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ORIGINAL PAPER

Cuttlefishes (Cephalopoda, Sepiidae): the bare bones—an hypothesis of relationships

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Abstract

Based on a comprehensive analysis of molecular sequence data, the Sepiidae genera *Acanthosepion* Rochebrune, 1884; *Ascarosepion* Rochebrune, 1884; *Aurosepina* Jothinayagam, 1987; *Decorisepia* Iredale, 1926; *Doratosepion* Rochebrune, 1884; *Rhombosepion* Rochebrune, 1884 and *Spathidosepion* Rochebrune, 1884 are here re-instated and formally recognised as valid. *Sepia* Linnaeus, 1758 and *Sepiella* Gray, 1849 are retained, but *Metasepia* Hoyle, 1885 is placed in alternative combination with *Ascarosepion*. The subgenus *Digitosepia* Lipiński, 2020 is well supported and is herein elevated to generic status. *Sepia trygonina* (Rochebrune, 1884) and *Sepia hieronis* (Robson, 1924) are placed in new monotypic genera *Erythalassa* gen. nov. and *Lusepia* gen. nov. respectively. *Hemisepius* Steenstrup, 1875, also monotypic, is recognised as valid based on a unique synapomorphy: the presence of a fleshy ridge on each side of the antero-ventral mantle that bears a longitudinal row of black pores, however, *H. typicus* Steenstrup, 1875, was not included in our molecular analysis as tissue samples could not be obtained. *Sepia tuberculata* Lamarck, 1798, the type species for the nominal genus *Spathidosepion*, was not included for the same reason. Based on the morphological similarity between *S. tuberculata* and the sequenced taxa, *S. papillata* Quoy & Gaimard, 1832 and *S. angulata* Roeleveld, 1972 we tentatively assign these two taxa to *Spathidosepion* pending future confirmation. Where possible, each genus is diagnosed based on a combination of morphological and molecular characters.

Keywords Sepiidae · *Sepia* · *Metasepia* · *Sepiella* · Phylogeny

Abbreviations

Ac.	*Acanthosepion*
As.	*Ascarosepion*
Au.	*Aurosepina*
ClRC	Club Row Count (i.e., the number of club suckers in oblique transverse rows)
De.	*Decorisepia*
Di.	*Digitosepia*
Do.	*Doratosepion*
ML	Mantle length
S.	*Sepia*
Sl.	*Sepiella*
Sp.	*Spathidosepion*

Introduction

Cuttlefishes are found in temperate to tropical waters over continental shelves and slopes, from the western Pacific, the Indian Ocean and to the eastern Atlantic, as far north as the North Sea. This species-rich family is well defined as a discrete monophyletic taxonomic unit (Allcock et al. 2014).

Cuttlefish diversity can be partly explained by their biology and biogeography. Juveniles (with a few notable exceptions) are primarily benthic following hatching and there is no paralarval stage (Young et al. 1998; Neige 2003); adults are demersal, mostly occurring in the neritic zone, although some species inhabit deeper waters. As is the case for many

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marine taxa (Hoeksema 2007; Sanciangco et al. 2013), the Indo Pacific harbours their greatest diversity (Rosa et al. 2019). Multiple processes have led to high levels of faunal biodiversity in the region (Halas and Winterbottom 2009).

The study and naming of cuttlefishes according to modern taxonomy dates to Linnaeus (1758), with the genus *Sepia* first recognised to include all cephalopods without an external shell. Lamarck (1799) limited the genus to include only those cephalopods with an internal calcareous shell. At that time, only two species, *S. officinalis* Linnaeus, 1758 and *S. tuberculata* Lamarck, 1798 were known. In 1845, d'Orbigny listed 21 species, most of which are still valid. He classified them into two groups based on the arrangement and relative sizes of suckers on the arms and tentacular clubs. Gray (1849) partially adopted d'Orbigny's classification and additionally included cuttlebone characters. He coined the name *Sepiella*, then known only from cuttlebones (and not whole animal soft parts), for species with cuttlebones that were described as 'oblong, posterior end expanded, produced, cartilaginous, not beaked, convex beneath' (Gray 1849: 106). Later, Steenstrup (1875: 468) erected *Hemisepius* with *H. typicus* as the type species based on the animal and the cuttlebone. He also redescribed *Sepiella* based on the shell and soft parts, raising it to generic status (Steenstrup 1880). Rochebrune (1884) subsequently proposed ten genera based on cuttlebone characters. Hoyle (1886), who described the subgenus *Metasepia* in 1885, did not concur with Rochebrune's classification, stating that the defining characters were at best of subgeneric value. In 1923, Naef revisited the issue of sepiid relationships and proposed that the Sepiidae be classified in three genera: *Sepiella*, *Hemisepius* and *Sepia*, and further divided *Sepia* into seven subgenera based on characteristics of the animals' soft parts and their cuttlebones. While many species had been insufficiently described at that time, he concluded that a natural system would be readily determined if the member taxa for each group could be fully described.

Sasaki (1929), Adam (1944), and Adam and Rees (1966) did not support Rochebrune's classification describing it, in summary, contradictory and unnatural, but did not comment in detail on Naef's (1923) proposal. In 1954, Iredale divided the Australian species into three families, four subfamilies and thirteen genera. Iredale (1926, 1954) described many Australian species based on features of the cuttlebone alone. Adam and Rees (1966) firmly criticised Iredale's classification, and particularly his systematic conclusions pertaining to the higher-level taxonomic categories that he defined with few supporting diagnostic characters, in addition to his excessive splitting of species that Adam and Rees (1966) attributed to individual, sexual or geographic variation. Nonetheless, with knowledge of the animals' soft parts, a number of Iredale's species that were synonymised, or of uncertain status, have subsequently proved to be valid.

Among the abovementioned treatments, Adam and Rees (1966) provide the most comprehensive recent revisionary account of the family. These authors retain the genera *Sepia* and *Sepiella* (recognising *Hemisepius* and *Metasepia* as subgenera within *Sepia*) but do recognise some species-groups, although Adam indicated in personal communication cited in Roeleveld (1972: 268) that they did not apply any systematic value to the groups and they were used simply to flag similar species to assist in the study of interspecific relationships. In fact, Adam and Rees (1966: 130–144) go to great lengths to explain why their groupings could not be formally separated into different genera and subgenera. A few years later, the Sepiidae of South African waters were clarified by Roeleveld (1972), and in her discussion she refers to the groups outlined in Adam and Rees (1966) and was able to assign the southern African representatives to these groups, with the caveat that the degree of affinity within the different groups varies.

More recently, Khromov (1987, 1990) proposed a classification of the Sepiidae, based on both extant and fossil taxa. In their 'Synopsis of Sepiidae outside Australian waters', Khromov et al. (1998) recognised three genera, *Sepia, Sepiella,* and *Metasepia,* and this classification has largely remained the status quo since then. Within *Sepia*, six species-complexes (rather than subgenera) were recognised: *Sepia sensu stricto*, *Acanthosepion* Rochebrune, 1884; *Anomalosepia* Khromov, 1987; *Doratosepion* Rochebrune, 1884; *Hemisepius* and *Rhombosepion* Rochebrune, 1884. Lu (1998) also divided *Sepia* into species-groups. The complexes defined by these workers are not entirely congruent and are based largely on subjective and, to some extent, intuitive methods. Not all species fit within this framework and whether they comprise monophyletic groups has not been tested. Current classifications, such as Mangold and Young (2016) and WoRMs (2023), assign all species to three genera: *Metasepia*, *Sepia* and *Sepiella*. *Metasepia* includes two species, *Sepiella* (abbreviated below as *Sl.*) contains seven species, while the remaining 109 species are placed in the catch-all genus *Sepia*.

In short, despite Naef's (1923) optimism, clarification of the relationships among the Sepiidae based on morphological traits has remained exceedingly perplexing.

The naming of genera, subgenera and species-groups has been based on few characters, mainly pertaining to the cuttlebone, and the tentacular club. While very useful enablers for species identification purposes, whether their morphology is indicative of shared history is largely unknown. It is well known that morphological traits can converge due to similar environmental pressures. As suggested by Ward et al. (2022), reliance on the cuttlebone as a way of recognising species-groups may be problematic, reflecting less about the evolutionary relationships among members of the group than convergence based on traits related to habitat depth, with bone morphology reflecting the physical and physiological constraints imposed by living at particular depths. Similarly, the arrangement of tentacular club suckers may be more of a functional adaptation relating to the nature of available prey species rather than a shared history. Until a robust classification is devised, it is difficult to ascertain the path of character evolution and decide which taxa and characters should be a focus for more detailed morphological examination.

In this study we focus on molecular traits in an attempt to reconstruct sepiid phylogeny based on reliably identified cuttlefish species, including most type species for each of the previously recognised genera. To date, there are few molecular studies that include large numbers of sepiids and no consistent set of genes has been used to clarify relationships (Allcock et al. 2014). Phylogenies from the most extensive studies include: Bonnaud et al. (2006) [12S rRNA, 16S rRNA, *COII*]; Yoshida et al. (2006) [12S rRNA, 16S rRNA, *COI*]; Yoshida et al. (2010) [*COI*, *cytochrome b* and *ND5*], and Lindgren et al. (2012) [whole evidence approach 4–10 genes]. Yoshida et al. (2006), included eleven sepiids from Japanese waters, *Sepia officinalis* from the Mediterranean and five species that had previously been sequenced by other researchers. Four clades were recovered from the analysis, recognised as the '*Sepia* species complex', a clade including *S. officinalis, S. hierredda* Rang [in Férussac & d'Orbigny], 1835; *S. bertheloti* d'Orbigny [in Férussac & d'Orbigny], 1835; *S. pharaonis* Ehrenberg, 1831 and *Sl. japonica* Sasaki, 1929; a *M. tullbergi* (Appellöf, 1886) + *S. latimanus* Quoy & Gaimard, 1832 clade; a *S. esculenta* Hoyle, 1885; *S. madokai* Adam, 1939a; *S. aculeata* Van Hasselt [in Férussac & d'Orbigny], 1835 and *S. lycidas* Gray, 1849 clade, and a *Doratosepion* species-complex that included *S. kobiensis* Hoyle, 1885; *S. lorigera* Wűlker, 1910; *S. pardex* Sasaki, 1913 and *S. peterseni* Appellöf, 1886. *Sepia elegans* Blainville, 1827 resolved as a separate lineage representing a possible fifth clade. The molecular phylogeny was not congruent with the arrangement of tentacular club suckers, but two groups, one with a broad cuttlebone, and the other with a lanceolate cuttlebone were supported by the molecular data. Members of the *Doratosepion* group were also characterised by the absence of a membranous structure suspended between cuttlebone pillars as ascertained following scanning electron microscopy. In a later study including 16 species of east Asian sepiids Yoshida et al. (2010) [*COI*, *Cytb* and *ND5*] reconfirmed the existence of four groups with high support values, finding support for an *Acanthosepion* clade, *Metasepia* + *S. latimanus*, the *Doratosepion* clade and an east Atlantic *Sepia* + *Sepiella* clade. Yoshida et al. (2010) proposed hypotheses regarding the possible evolution of these clades. Their data supports *Acanthosepion* as a possible ancestor of other groups. As *Acanthosepion* is restricted to Asian waters, the authors postulated that extant cuttlefishes evolved from a common Asian ancestor.

Yoshida et al. (2010) concluded that the absence of a cuttlebone posterior spine has occurred in different lineages, as has the lateral narrowing of the cuttlebone, and thus these traits are not necessarily associated with phylogenetic relationships. They also supported the view that there seems to be very little clustering by geographic location (Ward and von Boletzky 1984; Bonnaud et al. 2006).

Herein, we aimed to study a greater number of species with broader geographic coverage than has been attempted previously, in the hope that we could develop a more robust hypothesis of relationships and provide greater taxonomic stability. Specifically, we collected material globally, including as many type species as possible, and sequenced multiple genes for each species with the objective of building a robust phylogenetic tree. Furthermore, we interrogated a database of morphological traits compiled over many years to determine characters which, in combination, diagnosed well-supported clades in the molecular phylogeny. Thus, we present a revised phylogeny for Sepiidae that includes approximately half of the known diversity in the family and propose a generic-level classification that reflects this phylogeny. This framework can provide a focus for future research, particularly to re-examine possible pathways of character evolution and biogeographic history within this enigmatic cephalopod family.

Materials and methods

Acquisition and identification of tissues and vouchers

Tissue samples for DNA sequencing were obtained via colleagues from various sources (see acknowledgements) including tissue banks of the Australian Museum Research Institute (Sydney, Australia), National Museum of Nature and Science (Tokyo, Japan), Museum Victoria (Carlton, Australia), South Australian Museum (Adelaide, Australia) and the Natural History Museum, National University of Singapore, Singapore (Singapore). Voucher specimens exist for nearly all sequenced material (Table 1) and all were reliably identified based on morphology. We sequenced 50 species with a wide geographic spread, and that encompassed a broad range of the known morphological variability within Sepiidae, including as many type species for the previously recognised genera/subgenera as possible. The type localities of all taxa are included in Table 1 to indicate the proximity of sequenced taxa to their representative type localities.

Unfortunately, few species were available from the exact type localities for each species, although the true type localities of many species first described from beach washed cuttlebones is unknown because the bones may have drifted post-mortem (Voss 1974, Reid 2016). One known issue in this regard pertains to the possibility of hitherto unrecognised or cryptic species being included.

Molecular sequencing

Genomic DNA was extracted from the tissues using a NucleoSpin® Tissue kit (Macherey–Nagel, Germany). Partial sequences of *nuclear histone H3* (*H3*), *cytochrome c oxidase subunit I* (*COI*), *cytochrome c oxidase subunit III* (*COIII*), 12S rRNA (12S) and 16S rRNA (16S) were amplified by polymerase chain reaction (PCR) using the published primers of Svenson and Whiting (2004), Folmer et al. (1994), Kassahn et al. (2003), Takumiya et al. (2005), and Palumbi et al. (1991) respectively. PCR was carried out in 25 µl reaction mixtures containing 2.5 µl of template DNA (approximately 125 ng), 12.5 µl Premix–GoTaq G2 Green Mastermix (Promega, Madison, WI, USA Madison, WI), 9 µl of sterile distilled water, and 0.5 µl of forward/reverse primer at 10 µM) with initial denaturation at 94 °C (2 min), followed by 35 cycles of 94 °C (40 s), 50 °C (40 s), and 72 °C (90 s), and a final extension step of 72 °C (10 min). Where standard PCR failed to yield product, the protocol was repeated preheating the reaction mixture prior to the addition of primers. PCR products were checked on 2% agarose gels and purified using NucleoSpin® Gel and PCR Clean-up kits (Macherey–Nagel, Germany). Purified PCR products were commercially sequenced by *Eurofins*, Germany.

H3 yielded only poor quality sequences with low PHRED scores and consequently these sequences were not used in subsequent analyses. A substitution saturation test by Xia et al. (2003) and Xia and Lemey (2009) performed in DAMBE (Xia and Xie 2001) showed *COIII* to be saturated. RY coding and coding with degenerate nucleotides did not solve the problem and thus *COIII* sequences were not used in subsequent analyses. Thus *COI*, 12S rRNA and 16S rRNA sequences were retained for analyses.

Other data

In addition to those samples that we sequenced ourselves, we downloaded the *COI*, 12S rRNA and 16S rRNA sequences from GenBank for all sepiid species for which an entire mitochondrial genome had been sequenced. We further audited all sepiid sequences available in the Nucleotide database of GenBank to see which species had been sequenced for at least two of *COI*, 12S and 16S. We took a conservative view when downloading sequences for inclusion as we did not wish to include specimens that had been misidentified. We thus only included sequences when either (a) the specimens had been identified by an acknowledged expert in sepiid taxonomy, or (b) there were multiple sequences of that species on GenBank and trees built from individual genes provided evidence that specimens had been correctly identified. Included sequences are listed in Supplementary Information 1, while Supplementary Information 2 provides a detailed rationale for inclusion and exclusion of GenBank accessioned sequences. We also searched Sequence Read Archives to see whether there were NGS data from which we could retrieve our genes of interest, but all sepiid SRA data pertained to species already included in our analysis. Finally, we included unpublished sequences of *S. orbignyana* Férussac [in d'Orbigny], 1826 that one of us (ALA) had from another project, even though there was no voucher specimen available for these sequences.

Outgroups

Since sepiids appear to be sister to all other decapodiform taxa (e.g., Strugnell et al. 2017; Tanner et al. 2017), we downloaded *COI*, 12S and 16S sequences from whole mitochondrial genome sequences on Genbank for a representative taxon of each major decapodiform lineage (Oegopsida, *Architeuthis dux* Steenstrup, 1857, NC_011581; Myopsida, *Doryteuthis opalescens* (S. S. Berry, 1911), NC_012840; Sepiolida, *Semirossia patagonica* (E. A. Smith, 1881), NC_016425; Spirulida, *Spirula spirula* (Linnaeus, 1758) NC_034682; Idiosepiida, *Idiosepius hallami* Reid & Strugnell, 2018, KF647895) to serve as outgroups.

Alignment preparation

COI sequences were translated, aligned as amino-acid sequences using ClustalX with default settings in Mega v.7, and trimmed to a 636 base-pair sequence matrix. 12S and 16S sequences were aligned in MAFFT version 7 on the online server available at https://mafft.cbrc.jp/ (Katoh et al. 2019) using the E-INS-I iterative refinement method that is recommended for sequences with multiple conserved domains and long gaps, and with a 1PAM scoring matrix. The difficult to align loops were removed using the Gblocks server available at http://molevol.cmima.csic.es/castresana/Gblocks_server.html (Castresana 2000) with less strict settings. Gblocks reduced the 16S alignment from 537 to 460 bp and the 12S alignment from 436 to 316 bp. Thus, our final sequence matrix comprised 71 ingroup sequences 1412 bp long (*COI* 1–636; 16S 637–1096; 12S 1097–1412), and five outgroup taxa, with a very limited amount of missing data (Table 1, Supplementary Information 1).

Molecular analyses

A Maximum Likelihood (ML) tree was constructed using IQ-Tree 2.0 (Nguyen et al. 2015) using a 3-partition scheme, whereby the first and second codons of *COI* comprised one partition, the third codons of *COI* comprised another, and

Table 1 Museum catalogue and GenBank accession numbers for specimens for newly sequenced material and type locations for included taxa

Species	Museum voucher	Voucher collection location	Type localities (after Sweeney, 2021)	GenBank accession numbers		
				COI	12S	16S
M. pfefferi (Hoyle, 1885)	WAM S29628	Australia. Western Australia, Shark Bay	Australia, Queensland, Masthead I. [cuttlebone]	OP825044	OP851641	OP851591
M. tullbergi (Appellöf, 1886)	NSMT MO 74860	Vietnam, Nha Trang, Central Market	Japan, Nagasaki	OP825045	OP851642	OP851592
Sepia andreana Steenstrup, 1875	NSMT MO 75875	Japan, Miyagi Pref., off Joban, off Sendai	Japan, Hakodate		OP851643	OP851593
S. angulata Roeleveld, 1972	AM C.572196	South Africa, off the coast	South Africa. Bloubergstrand 33°48′S 18°27′E [cuttlebone]	OP825046	OP851644	OP851594
S. apama Gray, 1849	AM C.474142	Australia, NSW, Cronulla, off Oak Park	Australia, South Australia, Port Adelaide [cuttlebone]	OP825047	OP851645	OP851595
S. arabica Massy, 1916	AM C.483506	Pakistan, Karachi, West Wharf	Syntypes: Lacadive Sea and Persian Gulf	OP825048	OP851646	OP851596
S. australis Quoy & Gaimard, 1832	AM C.572188	South Africa, off the coast	South Africa, Cape of Good Hope, Banc des Aiguilles	OP825049	OP851647	OP851597
S. bandensis Adam, 1939b	AM C.477609	Timor-Leste, east of Aturo Island	Indonesia, Banda Neira	OP825050	OP851648	OP851598
S. barosei Lipiński, 2020a	SAMC MB A089309	South Africa, eastern Agulhas Bank	South Africa, eastern Agulhas Bank	OP825051	OP851649	OP851599
S. braggi Verco, 1907	AM C.500857	Australia, Western Australia, off Jurien Bay	Australia, South Australia, Glenelg [cuttlebone]	OP825052	OP851650	OP851600
S. cultrata Hoyle, 1885	AM C.500883	Australia, Southern Ocean	Australia, NSW, off Twofold Bay 36°59′S 150°20′E		OP851651	OP851601
S. dubia Adam & Rees, 1966	(no voucher)	South Africa, off the coast	South Africa, False Bay	OP825053	OP851652	OP851602
S. erostrata Sasaki, 1929	NSMT MO 74429	Japan, Kanagawa Pref., Miura, off Bishamon	Japan, Sagami Province, Manazuru		OP851653	OP851603
S. esculenta Hoyle, 1885	NSMT MO 71643	Japan, Miyakubo, Seto Inland Sea	Japan, Yokohama, market	OP825054	OP851654	OP851604
S. faurei Roeleveld, 1972	SAMC MB A089312	South Africa, off the coast	South Africa, E of Cape Seal, 37°07′S 23°24′E	OP825055	OP851655	OP851605
S. foliopeza Okutani & Tagawa, 1987	NSMT MO 75608	China, East China Sea	East China Sea		OP851656	OP851606
S. hedleyi Berry, 1918	AM C.487273.001	Australia, off Ulladulla,	South Australia, S of Kangaroo I., Investigator Strait	OP825056	OP851657	OP851607
S. hieronis (Robson, 1924)	AM C.572193	South Africa, off the coast	South Africa, off Cape Town	OP825057	OP851658	OP851608
S. kobiensis Hoyle, 1885	NSMT MO 71644	Japan, Okiya-akishima, Seto Inland Sea	Japan, Bay of Kobe, 34°39′N 135°14′E	OP825058	OP851659	OP851609
S. latimanus Quoy & Gaimard, 1832	AM C.476101.003	Timor-Leste, Dili, street vendor	New Guinea, Port Dorey	OP825059	OP851660	OP851610
S. limata (Iredale, 1926)	AM C.456687	Australia, off Sydney,	Australia, NSW, Manly Beach [cuttlebone]	OP825060	OP851661	OP851611
S. longipes Sasaki, 1913	NSMT MO 71724	Japan, off Kashima	Japan, Kazusa Province, Choshi	OP825061	OP851662	OP851612
S. lorigera Wülker, 1910	NSMT MO 75924	Japan, no exact location data	Japan, Misaki		OP851663	OP851613
S. lycidas Gray, 1849	NMST MO 71645	Japan, Takehara supermarket	China, Canton market	OP825062		OP851614
S. madokai Adam, 1939a	NSMT MO 71662	Japan, Mimase Fishing Port (Kouchi)	Japan, Tokyo Bay	OP825063	OP851664	OP851615
S. mestus Gray, 1849	AM C.553308	Australia, NSW, off Manly	Australia [cuttlebone]	OP825064	OP851665	OP851616
S. novaehollandiae Hoyle, 1909	WAM S34840	Australia, Western Australia, Geographe Bay, N of Bunker Bay	South Australia, Kangaroo I. [cuttlebone]	OP825065	OP851666	OP851617
S. omani Adam & Rees, 1966	AM C.483505	Pakistan, Karachi, West Wharf	Gulf of Oman, 25°10′48″–25°09′48″N 56°47′30″E	OP825066	OP851667	OP851618
S. opipara (Iredale, 1926)	AM C.532856	Australia, NSW, Coffs Harbour	Australia, Queensland, Capricorn Group, Masthead I. [cuttlebone]	OP825067	OP851668	OP851619
S. orbignyana Férussac, 1826	(no voucher)	Ireland, Celtic Sea	France, La Rochelle [cuttlebone]	OP825068	OP851669	OP851620
S. papillata Quoy & Gaimard, 1832	AM C.572184	South Africa, off the coast	South Australia, Cape of Good Hope		OP851670	OP851621
S. papuensis Hoyle, 1885	WAM S90649	Australia, Western Australia, Shark Bay	Arafura Sea, S of Papua, 9°59′S 139°42′E	OP825069	OP851671	OP851622

Table 1 (continued)

Species	Museum voucher	Voucher collection location	Type localities (after Sweeney, 2021)	GenBank accession numbers		
				COI	12S	16S
S. peterseni Appellöf, 1886	NMST MO 72127	Japan, off Tosa Bay	Japan, Nagasaki	OP825070	OP851672	OP851623
S. 'pharaonis'[a] Ehrenberg, 1831	WAM S34838	Australia, Houtman Abrolhos Isds	Red Sea, Gulf of Suez	OP825071	OP851673	OP851624
S. plangon Gray, 1849	AM C.269862	Australia, NSW, off Woolwich	Australia, Port Jackson [cuttlebone]		OP851674	OP851625
S. prashadi Winckworth, 1936	AM C.483527	Pakistan, Karachi, West Wharf	India, Madras, Beach	OP825072	OP851675	OP851626
S. ramani[a] Neethiselvan, 2001	AM C.483507	Pakistan, Karachi, West Wharf	Red Sea, Gulf of Suez	OP825073	OP851676	OP851627
S. robsoni (Massy, 1927)	(no voucher)	South Africa, off the coast	South Africa, Hout Bay	OP825074	OP851677	OP851628
S. roeleveldi Lipiński, 2020a	SAMC MB A089307	South Africa, Aghulas Bank	South Africa, Benguela Current	OP825075	OP851678	OP851629
	(no voucher)	South Africa, Aghulas Bank		OP825076	OP851679	OP851630
S. rozella (Iredale, 1926)	AM C.532854	Australia, NSW, Coffs Harbour	Australia, Manly Beach [cuttlebone]	OP825077	OP851680	OP851631
S. shazae Lipiński & Leslie, 2018	(no voucher)	South Africa, southern Benguela System	South Africa, southern Benguela System	OP825078	OP851681	OP851632
S. smithi Hoyle, 1885	AM C.532847	Australia, Qld., Moreton Bay	Arafura Sea, S of Papua, 9°59′S 139°42′E	OP825079	OP851682	OP851633
S. stellifera Homenko & Khromov, 1984	AM C.483511	Pakistan, Karachi, West Wharf	East Arabian Sea	OP825080	OP851683	
S. tenuipes Sasaki, 1929	NSMT MO 71676	Japan, Mimase Fishing Port (Kouchi),	Japan, Ibaraki Prefecture		OP851684	OP851634
S. tokioensis Ortmann, 1888	NSMT MO 74453	Japan, Kanagawa Pref., Miura, off Bishamon	Japan, Tokyo Bay		OP851685	
S. trygonina (Rochebrune, 1884)	AM C.483518	Pakistan, Karachi, West Wharf	Red Sea	OP825081	OP851686	OP851636
S. vermiculata Quoy & Gaimard, 1832	AM C.483531	South Africa, off the coast	Cape of Good Hope	OP825082	OP851687	OP851637
Sepiella inermis (Van Hasselt [in Férussac & d'Orbigny], 1835)	AM C.483531	Pakistan, Karachi, West Wharf	Indonesia, Java	OP825083	OP851688	
	ZRC.MOL.3205	Singapore, Terumbu Pempang Laut		OP825084	OP851689	OP851638
	NSMT MO 74862	Vietnam, Nha Trang, Fish Landing Place		OP825085	OP851690	OP851639

Where type specimens are cuttlebones only (indicated in square brackets), the type localities are approximate only due to likely post-mortem drift; equally those obtained in fishmarkets have no provenance

AM Australian Museum, Sydney; *NSMT* National Museum of Nature and Science, Tokyo, Japan; *SAMC* South African Museum, Cape Town South Africa; *WAM* Western Australian Museum, Perth; *ZRC* Lee Kong Chian Natural History Museum, Singapore

[a] *Sepia ramani* is part of a species-complex. Neither of the tissue samples available to us were obtained from close to the type locality of *Sepia pharaonis*, but clearly conform to this species-group. (See Discussion and Supplementary Information 4)

the final partition comprised the concatenated ribosomal RNA genes. IQTree called ModelFinder (Kalyaanamoorthy et al. 2017), and selected and applied the best fit model to each partition. IQTree applied the TN model (Tamura and Nei 1993) with empirical base frequencies, a proportion of invariant sites and the discrete Gamma model (Yang 1994) with four rate categories to the first partition; TPM2 (where the A–C substitution rate equals the A–T substitution rate, A–G equals C–T, and C–G equals G–T) with empirical base frequencies, and a discrete Gamma model with four rate categories to the second partition; and the General Time Reversable model (Tavare 1986) with empirical base frequencies, a proportion of invariant sites, and the discrete Gamma model with four rate categories to the third. A consensus tree was constructed from 1000 standard bootstraps (Felsenstein 1985).

Bayesian trees were built in MrBayes, with partitions as detailed above but with the GTR model, a proportion of invariant sites and a Gamma model applied to each partition, with four Monte Carlo Markov chains run simultaneously for 1,000,000 generations, sampling every 100 generations, with 25% discarded as burn-in. Stationarity of runs was assessed through standard deviation of split frequencies (<0.02) and ESS and plot shape in Tracer v.1.7.1. Each Bayesian run was repeated to ensure that global optima rather than local optima were reached.

The ML tree is presented, with major clades highlighted using a colour-blind friendly colour ramp generated in the R (version 4.1.2; R Core Team 2022) package viridis (Garnier et al. 2021). For the major highlighted clades, for supported relationships among those clades, and for specific intraclade relationships, posterior probabilities from the Bayesian Inference analysis are superimposed on the ML tree. The full Bayesian tree is presented in Supplementary Information 3. We consider clades with boostrap support > 70 to be well supported.

Morphology

Morphological data were derived from examination of preserved specimens from museum collections where possible and published literature. A comprehensive data set was coded in Mesquite 3.7 (Maddison and Maddison 2021). Species were grouped in Mesquite based on the clades identified in the molecular analysis in an attempt to visualise morphological traits that can be used to define each clade.

Results

New sequences were submitted to Genbank under Accession numbers OP825044–OP825085 (*COI*), OP851641–OP851690 (12S), OP851591–OP851639 (16S) (Table 1). Nine clades, marked as coloured bands and numbered sequentially from the top in Fig. 1, as well as four distinct lineages not closely related to any of these clades, were recovered in both Maximum Likelihood (ML; Fig. 1) and Bayesian Inference (BI; Supplementary Information 3) analyses.

Description of major clades

Clade 1 contains 13 termini and is well supported (BS = 83, PP = 1). There is limited support for any within clade structure, except for a sister-taxon relationship between *S. smithi* Hoyle, 1885 and *S. elliptica* Hoyle, 1885. The specimen identified as *S. ramani* Neethiselvan, 2001 is closely associated with specimens identified as *S. pharaonis*, although these three specimens do not form a well-supported clade.

Clade 2 contains 15 termini. It is well supported (BS = 92, PP = 1). *Metasepia tullbergi* and *M. pfefferi* (Hoyle, 1885) are sister taxa within this clade with high support (BS = 89, PP = 1). Their differentiation from other species in the clade is not well defined. There is no other evident within-clade structure.

Clade 3 contains species identified as *Sepiella inermis* (Van Hasselt [in Férussac & d'Orbigny], 1835), *Sl. japonica*, and *Sl. maindroni* Rochebrune, 1884 and has full support (BS = 100; PP = 1). Clade 3 clearly contains three species, but the names applied to specimens are not congruent with those taxa. *Sepiella maindroni* is a junior synonym of *Sl. inermis* according to WoRMS (2023) but analysis of all sepiid *COI* data available on GenBank (Supplementary Information 4) suggests that the name *Sl. maindroni* is in fact commonly applied to *Sl. japonica*; indeed NC017749 and NC028731 appear to be the same species, which we assume to be *Sl. japonica*. This same wider analysis of *COI* data also recovered three closely related clades of *Sepiella:* a large clade identified as *Sl. inermis*, a large clade of specimens identified either as *Sl. japonica* or *Sl. maindroni* (assumed to represent *Sl. japonica*), and a small clade of just two termini. These two termini comprise AM C.483531 from Pakistan sequenced herein, as well as a specimen from the Arabian Sea, accessioned to GenBank as KC409394. AM C.483531 is superficially similar in morphology to *Sl. inermis.* It could represent an undescribed species of *Sepiella* but could also pertain to one of several species of the genus known from only limited samples around their type localities. Further work in the Indian Ocean is likely required to properly delimit species in this genus.

Sepia bertheloti falls as a separate lineage outside our numbered clades. It is sister to Clade 4 in both the ML and BI trees, but the relationship is not well supported (BS = 59; PP = 0.75). The position of this taxon is therefore unclear so it is not treated further at this time.

Clade 4 contains three termini and is well supported (BS = 90, PP = 1). *Sepia hierredda* and *S. vermiculata* Quoy & Gaimard, 1832 are sister taxa (BS = 100), with *S. officinalis* sister to these.

Clade 5 contains four species and is well supported (BS = 94, PP = 1). Within the clade, *Sepia omani* Adam & Rees, 1966 and *S. prashadi* Winckworth, 1936 are sister taxa (BS = 100), as are *S. elegans* and *S. orbignyana* (BS = 100).

Clade 6 contains just two species, *S. angulata* Roeleveld, 1972 and *S. papillata* Quoy & Gaimard, 1832, united with full support (BS = 100, PP = 1.0).

Clade 7 contains 13 united termini and is well supported (BS = 99, PP = 1). Many members of this clade appear to be very closely related with short branch lengths.

Two other species, *Sepia arabica* Massy, 1916 and *Sepia trygonina* (Rochebrune, 1884) form subsequent sister species to Clade 7 but on much longer branches. Because of this difference in branch lengths, and the much lower support for the wider clade(s), we have treated *S. arabica* and *S. trygonina* as separate lineages.

Clade 8 unites three species, *S. australis* Quoy & Gaimard, 1832, *S. hedleyi* Berry, 1918, and *S. madokai*, and is well supported (BS = 97, PP = 1). Within this clade, *S. hedleyi* and *S. madokai* are very closely related sister taxa (short branch lengths, BS = 100).

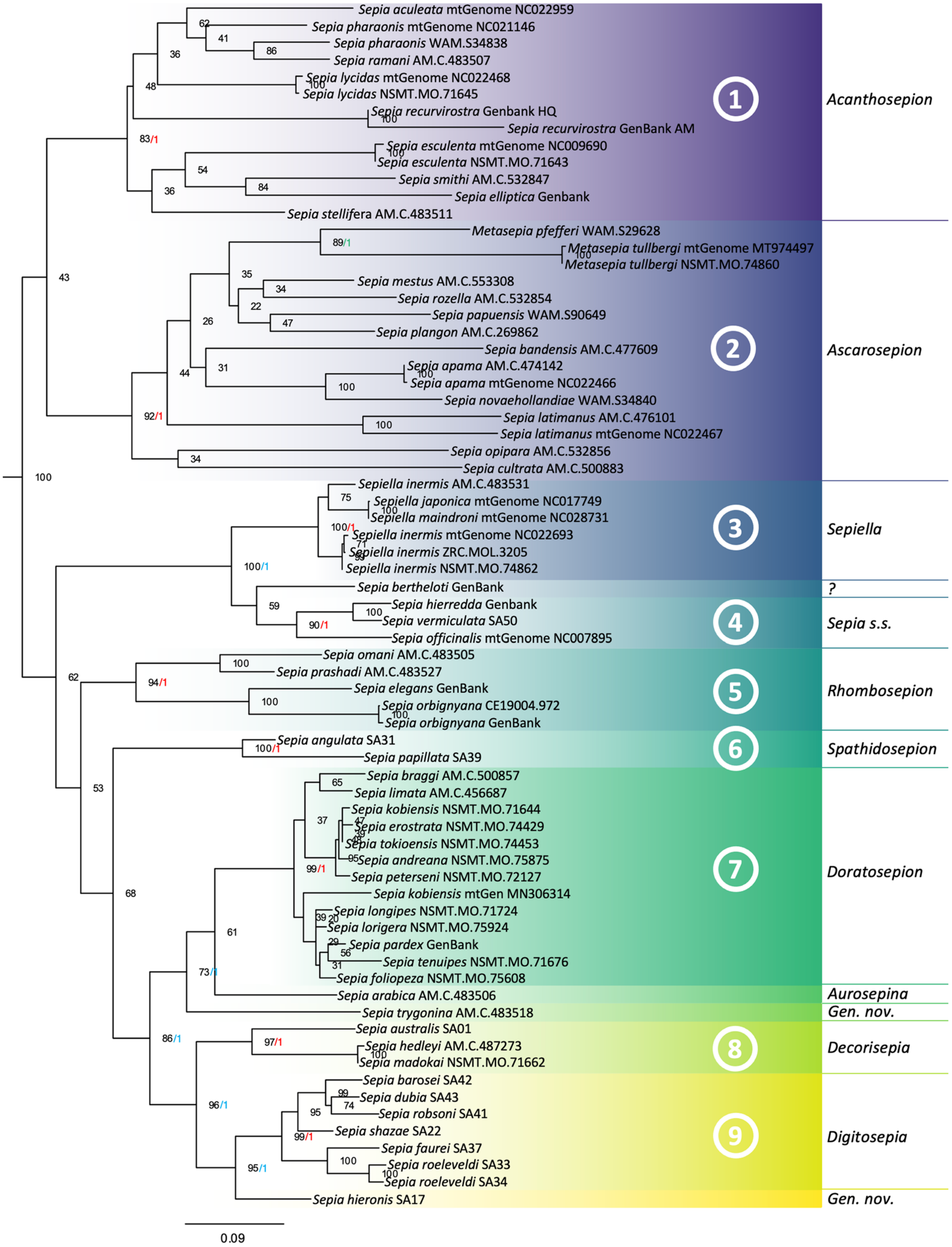

Fig. 1 Maximum likelihood tree built in IQTree using a 3-partition model. ML support values generated from 1000 standard bootstraps (BS) and Bayesian Inference posterior probabilities (PPs) are indicated as BS/PP on nodes. PPs included for selected nodes only and colour coded: numbered clades in red, interclade nodes in blue, intraclade nodes in green. For Bayesian Tree with all PPs see Supplementary Information 3. Tree rooted on representatives of the orders Idiosepiida, Oegopsida, Spirulida, Myopsida, and Sepiolida. Root not shown. Suggested genus names for clades given on the right hand side (see taxonomic section)

Clade 9 contains seven termini representing six nominal species, several of which are recently described, from southern Africa. The clade is well supported (BS = 99, PP = 1); it is one of few clades with well-supported intraclade relationships. *Sepia dubia* Adam & Rees, 1966; *S. barosei* Lipiński, 2020a and *S. robsoni* (Massy, 1927) are closely related (BS = 95), with *S. shazae* Lipiński & Leslie, 2018 sister to these. *Sepia faurei* Roeleveld, 1972 and *S. roeleveldi* Lipiński, 2020a are sister taxa (BS = 100) and sister to the other four species.

Sepia hieronis (Robson, 1924) is in a well-supported sister-taxon relationship to Clade 9 (BS = 95, PP = 1) but, due to the branch lengths separating *S. hieronis* and Clade 9, we treat *S. hieronis* as a separate lineage.

Where two or more individuals of any given species were included in our tree (mostly where complete mitochondrial genomes existed and were downloaded and added to our matrix), these generally resolved as sister taxa as expected. Exceptions are as follows. We included two *Sepia pharaonis* and one *Sepia ramani*, a species that was previously split from the *pharaonis* species-complex. These three samples do group together, but the *S. pharaonis* samples are not sister, reflecting the need for further revision of this complex. The sequences from the whole mitochondrial genome of *S. kobiensis* from GenBank (MN306314) do not fall sister to our *S. kobiensis* sample (NSMT MO 71644). One of us (TK) rechecked the voucher of NSMT MO 71644 and we are confident that this specimen does represent *S. kobiensis*. Of further note is the long branch length of one *S. recurvirostra* Steenstrup, 1875 specimen. This may reflect a genuine difference, but the 12S rRNA sequence available on GenBank accounts for most of the difference and, as aligned with other 12S rRNA sequences from sepiids, looks as though it might have been degraded at the 3' end. Without access to the electropherogram, it is impossible to draw further conclusions.

Relationships among and between clades

Many deep nodes were poorly supported. However, a relationship among Clades 8, 9 and *S. hieronis* is well supported (BS = 96, PP = 1), and a relationship between this superclade and the superclade composed of Clade 7 and *S. arabica* and *S. trygonina* is also well supported (BS = 86, PP = 1). The only other supported interclade relationship is that uniting Clade 3, *S. bertheloti*, and Clade 4, which is fully supported (BS = 100, PP = 1).

Revised generic level classification

Based on the nine clades recovered from the molecular analyses, we propose that each is recognised at the generic level according to its member type species as shown in Table 2 (clades 1, 2, 4, 5, 7, 8, 9), or, where the type species was not sequenced, according to morphological similarities of sequenced species to type species (clades 3 and 6). Most clades can be assigned to available names within the family (see Table 3), so these are herein taken out of their former synonymy with *Sepia*. Clade 1, which includes *S. aculeata*, is recognised as *Acanthosepion* Rochebrune, 1884. Clade 2 includes *S. mestus* Gray, 1849, so its member species are assigned to the genus *Ascarosepion* Rochebrune, 1884. This renders the genus *Metasepia* as invalid. While its two member species (both included here) have some clearly distinct morphological traits, the retention of *Metasepia*, clearly embedded within Clade 2 cannot be supported on phylogenetic grounds. We therefore place *Metasepia* in alternative combination with *Ascarosepion*. While the type species of *Sepiella*, *Sl. ornata*, was not available for sequencing in this study, the included taxa form a well-supported clade and are also defined based on morphological characters, so there is no doubt that *Sepiella* (Clade 3) remains a valid genus. Clade 4 corresponds to the genus *Sepia*, the type genus for the family Sepiidae, and includes *S. officinalis* (type species of this genus) together with *S. hierredda* and *S. vermiculata*. Clade 5 includes the type species of the genus *Rhombosepion*, namely *S. elegans*, so this clade is assigned to that genus. Clade 6 is well supported and includes two taxa, neither of which are type species for any genus. However, *S. papillata* is very similar morphologically to *S. tuberculata*, the type species for *Spathidosepion* Rochebrune, 1884, so we assign this name to Clade 6. Clade 7 includes the type species for the genus *Doratosepion* Rochebrune, 1884, *S. andreana* Steenstrup, 1875. Clade 8 is defined as *Decorisepia* Iredale, 1926 due to the inclusion of the type species, *S. hedleyi*. Clade 9, includes the type species, *S. robsoni* for the subgenus *Digitosepia* Lipiński, 2020a. Given this clade's strong support, we herein elevate the subgenus to full generic status. This clade includes a number of other taxa that have been previously recognised in the *Hemisepius* species-group [Adam and Rees (1966); Roeleveld (1972); Khromov et al. (1998); Lipinski (2020a)]. However, in the absence of molecular data for the type species *H. typicus* Steenstrup, 1875, *Digitosepia* is the best name we can apply to this clade. *Hemisepius typicus* is currently alone among the Sepiidae in the possession of a unique synapomorphy, namely the presence of lateral pores on each side of the ventral mantle. We therefore tentatively recognise *Hemisepius* as a valid genus on morphological grounds and include it among the taxa we recognise below.

Sepia arabica, which clearly falls on its own long branch, possibly sister to the *Doratosepion* clade, is the type species for *Aurosepina* Jothinayagam, 1987, and is thus assigned to that genus. *Sepia trygonina* has previously been included in *Doratosepion* but its long branch length sets it apart from

Table 2 Clades receiving consistent support. Bold text indicates type species that have been used to infer the clade name. BS, Bootstrap support; PP, Posterior probability

Clade	Included species	BS	PP
Acanthosepion	***aculeata***, *elliptica, esculenta, lycidas, pharaonis, ramani, recurvirostra, smithi, stellifera*	83	1
Ascarosepion	***mestus***, *apama, bandensis, cultrata, latimanus, novaehollandiae, opipara, papuensis, pfefferi, plangon, rozella, tullbergi*	92	1
Aurosepina	***arabica***		
Decorisepia	*australis*, ***hedleyi***, *madokai*	97	1
Digitosepia	***robsoni***, *barosei, dubia, faurei, shazae, roeleveldi*	99	1
Doratosepion	***andreana***, *braggi, erostrata, foliopeza, kobensis, limata, longipes, lorigera, pardex, peterseni, tenuipes, tokioensis, trygonina*	99	1
Rhombosepion	***elegans***, *omani, orbignyana, prashadi*	94	1
Sepia s.s	***officinalis***, *hierredda, vermiculata*	90	1
Sepiella	*inermis, maindroni, japonica*	100	1
Spathidosepion	*angulata, papillata*	100	1

Table 3 Sepiid genera and their type species

Genus	Type species
Sepia Linnaeus, 1758	*officinalis* Linnaeus, 1758
Sepiella Gray, 1849	*ornata* Rang, 1837
Hemisepius Steenstrup, 1875	*typicus* Steenstrup, 1875
Acanthosepion Rochebrune, 1884	*aculeata* Van Hasselt [in Férussac & d'Orbigny], 1835
Ascarosepion Rochebrune, 1884	*verreauxi* Rochebrune, 1884 (= *mestus* Gray, 1849)
Diptherosepion Rochebrune, 1884	*ornata* Rang, 1837 (= *ornata* Rang, 1837)
Doratosepion Rochebrune, 1884	*andreana* Steenstrup, 1875
Lophosepion Rochebrune, 1884	*lefebrei* d'Orbigny, 1839–1842 (= *gibba* Ehrenberg, 1831)
Rhombosepion Rochebrune, 1884	*rupellaria* d'Orbigny, 1834 [in Férussac & d'Orbigny 1834–1848] (= *elegans* Blainville, 1827)
Spathidosepion Rochebrune, 1884	*tuberculata* Lamarck, 1798
Metasepia Hoyle, 1885	*pfefferi* Hoyle, 1885
Andreaesepia Grimpe, 1922	*andreana* Steenstrup, 1875
Eusepia Naef, 1923	*officinalis* Linnaeus, 1758
Parasepia Naef, 1923	*orbignyana* Férussac [in d'Orbigny], 1826
Platysepia Naef, 1923	*esculenta* Hoyle, 1885
Amplisepia Iredale, 1926	*apama* Gray, 1849
Arctosepia Iredale, 1926	*limata* Iredale, 1926
Crumenasepia Iredale, 1926	*hulliana* Iredale, 1926) [= *pharaonis* Ehrenberg (1831)]
Decorisepia Iredale, 1926	*rex* Iredale (1926) (= *hedleyi* Berry, 1918)
Fiscisepia Iredale, 1926	*ellipticum adjacens* Iredale, 1926 (= *elliptica* Hoyle, 1885)
Glyptosepia Iredale, 1926	*opipara* Iredale, 1926
Mesembrisepia Iredale, 1926	*macandrewi* Iredale, 1926 (= *novaehollandiae* Hoyle, 1909)
Ponderisepia Iredale, 1926	*eclogaria* Iredale,1926 (= *latimanus* Quoy & Gaimard, 1832)
Solitosepia Iredale, 1926	*liliana* Iredale, 1926 (= *mestus* Gray, 1849)
Tenuisepia Cotton, 1932	*mira* Cotton, 1932
Blandosepia Iredale, 1940	*baxteri* Iredale, 1940
Anomalosepia Khromov, 1987	*omani* Adam & Rees, 1966
Aurosepina Jothinayagam, 1987	*arabica* Massy, 1916

Information from "Taxa Associated with the Family Sepiidae Keferstein, 1866" on the cephalopod Tree of Life webpages at http://www.tolweb.org others within the clade and, given its unique and distinct morphology, we ascribe it to a new monotypic genus. As discussed below, based on a number of morphological traits that set it apart from *Digitosepia*, we also assign *S. hieronis* to a new genus. A list of all taxa included in this study, together with their current classification and proposed taxonomy is provided in Supplementary Information 5. Where species have been moved from *Sepia* (gender feminine) to a genus whose gender is neuter, we provide some deduced etymological information in support of decisions on amending species name endings (Supplementary Information 6).

Individual clades are diagnosed by combinations of characters. In most cases, diagnoses are therefore polythetic as defined in Dubois (2017): involving a variable combination of properties, none of which is necessarily present in every member of the genus. Diagnoses have been based on the type species for each genus and emended to apply to all our member taxa where this information is known. The most significant diagnostic characters are italicised. It is anticipated that each generic diagnosis will be refined over time as additional taxa are assigned to each clade, particularly as additional molecular data become available, and as members of each genus are studied in more detail to look for further unifying characters. Clades are listed below alphabetically by genus name.

Sepiidae Leach, 1817

Acanthosepion Rochebrune, 1884

(Figs. 1, 2, 3, 4a)

Type species. *Sepia aculeata* Van Hasselt, 1835, pl. 5bis, in Férussac, AE de, & A d'Orbigny, 1834–1848. *Histoire Naturelle Générale et Particulière des Céphalopodes Acétabulifères Vivants et Fossiles*. lvi + 361 pages, Atlas with 144 plates. Paris. *Type locality:* Indonesia, Java (cuttlebones only).

Diagnosis (modified from Rochebrune, 1884). Mantle oblong (half as broad as long). Ventral mantle margin emarginate, without distinct lateral angles. Posterior gland and gland pore absent. Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression that corresponds to ridge. Male and female arm lengths subequal; suckers usually tetraserial. Hectocotylus present, left ventral arm modified; sucker size normal proximally, reduced medially, then normal to arm tip; from proximal to distal end of arm, ~ 3 rows of normal suckers; ~ 5–6 rows of markedly reduced suckers; suckers in two dorsal series smaller than remaining suckers; arm sometimes with deep median furrow; suckers in two dorsal and two ventral series displaced laterally. Club sucker-bearing face convex or flattened; ClRC variable, 8–22 suckers in oblique transverse rows; dorsal and ventral protective membranes not fused at base of club (although in *Ac. ellipticum* the membranes are not fused in small animals but fused in adults); dorsal and ventral membranes the same length; extend beyond carpus along stalk or terminate at posterior end of carpus. Buccal membrane with, or without, few, minute suckers.

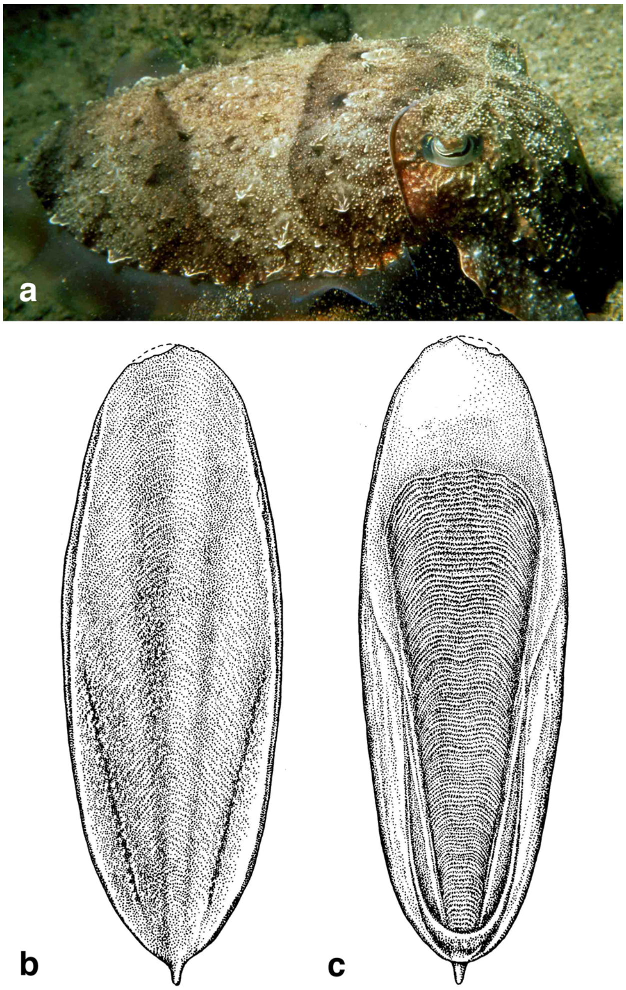

Fig. 2 *Acanthosepion aculeatum* (Van Hasselt [in Férussac & d'Orbigny], 1835). **a** live animal; **b** cuttlebone dorsal view; **c** cuttlebone ventral view. [**a** John Forsythe; **b**, **c** Reid et al. (2005), fig. 112 (in part)]

Dorsal mantle sometimes with longitudinal row of ~ eight ridge-like papillae along each side, close to base of each fin; body covered with numerous large papillae and scattered small tubercles (Fig. 2a). Dorsal 'eye' spots absent. Fins dorsally with pale reflective line along base. Eggs white, sometimes sand-coated.

Cuttlebone (Fig. 2b, c) length approximately equal to mantle length; outline oval to oblong; anterior margin triangular or bluntly rounded; dorsal median rib (when present)

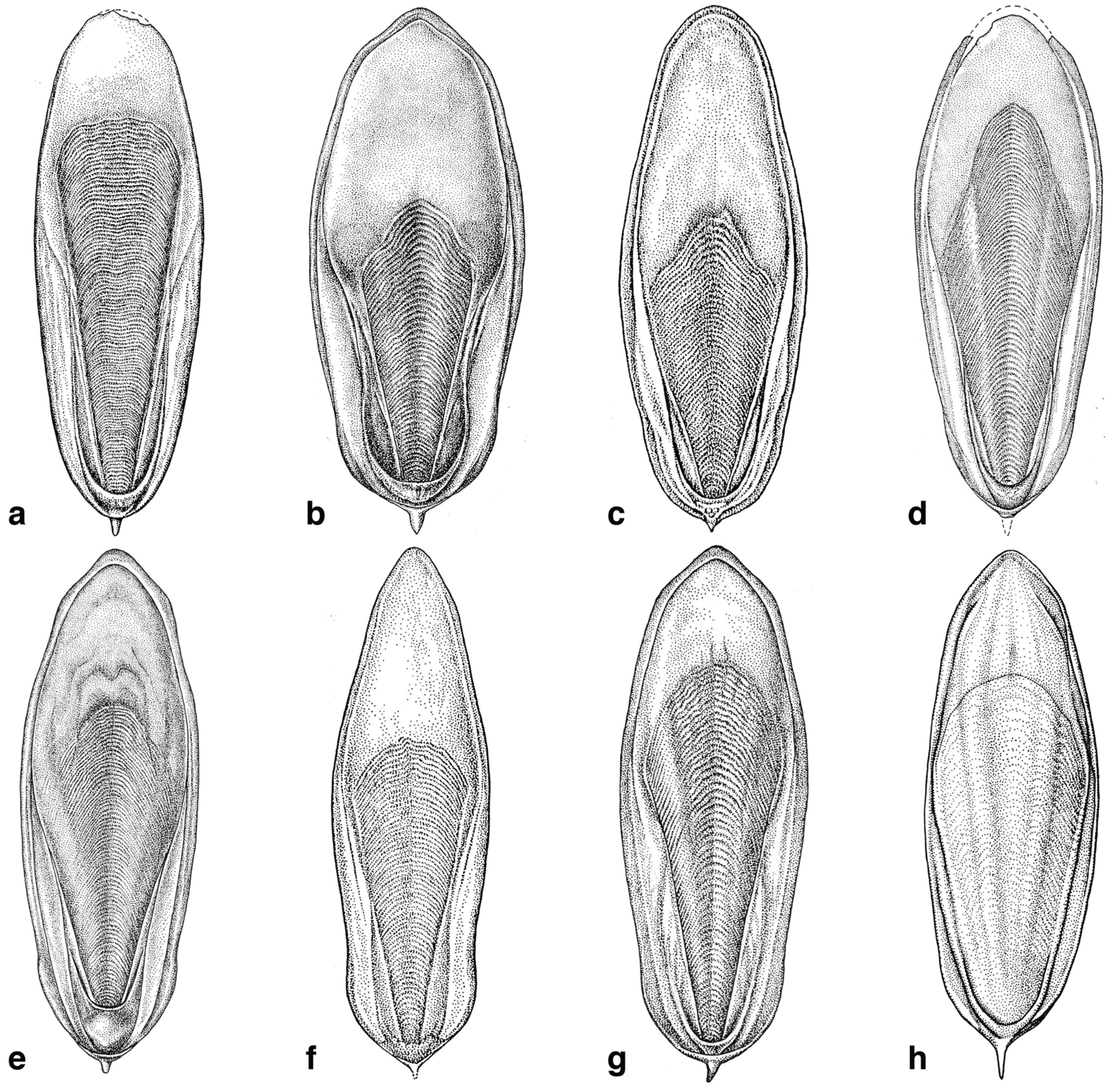

Fig. 3 *Acanthosepion* cuttlebones, ventral view. **a** *Ac. aculeatum* (Van Hasselt [in Férussac & d'Orbigny], 1835); **b** *Ac. ellipticum* (Hoyle, 1885); **c** *Ac. esculentum* (Hoyle, 1885); **d** *Ac. lycidas* (Gray, 1849); **e** *Ac. pharaonis* (Ehrenberg, 1831); **f** *Ac. recurvirostrum* (Steenstrup, 1875); **g** *Ac. smithi* (Hoyle, 1885); **h** *Ac. stelliferum* (Homenko & Khromov, 1984). [**a**–**h** Reid et al. (2005)]

broadens anteriorly; lateral ribs present, distinct; chitin present, wide patch posteriorly and narrow rim borders lateral margins of cuttlebone; spine present, long, pointed; keel present or absent; anterior striae U-shaped; inner cone limbs narrow anteriorly, broaden posteriorly, *often thickened; recurved with secondary folding of the inner cone over the posterior part of phragmocone, not joined to it, often forming a cup-like structure and elevated forming a gap* (Fig. 3); outer cone narrow anteriorly, broadens posteriorly, not flared ventro-laterally; outer cone limbs forming thin rim ventral to spine.

Distribution. Eastern Africa through northern Indian Ocean to western Pacific Ocean: northern Japan to northern Australia (Fig. 4a).

Remarks. Rochebrune (1884: 100) defined the arm sucker arrangement in *Acanthosepion* as follows (translated from French): '*arranged in oblique rows of four rows in the first two thirds of the length, and in straight lines in two rows in the last third*'. The only species included in our analysis that has biserial suckers at the tips of the arms is *Ac. recurvirostrum.* In this species the suckers are biserial on the tips of arms 1–3 in both sexes. This character needs to be checked in other species included in this genus, but the type species *Ac. aculeatum* (contrary to Rochebrune's diagnosis) has tetraserial suckers on all arms.

See also Remarks under *Ascarosepion* below.

Member taxa (this study): *Acanthosepion aculeatum* (Van Hasselt [in Férussac & d'Orbigny], 1835); *Ac. ellipticum*

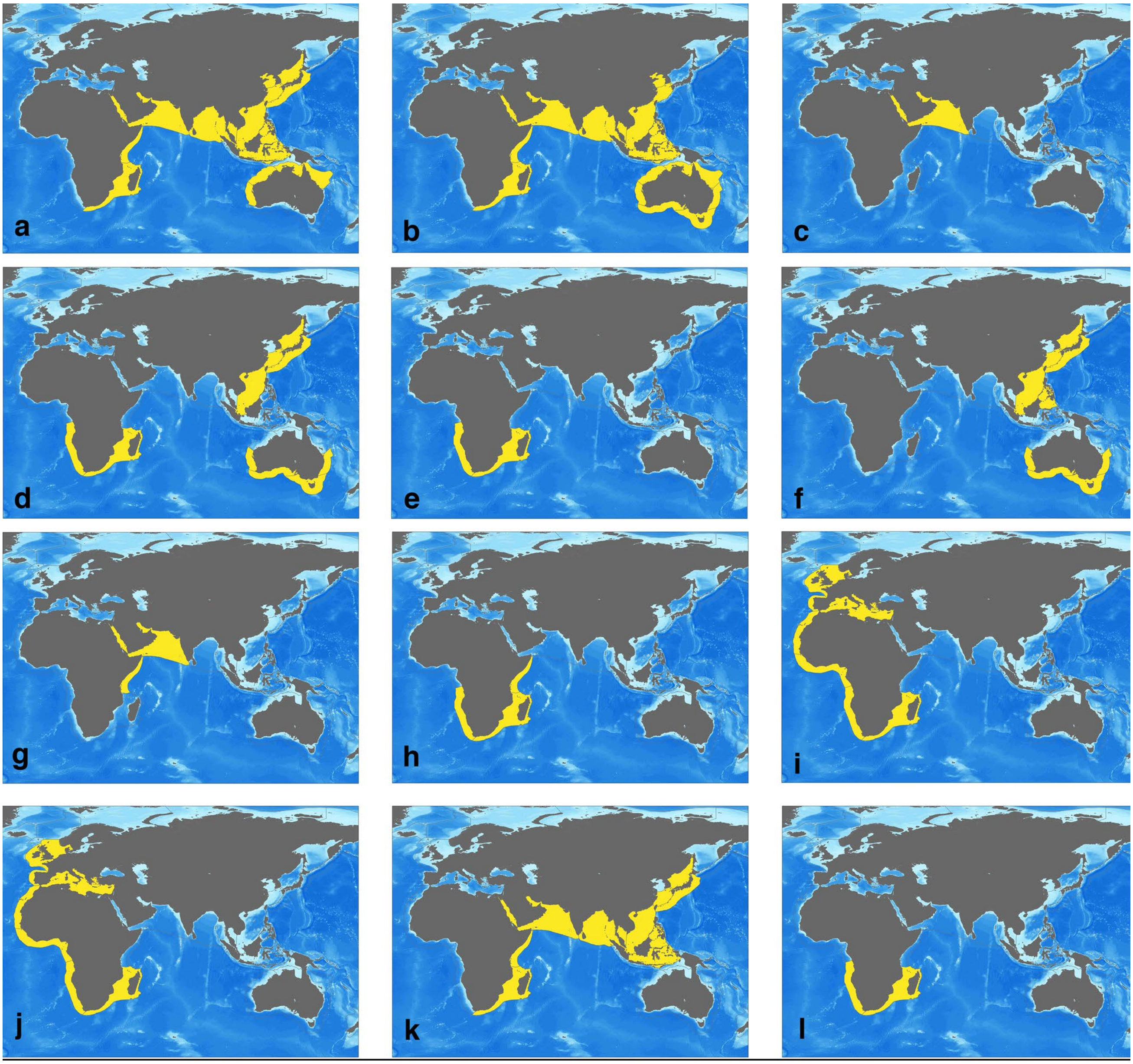

Fig. 4 Clade distributions within Large Marine Ecosystems (LMEs) globally. **a** *Acanthosepion*; **b** *Ascarosepion*; **c** *Aurosepina*; **d** *Decorisepia*; **e** *Digitosepia*; **f** *Doratosepion*; **g** *Erythalassa*, gen. nov.; **h** *Lusepia*, gen. nov.; **i** *Rhombosepion*; **j** *Sepia*; **k** *Sepiella*; **l** *Spathidosepion*. Distributions determined from IUCN Red List data. The IUCN Red List compiles occurrence in LMEs for each species. Herein we collated information for every species occurring in our named clades in Fig. 1

(Hoyle, 1885); *Ac. esculentum* (Hoyle, 1885); *Ac. lycidas* (Gray, 1849); *Ac. pharaonis* (Ehrenberg, 1831); *Ac. recurvirostrum* (Steenstrup, 1875); *Ac. smithi* (Hoyle, 1885); *Ac. stelliferum* (Homenko & Khromov, 1984).

Ascarosepion Rochebrune, 1884

(Figs. 1, 4b, 5, 6)

Type species. *Ascarosepion verreauxi* Rochebrune, 1884. Étude monographique de la famille des Sepiadae. Bull. Soc. philomath. Paris, 7(8): 74–122, pls 3–6. [98, pl. 5]. *Type locality:* Australia, Sydney. [= *Sepia mestus* Gray, 1849. Catalogue of the Mollusca in the British Museum. Part I. Cephalopoda Antepedia. 164 pages. London:108. *Type locality:* Australia, New South Wales, Manly Beach (cuttlebones only).]

Diagnosis [modified from Rochebrune (1884)]. Mantle oval; dorsal anterior margin rounded or triangular; ventral mantle margin emarginate, without distinct lateral angles. Posterior gland and gland pore absent. Mantle-locking

Fig. 5 *Ascarosepion mestus* (Gray, 1849). **a** live animal; **b** cuttlebone dorsal view; **c** cuttlebone ventral view. (**a** Becca Saunders; **b**, **c** David Paul)

cartilage curved, with semicircular ridge; funnel-locking cartilage with depression that corresponds to ridge. Male and female arms subequal in length [arms 1 shorter in *pfefferi*]. Arm suckers tetraserial, except in *As. papuense* males in which distal tips of arms 1–3 have biserial suckers. Hectocotylus present (left ventral arm) or absent; when present, suckers reduced proximally or normal proximally, reduced medially and normal distally; reduced suckers equal in size across rows or two dorsal rows smaller than ventral rows; sometimes wide, fleshy in modified portion. Tentacular club slightly recurved, crescent-shaped; sucker-bearing face flattened; *5–8 suckers in oblique transverse rows; suckers differing slightly in size; small, or several suckers of inner 2–3 rows slightly larger than rest;* swimming keel of club extends well beyond carpus; dorsal and ventral protective membranes fused or not fused at base of club; joined to stalk, or separated from stalk by a membrane. Buccal membrane without suckers; females with single median spermatheca in ventral part. Eggs white, or blackened with ink.

Dorsal mantle with scattered papillae or ridges. Paired dorsal eye spots present (Fig. 5a) or absent; fins with or without bands at base.

Cuttlebone length approximately equal to mantle length; outline broad, oval or diamond shaped (*As. pfefferi* and *As. tullbergi*); not strongly convex in lateral view, or strongly convex (in former two taxa); bone bluntly rounded anteriorly and posteriorly, or pointed, acute; not strongly recurved ventrally; dorsal ribs present or absent; spine present, absent or reduced to a tiny knob; spine with ventral keel in some species; striated zone concave or convex; sulcus present or absent, deep or shallow, narrow or wide; anterior striae inverted U-shaped; *inner cone limbs narrow anteriorly, broaden posteriorly, or narrow U-shaped; not raised to form ledge posteriorly; fused to outer cone sometimes thickened* (Figs. 5b, c; 6); outer cone narrow anteriorly, broadens posteriorly, usually not flared ventro-laterally.

Distribution. Southern Africa through northern Indian Ocean to western Pacific Ocean: southern Japan and Korea to Australia (Fig. 4b).

Remarks. Both sexes of *As. mestus* have a pair of adhesive pads of spongy tissue in a posterior ventro-lateral position on the mantle. The skin in this region appears crinkled in preserved specimens.

It is extremely difficult to determine, based on morphology alone, whether a species should be placed in *Acanthosepion* or *Ascarosepion.* The primary difference pertains to the cuttlebone inner cone that in *Acanthosepion* is recurved to cover the posterior tip of the phragmocone, and usually thickened, while in *Ascarosepion* the inner cone, while sometimes thickened, is joined throughout its length to the outer cone and not recurved ventrally (compare Figs. 3 and 6).

Ascarosepion pfefferi and *As. tullbergi* were formerly placed in the subgenus *Metasepia* Hoyle, 1885 and later elevated to genus by Iredale (1954). Hoyle's (1885: 145) generic diagnosis follows:

'*Body* short, rounded, thick dorsoventrally; *nuchal cartilage* without linear groove and *mantle* devoid of corresponding ridge; *siphon-pallial* articulation deep.

Tentacular club with unequal suckers.

Shell rhomboidal in outline, with no calcareous covering on the dorsal surface of the chitinous sheet; no *spine.'*

However, as Adam and Rees (1966) have noted, the cuttlebone is calcareous and it may be that Hoyle (1885) examined a decalcified specimen. The remaining diagnostic characters can be seen in other taxa (although the nature of the nuchal cartilage may be worth checking in other species; as far as we are aware this has not been widely recorded in species descriptions).

There are a number of morphological traits that unite *As. pfefferi* and *As. tullbergi* and set them apart from other members of this clade, including their distinctive and flamboyant colouration, and the diamond-shaped cuttlebone that is much shorter than the mantle and located in the anterior half to two thirds. Khromov (1987) used this latter trait to fully merit the recognition of *Metasepia* at the generic level.

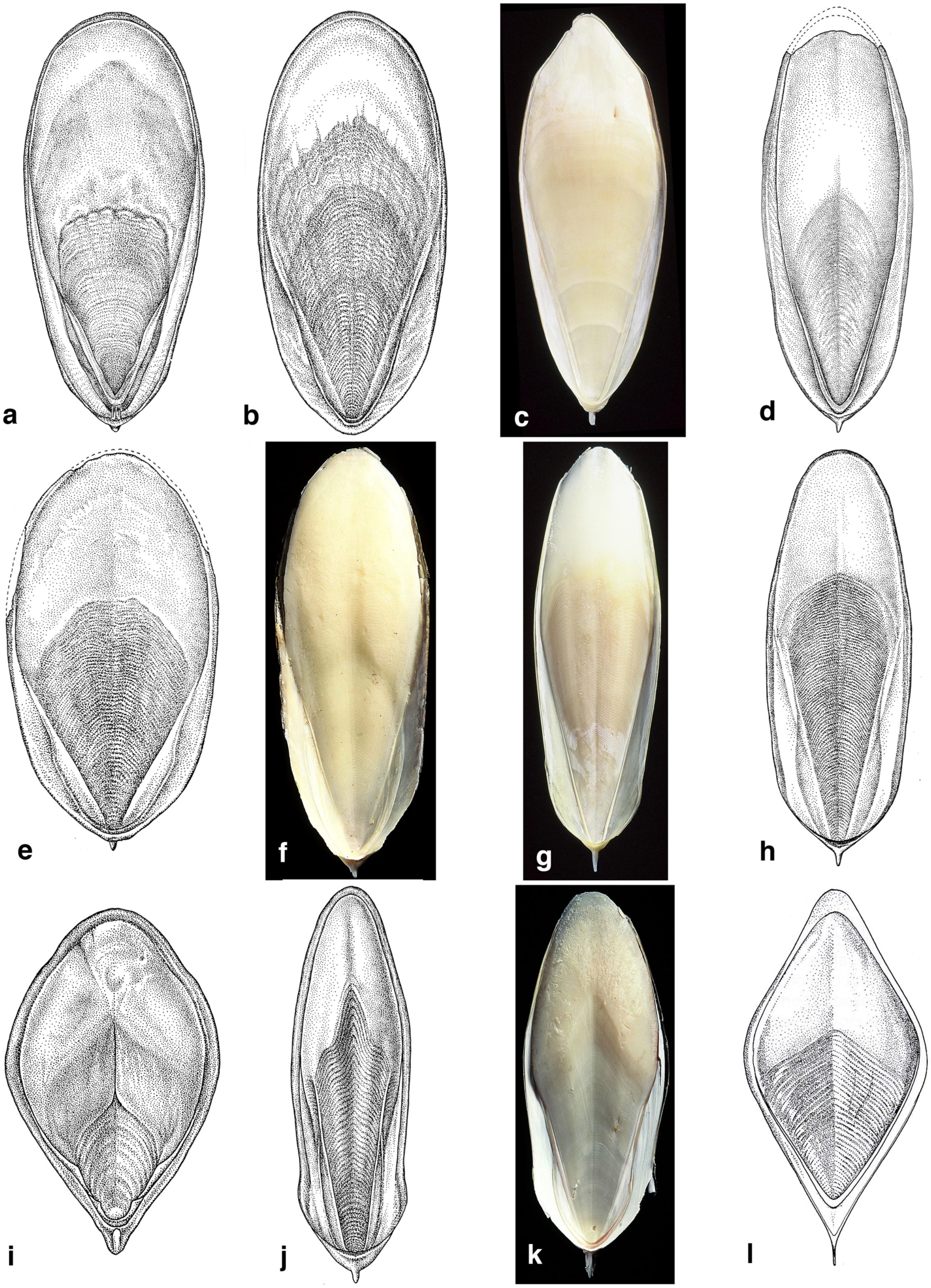

Fig. 6 *Ascarosepion* cuttlebones. **a** *As. apama* (Gray, 1849); **b** *As. bandense* (Adam, 1939b); **c** *As. cultratum* (Hoyle, 1885); **d** *As. latimanus* (Quoy & Gaimard, 1832); **e** *As. mestus* (Gray, 1849); **f** *As. novaehollandiae* (Hoyle, 1909); **g** *As. opiparum* (Iredale, 1926); **h** *As. papuense* (Hoyle, 1885); **i** *As. pfefferi* (Hoyle, 1885); **j** *As. plangon* (Gray, 1849); **k** *As. rozellum* (Iredale, 1926); **l** *As. tullbergi* (Appellöf, 1886). [**a**, **b**, **d**, **e**, **h–j**, **l** Reid et al. (2005); **c**, **f, g**, **k** David Paul]

He also refers to the absence of an outer cone (although the outer cone is, indeed, present but very narrow and thin), and the deep mantle (thick dorso-ventrally) and the position of the fins. While we agree that the cuttlebone position and overall morphology is distinctive, on that basis alone we cannot justify the retention of *Metasepia* based on phylogenetic grounds as revealed by our molecular analysis, so these taxa are placed in new combination with *Ascarosepion.*

Member taxa (this study): *Ascarosepion apama* (Gray, 1849); *As. bandense* (Adam, 1939b); *As. cultratum* (Hoyle, 1885); *As. latimanus* (Quoy & Gaimard, 1832); *As. mestus* (Gray, 1849); *As. novaehollandiae* (Hoyle, 1909); *As. opiparum* (Iredale, 1926); *As. papuense* (Hoyle, 1885); *As. pfefferi* (Hoyle, 1885); *As. plangon* (Gray, 1849); *As. rozellum* (Iredale, 1926); *As. tullbergi* (Appellöf, 1886).

Aurosepina **Jothinayagam, 1987**

(Figs. 1, 4c, 7)

Type species. Sepia arabica Massy, 1916. The Cephalopoda of the Indian Museum. *Records of the Indian Museum*, 12(part 5)(16): 185–247, 2 plates: 228. Plate XXIII: 1–5. *Type locality*: Laccadive Sea, 11°14′30″ N 74°57′15″ E. Persian Gulf, 26°20′ N 53°54′ E.

Diagnosis. Posterior gland and gland pore absent. Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression that corresponds to ridge. *Head with large, fleshy, ear-shaped lobes posterior to eyes* (Fig. 7a–c). Wide gap posteriorly between fins. Arm suckers tetraserial, small and widely spaced. *Arms 2 and 3 with a series of tubercles along their dorsal margins.* Hectocotylus present, left ventral arm modified on proximal third: suckers displaced toward lateral arm margins, with fleshy region devoid of suckers between rows; oral arm surfaces folded together longitudinally and nearly completely covered by protective membranes; suckers much smaller than normal arm suckers. Club crescent-shaped, small; with 5–6 small similar-sized suckers in oblique transverse rows; swimming keel of club as wide as sucker-bearing surface of club, extends slightly beyond carpus; dorsal and ventral protective membranes not fused at base of club; dorsal membrane much wider than ventral membrane. Buccal membrane without suckers.

Dorsal mantle with pale circular tubercles between 10 and 12 dark patches of concentrated chromatophores along base of fins. Dorsal side of arms 3 with rectangular brown patches.

Cuttlebone outline lanceolate, narrow (Fig. 7d); *widest anteriorly, posteriorly very narrow; recurved ventrally*. Dorsal surface granulose; wide bands of chitin border lateral margins; *spine absent*; dorso-posterior end of cuttlebone with short, median longitudinal keel; last loculus and striated zone strongly convex; shallow, sulcus confined to last loculus, broadest anteriorly, tapers posteriorly toward striated zone; *anterior striae V-shaped*; inner cone limbs uniform width, narrow V-shaped posteriorly; slightly raised to form rounded posterior ridge; *inner cone posteriorly with irregular calcareous ribs radiating into outer cone; outer cone limbs expanded posteriorly, rounded, paddle-shaped.*

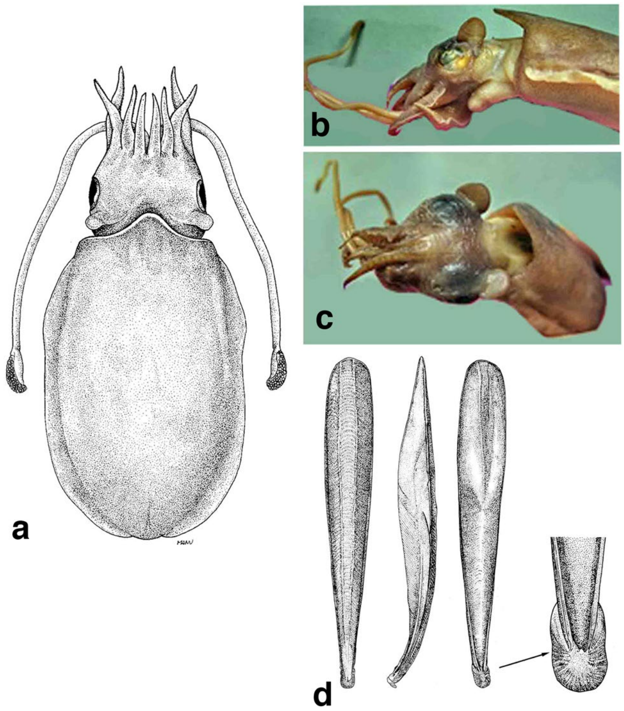

Fig. 7 *Aurosepina arabica* (Massy, 1916). **a** whole animal, dorsal view; **b** fresh specimen lateral view, showing pronounced flap posterior to eyes; **c** fresh specimen anterior dorsal view; **d** cuttlebone (left to right): dorsal view, lateral view, ventral view, enlargement of posterior end of cuttlebone, ventral view. [**a**, **d** Reid et al. (2005), fig. 118 (in part); **b**, **c**, Tooraj Valinassab]

Distribution. Indian Ocean: Red Sea, Gulf of Aden, Persian Gulf, western and southern India, Laccadive Islands (Fig. 4c).

Remarks. The cuttlebone is much broader anteriorly than posteriorly, unlike that seen in *Doratosepion*. The fleshy lobes posterior to the eyes are also very distinctive.

Adam and Rees (1966) describe only males from the Red Sea, but notably do not refer to the distinct rounded lobes, nor make any reference to the tubercles on arms 2 and 3. Jothinayagam (1987) in describing a male specimen of this species established the genus *Aurosepina* based on the ear-shaped skin flaps, unique cuttlebone morphology (in particular the radiating inner cone ribs and lack of a spine) and the presence of tubercles at the bases of arms 2 and 3; two on arms 2 and barbs or tubercles along the full length of the dorsal aboral surfaces of arms 3. Nateewathana (1996) did not recognise the genus as valid, feeling that the traits listed by Jothinayagam (1987) were not of a magnitude to warrant generic recognition, but if not species-level differences might warrant subgeneric recognition. However, given the long branch length uncovered in our molecular analysis and distinctive traits separating *Au. arabica* from its sister clade *Doratosepion*, we concur with Jothinayagam (1987) in recognising *Aurosepina* as valid.

Jothinayagam (1987) and Adam and Rees (1966) both refer to the absence of a spine on the posterior end of the cuttlebone. There looks to be a small spine in Adam and Rees (1966): Plate 23 Fig. 154b; this was the photograph used as a reference for the ink illustrations below. However, the posterior end of the bone figured in Adam and Rees (1966) may simply be slightly broken and bent dorsally.

Member taxon (this study): *Aurosepina arabica* (Massy 1916).

Decorisepia Iredale, 1926

(Figs. 1, 4d, 8)

Type species. *Decorisepia rex* Iredale, 1926. The cuttlefish "Bones" of the Sydney Beaches. Aust. Zool. 4:186–196, pls 22–23, 2 text figs. [193, pl. XXIII, figs. 9, 10] *Type locality:* Australia, New South Wales, Manly Beach. [= *Sepia hedleyi* Berry, S.S., 1918. Report on the Cephalopoda obtained by the F.I.S. "Endeavour" in the Great Australian Bight and other southern Australian localities. Biological Results of the Fishing Experiments carried on by the F.I.S. "Endeavour," 1909–14, 4(5):201–298, 67 figures, 29 plates: 258. *Type locality:* South Australia, Investigator Strait area (35°25′S 137°22′E), south of Kangaroo Is. (35°50′S 137°15′E).]

Diagnosis [modified from Iredale (1926)]. Posterior gland and gland pore absent. Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression that corresponds to ridge. Male and female arms subequal in length; arm suckers tetraserial throughout. Hectocotylus present; left ventral arm modified: 6–10 rows of normal suckers proximally, 6–10 rows of minute suckers medially, remaining suckers normal to arm tip; *suckers in two dorsal series smaller than those in two ventral series, dorsal and ventral series widely spaced, those in ventral two series may be aligned in a single row.* Tentacular club short, slightly recurved, not expanded, with 5–12 suckers in transverse rows, all similar sized, small, or with some enlarged suckers; dorsal and ventral protective membranes not fused at base of club; swimming keel extends beyond carpus along stalk. Female buccal membrane with spermathecae. Buccal membrane without suckers.

Skin smooth, without papillae (Fig. 8a).

Cuttlebone elliptical, acute anteriorly, narrower anteriorly; median rib present medio-dorsally (Fig. 8a); spine present, rounded in cross section, with or without keel; anterior striae inverted U-shape (or wavy M-shaped following sulcus in *S. australis*); *inner cone limbs uniform width, narrow, thickened, U-shaped posteriorly* (Fig. 8b); outer cone narrow, uniform width, not flared ventrolaterally.

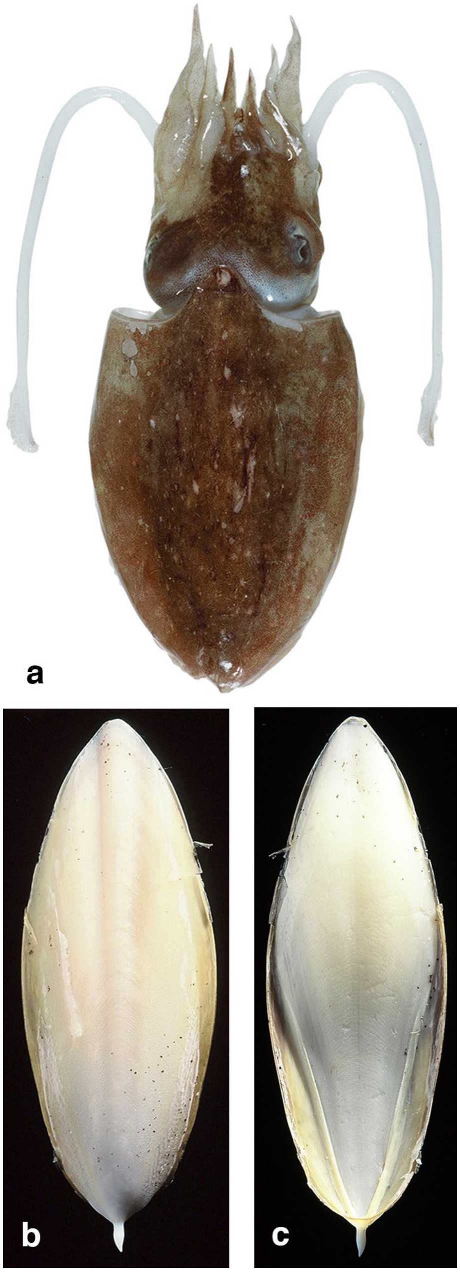

Fig. 8 *Decorisepia hedleyi* (Berry, 1918). **a** freshly caught specimen, dorsal view; **b** cuttlebone dorsal view; **c** cuttlebone ventral view. (**a** CSIRO Science Image AF9586; **b**, **c** David Paul)

Distribution. Southern Africa, Australia, northwestern Pacific from Japan to Taiwan. Possibly the Red Sea (*De. australis*) (Fig. 4d).

Remarks. The original definition of *Decorisepia* was based on the cuttlebone alone. Iredale (1926) diagnosed *Decorisepia* (with type species *Decorisepia rex* [now synonomised with *S. hedleyi* (Iredale 1926)] by the following traits: a rounded spine, inner cone lacking and outer cone large and 'scarcely calcareous'. However, *Sepia hedleyi* clearly has an inner cone, albeit a very narrow one with uniform width. It appears that Iredale (1926) has misinterpreted this structure. His fig. 7 (p. 189) that illustrates terms used in the description clearly shows a species in which the inner cone is characterised by secondary folding of the inner cone over the posterior part of the cuttlebone phragmocone. This secondary folding is not a characteristic of *Decorisepia*.

The tentacular club suckers in *De. hedleyi* and *De. madokai* are all small and uniform in size, while those of *De. australis* have ~ 4 suckers enlarged on the posterior end. The former two taxa do not have a keeled cuttlebone spine but there is a dorsal keel that extends along the posterio-dorsal side of the cuttlebone for some distance in *De. australis.*

Member taxa (this study). *Decorisepia australis* (Quoy & Gaimard, 1832); *De. hedleyi* (Berry, 1918); *De. madokai* (Adam, 1939a).

Digitosepia Lipiński, 2020

(Figs. 1, 4e)

Type species. *Rhombosepion robsoni* Massy, 1927. The Cephalopoda of the South African Museum. Annals of the South African Museum, 25(4):151–167, 2 plates. 159. *Type locality:* Africa: South Africa, Hout Bay. (Cuttlebone in poor condition.)

Diagnosis [modified from Lipiński (2020a)]. Small species (all less than 40 mm ML); mantle broad, oval; ventral mantle margin usually (but not in all species) emarginate medially, with distinct lateral angles. Posterior gland and gland pore absent. Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression that corresponds to ridge. No pores on ventral mantle. Ventral mantle with distinct ridge along each side. Some species with adhesive pads. Arm suckers biserial. Arms 1 tips with or without suckers and protective membranes. Hectocotylus present, *both ventral arms modified*: left ventral arm sucker size reduced proximally; ~ 10–15 rows of reduced suckers; reduced suckers much smaller than normal arm suckers; suckers displaced laterally; dorsalmost row smallest in zigzag arrangement, ventral suckers in straight line; oral surface in modified region swollen, fleshy with transverse ridges; right ventral arm with some enlarged suckers. Tentacular club short, crescent-shaped; sucker-bearing face flattened; with 4–8 suckers in oblique transverse rows; suckers all similar size, small; swimming keel of club usually extends well beyond club; dorsal and ventral protective membranes not fused at base of club. Buccal membrane without suckers.

Head and dorsal mantle with species-specific modifications that include clusters of papillae, warts, tubercles and or turrets [as defined by Lipiński (2020a)].

Cuttlebone not calcified or thinly calcified; outline ovoid, usually distinctly V-shaped anteriorly; bluntly rounded posteriorly; outer cone present; chitinous, not calcified. Indistinct median ridge in some species median sulcus absent; anterior striae wavy, straight, or slightly convex; *spine absent, or reduced to a blunt knob*; inner cone narrow, not raised to form ledge, uniform width; fused to outer cone; outer cone narrow anteriorly, very broad posteriorly.

Distribution. South Africa (Fig. 5e).

Remarks. Lipiński's (2020a) subgenus is here elevated to full generic status. Lipiński (2020a: 178) diagnosed the subgenus as including sepiids with a 'substantially modified cuttlebone', that includes the reduction of the inner cone to a thin band that is completely fused to the outer cone; striae moderately or strongly convex and the tips of the dorsal-most arm pair being completely devoid of suckers. Based on this diagnosis, Lipiński (2020a), retains *dubia, pulchra* and *shazae* in the subgenus *Sepia*. However, we have modified the generic diagnosis as the absence of suckers on the distal tips is not a trait shared by all members of the clade as revealed by molecular data. Among the species included in our analysis, *dubia* and *shazae* have suckers on the distal tips of the dorsal arms, however, they conform to *Digitosepia* in other respects and sit within the well-supported clade in our analysis that includes the *Digitosepia* type species, *Di. robsoni*.

The elaborate skin adornments that are characteristic for members of this clade serves to unify them. These modifications are permanent skin textural components and are likely composed (although yet to be verified) of cartilage or fibrous connective tissue as are the superocular cirri that are present in some incirrate octopods. In this respect they are unlike the various ridges, flaps and skin papillae that morph by muscular control in other cuttlefishes.

Lipiński (2020a) treats *S. typica* as distinct (under the subgenus *Hemisepius*). We concur with this view but give *Hemisepius* full generic status (see below).

Lipiński (2020a) indicates that many of the small South African sepiids in museum collections were preserved in 10% buffered formalin for varying amounts of time prior to transfer to 70% ethanol for long-term storage. Some of the cuttlebones were decalcified to varying degrees. It is unclear whether the lack of calcification or 'thin' calcification reported for members of this genus is an accurate trait, or in some cases could simply be due to the nature of preservation resulting in acidification of the storage media. It would be valuable in future if the cuttlebones could be removed from fresh specimens following capture and photographed prior to storage (preferably dry for species with small cuttlebones).

Members of this genus have previously been attributed to *Hemisepius*. *Hemisepius* is here limited to the species *H. typicus*. *Digitosepia* differs from *Hemisepius* due to the absence of ventral pores and the presence of significant skin modifications. *Hemisepius typicus* is only slightly papillose.

Member taxa (this study): *Digitosepia barosei* (Lipiński, 2020a); *Di. dubia* (Adam and Rees, 1966); *Di. faurei* (Roeleveld, 1972); *Di. robsoni* (Massy, 1927); *Di. roeleveldi* (Lipiński, 2020a).

Doratosepion Rochebrune, 1884

(Figs. 1, 4f, 9)

Type species. *Sepia andreana* Steenstrup, 1875. *Hemisepius*, ennyslaegt of Sepia-Blacksprutternes famile, Bemaerkinger om Sepia-Formerne. Almind. Kongelige dansk Videnskabernes Selskabs Skrifter, 10(5): 465–482, pl. 1, figs. 11–19. *Type locality*: Japan, Hakodate.

Diagnosis [modified from Rochebrune (1884)]. Mantle oblong; dorsal anterior margin triangular, acute; ventral mantle margin shallowly concave, without distinct lateral angles. Posterior gland and gland pore absent. Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression that corresponds to ridge. *Male arms usually modified: arms subequal, or arms 1 and/or 2 elongate (arms 3 elongate in* Do. braggi*)*; when elongate, may be attenuate, narrow and whip-like, or, in some species, broad, flared (Fig. 9a). *Female arm lengths subequal or some arm pairs may be elongate. Arm sucker arrangement may be tetraserial, or some arms, or parts thereof (usually distally) may have biserial suckers in one or both sexes; suckers may differ in size, some (usually biserial suckers may be minute and displaced laterally with gap in between).* Hectocotylus usually present, left ventral arm modified; *with reduced suckers distally*; reduced suckers may be much smaller than normal arm suckers; suckers evenly spaced on modified portion of arm, or rows may be displaced laterally with transverse grooves between, or deep median furrow. Club crescent-shaped with 4–10 suckers in oblique transverse rows; suckers similar or differing in size; swimming keel of club usually extends slightly beyond carpus along stalk; dorsal and ventral protective membranes usually not fused at base of club; joined to stalk; terminate at posterior end of carpus. Buccal membrane without suckers.

Dorsal mantle with longitudinal row of approximately six ridge-like papillae along each side, close to base of each fin. Arms 1–3 often with longitudinal orange-red pigmented stripe along aboral surfaces; narrow longitudinal iridescent band on each side close to fins.

Cuttlebone outline lanceolate; bone acuminate, acute anteriorly and posteriorly (Fig. 9b, c); dorsal median rib usually present; spine present; striated zone and last loculus convex; sulcus extends entire length of cuttlebone; sulcus shallow, narrow; anterior striae shallow m-shaped; inner cone uniform width, narrow, U-or V-shaped posteriorly, *usually raised and deflected ventrally forming a flat or rounded ledge separated from phragmocone; outer cone limbs usually expanded posteriorly forming two short 'wings', directed ventrally, forming recurved cup-like structure* (Fig. 9c).

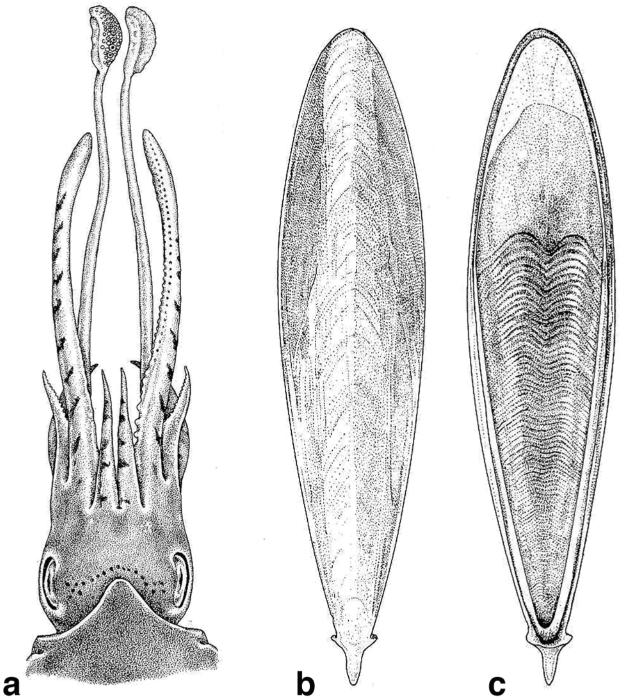

Fig. 9 *Doratosepion andreanum* (Steenstrup, 1875). **a** head of male, dorsal view; **b** cuttlebone dorsal view; **c** cuttlebone ventral view. [Reid et al. (2005) fig. 114 (in part)]

Distribution. Western Pacific and eastern Indian Oceans from Japan to Australia (Fig. 4f).

Remarks. Rochebrune (1884) defined this genus for Sepiidae with an elongate body, short arms with biserial suckers, short tentacular clubs with unequal suckers and a very elongated cuttlebone with two posterior 'wings' and a spine. This diagnosis was later rejected by Adam (1944) and Adam and Rees (1966).

Member taxa (this study): *Doratosepion andreanum* (Steenstrup, 1875); *Do. braggi* (Verco, 1907); *Do. erostratum* (Sasaki, 1929); *Do. foliopeza* (Okutani & Tagawa [in Okutani, Tagawa and Horikawa], 1987); *Do. kobiense* (Hoyle, 1885); *Do. limatum* (Iredale, 1926); *Do. longipes* (Sasaki, 1913); *Do. lorigerum* (Wülker, 1910)*; Do. pardex* (Sasaki, 1913); *Do. peterseni* (Appellöf, 1886); *Do. tenuipes* (Sasaki, 1929); *Do. tokioense* (Ortmann, 1888).

Erythalassa Reid, gen. nov.

(Figs. 1, 4g, 10)

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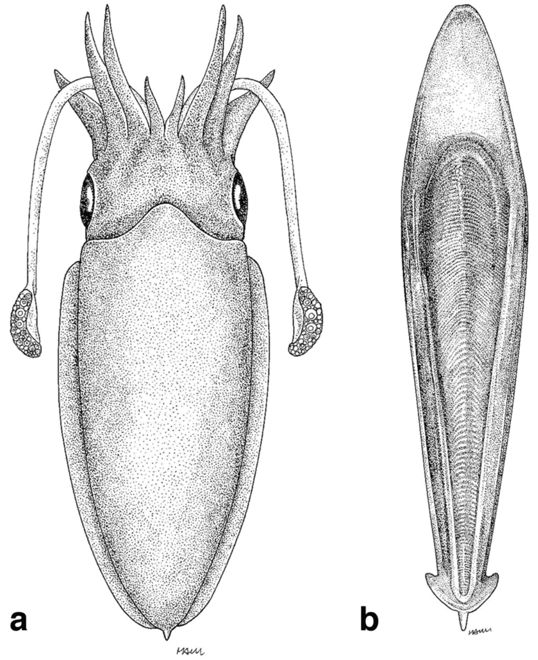

Fig. 10 *Erythalassa trygonina* (Rochebrune, 1884). **a** whole animal dorsal view; **b** cuttlebone ventral view. [Reid et al. (2005), fig. 192 (in part)]

Type species. *Doratosepion trygoninum* Rochebrune, 1884. Étude monographique de la famille des Sepiidae. *Bulletin des Sciences par la Société Philomatique de Paris*, 7(8): 74–122, pls 3–6: 97. Here designated. *Type locality*: Red Sea.

Diagnosis. Mantle oblong, acuminate posteriorly (Fig. 10a). Male and female arms differ in relative lengths, male arms 1 shorter than rest. Female arm lengths subequal. Arm sucker arrangement differs between sexes: *in males, arm suckers tetraserial; females, suckers on arms 1 and 4 tetraserial, suckers arms 2 and 3 tetraserial proximally, biserial on distal third of arms; female arms 2 and 3 suckers displaced laterally with gap between*. Hectocotylus present, left ventral arm modified: sucker size normal proximally, tetraserial for approximately four rows, *followed distally by modified region without suckers, then suckers normal to arm tip; oral surface of modified region surface hollowed out and covered by large transversely grooved protective membranes; ventral membrane wider than dorsal membrane, thick and curved inward*; some minute suckers marginally toward distal end of modified region. Club short, oval; with 8 suckers in oblique transverse rows; suckers differing markedly in size, 4–5 greatly enlarged suckers in longitudinal series towards posterior end of club. Buccal membrane in females without spermathecae. Ground colour (alcohol preserved specimens) purplish brown; fins males with dark purple band at base, adjacent to band or partially on it is a series of small oval or circular cream-coloured patches, often raised as low tubercles.

Cuttlebone outline, lanceolate; strongly recurved ventrally; dorsal surface pinkish; calcified medially, thickest posteriorly, slightly granulose with irregular longitudinal ridges; dorsal median rib present; indistinct; chitin present, wide bands border lateral margins of cuttlebone; spine curves dorsally, keel absent; sulcus extends entire length of cuttlebone; sulcus shallow, wide, flanked by rounded ribs (bordered by concave region with less distinct striae); anterior striae inverted U-shaped; inner cone lateral limbs overlie calcareous striated zone, anteriorly bordered, separated from outer cone by striated zone; inner cone limbs uniform width, narrow, U-shaped posteriorly; slightly raised to form rounded posterior ridge; *outer cone present; outer limbs expanded forming two long 'wings', directed ventrally, forming recurved cup-like structure* (Fig. 10b).

Distribution. Indian Ocean from Saya-de-Malha Bank and Zanzibar to South India, Red Sea, Persian Gulf (Fig. 4g).

Etymology. The generic name, *Erythalassa* is derived from the ancient Greek name for the Red Sea, Erythra Thalassa, the type locality for its type species *trygonina.* Gender feminine.

Member taxon (this study): *Erythalassa trygonina* (Rochebrune, 1884).

Lusepia Reid, gen. nov.

(Figs. 1, 4h, 11)

http://zoobank.org/urn:lsid:zoobank.org:act:E2CE66B1-5F68-4959-ABC4-78BB495D5A14

Type species. *Rhombosepion hieronis* Robson, 1924. On the Cephalopoda obtained in South African waters by Dr. J.D.F. Gilchrist in 1920–21. Proceedings of the Zoological Society of London 1924(2):589–686, 51 figures, 2 plates: 645. Here designated. *Type locality*: Africa: South Africa, Cape Town, 32°32′–33°03′S 17°29′–17°42′E.

Diagnosis. Fins very narrow. *Arms shortest dorsally*, *longest ventrally*; dorsal arms in males attenuated over distal third (Fig. 11a, b). Arm sucker arrangement differs between sexes. *Males: dorsal arm suckers biserial, minute on distal tips of dorsal arms; suckers of basal two thirds of arms 2 biserial, irregularly arranged (sometimes, tetraserial on middle third of arms), followed by 3–5 pairs greatly enlarged suckers* (Fig 11b), *distalmost of enlarged suckers elongate with long pedicels; distalmost suckers minute, tetraserial; arms 3 similar to arms 2 but middle third of arm with tetraserial suckers, enlarged suckers not as large as those on arms 2. Right ventral arm suckers on basal third same as arms 2 and 3, then suckers tetraserial on middle third of arms then 3–8 biserial rows, then about 5 rows of larger biserial suckers, distal arm tips with biserial suckers. Left*

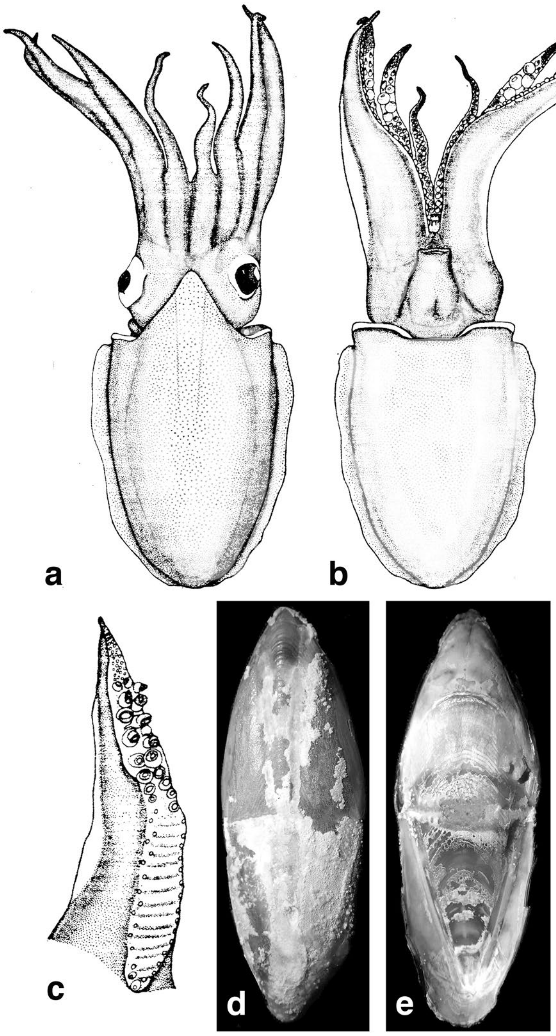

Fig. 11 *Lusepia hieronis* (Robson, 1924). **a** whole animal dorsal view; **b** whole animal ventral view; **c** hectocotylus; **d** cuttlebone dorsal view; **e** cuttlebone ventral view. [Modified from: **a** Roeleveld (1972), fig. 13b; **b** Roeleveld (1972), fig. 13a; **c** Roeleveld (1972), fig. 13c (male SAM A30563); **d**, **e** AM C.572187, Amanda Reid]

ventral arm hectocotylised: 1–3 normal suckers basally, followed distally by modified region that bears minute tetraserial suckers; dorsal and ventral series displaced laterally, ventral rows of suckers aligned in a single row; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges (Fig. 11c). *Distal to modified region suckers biserial, 9–10 pairs enlarged, rest minute to tip*. Females: all arms attenuate distally, *skin wrinkled basally next to sucker-bearing surface*. Suckers biserial on all arms, with some enlarged suckers in mature females.

Tentacular club with 8 suckers in transverse rows; suckers all similar size; swimming keel of club extends well beyond carpus; dorsal and ventral protective membranes not fused at base of club. Dorsal mantle and head sparsely papillose.

Cuttlebone length approximately equal to mantle length; outline oval; not strongly convex in lateral view; bone acuminate, acute anteriorly; acuminate, rounded posteriorly; not strongly recurved ventrally; entire surface calcified with reticulate granulose sculpture concentrated posteriolaterally and posteriorly in irregular longitudinal ridges; dorsal median rib present; distinct; broadens anteriorly; bordered laterally by distinct grooves (Fig. 11c); lateral ribs absent; spine absent, a blunt knob posteriorly; anterior striae inverted U-shaped; inner cone limbs uniform width, narrow V-shaped posteriorly (Fig. 11d); not raised to form ledge posteriorly; thickened slightly; outer cone narrow anteriorly, broadens posteriorly; lateral limbs not flared ventro-laterally.

Distribution. Africa: southern Namibia, to approximately 27°S to South Africa and east Africa from 17°S (Atlantic Ocean) to Kenya and Mozambique (Indian Ocean). Saya-de-Malha Bank (Fig. 4h).

Etymology. The genus is named for the esteemed researcher Chung Cheng Lu in honour and acknowledgement of the enormous contribution Lu has made to cephalopod research over many years. The name is derived from the combination of Chung Cheng Lu's family name with *Sepia*, the type genus for the family Sepiidae. Gender feminine.

Remarks. The molecular and morphological data indicate *Lusepia hieronis* is clearly distinct from those taxa in its sister clade *Digitosepia*, lacking the distinct skin modifications that characterise most members of this group.

It also differs in its unique morphology from *H. typicus*, so we do not consider it should be assigned to the only other possible nominal genus, *Hemisepius. Lusepia hieronis* differs from *H. typicus* due to the absence of ventral pores. The cuttlebone phragmocone is equal in length to the dorsal shield and is acute anteriorly, while in *H. typicus* the cuttlebone phragmocone is much shorter than the dorsal shield and the anterior margin is triangular, obtuse. In *Lusepia hieronis* outer cone is calcified; in *H. typicus* the outer cone is chitinous.

Member taxon (this study): Lusepia hieronis (Robson, 1924) by monotypy.

Hemisepius **Steenstrup, 1875**

(Fig. 12)

Type species. *Hemisepius typicus* Steenstrup, 1875. *Hemisepius*, en ny Slaegt af *Sepia*-Blacksperutternes Familie, med Bemaerkninger om *Sepia*-Formerne i Almindelighed. Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk, 10(7): 465–482, 2 plates: 468. *Type locality*: Africa: South Africa, Table Bay, 33°50′ S 18°27′ E.

Diagnosis [modified from Steenstrup (1875), and after Roeleveld (1972)]. Small species, up to approximately 25 mm ML. Ventral mantle margin emarginate, with distinct

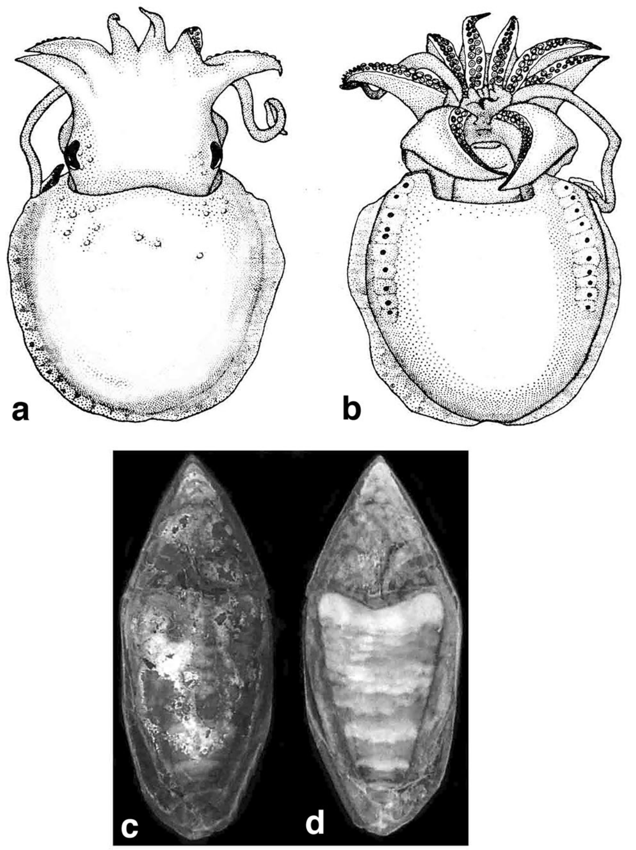

Fig. 12 *Hemisepius typicus* Steenstrup, 1875. **a** dorsal view; **b** ventral view showing ventrolateral pores (female SAM A29783); **c** cuttlebone dorsal view; **d** cuttlebone, ventral view. [**a**, **b** modified from Roeleveld (1972), fig. 17. **c**, **d** modified from Leslie et al. (2022), fig. 22, male, SAIAB 211602]

lateral angles. Posterior gland and gland pore absent. Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression that corresponds to ridge. *Fins fused posteriorly. Webs between arms 1–3 deep, reaching halfway along arms. Non-hectocotylised arm suckers biserial.* Male non-hectocotylised arm suckers: dorsal arms with 11 pairs of large suckers and few small suckers at tips, largest suckers broadest at base of arms, diminishing distally but 9th and 10th pair slightly broader; arms 2 similar, but 9th pair broader; arms 3 with 13–15 pairs of large suckers, 11th and 12th with greatest diameter; arms 4 with 15 pairs of large suckers, proximal much broader than on other arms, reduced distally with 11th to 14th pair larger. Hectocotylus present, left ventral arm modified: *sucker size reduced proximally, enlarged, then reduced distally to arm tip; 9–13 rows of reduced suckers (reduced suckers followed distally by 5–6 pairs of much larger suckers* [figured in Adam and Rees (1966)]; reduced suckers much smaller than normal arm suckers; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges; suckers in two dorsal two ventral series displaced laterally. Club short, oval, with 6 suckers in oblique transverse rows; swimming keel of club extends well beyond carpus; dorsal and ventral protective membranes not fused at base of club. Buccal membrane without suckers.

Dorsal mantle papillose (sparse); two pale, round tubercles with concentric chromatophores in middle of darker diamond-shaped region. Anterior half of ventral mantle in both sexes with fleshy ridge laterally on each side; ridges with 5–15 (usually 10–12) deep pores; pores situated in middle of distinct, roundish patch.

Cuttlebone thin, not calcified; phragmocone much shorter than dorsal shield; outline inversely obovate; bone triangular, obtuse anteriorly; curved posteriorly; outer cone present, chitinous.

Distribution. South Africa.

Remarks. This is the type species of Steenstrup's genus *Hemisepius.* Adam and Rees (1966) relegated *Hemisepius* to subgeneric status and included *S. dubia* in the subgenus, but *S. dubia* sits well within our *Digitosepia* clade. Thore (1945: 50) proposed that the smaller eastern forms be known as *H. typicus* var. *chuni.* A recent detailed analysis of quantitative and qualitative characters from across the full distributional range of this species has shown *H. typicus* to be a highly variable species (Leslie et al. 2022). A comprehensive molecular analysis is needed to further examine the status and population structure in this taxon.

Member taxon (this study): *Hemisepius typicus* Steenstrup, 1875.

Rhombosepion Rochebrune, 1884

(Figs. 1, 4i, 13)

Type species. *Sepia rupellaria* d'Orbigny, 1834 [in Férrusac & d'Orbigny, 1834–1848]. Histoire naturelle Générale et particulière des Céphalopodes acétabulifères vivants et fossils, Paris: i–lvi+1–361 & atlas, 144 pls. [274, Seiche pl, figs. 10–13]. *Type locality*: France, Island of Noir-moutiers and La Rochelle. [=*Sepia elegans* Blainville, 1827. Sèche, *Sepia* (Malacoz.). Dictionnaire des Sciences Naturelles, 48: 257–293 (July 1827): 284. *Type locality*: Sicily.]

Diagnosis [modified from Rochebrune (1884)]. Posterior gland and gland pore absent. Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression that corresponds to ridge. Ventral mantle margin emarginate, without distinct lateral angles. Male and female arms subequal in length. Arm suckers tetraserial or arms with some biserial suckers; arrangement differs between sexes. [In *R. elegans* males, arms 1 suckers biserial for few rows, rest tetraserial, arms 2 and 3 suckers tetraserial proximally, biserial at extreme distal tip, arms 4 suckers variously arranged (approximately 10 pairs biserial suckers arms 1–3, arms 4 with 2–4 rows biserial suckers); median suckers

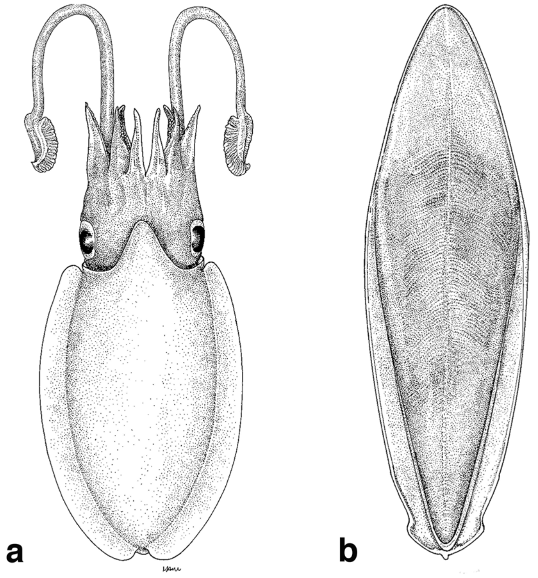

Fig. 13 *Rhombosepion elegans* Rochebrune, 1884. **a** whole animal, dorsal view; **b** cuttlebone, ventral view. [Reid et al. (2005), fig. 132 (in part); cuttlebone image modified from original]

with greater diameter than marginal ones. In females, suckers biserial proximally, tetraserial distally (5 rows biserial arms 1–3, 2–4 rows biserial arms 4)]. Hectocotylus present, left ventral arm modified; sucker size normal proximally, reduced medially, then normal to arm tip; reduced suckers minute, much smaller than normal arm suckers; suckers in two dorsal and two ventral series displaced laterally; suckers in two ventral series smaller than rest. Tentacular club short, oval; short; sucker-bearing face flattened; with 6–8 suckers in oblique transverse rows; *suckers differing markedly in size, some greatly enlarged*. Buccal membrane in females with single median spermatheca in ventral part. Body papillae present; ventral mantle with longitudinal row of six narrow ridges along each side close to fins. Eggs whitish in *R. elegans* and *R. orbignyanum.*

Cuttlebone acuminate, acute anteriorly and posteriorly, or bluntly rounded posteriorly; recurved ventrally; spine present with keel(s); dorso-posterior end of cuttlebone with short, median longitudinal ridge extending anteriorly; last loculus convex; narrow, shallow sulcus extends entire length of cuttlebone; anterior striae inverted U-shaped; inner cone limbs uniform width, narrow throughout or broaden posteriorly; V-shaped posteriorly; not raised to form ledge posteriorly; outer cone narrow throughout; lateral limbs not flared ventro-laterally.

Distribution. Northeastern Atlantic Ocean including the Mediterranean Sea, eastern and northern Indian Ocean (Fig. 4i).

Member taxa (this study): *Rhombosepion elegans* (Blainville, 1827); *R. omani* (Adam & Rees, 1966); *R. orbignyanum* (Férussac [in d'Orbigny], 1826); *R. prashadi* (Winckworth, 1936).

Sepia Linnaeus, 1758

(Figs. 1, 4j, 14)

Type species. *Sepia officinalis* Linnaeus, 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*, 658. *Type locality*: Eastern Atlantic. Type not traced.

Diagnosis [modified from Linnaeus (1758)]. Posterior gland and gland pore absent. Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression that corresponds to ridge. Non-hectocotylised arm sucker arrangement same in both sexes: arm suckers tetraserial or males may have biserial suckers at tips of arms. Hectocotylus present, left ventral arm modified; suckers normal proximally, reduced medially and normal to arm tip (Fig. 14a). Club with 5–6 suckers in oblique transverse rows; suckers differing in size; some large (Fig. 14b).

Cuttlebone outline oblong; not strongly convex in lateral view; bone acuminate, acute anteriorly; bluntly rounded posteriorly; spine present; sulcus present last loculus only, absent from striated zone; sulcus shallow, narrow; sulcus not flanked by rounded ribs; last loculus with shallow median indentation, not very pronounced; anterior striae inverted U-shaped, or shallow m-shaped; inner cone limbs narrow anteriorly, broaden posteriorly; not raised to form ledge posteriorly; not thickened; dull, not shiny; inner cone without calcareous ribs radiating into outer cone; outer cone

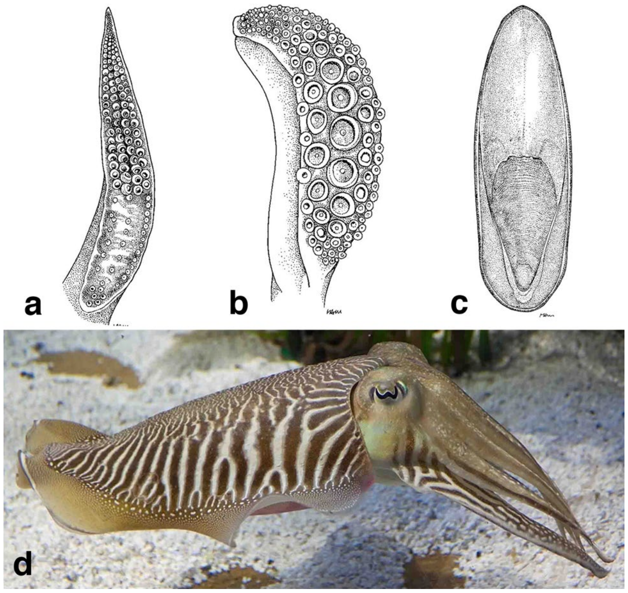

Fig. 14 *Sepia officinalis* Linnaeus, 1758. **a** hectocotylus; **b** tentacular club; **c** cuttlebone, ventral view **d** live animal, photo © Mexrix Dreamstime.com (Image ID 24638866). [**b–d** Reid et al. (2005), fig. 160 (in part)]

chitinous, spatulate, expanded; narrow anteriorly, broadens posteriorly (Fig. 14c).

Dorsal mantle with transverse zebra stripe pattern in mature males (Fig. 14d); fins pigmented.

Distribution. Eastern Atlantic, including the Mediterranean Sea, southwestern Indian ocean (eastern Africa) (Fig. 4j).

Remarks. Roeleveld (1972: 208) in her comprehensive account of the Sepiidae of southern Africa has noted that, '*S. officinalis* is the only species of *Sepia* known to occur in estuaries in southern Africa'. A description of breeding behaviour in a Dutch estuary is included in Norman (2000): 67–69. Its sister genus, *Sepiella,* also seems to tolerate a range of salinities.

Member taxa (this study): *S. hierredda* Rang, 1835; *S. officinalis* Linnaeus, 1758; *S. vermiculata* Quoy & Gaimard, 1832.

Sepiella **Gray, 1849**

(Figs. 1, 4k, 15)

Type species. *Sepia ornata* Rang, 1837. Documents pour servir à l'histoire naturelle des céphalopodes crypyobranches. Magasin de Zoologie, 7(Cl.V.): 1–77, 16 plates: 76. *Type locality*: Gulf of Guinea. Type not traced.

Diagnosis. Mantle oblong. *Mantle locking cartilage with triangular tubercle; funnel-locking cartilage with depression that corresponds to triangular tubercle. Gland and glandular pore on posterior tip of mantle, between fins* (Fig. 15a). Non-hectocotylised arm suckers tetraserial. *In males, chitinous inner ring of distal half of arm suckers with long, pointed teeth*. Hectocotylus present, left ventral arm modified; sucker size reduced proximally; ~ *10 rows of reduced suckers; suckers equal in size across rows; reduced suckers*

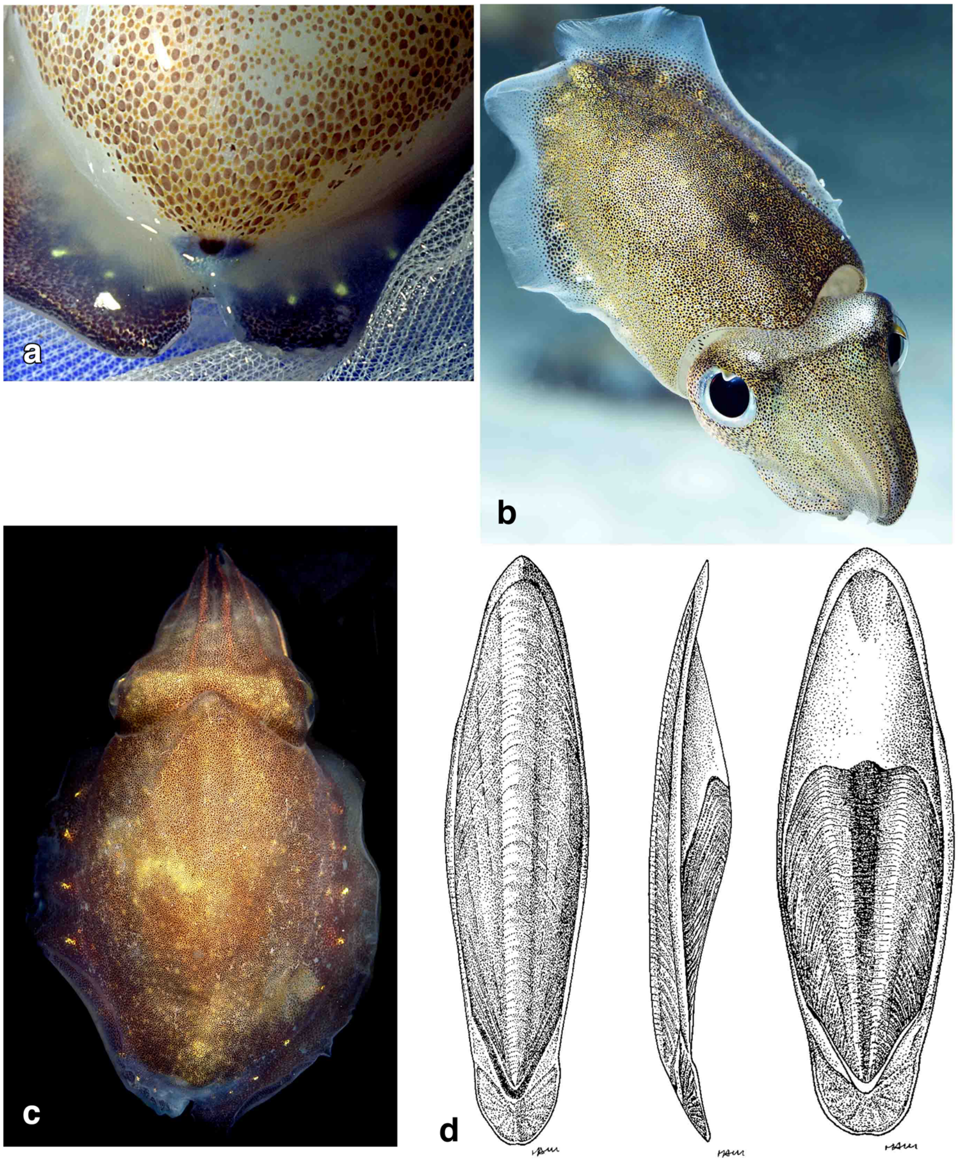

Fig. 15 *Sepiella inermis* (Van Hasselt [in Férussac & d'Orbigny], 1835). **a** posterioventral view showing glandular pore at tip of mantle; **b** live animal, dorsal view; **c** fresh caught animal *Sepiella ornata* (Rang, 1837): **d** (from left to right) cuttlebone dorsal, lateral and ventral views [**a, c** Mark Norman; **b** © BluehandDreamstime.com; **d** Reid et al. (2005), fig. 208 (in part)]

much smaller than normal arm suckers; oral surface of modified region wide, swollen, fleshy, with transversely grooved ridges; suckers in two dorsal two ventral series displaced laterally. Club with 10–14 suckers in transverse rows. Base of fins with rows of large spots (Fig. 15b, c).

Cuttlebone much shorter than mantle and located in anterior 2/3–3/4; outline oblong; bone acuminate, acute anteriorly; bluntly rounded posteriorly; *spine absent*; sulcus extends along striated zone only, shallow, narrow; sulcus flanked by rounded ribs; limbs of inner cone short, extend anteriorly to junction of striated zone and posterior termination of last loculus; inner cone limbs uniform width, narrow V-shaped posteriorly; not raised to form ledge posteriorly; not thickened; *outer cone present, chitinous, spatulate, expanded*, narrow anteriorly, broadens posteriorly, limbs expanded, extending posteriorly beyond inner cone, recurved ventrally (Fig. 15d).

Distribution. Indian Ocean from western African coast throughout the northern Indian Ocean and South China Sea to Japan and south to Australia (Fig. 4k).

Remarks. While the type species, *Sl. ornata* was not included in the molecular analysis, there is no doubt that the *Sepiella* clade includes a well-supported monophyletic group of taxa united by morphological traits.

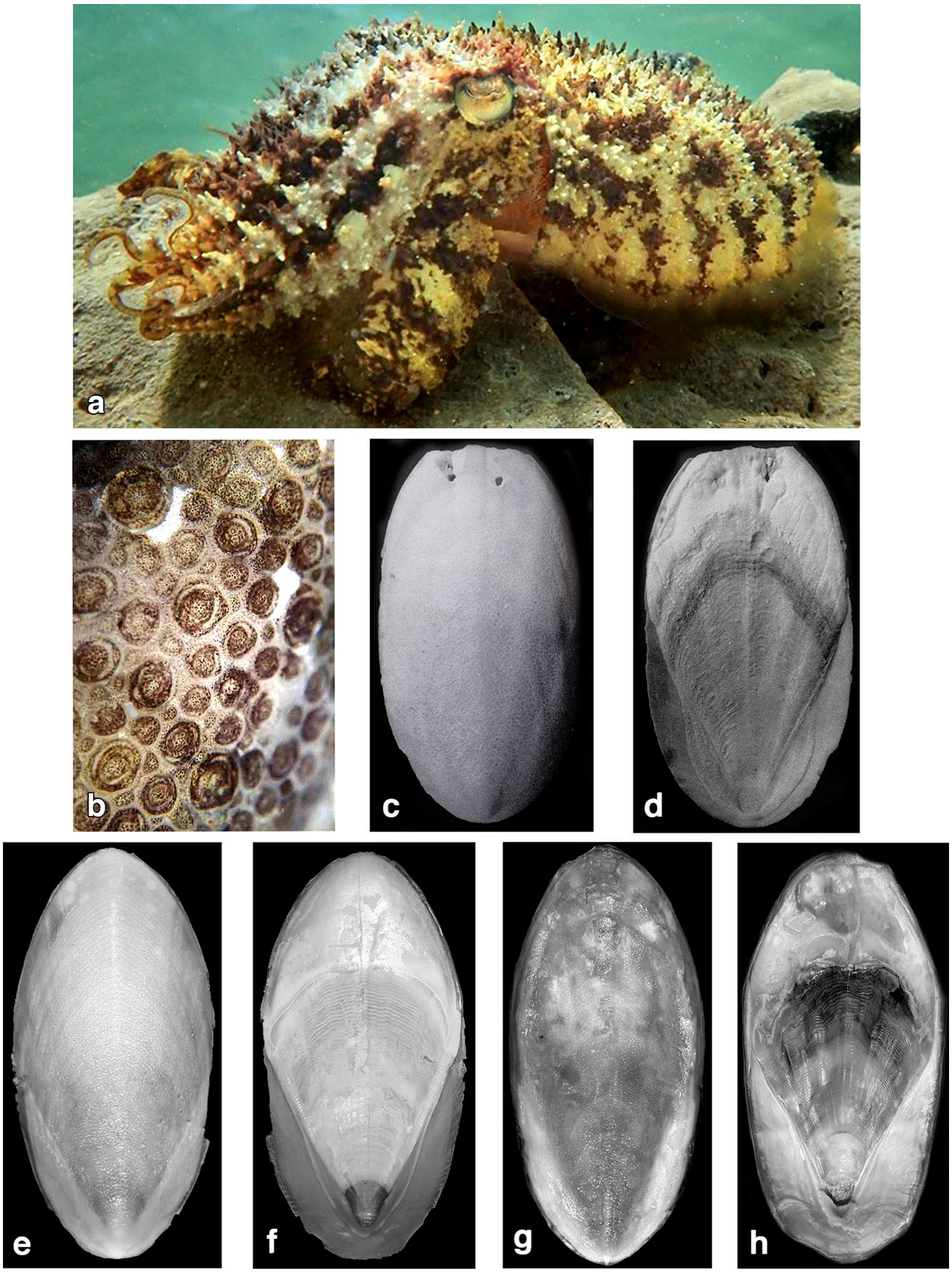

Fig. 16 *Spathidosepion tuberculatum* (Lamarck, 1798): **a** live animal; **b** enlargement of tubercles, fresh caught animal; **c** cuttlebone dorsal view; **d** cuttlebone ventral view. *Spathidosepion angulatum* (Roeleveld, 1972); **e** cuttlebone dorsal view; **f** cuttlebone ventral view; *Sp. papillatum* (Quoy & Gaimard, 1832) female; **g** cuttlebone dorsal view; **h** cuttlebone ventral view. [**a**, **b** Craig Foster; **c**, **d** figs. 169 and 170, Adam and Rees (1966); **e**, **f** A. Reid, AM C.572197; **g**, **h** A. Reid, AM C.572185]

Member taxa (this study): Sepiella inermis (Van Hasselt [in Férussac & d'Orbigny], 1835); *Sl. japonica* Sasaki, 1929.

Spathidosepion **Rochebrune, 1884**

(Figs. 1, 4l, 16)

Type species. *Sepia tuberculata* Lamarck, 1798. Extrait d'un Mémoire sur le genre de la Sèche, du Calmar et du Poulpe, vulgairement nommés, Polypes de mer. *Bulletin des Sciences, par la Société Philomatique de Paris*, 1(17): 129–131: 130. *Type locality*: Unknown.

Diagnosis. Mantle broad, oval. *Buccal membrane with papillae*. Webs uniting arms 1–3 deep, extending for approximately half the length of these arms. Distal tips of arms 1–3 may be long and attenuated (except in *Sp. papillatum*). Arm suckers tetraserial (eight rows on distal tips of arms in *Sp. papillatum* males). Hectocotylus present, left ventral arm modified; sucker size normal proximally, reduced medially, then normal to arm tip; reduced suckers, widely spaced; two dorsal two ventral series displaced laterally with wide gap between, suckers may appear as in a single row, or single zig-zag row. *Tentacular clubs long, slender*, with 8 suckers in oblique transverse rows; some suckers enlarged in *Sp. papillatum* and *Sp. tuberculatum*, markedly so in *Sp. papillatum*; dorsal and ventral protective membranes fused, or not fused at base of club. *Dorsal side of body, head and arms covered with coarse evenly spaced tubercles* (Fig. 16a, b); ventral mantle and ventral arms with wrinkled patches on each side (except in *Sp. angulatum*).

Cuttlebone broad, oval; not strongly convex in lateral view; bluntly rounded anteriorly and posteriorly; not strongly recurved ventrally; dorsal surface evenly convex; calcified with reticulate sculpture (especially posteriorly); dorsal median rib present; indistinct; broadens anteriorly; bordered laterally by distinct grooves (shallow); lateral ribs absent; chitin borders lateral and anterior margins of cuttlebone; spine absent, or reduced to a blunt knob; striated zone convex, strongly produced at junction with last loculus in *Sp. angulatum*; sulcus extends along striated zone only; anterior striae inverted V- or U-shaped; limbs of inner cone narrow, broaden posteriorly; inner cone limbs narrow anteriorly, broaden very slightly posteriorly and thickened, U-shaped; not raised to form ledge posteriorly, joined to outer cone; outer cone narrow anteriorly, broad posteriorly; lateral limbs flared ventro-laterally (Fig. 16c–h).

Distribution. Southern Africa (Fig. 4l).

Remarks. In the absence of available tissue for the type species *Sp. tuberculatum*, *Sp. angulatum* and *Sp. papillatum* (our Clade 6) are tentatively assigned to *Spathidosepion*, united by the presence of coarse tubercles and cuttlebones of very similar appearance. The correct assignment of our sequenced species to this clade requires future verification, however, at this time, there is not sufficient evidence to warrant assigning *Sp. angulatum* and *Sp. papillatum* to their own genus. There seems to be some variation in the sucker arrangement, but this may be a reflection of the degree of contraction of the arms.

Member taxa (this study): Spathidosepion angulatum (Roeleveld, 1972); *Sp. papillatum* (Quoy & Gaimard, 1832).

Discussion

Our tree contains more termini/species than included in previous cuttlefish phylogenetic studies. It is, however, completely congruent with some former studies. For example, the 12S rRNA tree of Bonnaud et al. (2006) clearly recovers groupings that correspond to our clades 1 (*Acanthosepion*), 2 (*Ascarosepion*), 3 + 4 (*Sepiella* and *Sepia*), and 5 (*Rhombosepion*), although with fewer species in each. Bonnaud et al. (2006) included two species not in our study: *Sepia filibrachia* Reid & Lu, 2005, was closely associated with *S. plangon* and *S. papuensis*, placing it in our Clade 2 (*Ascarosepion*). *Sepia whitleyana* (Iredale, 1926) was in a well-supported clade with *S. smithi, S. pharaonis, S. elliptica, S. recurvirostra*, and *S. aculeata*, placing it in our Clade 1 (*Acanthosepion*). Dai et al. (2012) recovered our Clade 1 and the *Sepiella* clade in separate neighbour-joining trees based on *COI* and 16S rRNA. However, their broad taxon study, which included squids and octopuses, included only a handful of sepiid species (eight) such that they did not recover other clades. The only included species outside our Clade 1 (*Acanthosepion*) and the *Sepiella* clade was *Metasepia tullbergi*; all species included by Dai et al. (2012) are included herein. Lin et al. (2004) did not recover our Clade 1 (*Acanthosepion*), but rather found *S. pharaonis* was sister to *Sl. maindroni*. However, a *COI* tree built of all available sepiid sequences (Supplementary Information 4) suggests that the *COI* sequences they included as *S. pharaonis* (AF359555) and *S. esculenta* (AF359554) are actually *Sl. japonica*. Their *S. robsoni COI* sequence (AF350495) falls as a slightly distant sister to a large clade of *S. esculenta* in a tree of all available *COI* sequences (Supplementary Information 4) and it is not clear what species AF350495 actually represents. It is important to note that the pioneers of cuttlefish phylogeny did not have the large database of comparative sequences that is now available to us, so recognising contaminant sequences at that time would have been extremely challenging. However, because it is helpful to all current researchers to recognise contaminants, we have included a list of sequences of sepiids thought to be misidentified (Supplementary Information 7). Yoshida et al. (2010) recognised that a *COI* sequence referred to *S. madokai* (AB192336) used in previous papers from their lab [Takumiya et al. (2005); Yoshida et al. (2006)] was not, in fact, *S. madokai*; analysis of all available sepiid *COI* sequences suggests it pertains to *Ac. esculentum*. Once that is considered, trees in Takumiya et al. (2005) and Yoshida et al. (2006), built on 12S + 16S + *COI* and 16S + *COI* respectively, are congruent with our study. Yoshida et al. (2006), who included more sepiid taxa (17), recovered Clades 1 (*Acanthosepion*), 2 (*Ascarosepion*), 3 (*Sepiella*), 4 (*Sepia*), (and the relationship between 3 (*Sepiella*), 4 (*Sepia*) and *S. bertheloti*), 5 (*Rhombosepion*) and 7 (*Doratosepion*), although each clade in their studies has fewer termini and clade 5 (*Rhombosepion*) is represented just by the lineage of *S. elegans*. Yoshida et al. (2010) increased the taxon sampling (to 23 termini, representing 20–22 sepiid species), and the resulting tree (based this time on *COI*, *Cytb* and *ND5*) even more closely resembles ours. The only deviation is in the placement of *S. elegans*. However, our large *COI* tree (Supplementary Information 4) reveals their *COI* sequences of *S. gibba* (AB430405) and *S. elegans* (AB430404) to actually be sequences of *Ac. pharaonis*, so the positions of these species in Yoshida et al. (2010) should be dismissed.

Thus, overall, there is considerable congruence between our tree and all previous cuttlefish phylogenies, including those that have used different genes. An obvious weakness is the lack of inclusion of nuclear genes in any study, and this reflects problems with nuclear genes in cephalopods generally. The markers developed by Strugnell et al. (2004, 2005; *pax6*, *ODH*, *rhodopsin*) are too conserved to be useful within families, and 18S rRNA and 28S rRNA potentially have issues with non-concerted evolution. We attempted herein to sequence *H3*, but we were not able to reliably sequence this gene for a sufficient number of taxa. While it is clear that confirmation of relationships with nuclear genes would be highly beneficial, the recovered topology appears to be stable across analyses (e.g., ML versus BI) and studies.

Changing the partition scheme and/or the outgroup (for example using representatives of just one other Decapodiformes order) has little effect on our topology (not shown). Bootstrap support values vary by only one or two points, as might be anyway expected in analyses that start in a random position in tree space. Thus, we are confident that this is a really stable topology. Our numbered clades were consistently well supported in all analyses. The ‘least’ supported is clade 1, with bootstrap support at 83. All other clades numbered and treated as genera have bootstrap support > 90 and all numbered clades have Bayesian Posterior Probabilities of 1. Because Sepiidae is a unique family, in its own order, there is no ‘close’ outgroup, use of which could potentially improve resolution within numbered clades. Likely, the low support for taxa such as *S. bertheloti,* and intra- and inter-clade topology can only be resolved by increased taxon sampling, and/or the use of more loci.

As previous researchers have found, it remains frustratingly difficult to find a clear set of morphological characters to define each genus. However, we hope that the present study will provide a framework for future more detailed anatomical investigations to define these groups. While we have attempted to investigate suites of characters in addition to those pertaining to the cuttlebone and tentacular club, it has not been possible yet to examine all species for each trait, and, importantly, whether these apply to members of both sexes. Cuttlefish morphological evolution seems to be extremely plastic. However, within this broader molecular framework it should now be possible to plot pathways of character evolution within each of the recognised clades and, in particular, to determine where character state reversals and convergence are likely to have occurred. There remains no doubt, however, that the cuttlebone remains a key diagnostic feature and has phylogenetic significance.

There are a number of features that appear to differ among clade members but have not yet been examined in sufficient detail across all taxa. These include meristic characters such as gill lamellae counts and total arm and club sucker counts. Quantitative morphological traits have, so far not proved informative, likely due, in part, to the difficulty in comparing taxa that have been similarly fixed and preserved post mortem, and at similar stages of maturity (Lupše 2017). Other characters worthy of further investigation and comparison among clades include: spermatophore ultrastructure, sucker rim anatomy (following scanning electron microscopy), and histological examination of textural skin components, as, for example seen in members of *Digitosepia.* Detailed ultrastructural comparison of cuttlebones of each species may prove informative as has been shown for representative *Doratosepion* (Yoshida et al. 2006, 2010) that lack a transverse membranous structure between upright pillars and such detailed examination could be broadened to include a greater number of species to determine whether this might be a unique synapomorphy for the *Doratosepion* clade. Behavioural traits, and elemental colour patterns, are also worthy of additional scrutiny. We agree with Yoshida et al. (2010) that the gross arrangement and size of suckers on the tentacular clubs, while significant for species identification is not consistent within clades and therefore indicative of relationships, although the ultrastructure of the sucker rims and their dentition may be worthy of further examination.

The addition of more species to the tree as fresh tissue becomes available will likely provide further indications of phylogenetic history. This particularly applies to the case of the very speciose *Doratosepion* group of taxa that may ultimately be further refined nomenclaturally when additional species are added to the molecular dataset.

Taxon selection and cryptic species

Recent molecular analyses of a number of cephalopod taxa indicate the presence of purported cryptic species, although ‘crypsis’ sometimes reflects a lack of detailed morphological analyses and the degree of molecular disparity at the population level has not been ascertained for many species. Particularly for widespread taxa, genetic drift may result in molecular differences that are not mirrored by species distinctiveness, so the wholesale naming of new species needs to be avoided. In addition, the degree of molecular difference representative of species boundaries varies among and within taxa, so a total evidence approach needs to be applied when making such decisions.

Crypsis is less likely to be a problem in Sepiidae than in some other cephalopod taxa, because they are characterised by a bottom-dwelling habit and direct development, suggesting comparatively limited dispersal capabilities. However, some taxa, such as *Acanthosepion 'pharaonis'* do appear to be widespread and comprise a complex of closely-related species.

The two nominal taxa of *'pharaonis'* included in our analysis are part of a species-complex recognised by Anderson et al. (2011). They clearly belong to this complex on morphological grounds. To validate their inclusion in the current study, we analysed all *COI* data available on GenBank as *S. 'pharaonis'* and *S. ramani* Neethiselvan, 2001, a taxon recognised as being very closely related to *Sepia pharaonis* when first described, whose validity was questioned by Anderson et al. (2011), and the status of which is not widely accepted. Both our samples fall well within a broader, and well-supported '*pharaonis'* clade. Based on this analysis, specimen AM.C.483507 from Karachi clearly belongs to a clade named the 'Iranian Clade' in Anderson et al. (2011), while our sample from northwestern Australia WAM.S34838 is sister to an unverified specimen from the Philippines (GenBank KJ168061.1) and these two samples in turn are most closely related to their 'Central Indian Ocean' clade (and, interestingly, not the Anderson et al. 2011 'Northeastern Australian clade). Furthermore, taxa identified as *S. ramani* do not form a monophyletic group in our broader *COI* analysis (Supplementary Information 4), so we agree that this taxon is invalid.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-023-04195-3.

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Author contributions ALA: conceived and designed this study. NL generated the majority of the sequence data; additional sequences by MT and ALA. Morphological data coding by AR. Identifications and morphological interpretations by AR and TK. The first draft of the manuscript was written by ALA and AR and all authors commented on the manuscript. All authors read and approved the final manuscript.

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Data/code availability Genetic sequence data are available from GenBank, https://www.ncbi.nlm.nih.gov/genbank/.

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

Ethics approval All specimens used in this study were collected according to current Animal Ethics procedures and were collected under appropriate permits.

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