviducal gland large, two-parted, proximal oviducal gland pale beige-cream-coloured, distal oviducal gland dark brown-pigmented, with greater dimensions (proximal oviducal gland length 61%–80 %, width 72%–81% overall gland dimensions), both oviducal gland parts longitudinally striate; distal oviduct length slightly less than oviducal gland (length 90%–95% oviducal gland).

Mature encased egg from distal oviduct (from TMAG E46505), with brittle casing, elongate and teardrop-shape (**Fig 11 P**), light honey-brown colour, 12.2 mm long × 5.8 mm wide (L:W ratio = 2.10). The casing forms a thick 'stalk' at one pole (likely not homologous with the stalk of classical cephalopod eggs), from 'stalk' longitudinal ridges head parallel to egg long axis (roughly 50−60), several branching from thicker ridges at the 'stalk'; antipodal to 'stalk' the ridges end abruptly at an irregularly-shaped smooth patch with finely dimpled texture. The whitish chorion fits well within the egg casing, with little free space.

Colouration: body surfaces and aboral surfaces of arms and webbing pale and largely unpigmented, with greyish-blue tone on fresh specimens (**Fig 10 J**), faintly pinkish on preserved specimens (**Fig 10 A, B**), small flecks and streaks of darker brown–maroon pigmentation on head and fins apparent on some specimens. Oral surfaces of webbing with distinct dark-bluish or purple-grey pigmentation, overlayed by colourless loose tissue, oral surfaces of arms paler (fresh condition **Fig 10 K**; preserved **Fig 10 C, E**). Suckers and cirri with a paler whitish or beige colour, contrasting against the adjacent arms and webbing. Areolar spots: present, arms I with 11 or 12 very-small areolar spots each, the first three pairs (for each dorsal arm) located on the head between the eyes. Arms II–IV each with 7–9 countable spots, starting immediately below the eye (arm II), between the eye and fin base (arm III), and near the fin base (arm IV). Spots extremely small, ~1 mm in diameter, each comprising a circular colourless area surrounded by a dark brown-pigmented ring, on many specimens the spots cannot be located, or are not clearly countable. Berry (1918) recorded 3–7 minute areolar spots along each arm.

[1] This slight reduction midway along the combined field could be a remnant of an ancestral condition, i.e., from animals with well separated PESF and DESF.

[2] On male MV F164064A arm IL, the 39th sucker (6.5 mm diameter) is followed by the 40th sucker (4.2 mm diameter).

Material examined.

WAM S113335, male (ML 58 mm), off Ulladulla, southern NSW, 35°25−29′S, 150°50−48′E, 549 m, FRV *Kapala*, Stn K71-13-06, 2.viii.1971 [donated to WAM by the Australian Museum, Sydney]. TMAG E46505, female (ML 56 mm), off eastern Victoria, SE Australia, 38°13'56"−14'37"S, 149°34'55"−33'31"E, 500−590 m, FRV *Southern Surveyor*, SS01/00, Stn 205, 23.iv.2000. MV F51086, male (ML 48.8 mm), off Cape Grim, 40°18'36"S, 143°16'48"E, 550 m, TFDA FV *Margaret Philippa*, MP0010001 (MP01 shot 1), 31.viii.1983 (coll. M. Cannon). MV F51088, female (ML 43 mm), SW of Cape Grim, 41°0'36"S, 143°31'12"E, 570–595 m, TFDA FV *Margaret Philippa*, MP0010004 (MP01 shot 4), 1.ix.1983 (coll. M. Cannon) [determined by G. L. Voss]. MV F164064 A, male (ML 51 mm), NW of Tasmania, 41°02'39"S, 143°53'06"E, 518–520 m, CSIRO RV *Soela*, SO1/85, Stn 17 (Engels high lift demersal trawl), 24.iv.1986. MV F164064 B, immature male (ML 37.3 mm), NW of Tasmania, 41°02'39"S, 143°53'06"E, 518–520 m, CSIRO RV *Soela*, SO1/85, Stn 17 (Engels high lift demersal trawl), 24.iv.1986.

Material not examined directly (photography and measurements provided).

Holotype. AM C.148253 [Berry registration No. S.S. 480], female, RV *Endeavour* Stn E5718, 42 miles SE of Genoa Peak (Victoria), 37°56'45"S, 150°10'35"E, 475.5 m (260 fathoms), i.1917 [very poor condition, dried & rehydrated].

Distribution: Type series collected from the Great Australian Bight (130°10–50′ E) and off southeastern Victoria (40–42 miles south-east of Genoa Peak), depth range 274–549 m (150–300 fathoms), the holotype and paratype both being from off Victoria (per Berry 1918; table 30). Material examined herein was from off southern NSW, southeastern Victoria (near the type locality), and off western Tasmania (500–595 m depth) (**Fig 1**). Overall, *E. persephone* seems to be widely distributed around southern Australia from NSW to the southwestern end of Western Australia, 274–595 m depth.

Table 7. *Exsuperoteuthis persephone* measurements and counts. *Damage. Measurements in mm.

ID	MV F51086	MV F164064 A	MV F164064 B	WAM S113335	TMAG E46505	MV F51088	AM C.148253 Holotype
Sex	Male	Male	Immature Male	Male	Female	Female	Female
TL	235	220	180	Unclear	220	180	NA
ML	48.8	51	37.3	~58	~56	43	NA
MW	54.3 (49.2)	65.7	52	61	65	48.8	35
HW	60.4	80.5 (70 EyO)	59.8 (49.6 EyO)	104	88 (60 EyO)	66.2 (55.6 EyO)	50
ED	33–36.5	35–36	24–26 (11 EyO)	~35 (lens 21–22)	~28–30	27–30	NA
FL (L/R)	37R	33 (36 outer edge, 29 inner)	NA (fins inverted)	~20**/42	NA (fins inverted)	19.8/15.6	20
FW (L/R)	16R	21	NA*	15/16	NA*	13/9.4	14
FuL	35	32.6	27	40	30	28.5	NA
PA	20	25	20	17	~16	~20	NA
GilI (L/R)	6/6	7/6 (W=13.4L, L=12.5L)	6/6	7/7	6/6	6/6 (W=11.8L, L=10.4L)	6
AL I (L/R)	166*/206	245/229*	140/113*	345/190*	130*/160	115*/137	150/165
AL II (L/R)	222/207	245/246	145/135	325/350	164/140*	138/142	160/160
AL III (L/R)	200/217	256/229	154/143	240*/319	167/181	139/125*	170/175
AL IV (L/R)	210/215	246/266	145/155	230*/272*	172/171	139/140	165/165
SC I (L/R)	55*/69	70/61*	66/40*	68/26*	38**/77	41*/67	78 R
SC II (L/R)	72/72	80/80	73/74	81/74*	76/50**	72/72	78 R
SC III (L/R)	78/87	74*/83	79/76	34*/79	82/77	70/51*	72 R
SC IV (L/R)	81/81	89/60*	79/81	35*/72	90/82	68/78	72 R
SuD	See enlarged suckers	See enlarged suckers	3.4^{Acet}, 2.7^{Inf} (IL, 32nd) 3.1^{Acet}, 2.2^{Inf} (IIIL, 15th)	See enlarged suckers	3.5 (IIIL, 11th) 3.6 (IIR, 20th)	2.6 (IIR, 20th) 2.5 (IR, 18th) 2.2 (IIR, 30th)	2+ (IR, 5th)
Enlarged sucker field position	4th/5th–36th/37th I 4th/5th–37th II 4th–35th or 38th III 5th–35th IV	4th–39th or 41st I 4th–37th or 40th II 4th–36th or 37th III 4th or 5th–38th IV	Not developed yet, immature	4th–40th I 4th–41st or 45th II 4th–40th III 4th–38th IV	NA	NA	NA
Enlarged sucker diameter	7.0^{Acet}, 4.4^{Inf} (IR, 33rd); 6.4^{Acet}, 4.3^{Inf} (IVL, 14th)	7.6^{Acet}, 5.6^{Inf} (IR, 29th); 6.8^{Acet}, 5.0^{Inf} (IR, 15th); 6.8^{Acet}, 4.4^{Inf} (IVR, 22nd)	Not developed yet, immature	10.8 ^{Acet}, 4.8^{Inf} (IIR, 16th); 10.4^{Acet}, 7.3^{Inf} (IR, 12th)	NA	NA	NA
CiL	3.45 (IR, 15-19th) 3.0 (IR, 18th)	4.4 (IIL, 21st–22nd) 4.3 (IR, 24th–25th) 3.6 (IR, 15th–16th)	3.9 (IIL, 20th–21st) 3.3 (IL, 18th–21st)	7.3–8.8 (IL, ~17th); 5.6 (IIR, 17th-18th)	~3.1 mid arm 2.0 (6th-7th)	2.55 (IR, 18–19th) 1.8 (IR, 18th–19th)	NA
Ci start sucker position	1 & 2	1 & 2	1 & 2	1 & 3	1 & 2	1 & 2 (2 & 3 on IR)	NA
WD A	111	92**	58	~100 (badly contracted)	103	90	100
WD B (L/R)	110/105	98/99	72/59	145	105/100	87/82	
WD C (L/R)	120/107	102/95	56/57	162	111/100	*/86	105

WD D (L/R)	117/109	102/98	62/71	160	108/108	85/86	
WD E	108*	105*	73*	~140	108	85	115
WN	NA	NA	NA	NA	NA	NA	
Areolar spots	11, arm IR	12, arm IR 7+, arm IIL/R 9, arm IIIL 8, arm IVL	9+, arm IL 7, arm IVL	Present?	Present?	11, arm IR	Present
Notes	Additional sucker measurements: 6.1^{acet}, 4.7^{inf} (IIIL, 11^{th}); 6.9^{Acet}, 4.6^{Inf} (IL, 30^{th})	Additional sucker measurements: Arm IL distal-most enlarged sucker 6.5^{acet} (39^{th}), 4.2^{acet} (40^{th}); 7.1^{acet}, 4.7^{inf} (IIR, 17^{th})	Additional sucker measurements: 2.8^{acet}, 2.0^{inf} (IL, 33^{rd}); 2.9^{acet}, 2.3^{inf} (IL, 19^{th})		DO 14.6 mm; DOG L=13, W=18; POG L=16, W=13.	DO 12.8; DOG L=8.25, W=14.6; POG L=5.35, W=11.8	

Etymology: Specific epithet after the mythological *Persephone*, the Ancient Greek queen of the underworld and husband of *Pluto*. Berry presumably chose this name in reference to the light colouration of this species (relative to *O. pluto*), relating to the periodic return of *Persephone* to the overworld and connection of this with light and spring.

Proposed vernacular name: Persephone's flapjack octopus.

Remarks: Berry (1918) made no clear reference to enlarged suckers in his description, and his type material was probably female (the type specimen matches females herein; per Berry's original photograph of its oral surfaces, Berry 1918, Plate 86). The *E. persephone* holotype is in extremely poor condition, having dried out at some point before being rehydrated (Australian Museum photography, now shown). However, Berry's (1918) original description seems to be sufficiently detailed to facilitate the identification of more recently collected material. *Exsuperoteuthis persephone* comb. nov. and *O. pluto* are sympatric along southern and southeastern Australia, and Berry differentiated *O. persephone* from *O. pluto* based on its colouration, and fewer gill lamellae (6. *vs.* 8 per gill). The colouration does seem useful in differentiating the species, with the pale aboral surfaces and bluish-slate oral surfaces being distinctive to *E. persephone*, and gill lamellae counts are also distinct. The series of small areolar spots also distinguishes *E. persephone* from *I. obscura* sp. nov. with its singular large areolar spot associated with each arm.

Lu (2010) examined *E. persephone* specimens as comparative material during his description of *O. dongshaensis* Lu, 2010. In this research Lu identified mature males of *E. persephone* permitting the diagnosis of the enlarged sucker configuration and digestive gland form, noting the DESF restricted to arms I and II, with these suckers smaller than PESF suckers and with a high number, but interestingly the same male specimens that Lu examined (examined herein from Museums Victoria) don't seem to have such a pattern of enlarged suckers, rather they have an enlarged sucker pattern consisting of a row of enlarged suckers spanning the whole medial region of each arm (a combined PESF and DESF). The male specimen from off New South Wales (WAM S113335), which had the same highly unusual sucker pattern, was consistent with this MV material, as was an Australian Museum specimen photographed in fresh condition (see **Fig 10 J, K**; also illustrated by Reid 2016, p. 301).

The enlargement of suckers on the male of this species is very distinctive, possibly a PESF that has extended across to the DESF (thus it would be incorrect to describe the distal field as missing, rather it is instead a combined enlarged sucker field). This configuration is only observed in two other species of '*Opisthoteuthis*' (herein also allocated to *Exsuperoteuthis*), *E. depressa* comb. nov. (Ijima & Ikeda, 1895) and *E. japonica* comb. nov. (Taki, 1962) (both from the northwestern Pacific off Japan). This immediately distinctive 'hectocotylization' in these three species was deemed sufficient to allocate them to the new genus *Exsuperoteuthis*.

Ijima & Ikeda (1895) described *O. depressa* from a single sexually immature male specimen collected near Sagami Bay (Japan) (HW across eyes 26 mm), this specimen lacked any sucker enlargement and from the original description is essentially indistinguishable from any other *Opisthoteuthis* (at the time only *O. agassizii* had been described). Though it did have 6 lamellae per gill, cirri commencing between suckers 1 & 2, and from illustrations had a bilobed digestive gland (Ijima & Ikeda 1895, Plate 33, fig. 7, 9). Meyer (1906) also described an *O. depressa* male that lacked sucker enlargement as this too was apparently sexually immature (both it and the holotype being very small), though he did describe and illustrate its reproductive system in detail (Meyer 1906, textfig. 8), and digestive system with bilobed digestive gland and elongate intestine (Meyer 1906, Plate 12, fig. 9, 11). Sasaki (1929) described further specimens from around Japan (Sagami, Satsuma, and Kii provinces), noting a sucker count on females ~50, but more importantly he described a mature male (HW across eyes 45 mm) with a distinct enlarged sucker field extending from

suckers 5–20 or 22 on all arms. These enlarged suckers had such large acetabular bases that they could not form a straight series, the crowding giving the appearance of a biserial or triserial sucker row (Sasaki 1929, textfig. 4). For comparison with *E. persephone*, several illustrations of *E. depressa* from Meyer (1906) and Sasaki (1929) have been redrawn herein in **Figure 12**.

E. persephone is similar to *E. depressa* in having a single combined enlarged sucker field in the males, spanning the proximal–distal arm region (**Fig 12 A**), having a bilobed digestive gland and an elongate intestine (~2× oesophagus length) (**Fig 12 B, C**), and in having a similar shell form (**Fig 12 D–G**). The shell of *E. depressa* is shallow (broad V-shape or arc) and lacks prominent saddle shoulders, similar to *E. persephone*. The clearest distinction in *E. persephone* relative to *E. depressa* is the greater number of enlarged suckers at 30–42 per arm, vs. 15–17 on the male *E. depressa*. Enlarged suckers of *E. persephone* are also proportionally smaller than those of *E. depressa*, Sasaki (1929) measured the largest sucker diameter of male *E. depressa* at 10 mm (22% of the HW of 45 mm), greater than *E. persephone* male maximum sucker diameter of 7.0–10.8 mm (9.4%–11.6% HW). The colouration is also a distinct difference between the Australian and Japanese species, the pale, somewhat colourless aboral surfaces of *E. persephone* not being comparable to the bright orange or orange-brown tones of *E. depressa* (see Norman 2000, p. 182).

Taki (1963) provided a brief description of *O. japonica* (following a Japanese description the year prior in Taki 1962) from two male specimens (Wakayama Prefecture, Japan, 152 m depth), it differed from *O. depressa* in that the enlarged suckers occurred from suckers 5–14, it lacked areolar spots, and had a shell and lower beak shape somewhat differing (the lateral ends of the shell being small spikes offset from the main saddle). However, from the provided photos (Taki 1963, Plate 3, fig. 2) the enlarged suckers run from suckers 5–19 or 20 (i.e., 15 enlarged suckers per arm), comparable to *E. depressa*, and the differences in the shell and beak could be due to damage or preservation artifacts. Given that *E. japonica* and *E. depressa* are sympatric off Japan, the former is herein recognized as a junior synonym of *E. depressa*, but a revision of Japanese opisthoteuthids is overdue and would help confirm this synonymy and untangle suspected misidentifications with other north Pacific taxa.

Genus *Insigniteuthis* gen. nov.

ZooBank LSID:
urn:lsid:zoobank.org:act:FD9123C8-2E73-4BFA-8C09-33328B632337

Type species: *Insigniteuthis obscura* **sp. nov.**, here designated.

Diagnosis: Opisthoteuthids with DESF variably on arms I–IV and comprised of a small number (~2–5) of greatly enlarged suckers (diameter > PESF) (see **Fig 2**). Digestive gland bilobed or unilobed.

Species allocated: *I. bruuni* **comb. nov.**, *I. albatrossi* **comb. nov.** (incl. synonymised *O. californiana*), *I. calypso* **comb. nov.**, *I. dongshaensis* **comb. nov.**, and *I. obscura* **sp. nov.**

Etymology: Derived from the Latin '*insignis*' meaning remarkable or obvious—in reference to remarkably distinctive distal enlarged suckers of mature males, combined with the Greek '*teuthis*' (τευθίς) meaning 'a squid'.

Remarks: This genus approximately encompasses O'Shea's (1999) 'Type 2' *Opisthoteuthis*, though *O. chathamensis* is retained in genus *Opisthoteuthis* given that its DESF is more consistent with that genus. It is interesting that the two members of genus *Insigniteuthis* wherein the DESF is present on all arms (*I. calypso* and *I. bruuni*), are also the only species with a unilobed digestive gland, and these two may be more closely related. *I. bruuni* as illustrated by Voss (1982) had 2–3 enlarged suckers in each DESF, but only immature specimens were examined, and the DESF suckers were small. Until the diameter of DESF suckers relative to PESF can be confirmed on mature males of this species, its placement in this genus is tentative (as detailed in the earlier discussion).

Insigniteuthis obscura sp. nov.

(Figure 13–15, Table 9 & 10)

ZooBank LSID:
urn:lsid:zoobank.org:act:A4569426-679A-4012-88C2-B4CDE7F50898

Type specimen lodged at the South Australian Museum, Adelaide (SAM D20278).

Synonymy.

Opisthoteuthis pluto (**in part**)—O'Hara *et al.* (2020)

Grimpoteuthis sp.—Trotter *et al.* (2022)

Diagnosis: Opisthoteuthid with 74–88 suckers per arm of adult, males with DESF of 3–5 enlarged suckers (with 2 or 3 greatly enlarged per DESF) on arms II–IV, DESF sucker diameter considerably exceeding maximum diameter of PESF suckers; web nodules absent; with dark brown−pink-purple aboral pigmentation, and a single large areolar spot near the base of each arm. Internally with digestive gland bilobed, 7 or 8 lamellae per gill, AG1 dominating AGC (approximately equal to size of combined AGC2 and 3), and with intestine approximately 1.6× oesophagus length.

Description: Mantle short, rounded posteriorly, width and length comparable (MWI 72%–118% male, 156% female) (**Fig 13 A–C**). Head considerably wider than mantle (HWI 104%–133% in males, 188% in female). Fins sub-terminally placed on mantle, relatively small (FLI 60%–80% male, 57–63% female). Fin width greatest near base, but with small constriction basally (FWI 35%–50% male, 68%–70% female), posterior fin edge straight, anterior and distal edges rounded. Eyes very large (EDI 49%–63% male and female), opening small and con-

Table 8. *Exsuperoteuthis persephone* indices. *Damage, **mantle greatly shrunken/distorted, indices likely slightly higher than actual.

Indices	MV F51086	MV F164064 A	MV F164064 B	WAM S113335 **	TMAG E46505	MV F51088	AM C.148253 Holotype
MWI	111%	129%	139%	105%	116%	113%	NA
HWI	124%	158% (137% EyO)	160% (133% EyO)	179%	157% (107% EyO)	154% (129% EyO)	NA
FuLI	72%	64%	72%	69%	54%	66%	NA
FLI (L/R)	76%R	65%	NA	72%R	NA	46%/36%	NA
FWI (L/R)	43%	64%	NA	38%	NA	66%/60%	NA
EDI	68%–75%	69%–71%	64%–70%	60%	54	63%–70%	NA
PAI	41%	49%	54%	29%	29%	47%	NA
Arm formula	II>IV>III>I*/ III>IV>II=I	III>IV>I=II/ IV>II>III=I*	III>IV=II>I/ IV>III>II>I*	I>II>III*>IV*/ II>III>IV*>I*	IV>III>II>I*/ III>IV>I>II*	IV=III>II>I*/ II>IV>I>III*	III>IV>II>I/ III>IV=I>II
Dorsal ALI	4.2× ML	4.7× ML	3.8× ML	5.9× ML	2.9× ML	3.2× ML	NA
Ventral ALI	4.4× ML	5.2× ML	4.2× ML	4.7*× ML	3.1× ML	3.3× ML	NA
SDI (normal)	See enlarged suckers	See enlarged suckers	9.1% 8.3%	See enlarged suckers	6.4% 6.3%	6.0% 5.8%	NA
Enlarged suckers	14.3% 13.1%	14.9% 13.3%	NA, Immature	18.6% 17.9%	NA	NA	NA
CLI	7.1%	8.6% 7.1%	10.4% 8.8%	15.2% 12.5% 9.6%	5.5%	5.9%	NA
Web formula	C>D>A=B>E A>D=E>C>B	E>C=D>B>A E>B=D>C>A	E=B>D>A>C E>D>B=A>C	C>D>B>E>A	C>E=D>B>A E=D>A>C=B	A>B>D=E (C*) A>D=C>E>B	E > C > A
WI A	54%	38%	41%	42% (Web B)	64%	66%	61%
WI E	50%	39%	47%	51%	63%	61%	70%

stricted. Funnel relatively long, tapering, (FuLI 46%–76% male and female), at least half funnel length free. Funnel organ V-shaped (but poorly preserved), lateral limbs of funnel organ thin out greatly where they converge distally. Pallial aperture gape small (PAI 35%–38% male, 46% female), enclosed around funnel. Olfactory papillae small, ovoid. Pallial adductor reduced to a narrow strap or band (per earlier species descriptions).

Gills: with 'half-orange' form, generally with 7 (and sometimes 8) primary lamellae per gill.

Optic nerve configuration: optic lobe large, ~rectangular, with optic nerves passing through each white body as four distinct bundles (right side white body exposed on male specimen) (**Fig 15 A**). White bodies relatively small, beige coloured (poorly preserved in specimen examined).

Internal shell: extracted from two specimens (male and female), both with some damage (**Fig 15 B–D**); very broad U-shape; saddle relatively short (SHI 35%–36%), narrow (SSI 50%–63%), outer (posterior) face concave, with strong groove, basal shelf absent; saddle shoulders well developed, with large concave outer face below each saddle prominence; shell wings diverge strongly from saddle mid-point at 56–58°, wings tapering to simple point (with tips only slightly flared relative to rest of wing); shell translucent, pale-yellow–orange.

Arms and webbing: arms thick, long (see **Fig 13** & **Fig 14**), approximately subequal (sometimes with dorsal or ventral arms longest, formula inconsistent), dorsal arm length 2.9–3.0× ML male, 3.4× ML female, ventral arms 2.7–3.2× ML (male and female). Arm I slightly more robust relative to other arms on males (mid-arm thickness 24 mm (I), 20 mm (II), 19.3 mm (IIIL), 19 mm (IVL), checked on SAM D72067). Web deep, simple, subequal (no consistent formula, though ventral sectors sometimes shorter), web A medial depth 53%–61% arm I length, web E medial depth 44%–60% arm IV length. Web nodules not apparent, but some thickening at web edge sometimes visible, web sectors attach along dorsal arm edges slightly more distal compared to ventral arm edges.

Suckers and cirri: maximum sucker count to 74–88 (comparable in males and females). Suckers sexually dimorphic, males with proximal and distal enlarged sucker fields (depicted **Fig 13 F, Fig 14 A, B**; schematized **Fig 14 C**). Male with proximal 3 suckers very small and slowly increasing in size, following 4–6 suckers comprise the proximal enlarged sucker field (PESF), the central 2–4 suckers being largest (PESF SDI ~6.8%–10.7%), with acetabulum swollen, globular, and partly elevated above arm tissue, infundibular ring and pad ⌀ ~70–80% acetabular ⌀, aperture large. Following mid-arm 'nor-

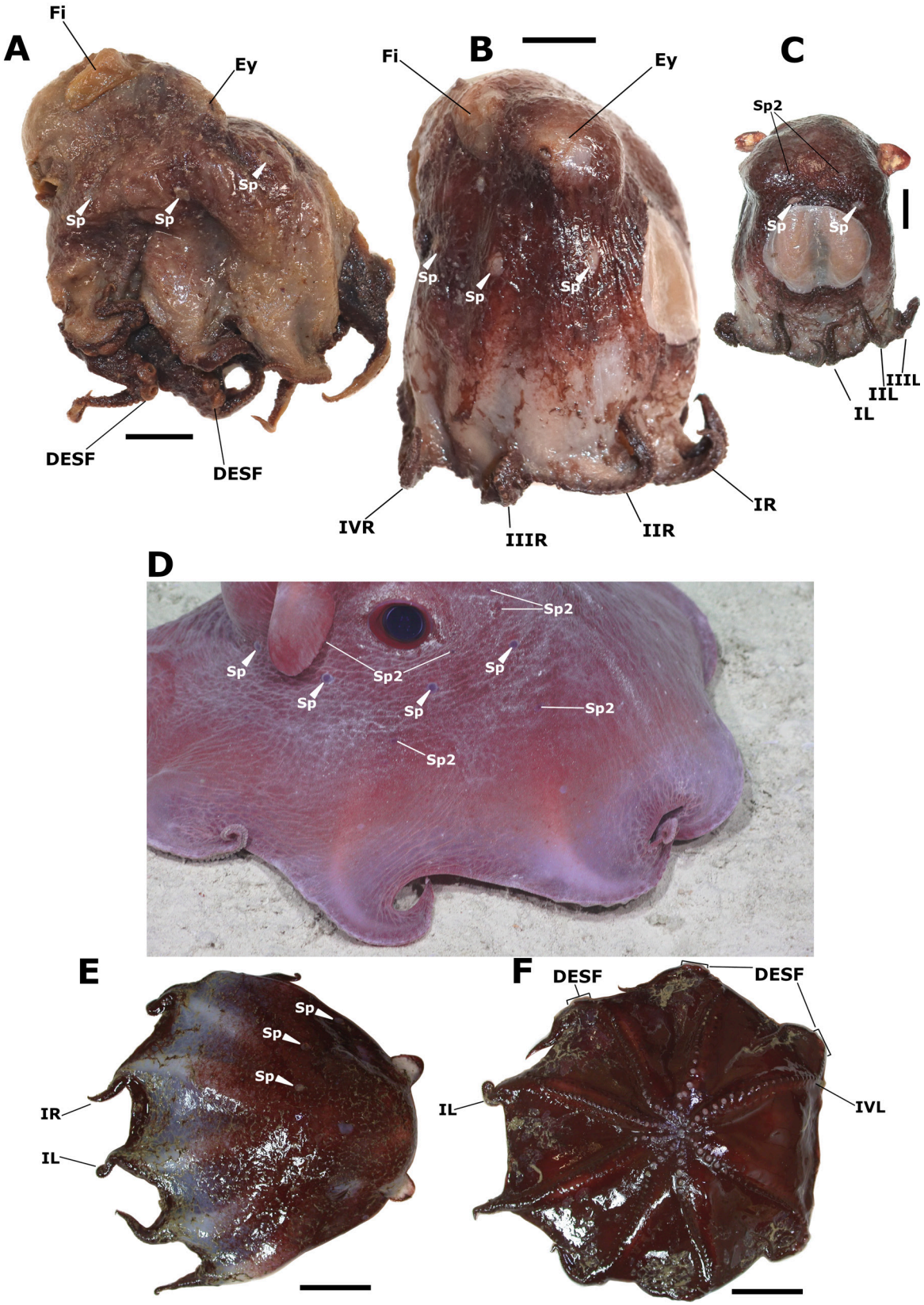

Figure 13. Whole aboral aspects of *Insigniteuthis obscura* sp. nov. depicting pigmentation and placement of large areolar spots. **A, B**) preserved specimens, male specimen, right side aspect (SAM D20278) (**A**), female (TMAG E44631) right side (**B**) and dorsal aspect (**C**). **D**) closeup of live specimen observed by ROV deployed by the RV *Falkor*, FK200126, 13.ii.2020 (image modified from original—Copyright: Schmidt Ocean Institute). **E, F**) freshly collected specimen (IN2017_V03, MV F245722) dorsal (**E**) and oral (**F**) aspects (Copyright: photographer Karen Gowlett-Holmes). Abbreviations/symbols: Ey—eye; Fi—fin; I–IV L/R—arm I–IV left/right; Sp—primary areolar spot; Sp2—secondary areolar spots. Scale bars = 20.0 mm (**A–C**), 50.0 mm (**E**, **F**).

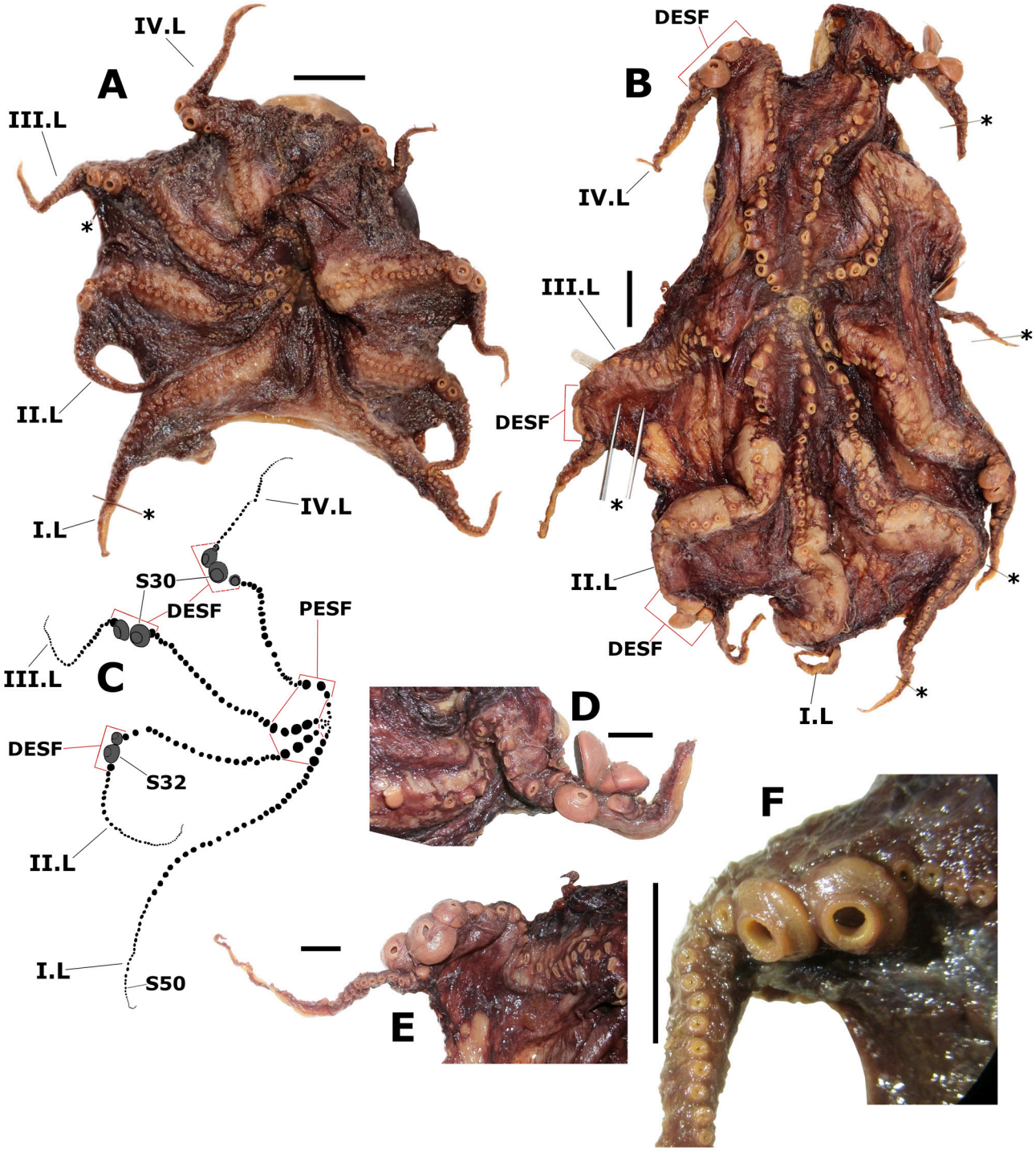

Figure 14. Arm and sucker detail of *Insigniteuthis obscura* sp. nov. **A**, **B**) oral aspects of male specimens depicting the enlarged sucker fields of a smaller (**A**) and larger specimen (**B**) (SAM D20278 and SAM D72067 respectively). **C**) schematic of relative sucker size of male *O. pluto* (based on '**A**'). **D–F**) close-up aspects of distal enlarged suckers, '**D**' & '**E**' are from a larger male (D72067, '**D**' showing some enlarged suckers in lateral profile), '**F**' depicts distal enlarged suckers of a somewhat smaller male (D20278) with enlarged suckers fewer in number and more imbedded. Abbreviations/symbols: *—prop used to pin down structures in photography; DESF—distal enlarged sucker field; I–IV.L—arm I–IV left; PESF—proximal enlarged sucker field; S30–50—sucker number 30–50. Scale bars= 20.0 mm (**A–C**), 10.0 mm (**D–F**).

mal' suckers reduced in size (SDI 4.4%–5.3%), more sunken into arm tissue.

DESF present on arms II–IV, comprising generally 4 suckers (sometimes 3 or 5) positioned between suckers 28–36; each DESF with 2 or 3 grossly enlarged suckers (generally the central 2, or proximal 2 or 3 in each DESF) with the other enlarged suckers being considerably smaller (see **Fig 14 D–F**). Largest DESF suckers with SDI 15%–23%, far exceeding diameters of PESF suckers. Largest and grossly enlarged DESF suckers ~conical, acetabula greatly enlarged, swollen, but with a truncat-

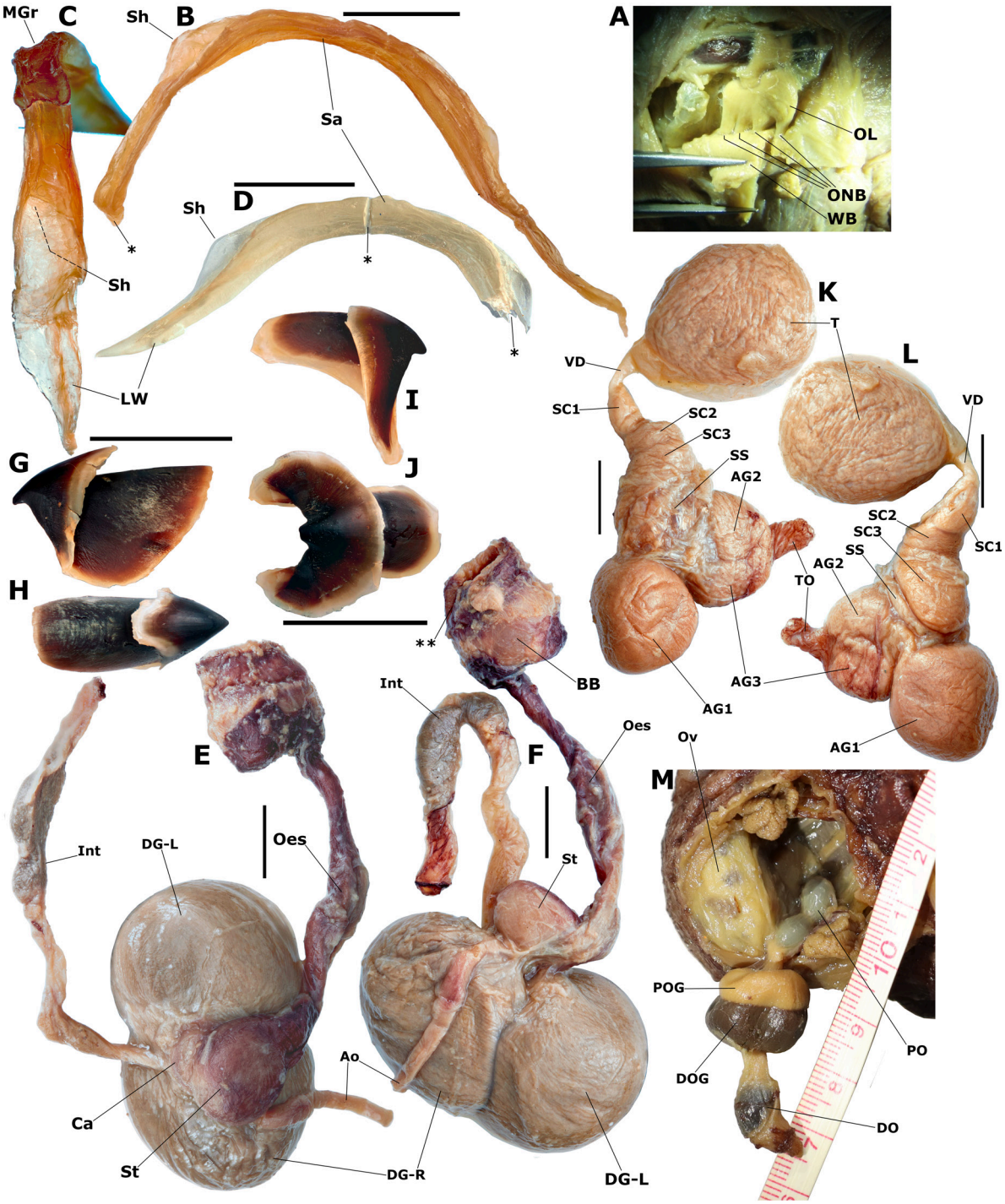

Figure 15. Internal morphology of *Insigniteuthis obscura* sp. nov. (male, SAM D72067). **A**) right-side retinal nerve branching pattern through white body (white body partly damaged). **B–D**) internal shell with dorsal (**B**) and lateral (**C**) aspects from a male specimen (SAM D72067), and dorsal aspect of shell from a female (**D**, TMAG E44631). **E**, **F**) dorsal and ventral aspects of the digestive system (SAM D72067), buccal bulb is positioned laterally (with dorsal edge at right and left in '**E**' & '**F**' respectively). **G–J**) beaks (SAM D72067) with upper beak lateral and dorsal aspects (**G**, **H**), and lower beak lateral and ventral aspects (**I**, **J**). **K**, **L**) male reproductive system (SAM D72067). **M**) female reproductive system (TMAG E44631), with oocytes in both distal and proximal oviduct. Abbreviations/symbols: *—broken sections of shell; **—cuts to remove beak; AG1–3—accessory gland part 1–3; An—anus; Ao—aorta; BB—buccal bulb; Ca—caecum; DG—digestive gland (DG-R & -L are right and left lobes); DO—distal oviduct; DOG—distal oviducal gland; Fu—funnel; FO—funnel organ; Int—intestine; LW—lateral wing of shell; MGr—median groove of shell; Oes—oesophagus; OL—optic lobe; ONB—optic nerve bundle; Ov—ovary sac; Pa—pancreas; PO—proximal oviduct; POG—proximal oviducal gland; Sa—saddle; 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; WB—white body. Scale bars = 10.0 mm, image ruler in mm marks (**M**).

Table 9. *Insigniteuthis obscura* sp. nov. measurements and counts. Measurements in mm. *Badly damaged (measurement uncertain).

ID	TMAG E44631	SAM D72067	SAM D20278 Holotype	SAM D68457
Sex	Female Mature	Male Mature	Male Mature	Male Mature
TL		~220 (arms distorted)	~152	~160
ML	~35	72	40	~45*
MW	~56	52	40 (47 at inner fin edge)	~35*
HW	64	75	53	~55*
ED	~20	45(L)	23–25	22
FL (L/R)	22/20	44/46	24/25	~36*
FW (L/R)	15/14	22/16	10/12	~11*
FuL	20	33	24 (10 free)	34
PA	16	25	15	16
Gill LC (L/R)	8/7	7/7	7/7	7/7
AL I (L/R)	114/105	211/200	110/112	130/133
AL II (L/R)	118/110	212/177*	117/112	135/134
AL III (L/R)	113/106	195/185*	112/112-3	133/120
AL IV (L/R)	106/102	190/192	119/116	134/142
SC I (L/R)	74/71	77/72	65/72	61*/63*
SC II (L/R)	73/72	83/64*	74/63	74/75
SC III (L/R)	71/70	88/64*	67/72	71/53*
SC IV (L/R)	78/75	58/50	71/68	74/74
SuD (normal)	1.9 (25th, IIR)	3.8 (mid arm, IIIL)	1.9 (mid arm, IIL)	~2.0 (mid arm)
PESF position	NA	4–8 or 9 (5th–7th or 8th largest)	4–8 (5th or 6th largest)	4–7 (or 8 on arms IV)
SuD (PESF)	NA	6.4 ^{Acet}, 4.6 ^{Inf} (IIL, 6th) 6.0 ^{Acet}, 4.5 ^{Inf} (IVL, 7th)	3.0 ^{Acet} (IIL, 6th) 2.7 ^{Acet} (IL, 7th)	4.8 ^{Acet}, 3.3 ^{Inf} (IVL) 4.2 ^{Acet}, 3.6 ^{Inf} (IIL)
DESF position	NA	NA arm I 33–36/32–35 (34-35/33-34 ^{largest}) II 31–34 (32–33 ^{largest})/34–36* III 33–35/33–36 (33–34 ^{largest}) IV	NA arm I 31–33 (31–32 ^{largest}) II 28–32 (29–31 ^{largest}) III 29–32 (30–31 ^{largest}) IV	NA arm I 32–34 (33 ^{largest}) II 31–33/31–34 (31–33 ^{largest}) III 32–34/33–36 (32-33/34-35 ^{largest}) IV
SuD (DESF)	NA	13.0 ^{Acet}, 6.8 ^{Inf} (IIIL) 11.2 ^{Acet}, 7.6 ^{Inf} (IVL)	5.8 ^{Acet}, 3.5^{Inf} (IIL) 6.6 ^{Acet}, 4.0^{Inf} (IIIL)	10.2 ^{Acet}, 5.2 ^{Inf} (IVR) 9.8 ^{Acet}, 5.2 ^{Inf} (IVL) (3.4 ^{Acet}, 2.4 ^{Inf}, flanking suckers)
CiL	~1.9 (sucker 19-20 IR)	3.0–3.2 (retracted)	2.1 mid arm IL	1.6
Ci start	2–4	3 & 4	2–4	2–4
WD A	70	128	50	70
WD B (L/R)	72	106	62/66	68/68
WD C (L/R)	72	90	68/	62/62
WD D (L/R)	68	94	61/	*/62
WD E	64	94	52	*
WN	Not discernible (some thickening)	NA	NA	NA
Areolar spots	2, arm I 1, arm II–IV	Present (skin often too damaged)	1 each arm base	Too damaged
Notes	Bilobed DG		~40 mm from mid DESF to arm tip free of webbing.	Badly mangled

ed (i.e., flattened) base. Infundibular structures of grossly enlarged suckers proportionally small, infundibular ⌀ ~50–68% acetabular ⌀, infundibular ring and pad poorly differentiated, forming simple ring around a large aperture. Following the DESF, suckers drop to diameter less

than mid-arm suckers, continuing to arm tips with minute size.

Females with the first 3 or 4 suckers very small and increasing in size, reaching greatest dimensions over mid-arm, SDI 5.4%, suckers slowly decrease in size in the distal arm-third.

Cirri commence between suckers 2–4, reaching greatest length by ~⅓ arm length and over central arm, CLI 3.6%–5.4%, diminishing in length to arm tips. Cirri located in small retractile pockets on some specimens (possibly a preservation artifact).

Digestive system: dissected from male specimen (see **Fig 15 E, F**); buccal bulb very large (slightly exceeding combined stomach/caecum in greatest dimensions); no salivary glands (anterior or posterior) apparent externally on the buccal bulb or oesophagus, but anterior salivary glands were present within the postero-ventral portion of the buccal bulb (partly visible by stripping away membrane of the bulb); odontophore small, narrow, lacking radula or chitinous lining; labial palps (lacking palatine teeth); salivary papillae well-developed. Upper beak (**Fig 15 G, H**) tall, height 72% beak length (or 80% width), hood moderately tall (hood length 59% beak length); rostrum blunt, deflected down slightly, jaw cutting edge smooth (without teeth), hood crest rounded (convex); lateral walls near-parallel, without lateral grooves/flexures, dorsal edge relatively straight (slightly convex), posterior edges gently convex, crest of posterodorsal apex rounded. Lower beak (**Fig 15 I, J**) tall (height 62% width), with relatively short hood (hood length 52% beak length), elongate wings (wing length 95% beak length) with only weak diagonal flexure; rostrum small, blunt, hood crest rounded. Oesophagus expanded midway as simple crop (without diverticula); stomach simple, rounded, muscular; caecum small, ~½ stomach greatest dimensions, simple, without spiral coiling; digestive gland bilobed, greenish; hepatic ducts short; intestine long, approximately 1.6× oesophagus length, with distinct coil in the distal half where it is also slightly distended; ink sac and anal flaps absent. Digestive system with dark purplish membrane over buccal bulb, oesophagus, and stomach, as well as the rectum where it projects into the mantle cavity, caecum and intestine lack pigmentation.

Male reproductive system: dissected from mature male (**Fig 15 K, L**); testis ovoid, vas deferens thin, relatively short; spermatophoric complex three-parted (SC1–3), SC3 largest (exceeding combined dimensions of SC1 and 2); spermatophoric sac (Needham's sac) large, folded, similar to SC3 in size, located between SC3 and the accessory gland complex; AGC exceeds SC1–3 in overall dimensions, dominated by the separated and rounded AG1, whereas AG2 and 3 are fused closely together as a single ovoid structure (a medial seam visibly separates AG2 and 3) truncated where it abuts the spermatophoric sac, with greatest dimensions slightly less than AG1; terminal organ projecting from conjoined AG2 and 3 medially, short, thick (length slightly over ⅓ combined AG2 & 3 greatest dimension).

Female reproductive system: illustrated partly *in situ* (distal parts dissected free) (**Fig 15 M**); ovary large, occupying posterior half of mantle; proximal oviduct elongate, containing at least two oocytes (each ~7 mm long); oviducal gland large, rounded, two parted, proximal oviducal gland pale-beige, distal oviducal gland dark brown and slightly larger (proximal oviducal gland ~90% width of distal part, length ~46% oviducal gland's length); distal oviduct longer than oviducal gland, 1.5× its length, projecting into mantle cavity. Encased egg in distal oviduct present (not dissected free as it was broken), length of encased egg ~10 mm.

Colouration: surfaces of mantle, head, fins, and aboral arms/webbing, dark maroon-pigmented on preserved specimens (**Fig 13 A–C**); living animals (identified by distinctive areolar spot pattern, discussed next) indicate a more pink-purple pigmentation in life, with pigment reduced on distal arm (**Fig 13 D**); freshly collected specimens similar but darker in pigmentation (**Fig 13 E**). Oral surfaces of webbing and arms darker than aboral faces, maroon in colouration (fresh condition, **Fig 13 F**; preserved **Fig 14 A, B**). Sucker infundibuli and acetabular chambers of distal enlarged suckers, and cirri, contrasting with a paler colouration, more yellowish to beige. Areolar spots: distinctive, with single large spot near base of each arm (measuring ~3 mm across), appearing as an unpigmented patch on preserved specimens, and as more bluish-purple and more sharply defined spot in life (**Fig 13 A–E**). On the dorsal arms, two pairs of much smaller spots were discernible between the eyes and one just distal to the enlarged spot (but only half the size of the enlarged spot), with at least one or two smaller spots also apparent on arms II and III (though inconsistently).

Material examined.

Holotype.

SAM D20278, male (ML 40 mm), 222 km SW of Cape Adieu, Great Australian Bight, 33°58′S, 131°22′E, 1000 m, trawl, FV *Saxon Progress*, xi.1989 (coll. D. Wheenan).

Paratypes.

SAM D72067, male (ML 72 mm), 83 km SW of Currie Head, Tasmania, 40°38–39′S, 143°25–27′E, 940–965 m, trawl (Orange Roughy), RV *Soela*, Cruise SO 2/89 Stn 37, 7.iii.1989. SAM D68457, male (ML 35 mm), 241 km SSW of Cape Adieu, Great Australian Bight, 34°09'S, 131°27'E, 1210–1089 m, FV *Longva III*, 16.xii.1989 [mangled]. TMAG E44631, female (ML 35 mm), St Helens Hill, off eastern Tasmania, 41.2225−2100°S, 148.7446−7401°E, 942–1035 m, FV *Saxon Progress*, Cruise SXP199903 [SXP 3/99] Stn 38, 28.vii.1999.

Table 10. *Insigniteuthis obscura* sp. nov. indices and formulas. *Arm I damaged (Dorsal ALI using longer arm II, WI A is relative to longer arm II); **fin length likely overestimate as mantle tissue around fin bases largely destroyed.

Indices	TMAG E44631	SAM D72067	SAM D20278 Holotype	SAM D68457**
MWI	156%	72.2%	117.5%	78%
HWI	183%	104.2%	132.5%	122%
FuLI	57%	45.8%	60%	76%
FLI (L/R)	57%–63%	61%–64%	60%–63%	~80%**
FWI (L/R)	68%–70%	35%–50%	42%–48%	~31%
EDI	57%	62.5%	58%–63%	49%
PAI	46%	34.7%	37.5%	36%
Arm formula	II>I>III>IV / II>III>I>IV	II>I>III>IV / I>IV>III*>II*	IV>II>III>I / IV>I=II=III	II>III=IV>I / IV>I=II>III
Dorsal ALI	3.4× ML (arm II)	2.9× ML	2.9× ML (arm II)	3.0× ML (arm II)
Ventral ALI	3.0× ML	2.7× ML	3.0× ML	3.2× ML
SDI	5.4%	5.3%	4.8%	4.4%
SDI PESF	NA	8.3%–8.9%	6.8%–7.5%	9.3%–10.7%
SDI DESF	NA	15.6%–18.1%	14.5%–16.5%	21.8%–22.7%
CLI	5.4%	4.4%	5.3%	3.6%
Web formula	B=C>A>D>E	A>B>D=E>C	C>B>D>E>A*	A>B>C=D>E*
WI A	61%	61%	59% (B % arm I)	53%
WI E	60%	49%	44%	44% (D % arm IV)

Distribution: Material examined was from the Great Australian Bight, off western Tasmania, and off eastern Tasmania, 940–1210 m depth. The live observation by RV *Falkor* (FK200126) was at Hood Canyon, off Bremer Bay, southwestern Australia (1118 m) (depicted in Trotter *et al.* (2022) as *Grimpoteuthis* sp.), while recently collected material from CSIRO voyage IN2017_V03 was collected over 999–1257 m depth from off northern NSW (28.1–30.1°S, 153.6–154.1°E) (see remarks). Overall, this species likely occurs broadly off the eastern and southern Australian coasts per **Figure 1**, ~ 900–1300 m depth.

Etymology: From the Latin '*obscura*' (feminine) meaning 'shadowy' or 'obscure', in reference to uncertainty and obscurity with regard to the identification of the specimens (being confused with *O. pluto*).

Remarks: There has been considerable literature confusion between this species and *O. pluto* (briefly described earlier). Nesis (1987) was the first to note greatly enlarged suckers in DESF for *O. pluto* (p. 288 "Males have 3–4 enlarged suckers in distal parts of 3rd–4th arms near web edge."). Lu (2010), examining material from off NSW, South Australia, and Western Australia that he attributed to *O. pluto*, reported a bilobed digestive gland and 2–4 greatly enlarged DESF suckers on arms II–IV.

However, it was evident from examination of Berry's *O. pluto* type series material and a fresh male specimen collected from the same location, that *O. pluto* doesn't have a distinct DESF, and has a unilobed digestive gland. The specimens with the greatly enlarged DESF on arms II–IV were thus left without a name and are described herein as *I. obscura* sp. nov.

The presence of a distal enlarged sucker field on only arms II–IV is technically shared with *O. massyae* (Grimpe, 1920) within the Opisthoteuthidae. However, *O. massyae* can be easily distinguished by the much greater number of suckers in the DESF (9–11) and the small size of the DESF suckers relative to the proximal (thus placing it in genus *Opisthoteuthis*). *I. dongshaensis* comb. nov. has the DESF restricted to arms III and IV (but otherwise resembles *I. obscura* sp. nov. in the number of suckers per DESF (3 or 4)), as well as bilobed digestive gland; *I. dongshaensis* can also be distinguished by lower gill lamellae counts (typically 6 per gill and only rarely 7), and a differently-shaped internal shell (much more strongly U- or V-shaped and with larger 'shoulders'; see Lu 2010, fig. 4).

Mature male *I. obscura* sp. nov. are almost impossible to misidentify given the enlarged suckers (unique among opisthoteuthids), but females are more difficult to identify. However, the unique areolar spot pattern, with a single unusually large spot at the base of each arm, along with the reddish or maroon pigmentation, should allow reliable identification of female *I. obscura* if skin is relatively intact.

Recently, as part of the CSIRO voyage IN2017_V03, several *I. obscura* were collected over a depth range of 999–1257 m from eastern Australia, being easily identifiable from the small number of greatly enlarged DESF suckers (at least on the male MV F245722) and the single large areolar spot near the base of each arm (see **Fig 13 E, F**). These specimens were misidentified as *O. pluto* by O'Hara *et al.* (2020), while another from 2692–2760 m depth was likely a *Grimpoteuthis* (possibly *G. greeni*) given the form and placement of its fins as well as elongate cirri (as discussed in remarks section for *O. pluto* earlier).

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