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Morphological disparity in extant and extinct sepiid phragmocones: morphological adaptations for phragmocone strength compared to those related to cameral liquid emptying hypotheses

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Abstract

The phragmocone-bearing coleoid cephalopods *Sepia*, *Sepiella*, *Metasepia* and *Hemisepius* (sepiids) are the most diverse of all extant chambered cephalopods and show the highest disparity. As such, they have a great potential to serve as model organisms to better understand the paleobiology not only of extinct coleoids, but of extinct nautiloids and ammonoids as well. Here, we present new measurements from the phragmocones of *Sepia* and *Sepiella* and relate these to known maximum depths. While these latter data remain few for some species, in aggregate they provide progress allowing this work. In so doing, we expand upon the great legacy of Sigurd von Boletzky. We show that deep water-inhabiting sepiids have phragmocones with a higher number of septa per length, a smaller area covered by the last chamber in relation to the volume of all previous phragmocone chambers, are smaller in size (length and volume), and bear dorsal shields that have strengthening central rib(s) compared to most species from shallower water; the very small endemic species of South Africa may be an exception. We show that the various subgenera defined by Khromov (1987) are not monophyletic clades but morphological groupings explicitly related to depth, partially evolved convergently. We conclude with analyses of Australian sepiid assemblages and show that these are depth related in ways analogous to ammonite and/or nautiloid assemblages of the past that are later commingled through post-mortal drift.

Keywords: Coleoidea, Cephalopoda, Development, Ecology, Evolution, Systematics

Introduction

The phragmocone-bearing cephalopods *Sepia*, *Sepiella*, *Hemisepius* and *Metasepia* (“sepiids”; see Fig. 1) are among the most speciose of all cephalopods (Adam & Rees, 1966; Jereb & Roper, 2005; Neige, 2021; Nesis, 1987; Okutani, 1995; Roeleveld, 1972). All contain hard

parts that serve as buoyancy devices (the phragmocone; e.g., Denton & Gilpin-Brown, 1959, 1961a, 1961b, 1961c; Birchall & Thomas, 1983). These (Fig. 2) are constructed with enclosed, gas-filled spaces maintained at pressures lower than ambient, and thus have finite depth limits imposed by the mechanical properties of their chambered shell (Denton & Gilpin Brown, 1973; Sherrard, 2000; Ward, 2000; Ward & Boletzky, 1984). Yet, in addition to depth limitations imposed by mechanical design, it is also known that there are depth limits imposed by *physiological* properties as well as mechanical: at depths exceeding these “physiological depth limits”, the

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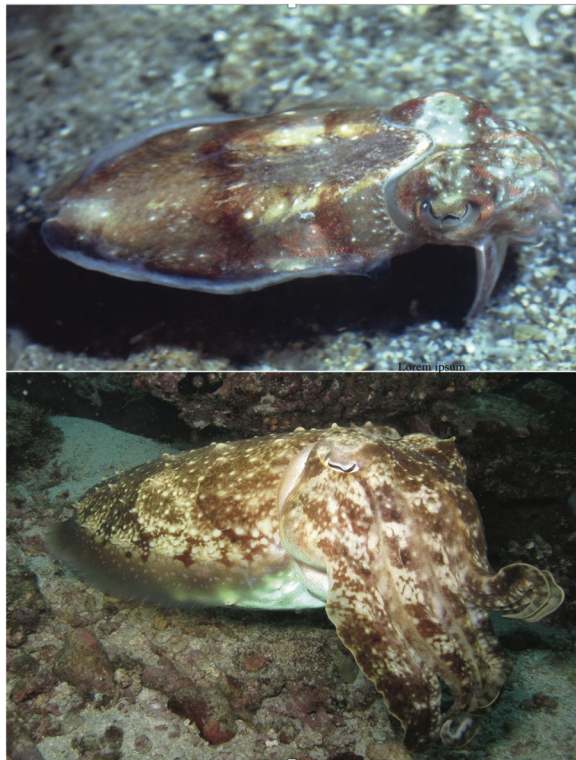


Fig. 1 Above: *Sepia orbignyana*, brought up by trawl from 400 m for photograph. Mantle length 70 mm. Note use of tentacles for keeping station above bottom. This species observed to slowly use tentacles for crawling along bottom. Prototypic deep-water squid. Photo by P. Ward, Banyuls sur Mer. Below: *Sepia latimanus*, photographed in situ, 20 m depth. Mantle length 200 mm. This species is an active, nektonic predator, patrolling reef wall edges for prey. Prototypic shallow water sepiid. Photo by Jerome Napala, Sogod Bay, Southern Leyte

phragmocones will fill with liquid forced into the gas spaces, eventually mooring the animal to the bottom (Ward, 1987). This second imposition that increasingly is being understood as an evolutionary driver towards phragmocone design is perhaps as important as the better-known strength aspects of chambered cephalopod design for nautiloids, ammonoids, belemnoids as well as sepiids both extant and extinct (e.g., Daniel et al., 1997; Hewitt & Pedley, 1978; Hewitt et al., 1989; Klug & Hoffmann, 2015; Lemanis et al., 2016; Peterman et al., 2021; Ward et al., 1980; Westermann, 1973, 1975, 1977). In this paper, we present new measurements from cuttlebones of species with known maximum depths as a means of exploring the dual, and perhaps competing set of evolutionary drivers—constraints imposed by shell strength compared to constraints of buoyancy optimization—of chambered cephalopod shell and phragmocone construction. Elsewhere, this dichotomy has been informally described or discussed as “Depth vs. Emptying Paradigms” (Checa et al., 2015; Kulicki, 1979; Ward, 1987). In

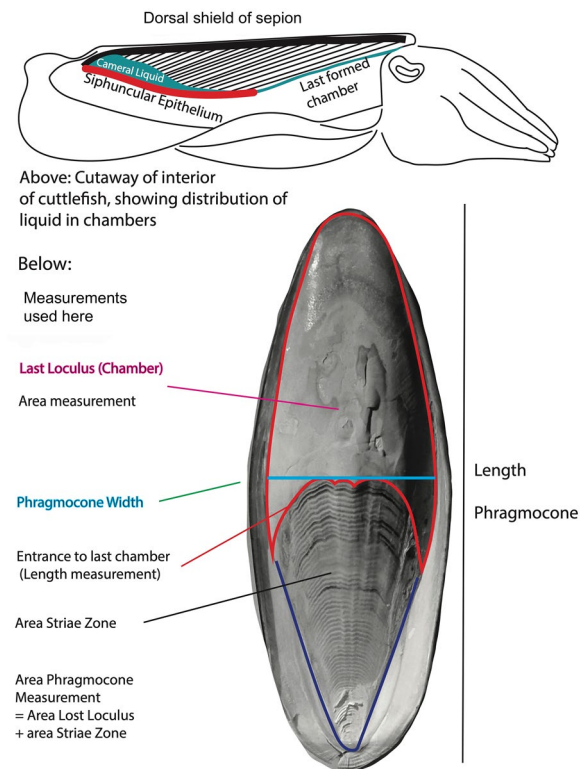


Fig. 2 Position of phragmocone within sepiid, showing relative positions of chambers, siphuncle, and cameral liquid within chambers in a growing sepiid. Below: cuttlebone of mature *Sepia officinalis* illustrating relevant morphology and measures made for this study

this paper we demonstrate specific, measurable features of the phragmocone in sepiids that will hopefully guide future research into buoyancy as well as strength as morphological drivers of shape.

Scientific background

The elucidation of how cuttlefish produce, and then empty chambers was the seminal set of discoveries that enabled understanding of neutral buoyancy formation and then subsequent maintenance in all chambered cephalopods, as demonstrated by the 1960s and 1970s papers of Denton and Gilpin Brown, summarized in Denton, 1974. There is no siphuncular tube in *Sepia*; instead, liquid exchange occurs along a wide zone (the striae or siphuncular zone) on the posterior part of the ventral cuttlebone. New septa are secreted on the ventral side of the cuttlebone, which can be divided into an anterior smooth zone or last loculus, and posterior siphuncular or striae zone.

More than a half century ago, this pioneering work of Denton and Gilpin Brown (1959, 1961a, 1961b), Denton et al. (1961) demonstrated how the “cuttlebones” of the sepiids are constructed through sequential formation

of liquid-filled chambers that, when sufficiently calcified, are emptied by osmotic processes (“local osmosis”; Mathias & Wang, 2005) at rates that produce an overall, neutral buoyancy in the sea. Soon thereafter, alerted to the presence of cameral liquid in sepiids, Bidder (1962) made the seminal discovery of homologous liquid in the chambers of living *Nautilus* species.

Denton and Gilpin Brown thus not only discovered the process by which chambers are first produced, and then osmotically emptied off the liquid that fills a new chamber, but also measured gas pressures from newly emptied chambers, finding it always less than one atmosphere, irrespective of depth of the living animal. Because of this, they realized that cuttlebones have a finite depth, beneath which they would implode. Thus, they encapsulated the two great aspects of phragmocone-bearing animals’ biology, and their limits: emptying liquid and avoiding implosion by depth. From this, more than half a century of research has completely changed the perception and understanding of the many extinct chambered cephalopods, profuse research branches grown from those first scientific studies, made on sepiids (e.g., Daniel et al., 1997; Hewitt et al., 1989; Klug & Hoffmann, 2015; Lemanis et al., 2016; Peterman et al., 2021; Ward et al., 1980; Westermann, 1973, 1975, 1977).

From *Sepia officinalis*, Denton and Gilpin Brown (1966) then moved to analogous studies on the buoyancy and new chamber formation in *Nautilus*. Much information has accrued from those, and then later studies by others of the extant nautilids and their buoyancy, and their depth-related constructions of both soft and hard parts. Still, the remarkable conservatism and low degree of disparity of extant nautilid shell architecture has limited their use as means of establishing how depth, and the effect that increasing depth, imposes limitations on those parts of the phragmocone involved in neutral buoyancy attainment and maintenance. Yet comparative anatomy (both soft and hard parts) morphology between deep-, and shallow-dwelling, phragmocone-bearing cephalopods can certainly provide new information and understating about the (possibly antagonistic) relationships between morphological adaptations to phragmocone strength, and those producing efficiency of phragmocone cameral liquid emptying and buoyancy needs. These include buoyancy change in response to sudden addition or reduction of density of the entire animal through a variety of events, varying between predatory attack causing significant loss of shell (positive buoyancy), to the buoyancy consequences of large, opportunistic feeding of high-density food material (negative buoyancy). Or, perhaps as importantly, buoyancy that is increased or decreased soon after sudden depth change done at

scales or rates of time that overwhelm or underwhelm the balance between salt in cameral liquid and salt in the siphuncular epithelium, separated by membrane.

As an example, the approximately half dozen extant *Nautilus* and two *Allonautilus* species are all so similar in phragmocone morphology that, unfortunately, they are of less use for understanding the paleobiology of extinct ectocochliates than they would be if there was a wider disparity of phragmocone “design” currently available in these nautilids. But in *Sepia*, *Sepiella*, *Hemisepius*, and *Metasepia* there is a large disparity of morphology (Neige, 2003a, 2003b) and examples among them of hard and soft part design that might prove useful experimentally, or as useful in providing clues to larger evolutionary and or ecological questions related to buoyancy, its use, and its limitations in chambered cephalopods. Thus, in contrast to the relatively low diversity and disparity of extant nautilids, the extant (and to an increasing extent, the extinct) sepiids are being shown to be over an order of magnitude more diverse than the extant nautilids in species richness (Lu, 1998; Neige, 2003a, 2003b; Okutani, 1995; Okutani et al., 1987; Reid, 2000; Reid et al., 2005) and have a far greater disparity of phragmocone morphology (Neige, 2006; Neige & von Boletzky, 1997).

It is not just in the study of buoyancy that a great, recent flowering of research has appeared on sepiids. The morphological analyses of cuttlebones by both biologists (Bandel & von Boletzky, 1979; Birchall & Thomas, 1983; Checa et al., 2015; Florek et al., 2009; Tanabe et al., 1985) and, strikingly, engineers (Battistella et al., 2012; Le Pabic et al., 2019) have produced surprising new information about not only the evolution of sepiids, but also about the material construction of cuttlebones that are increasingly providing new paradigms for materials research. These latter findings include information that have led to proposals of producing new, bionic materials of great strength but light weight (Battistella et al., 2012; Yang et al., 2020). Other new studies (Checa et al., 2015) have expanded our understanding of how liquids might function within phragmocones in ways beyond simply serving as ballast, but in fact are part of internal shell formation processes, and we find this latter study particularly revolutionary for fluid dynamics as well as for its better understanding biology.

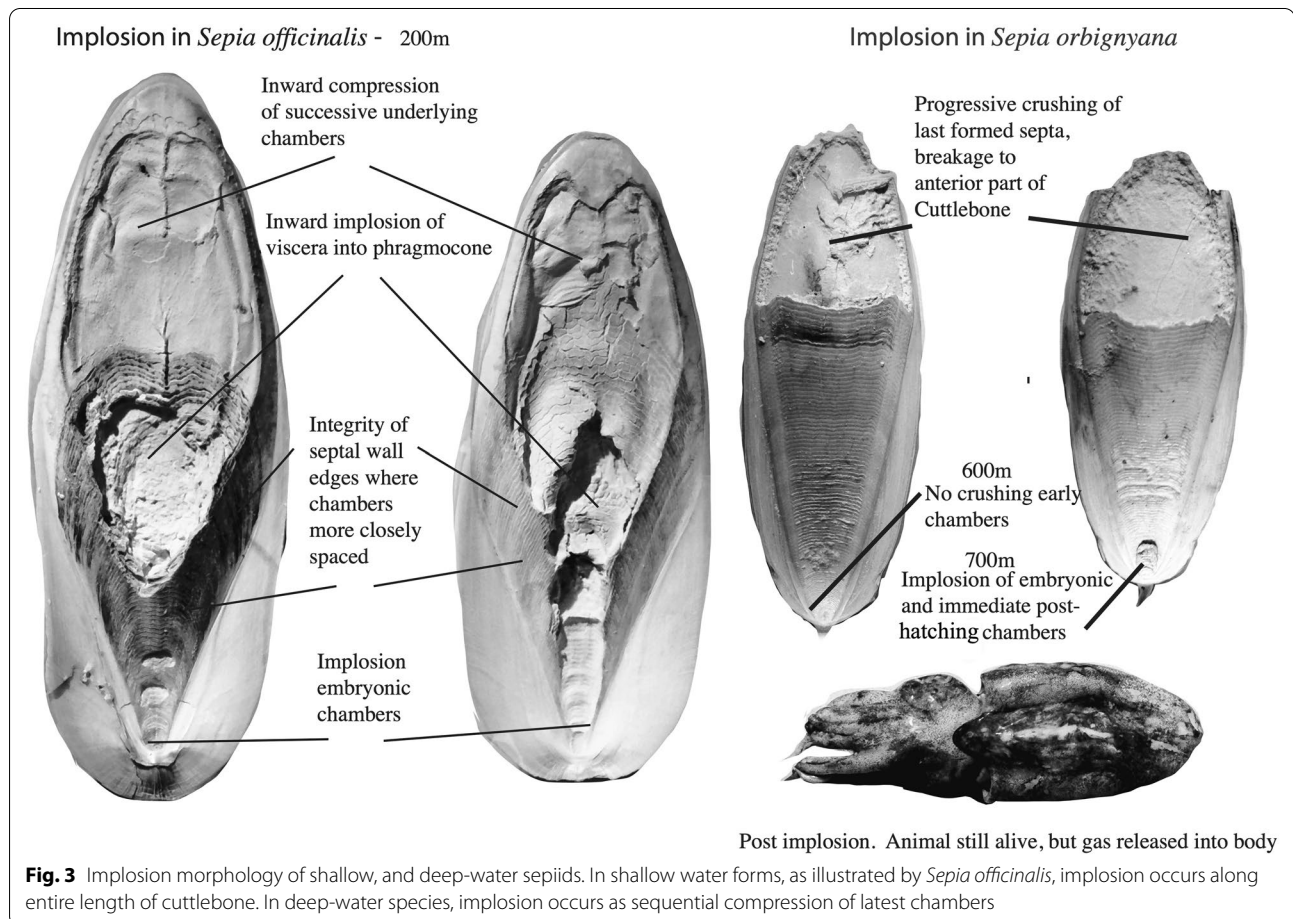
Yet, surprisingly, studies of the *variety* of phragmocone variability in sepiids—as a means of better understanding one of the key aspects of chambered cephalopod research of extinct species, the strength versus emptying aspects noted above—are rare. Very few published studies have explicitly addressed shell strength in sepiids as a means of applying understanding derived from cuttlebone design to broader questions of paleobiology and phragmocone function in extinct cephalopods, and

few to none concerning the challenges posed by great depth to osmotic emptying of chambers (and keeping them empty) among the deepest living sepiids in terms of either biological or paleobiological questions.

As in so much concerning the biology of phragmocone-bearing cephalopods, Denton and Gilpin Brown (1973) reported on cuttlebone strength against implosion in their pioneering research. They found that the cuttlebones of *Sepia officinalis* imploded at 24 atm, corresponding to a depth of about 240 m. A decade later, Ward and Boletzky (1984) confirmed these results and also tested shell strength in the Mediterranean species *S. elegans* and *S. orbignyana* through implosion experiments, and it is instructive to compare the difference in implosion morphology between the shallower (*S. officinalis*) and deeper (*S. orbignyana* and *S. elegans*) of the tested species, as shown in our Fig. 3, from photographs taken during that prior study. Since these two latter species are routinely captured at depths greater than the implosion depth of *S. officinalis* (Mangold, 1966), it was clear that some aspect of cuttlebone morphology in the

Mediterranean species allowed greater habitat depth than in *S. officinalis*.

Ward and Boletzky further showed that implosion occurs between 400 and 600 m in *S. elegans* and between 550 and 600 m for *S. orbignyana*. They also discovered that not only did implosion depths greatly differ in these three taxa, but that the *mode* of implosion (the parts of the phragmocone undergoing material failure) differed as well, suggesting that shell strength in sepiids is related to specific morphological adaptations of the cuttlebone. A final discovery was that implosion depth of hatchling *S. officinalis* was approximately 25% that of the adults, suggesting that the juvenile sepiids (cuttlebones) are far more depth sensitive than those in the adult, as shown in Figs. 3 and 4. To date, however, there has been no further discourse concerning the implications for dispersal, and thus effects on speciation, coming from this salient fact. We do not even know if this difference in strength of juveniles compared to adults of the same is present in other sepiid species—or in ammonites and or nautilids, for example.



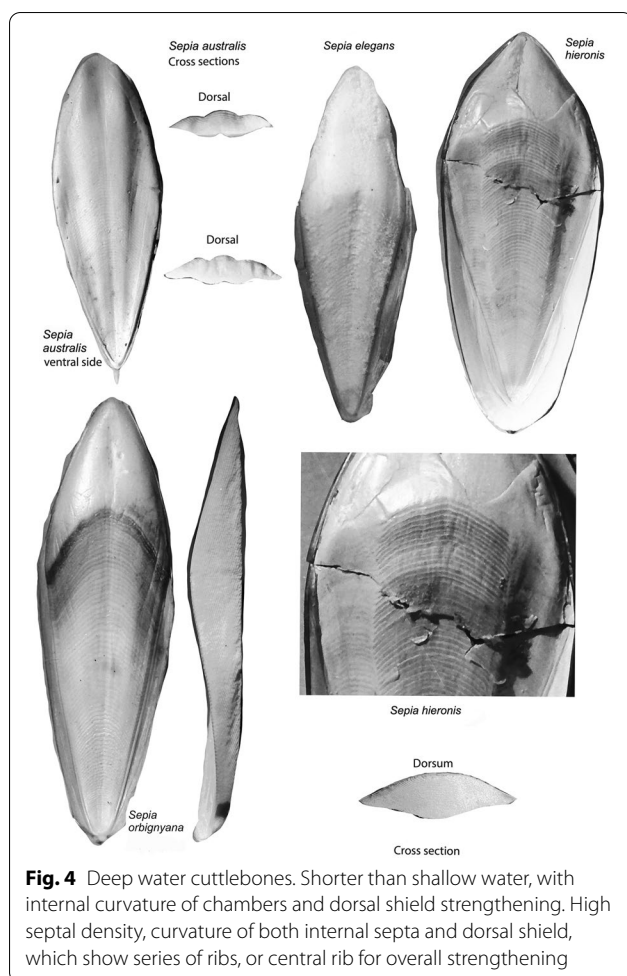


Fig. 4 Deep water cuttlebones. Shorter than shallow water, with internal curvature of chambers and dorsal shield strengthening. High septal density, curvature of both internal septa and dorsal shield, which show series of ribs, or central rib for overall strengthening

Unlike the phragmocones of *Nautilus* and the majority of extinct chambered cephalopods, the phragmocones (sepiion, cuttlebone) in the Sepiidae is entirely internal. The chambers of the cuttlebone are long, broad, and extremely thin compared to chambers of most ectocochleate cephalopods. The chamber walls (which are homologous to the septal necks in nautiloids and ammonoids, rather than the septa; Bandel & Boletzky, 1979) are supported by calcareous, vertical columns and walls. The chambers are delimited by calcareous and organic septa in most but not all sepiids; a large group informally assigned to the subgenus *Sepia* (*Doratosepia*) have been discovered to be the only sepiids without intercameral organic lamellae (Okutani et al., 1987). The structural, genetic, and ecological ramifications of this remain unknown but it is surprising that it was not until recently that this observation was made and its genetic and phylogenetic use as a potential taxonomic character should be further explored. The group defined by Khromov (1987) as *Doratosepia* thus appears to lack the intercameral

lamellae composed of layered organic material within the chambers and parallel the septa are entirely lacking. These are all (apparently) capable of living at depths greater than 200 m.

Subsequent studies linking specific cuttlebone morphology to depth were made by Gower and Vincent (1996), Ward (2000), and Sherrard (2000). All of these papers considered various aspects of cuttlebone construction in terms of the strength hypothesis only; to date, there has been no study attempting to relate any aspect of cuttlebone form as adaptation to the constraints on emptying imposed by increasing depth other than inferences to this by Checa et. al. (2015).

A surprising aspect of sepiid biology is how speciose they are (for example, see Nesis, 1987; Jereb & Roper, 2005), and it may well be that the high number of species is to some degree a consequence of depth-related isolation, causing poor dispersal ability leading to allopatric speciation. Thus it may be that strength, and perhaps osmotic emptying limitation impose isolation, so that local, daughter populations of sepiids arriving at new habitats from a larger population (such as by a sweepstakes, chance event) are then separated by reduced or absent gene flow, and thus readily speciate in their new habitat. New research (Barord et al., in review; Combosch & Giribet, 2016) now show that *Nautilus* is far more speciose than has previously been accepted, with perhaps a dozen species currently extant, and in this *Nautilus* is equivalent to *Sepia* in having a large hatchling incapable of dispersal across deep water bottoms, and hence is easily, genetically isolated. For whatever reasons, there are more than a hundred named species (Adam & Rees, 1966; Reid et al., 2005) and in this number, they rival the known number of species of *octopods*. Yet, the latter have no hard-part dictated depth limits and are found to high latitudes in all the world's oceans. By contrast, the sepiids are limited to but half the globe and are unknown from Arctic or Antarctic waters; by area of sea bottom over which (or in some cases for sepiids, within) they live, sepiids inhabit a lower percentage of the sea compared to octopods. Yet they are highly speciose. The presence of a weak and collapsible cuttlebone in large hatchlings is perhaps one reason.

Because of the large number of species, there have been multiple attempts at taxonomy above the species level. Prior to the advent of gene-based systematics, morphology-only-based models of sepiid phylogeny used both hard and soft parts as characters, with different levels of weighting of soft versus hard-part characters. One of these studies by Khromov (1987; but see Khromov, 1998 for a revision of this) was based mainly on cuttlebone (hard part) morphology, but was considered by that

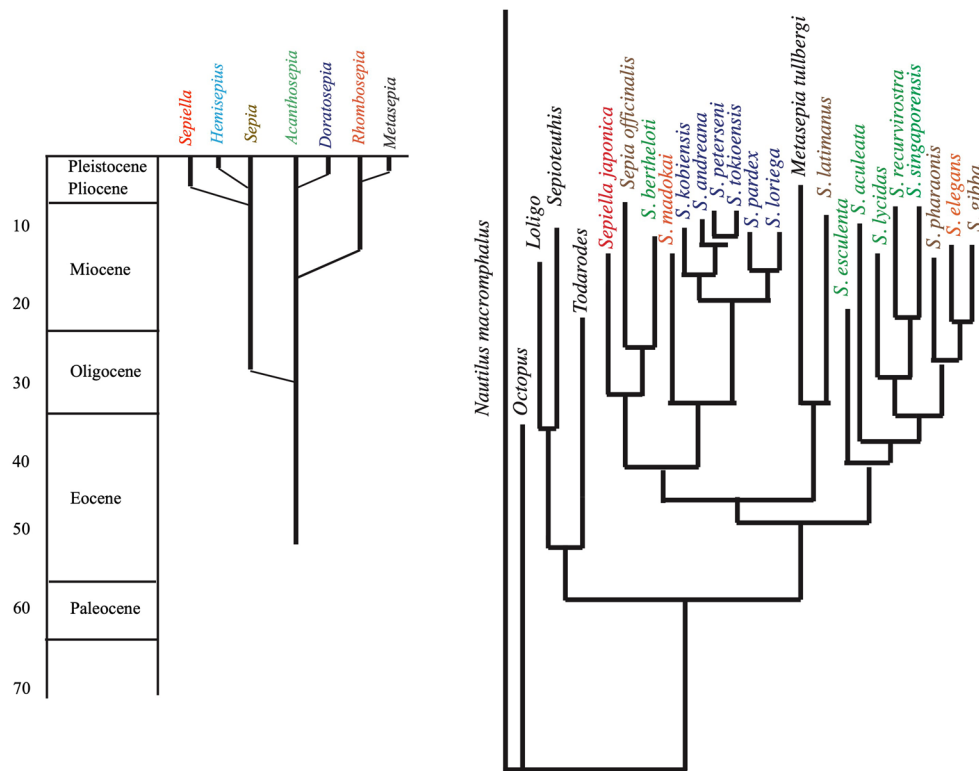


Fig. 5 Khromov—phylogeny (modified after Yoshida et al. 2006). On left, geological ranges of the various Khromov defined subgenera. On right, DNA based phylogeny of sepiids, falsifying the Khromov “subgenera” as actual clades

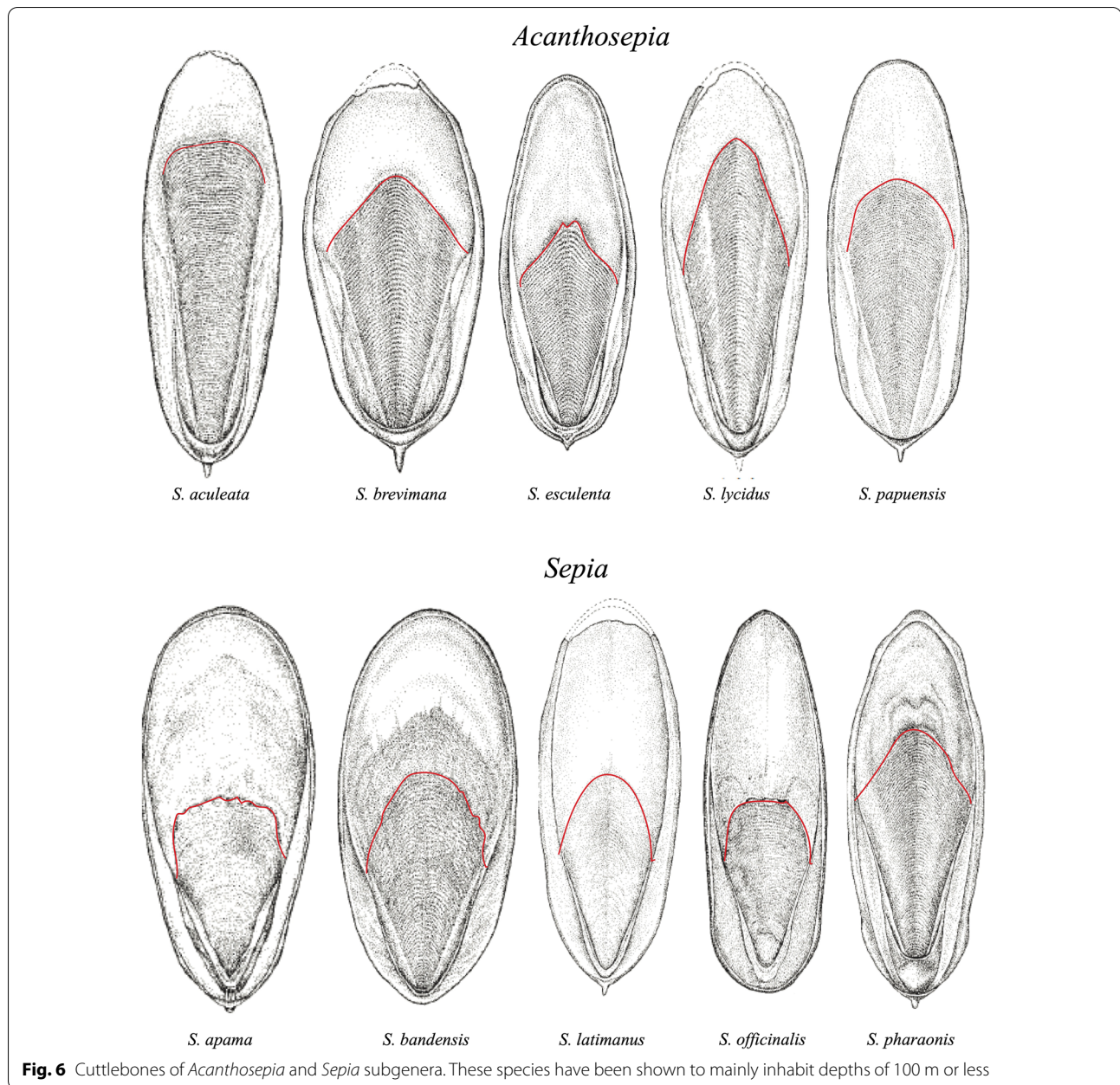
author to be a valid phylogenetic model (Fig. 5). Khromov defined multiple “subgenera”, and we illustrate the cuttlebones of selected species placed in these taxa in Figs. 6, 7, 8.

Khromov (1987) assigned first appearance dates using geological time units to reinforce his inference that his “subgenera” were clades. However, subsequent studies based on various genes have largely falsified Khromov’s (1987) phylogeny (Bonnaud et al., 1994, 1996, 1997; Yoshida et al., 2006); an example of this is shown in our Fig. 5. Only the subgenus *Doratosepia* shows substantial support (Fig. 5).

As we note below, rather than be evolutionary clades, we propose that Khromov’s, (1987) “subgenera” represent cuttlebone shape categories adapted to varying depths and perhaps modes of life (benthic ambushers versus active, demersal swimming and/or hunting in mid-water). Eventually, it is hoped that a better understanding of the various trophic positions (levels) of sepiids within their respective communities will incorporate hard and soft part morphology including behavior, predators, prey, and the morphology of the tentacular clubs (which have four distinct patterns and sizes of suckers; see Nesis, 1987). Is there particular kind of prey that a few, larger

suckers are optimal for, compared to the species with clubs that are covered with a large number of much smaller suckers? As such, the communities with multiple, shared sepiids could provide valuable clues to the modes of life of ammonoid in past ecosystems with many sympatrically living species.

Our goal is thus to explore hypotheses explaining cuttlebone morphology related to adaptation against mechanical failure caused by ambient pressure, and, as well, to consider those structures that may be related to avoiding loss of buoyancy control through phragmocone flooding by overpressure of great depth (or that allow rapid depth to change) without exceeding osmotic pressure limitations imposed by the solute contents within the siphuncular epithelium at the siphuncle/chamber intersection. While the optimal way to test specific hypotheses about such morphology would require in-water experiments at great depth, or the use of pressure tanks. Our own work on *Nautilus* (Ward, 1987, where over multiple years the test of nautilus’ ability to empty chambers are depths greater than 240 m were completed only with great difficulty), trying such studies on Cuttlefish at 400 to 600 m, for instance, is impractical and hence here we necessarily reply on

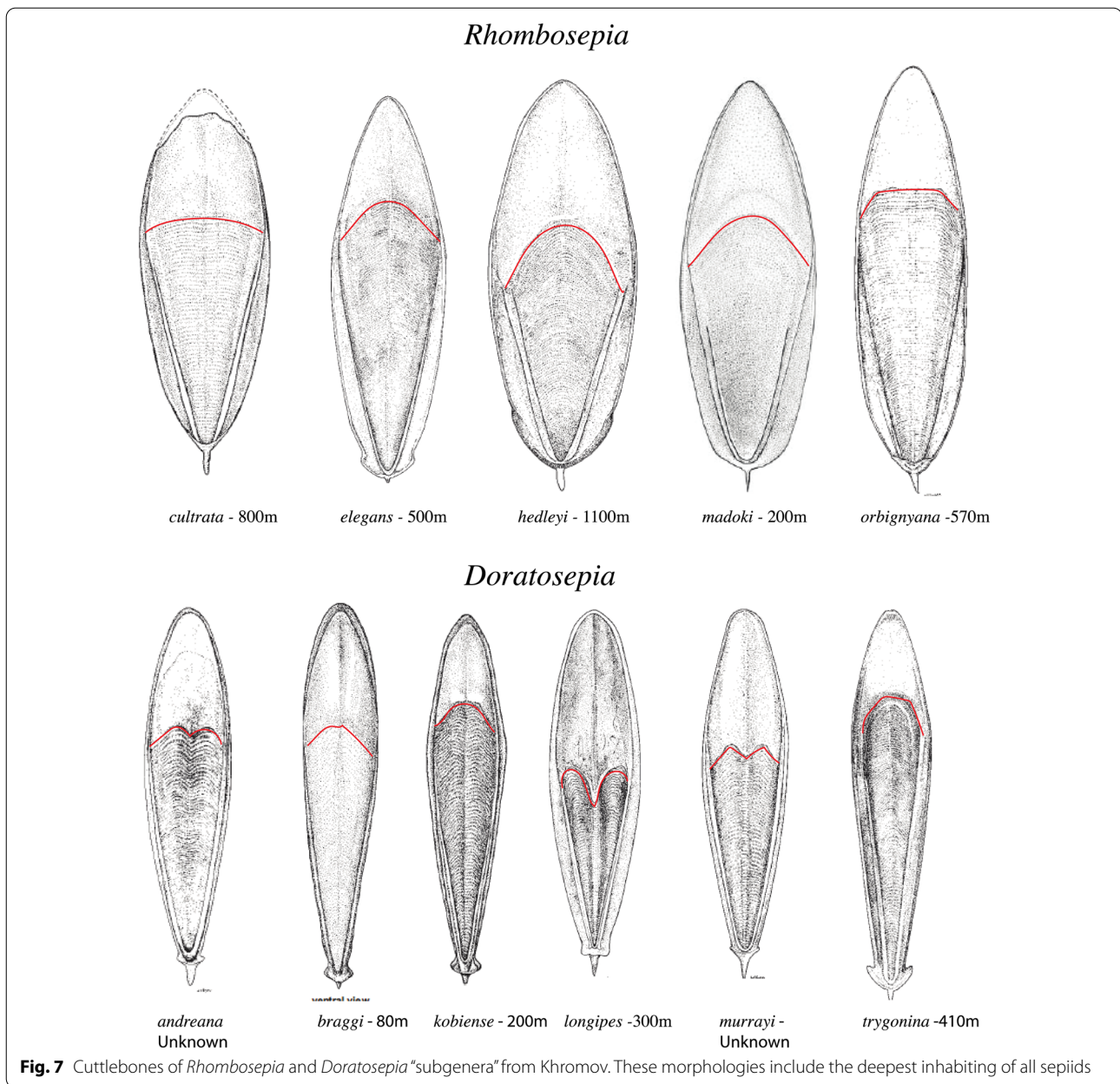


less direct kinds of tests, observational in nature from cuttlebones.

All of these results hopefully provide useful analogues to understanding the make-up communities of phragmocone-bearing cephalopods of the past, particularly in the context of depth distribution prior to the common “mixing” prior to deposition of phragmocones from deceased animals that can take place through post-mortal drift. In particular, from a whole-animal point of view, we test hypotheses concerning the relationship between habitation depth and phragmocone construction (including

shapes and relationships of chamber morphology and their contact with the siphuncle in the “striae” zone).

We conclude with comparisons of the depth-related cuttlebone assemblages in extant environments as analogues to paleocommunity associations of co-occurring ammonites and or/nautiloids; presumably, these were living in depth-stratified assemblages based on morphology yet mixed after death. We use new data from the living sepiid associations around Australia as a means of showing how multiple sepiid species of Australia do represent shallow to deep depth gradients, using newly published



on the distribution data of cuttlebones around Australia (Reid, 2016) as a source, and from this distribution data show how the separate communities found around that continent are depth distributed.

To these ends, here we look more closely at the relationships of what appear to be depth-related sepiid taxa that share certain morphological attributes. An evolutionary model is one, or a small number of sepiids invading a new biogeographic region, and then speciating to fill various depth zones and the modes of life best suited for those depths with the different,

depth-defined ecosystems and environmental conditions to be encountered at those biogeographic sites and their various depths. The questions examined here are: are there previously overlooked relationships between the morphology (length) to the opening to the phragmocone and depth? Are there relationships of the Khromov subgenera to depth? Is cuttlebone size related to depth? Are number of chambers in a given species related to depth? Does the dorsal side of the cuttlebone show morphology in deeper water species not found in shallower species?

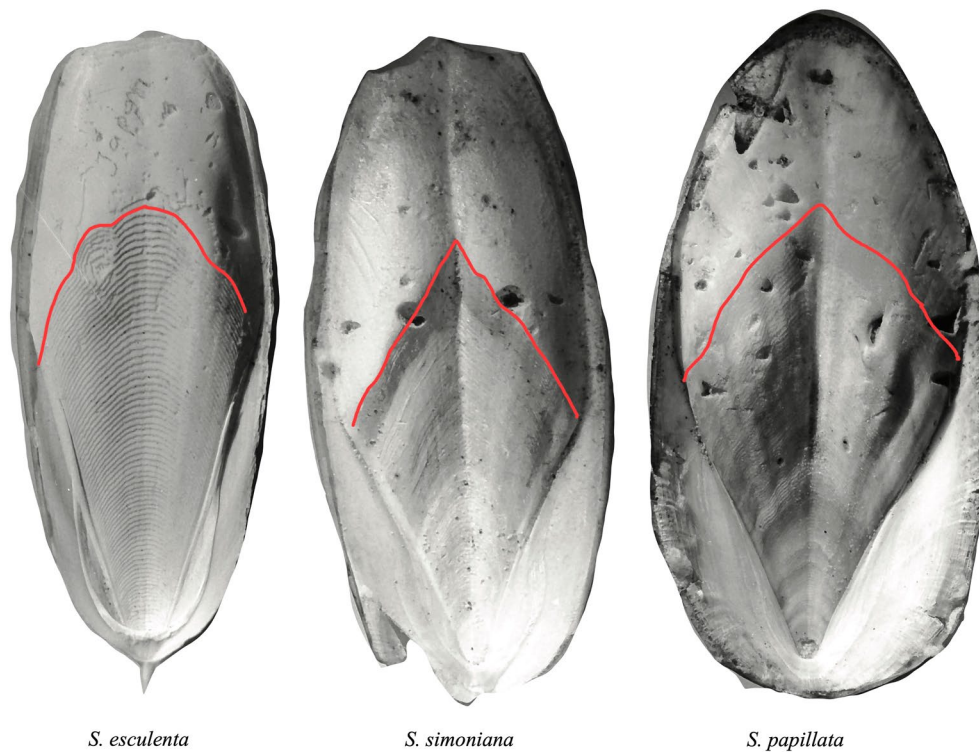


Fig. 8 Shallow water sepiids. Broad, flat, low septal density. The last locus makes up a significant proportion of the total phragmocone volume; the overall sepioid is flat for its width; the dorsal side of sepioid has no ribbing for strengthening. Red line shows position of last locus contact with siphuncular epithelium

Materials and methods

Our working hypothesis is that the assemblages of species identified as phylogenetically distinct subgenera defined by Khromov, (1987) are, in fact, groups of species sometimes coming from clades, but often unrelated convergences that arrived at similar cuttlebone morphologies because of sharing similar depth and probably behavioral adaptations. We thus have taken measures from different parts of cuttlebones that have been assigned to the various Khromov subgenera.

The species data included in this study are taken from museum specimens, or from photographs assembled from various publications. Photographs of actual specimens for most of the species analyzed here were taken from material stored in the Natural History Museum in London, in the South African Museum in Cape Town, the Australian Museum in Sydney, and the Burke Museum, University of Washington (material of over half of all named species are available there). Photographs of all specimens were assembled onto digital media and then measured, using the measurements delineated in Fig. 2, and then analyzed using ImageJ (NIH). Measurements included (1) *cuttlebone length, comparative lengths of the striae zone to length of last locus*; (2) *comparative areas*

of each when viewed from the ventral side of the cuttlebone; (3) *perimeter length of the opening to the phragmocone*, and (4) *number of septa in the striae zone*.

The measurements used here are unlike most hard-part measurements of sepions in the literature, which use standard length and width measures (which by necessity thus include both wings on the side, and spines in length measurements). Instead we measured the actual width of *chambers*, including estimates of the position of embryonic chambers in this sepions where earliest chambers are covered with conchiolin. We then used the NIH program ImageJ (version 1.53) to make the following measurements: maximum length of phragmocone, width of phragmocone at the widest part of last locus (last chamber), length of opening (of the last chamber) to contact with the siphuncle; area measurements of the last locus from each photograph, area of the entire phragmocone, area the last locus, number of chambers. Each measurement was made multiple times to insure reproducibility, and the error are estimated to be less than 1% for direct, length width measures, and approximately 5% for area measures using ImageJ. We have also assembled data on the maximum known depth of various species from the literature (Reid, 2016; Sherrard, 2000; Ward,

2000). While these latter data are perhaps the greatest source of area in this work, and it is hoped that there will be much improvement of actual maximum depth limits of various sepiids, that there appear to be robust relationships between morphology and currently known depths allows progress in these bathymetric relationships. Avoiding the use of bathymetry because it could be “improved” will negate progress in the understanding of sepiids.

In order to address the question for convergent evolution of sepioid morphology driven by diving depth versus sepioid shape as primary apomorphy, we have grouped the species analyzed in this paper into assemblages following Khromov (1987). Species that had not yet been formally described at the time of that publication, or that were not discussed by Khromov, (1987), have been placed into his subdivisions based on morphology. These are: *Acanthosepia*, *Sepia*, *Anomalosepia*, *Doratosepia*, and *Sepiella*. We omitted *Hemisepius* and *Metasepia* because of their lack of a calcareous sepioid.

The analyses performed were designed to search for relationships between depth and aspects of phragmocone morphology. Data were first loaded into excel files, and then transferred into PRISM statistical software. Statistical analyses were performed using PRISM, as were the graphs that we show here.

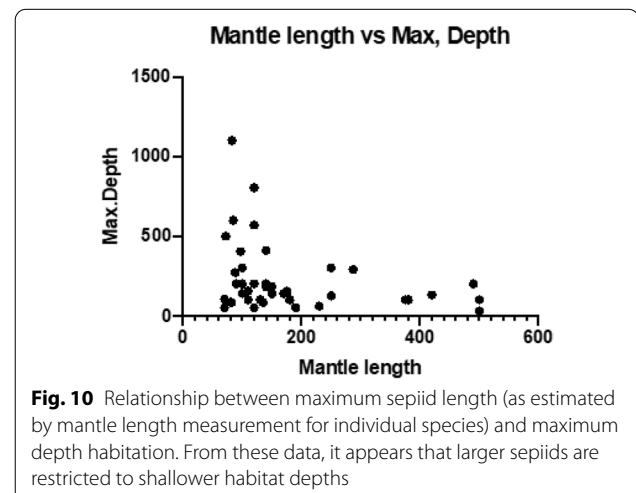
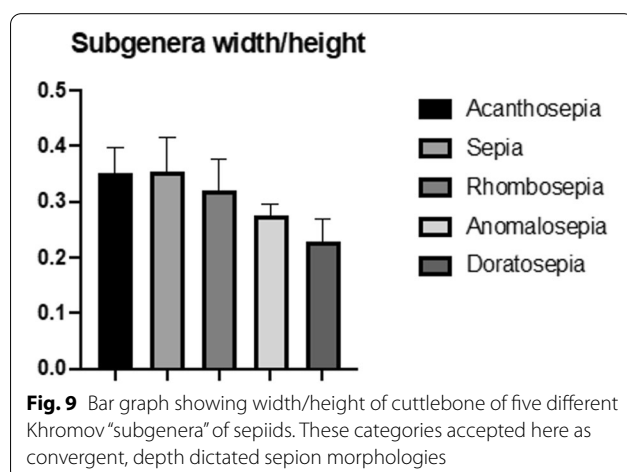
We made the following analyses: Khromov subgenera were plotted against the mean width/length of their cuttlebones (Fig. 9); relationship between mantle length and maximum depth (Fig. 10); mean number of septa per cuttlebone (Fig. 11A) and Area of last locus (Fig. 11B) plotted against depth; maximum depths of the various Khromov subgenera (Fig. 12); and comparison of maximum depths of cuttlebones with and without dorsal shield modifications such as longitudinal ribbing (Fig. 13). These results are discussed in more detail below.

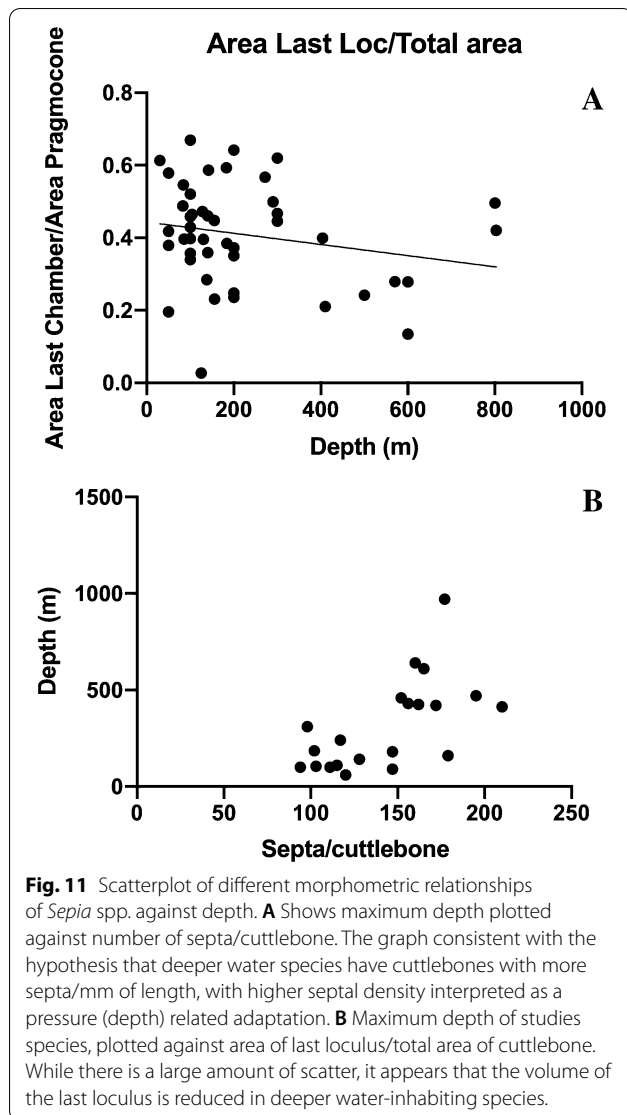
Results

The results from individual measurements and comparison of combined measures such as ratios from single measurements are listed in Table 1. Each of these sets of data are as follows.

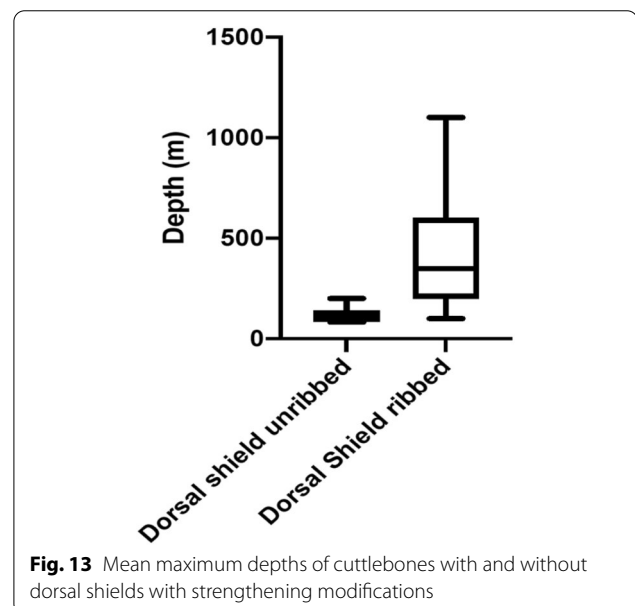
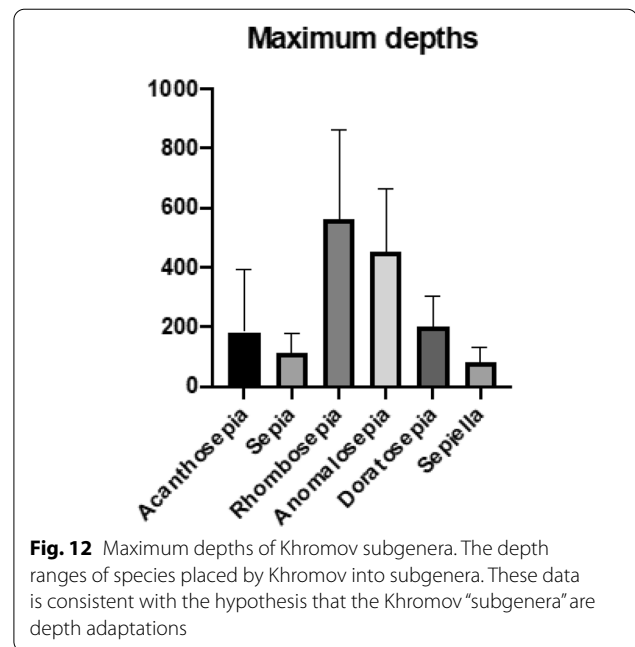
Length versus width of phragmocones as a proxy for cuttlebone shapes. The spectrum of cuttlebone shapes theoretical and actually evolved was previously published in Ward, (2000), using plots of maximum cuttlebone length against a width/length ratio. Although a wide spectrum of cuttlebone shapes can be envisioned, this diagram showed that cuttlebone form actually inhabits a fairly narrow range of shell shapes. The overall density diagram was roughly triangular in shape, with a high density of cuttlebones in the short, narrow to wide areas, and decreasing with variability as length increases. The largest cuttlebones (> 100 mm) are very restricted in terms of width (between 30 and 40% of total length; *S. officinalis* is an example of such a shape). The isolated region in the upper left of the diagram represents species of the taxa *Metasepia* and *S. (Hemisepius)*, which have very small and very broad cuttlebones composed partially of chitin; however, as stated previously, we did not include species in these two taxa in most analyses presented here.

Chamber spacing. Cuttlefish species that have been observed to have more chambers (no. of septa/cuttlebone) have a higher tendency to have a higher depth limit (Fig. 11A). Although this relationship is not strong, the data at hand indicate light correlation between these parameters. Other morphometric data such as the area of last locus to total phragmocone area were examined as a further possible aspect of depth potential; as can be seen in Fig. 11B, the deeper water sepiids in *Anomalosepia*, *Rhombosepia* and *Doratosepia* visually appear to have smaller last locus surface areas than is present in *Sepia* and *Acanthosepia*. However, these figures do





not take overall volume into account, nor is such data currently available (although it would be obtainable by measuring volumes of last chambers to total phragmocone volume in actual cuttlebones, if such material was uniformly available for actual volume measurement). In fact, such measures are not currently allowed to be conducted upon museum curated material. Be it as may, our Fig. 11B shows there is no correlation ($r^2=0.02$) in the relationship between the area of the last locus over the total area of the cuttlebone against the maximum depth. This implies that the size of the *area* of the last locus relative to its cuttlebone size may not have a highly significant role in its ability to reach extreme depths (> 200 m), although, again, whether or not the volume relationships may tell a different story.



Relation of morphology and depth in sepiid dataset presented here. The relationship between maximum observed depth and maximum cuttlebone length as well as the same depth findings plotted against maximum length and breadth/length ratio for the sampled species is shown in Fig. 10. It appears that sepiid taxa with very wide cuttlebones are confined to shallow water (<200 m). Narrow and shorter cuttlebones of intermediate width can be either shallow or deep, although as is so often the case, exceptions occur. For instance, in the review process we were

Table 1 Measurements of Sepiid cuttlebones arranged in different subgenera, showing ratios of different morphological features

	Known maximum depth (m)	Mantle length (mm)	Width/length	Length of siphon/area of lost locus	% last locus/total area	Length of siphon/area of last locus	% last locus/total area
<i>Acanthosepia</i>							
<i>S. stellifera</i>	200	120	0.339	0.016	0.24777758	0.06274	0.24777758
<i>S. smithi</i>	138	150	0.334	0.013	0.284545469	0.04581	0.28454547
<i>S. lycidas</i>	100	380	0.336	0.015	0.356751892	0.04103	0.35675189
<i>S. brevimana</i>	100	110	0.456	0.009	0.397916395	0.0238	0.39791639
<i>S. savignyi</i>	50	190	0.38	0.007	0.417670274	0.01673	0.41767027
<i>S. cultrata</i>	803	120	0.35	0.006	0.420648653	0.01342	0.42064865
<i>S. recurvirostra</i>	140	170	0.287	0.009	0.460575349	0.01954	0.46057535
<i>S. whitleyana</i>	128		0.37	0.005	0.472523984	0.00967	0.47252398
<i>S. esculenta</i>	100	180	0.316	0.005	0.520144394	0.01032	0.52014439
<i>S. rozella</i>	183	140	0.341	0.006	0.592817625	0.0107	0.59281763
<i>Sepia</i>							
<i>S. zanzibarica</i>	125	250	0.322	0.11	0.02693217	4.07948	0.02693217
<i>S. tuberculata</i>	–	–	0.472	–	0.195675073	–	0.19567507
<i>S. probahari</i>	100	130	0.329	0.014	0.339751092	0.04241	0.33975109
<i>S. bandensis</i>	50	70	0.443	0.01	0.378875429	0.02641	0.37887543
<i>S. pharaonis</i>	130	420	0.331	–	0.39541982	–	0.39541982
<i>S. ramani</i>	100	375	0.281	0.012	0.428986858	0.02855	0.42898686
<i>S. papuensis</i>	155	110	0.32	0.007	0.447618688	0.01549	0.44761869
<i>S. hierredda</i>	100	500	0.309	0.009	0.458652092	0.01995	0.45865209
<i>S. plangon</i>	83	135	0.285	0.011	0.487355363	0.02283	0.48735536
<i>S. vermiculata</i>	290	287	0.386	0.006	0.498728265	0.01255	0.49872826
<i>S. grahami</i>	84	82	0.451	0.005	0.545447934	0.00935	0.54544793
<i>S. simoniana</i>	–	–	0.374	0.001	0.558504808	0.00116	0.55850481
<i>S. elobyana</i>	–	53	0.365	0.006	0.569278109	0.01007	0.56927811
<i>S. elliptica</i>	142	175	0.381	0.005	0.586393149	0.00839	0.58639315
<i>S. latimanus</i>	30	500	0.275	0.005	0.612875219	0.00803	0.61287522
<i>S. officinalis verm</i>	–	–	0.331	0.001	0.641126918	0.00172	0.64112692
<i>S. officinalis</i>	200	490	0.294	0.005	0.641608779	0.00803	0.64160878
<i>S. apama</i>	100	500	0.431	0.006	0.669212788	0.00928	0.66921279
<i>S. bandensis</i>							
<i>Rhombosepia</i>							
<i>S. elegans</i>	500	72	0.268	0.01	0.241716749	0.04213	0.24171675
<i>S. hierornis</i>	–	–	0.392	–	0.278139121	–	0.27813912
<i>S. orbignyana</i>	570	120	0.259	0.01	0.278682579	0.0351	0.27868258
<i>S. madokai</i>	200	100	0.329	0.008	0.372213483	0.02098	0.37221348
<i>S. sulcata</i>	404	97	0.289	0.007	0.399168231	0.01776	0.39916823
<i>S. hedleyi</i>	1100	83	0.378	0.007	0.49543419	0.01373	0.49543419
<i>Anomalosepia</i>							
<i>S. australis</i>	345	85	0.29	0.018	0.134320913	0.13458	0.13432091
<i>S. omani</i>	210	100	0.264	0.005	0.445989493	0.01115	0.44598949
<i>Doratosepia</i>							
<i>S. trygonina</i>	410	140	0.195	0.011	0.210641424	0.05409	0.21064142
<i>S. bertheloti</i>	156	175	0.248	–	0.23076413	–	0.23076413
<i>S. kobiense</i>	200	90	0.201	0.011	0.235882452	0.04847	0.23588245
<i>S. prashadi</i>	200	140	0.261	0.008	0.350295697	0.0236	0.3502957
<i>S. vossi</i>	140	100	0.292	0.008	0.358668649	0.02334	0.35866865
<i>S. opipara</i>	184	150	0.295	0.008	0.384575282	0.02137	0.38457528

Table 1 (continued)

	Known maximum depth (m)	Mantle length (mm)	Width/length	Length of siphon/area of lost loculus	% last loculus/total area	Length of siphon/area of last loculus	% last loculus/total area
<i>S. braggi</i>	86	80	0.202	0.007	0.396286439	0.01703	0.39628644
<i>S. vietnamica</i>	104	70	0.226	0.006	0.464228268	0.01363	0.46422827
<i>S. lorigera</i>	300	250	0.21	0.006	0.467224547	0.01268	0.46722455
<i>S. arabica</i>	272	88	0.156	0.006	0.566749124	0.01116	0.56674912
<i>S. andreana</i>	50	120	0.222	0.007	0.578033004	0.01291	0.578033
<i>S. longipes</i>	300	250	0.23	0.007	0.619835128	0.01057	0.61983513
<i>Sepiella</i>							
<i>S. japonica</i>	50		0.294	0.009	0.411410711	0.02108	0.41141071

informed that *Sepia roelefeldi* Lipinski has a broad cuttlebone, but has been found to 497 m, while *S. typica* now known to 501 m, and *S. robsoni* to –449 m were pointed out to us as exceptions (Lipinski, pers. comm). These taxa merit detailed further morphological examination of their pillar structures and other aspects that could contribute strength against implosion.

Nevertheless, taking the entire disparity of cuttlebone shape together, it appears that large cuttlebones are most commonly found in, or even restricted to, shallow water; small cuttlebones, however, can be shallow or deep. Length per se is probably irrelevant; length, however, is related to cross-sectional shape. Larger cuttlebones by necessity have broader widths, and hence less curved cross-sections. Cuttlebones with highly curved cross-sectional shapes appear better adapted to withstand higher hydrostatic pressure (compression as well as tension) produced by stresses directed normal to all surfaces of the cuttlebone. The weakly curving septa, which define the cross-sectional shapes, as well as more widely spaced pillar structures between septa may be the cause of the structural weakness of the larger cuttlebones. Smaller cuttlebones have more highly curved cross-sections, and shorter pillars. That some of these latter species are found in shallow water suggests that either they have a low septal density and are weakened by this factor, or that they are adapted for deeper water but live in shallow water.

Discussion

Morphological features of chambered cephalopods cited in the literature as shell-strengthening adaptations include increased complexity of septa, increase in septal spacing, septal thickness, septal shell construction and shell wall modification (e.g., Daniel et al., 1997; Hewitt et al., 1989; Hoffmann et al., 2018; Klug & Hoffmann, 2015; Lemanis et al., 2016; Lukeneder et al., 2008; Peterman et al., 2021; Ward et al., 1980; Westermann, 1973, 1975, 1977). All of these factors may be utilized in

sepiids, but the relative degree of each shell-strengthening mechanism remains obscure. Cross-sectional complexity (through small size, and hence high septal curvature or through the evolution of various folds and sulci running the length of the cuttlebone), and to a lesser degree septal crowding may be adaptations used by sepiids to strengthen their shells against hydrostatic pressure; other, as yet unobserved adaptations may also be present as well. What appears to be correlation between these features and depth habitation in the sepiids suggests that mechanical adaptation to increased strength may be a primary ecological driver in the evolution of the Sepiidae. But what about buoyancy concerns?

Less clear than apparent morphological adaptations to cuttlebone ambient pressure across a range of depths inhabited by cuttlefish are morphological aspects of cuttlebone construction that relate either predominantly to, or at least in part to, the need for chamber emptying (or at least a cessation of reflooding of chambers (and avoiding refilling already emptied chambers) in very deep water. These aspects occur in growing animals as a process of new chamber formation, or in adults entering greater depths and thus pressures, thereby encountering inadvertent chamber refilling by ambient pressure over-matching osmotic pressure produced within the canaliculi and microscopic folds of the siphuncular epithelium, as noted by Denton, (1974), Ward, (1987) for *Nautilus*. Just such chamber refilling was observed in experiments where caged *Nautilus macromphalus* were maintained for more than 5 days at more than 500 m in depth (also in Ward, 1987).

It is here that the phragmocone construction of the deepest water-inhabiting species might provide clues. The measurements above suggest that a characteristic of deep-water species is their small size but also thinner cuttlebones with a significantly larger internal curvature of more widely spaced chamber walls. Examples of several of the deepest diving known cuttlefish are shown

in Fig. 8, showing cuttlebone details for *Sepia australis*, *S. orbignyana*, *S. elegans*, and *S. hieronis*. These species appear to be able to live, or at least visit for unknown periods of time, at depths greater than 500 m. The deepest published depth of a *Sepia* species is nearly 1000 m (Reid, 2016). This is remarkable taking the very small thickness of the sepiion walls into account. They reach depths comparable to the maximum habitation depths of extant *Nautilus* species.

The depth limit imposed by “simple osmosis” is 240 m—the depth at which the osmotic pressure differential between fresh and salt water separated by a semipermeable membrane equals the 24 atmospheres of ambient pressure at that depth. Studies (Greenwald & Ward, 1987 1987; Ward, 1987) have shown that, at least in *Nautilus*, emptying can take place at depths greater than 240 m, presumably through a process of “local osmosis”, or solute coupled transport (Mathias & Wang, 2005). To date no such studies or observations have been made on sepiids, and such studies would prove challenging because of the extremely small size of single chambers and their topographic position in deep-water cuttlefish, even if such experiments were conducted within pressure chambers in surface laboratory settings. Yet, there are observations that there appear to be extreme modifications of the siphuncle in the deeply living dibranchiate squid *Spirula* (which has been caught at depths of 1600 m) as possible responses to either building chambers at such high ambient pressures, or more probably simply avoiding the inadvertent refilling of partially or completely emptied chambers. In turn, this suggests that deep-water cuttlefish may as well have adaptations to avoid refilling when visiting depths greater than perhaps 300 m.

One possibility to avoid refilling is reducing the volume of any single chamber compared to the entire phragmocone volume. Thereby, if a progressive, chamber by chamber implosion begins in the last formed chambers (the kind of implosion observed in *S. orbignyana*: Ward & Boletzky, 1984), the flooded chambers would not create a negative buoyancy beyond the animal’s ability to regain shallower depths.

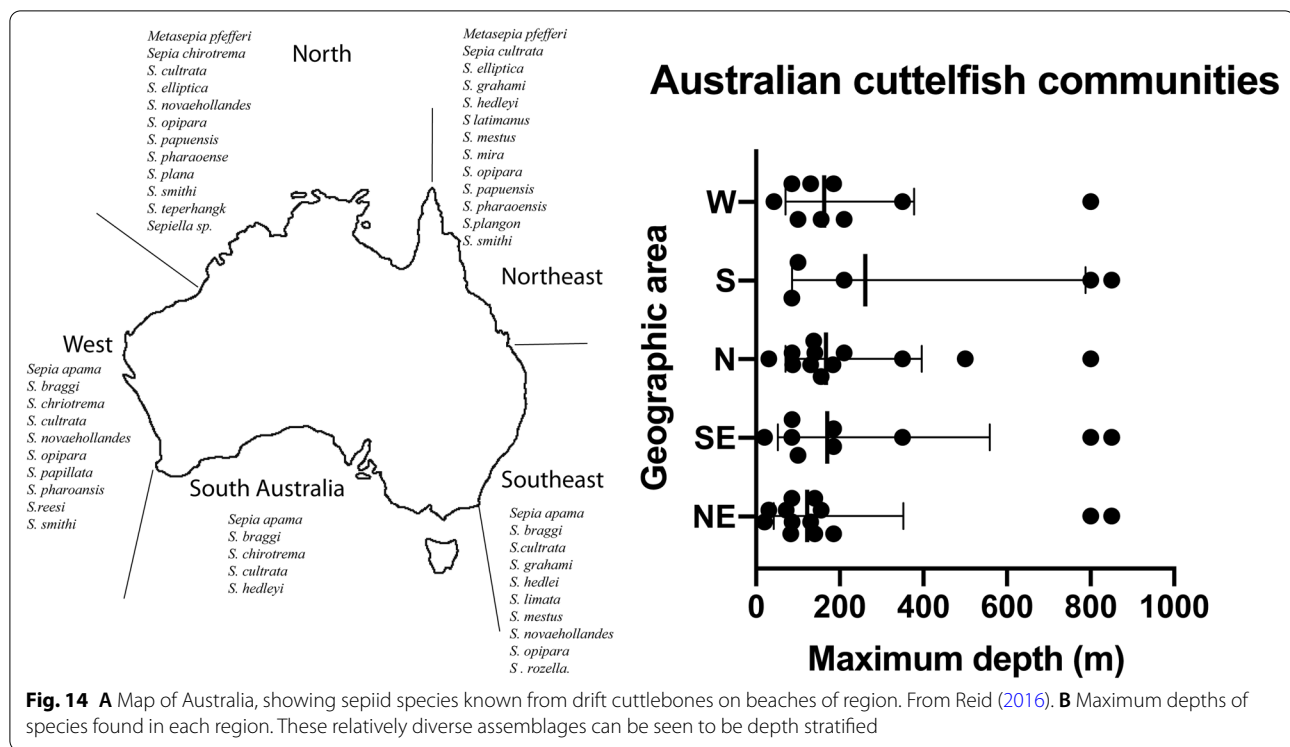
A second possibility is that, by reducing the length of the chamber opening where the flooding would begin, where the siphuncle is in contact with the chamber opening, that flooding would be reduced. Again, our measurements suggest that this is the case. In deeper water species, the length of the opening (which is an estimate for the actual area of opening) compared to the area of the last loculus (itself an estimator of the volume of the last loculus) is also smaller in deeper water species than shallower species.

Finally, and perhaps most interestingly, the new observations by Checa et al. (2015) on the nature of cameral

liquid, or perhaps, in cold water, cameral “gel” in *Sepia officinalis* makes us wonder about the nature of chamber liquid in deeper water species. In analogous fashion, the recent engineering observations on cuttlebones makes it conceivable that the known, higher density of pillars in deeper water cuttlebones, combined with the greater sinuosity of pillar/chamber wall contact in deep-water water species might be a means of reducing the rate of inadvertent flooding through simple, essentially structural “roadblocks”. In the very thin chambers, all of these factors could combine through changing density of cameral liquid over the length of a single chamber from near to far from the siphuncular epithelium to enable habitation of deep-water cuttlefish. Perhaps more importantly, this would allow them to make rapid descents on steep deep water slopes. By contrast, the opposite of these structures in the large, shallow water cuttlefish may be adaptations to rapidly add and remove cameral liquid to enable a rapid density change. This would be similar to the observations by Denton and Gilpin Brown (1961b) on *S. officinalis* doing diurnal buoyancy changes in support of burrowing in diurnal fashion. For such larger scale movement of cameral liquid, the opening of into and out of the last formed chamber and chambers would be optimally large.

The ability to live at varied depths may be an important driver of sepiid evolution, and perhaps of ancient, chambered cephalopods as well. Sepiids disperse largely along coastlines; and most species appear to be entirely nekto-benthic in habit. This is not the case for the large, demersal species *Sepia apama*, *S. latimanus* and *S. pharaonis*. At least as adults, these latter species live off the bottom (our personal underwater observations). As for the majority of smaller sepiids, their relatively shallow implosion depths and complete lack of free-living, open water habits in either the newly hatched or juveniles or adults precludes any important over-deep bottom dispersal (where hatchlings move in the upper water column, over bottoms that far exceed the implosion depth), such as the planktonic dispersal of most gastropods, bivalves, and even many *Octopus* species. It appears that sepiids assume a benthonic existence immediately upon hatching (Villanueva et al., 2016). Nature, of course, is full of exceptions, and we have been informed of two, smaller sepiid species recently described from waters off South Africa (Lipinski 2020a, 2020b; Lipinski & Leslie, 2018) where a nektonic rather than nekto-benthonic existence also occurs.

This mode of dispersal is perhaps exemplified by the present-day biogeographic ranges of the sepiids. For example, although abundant and diverse in West African and European waters, no sepiids exist in coastal areas of either North or South America. As another



example, Australia is thought to have over thirty sepiid species (Fig. 14), while new nearby New Zealand has none (Adam & Rees, 1966; Reid, 2016; Reid et al., 2005). These differences cannot alone be due to environmental differences between these areas. The sepiids are not there probably because they cannot get there. The ones that do (or did) arrive in new places might then have evolved into depth segregated species. Thus, a critical question: *can a shallow water species produce new species that can inhabit greater depths than the mother species; conversely can deep-water species then evolve into shallow water species.*

Although sepiids cannot move across bodies of water deeper than their implosion depth (a maximum of perhaps 1000 m), they are capable of widespread dispersal along coastlines, and many species seemingly can endure great variations in temperatures. This leads to wide ranges of many species. *Sepia officinalis*, for example, is continuously found from Northern Europe to the east coast of southern Africa (Neige, 2003a, 2003b); *S. pharaonis* is found from the Red Sea to Hong Kong. Many of the Australian species are found distributed around that continent. Reproductive isolation leading to speciation may be related to geographic isolation (Fig. 14).

In the tropical Pacific region, only *Sepia latimanus* is known in archipelagos that are separated by hundreds of kilometers of open ocean; they are found on Fiji, Vanuatu, the Solomons, and other archipelagos but no other

sepiids apparently were able to cross these distances, apparently not the deep water but smaller species (Neige, 2003a, 2003b).

Sepiid habitat and ectocochleate taphonomy

Regionally, various sepiid species may live quite close to each other. This can be explained by different prey preferences or by different habitats and particularly habitat depths. When examining associations of extinct ectocochleates such as ammonoids and nautiloids, striking numbers of species may co-occur. For example, in the Moroccan Eifelian (Middle Devonian), 12 ammonoid species + ca. 5 nautiloid species occur in one layer (Klug, 2001; Monnet et al., 2011). In the Smithian (Early Triassic) of South China, up to 24 species of ammonoids were documented for a single bed (Brayard & Bucher, 2008). In the Toarcian (Early Jurassic) of the Causses in France, several layers yielded nearly 20 ammonoid species (Guex, 1975). As a last example, Reboulet et. al. (2005) report a generic richness of up to 18 genera per stratum from the Breistroffer interval in the Albian (Early Cretaceous) of France.

In palaeontological associations, the question for systematic, taphonomic and sampling biases arise immediately when discussing such numbers:

- Are contained taxa highly variable and oversplit?
This cannot be ruled out and likely varies between researchers, localities, and modes of preservation. However, it appears unlikely that all 20 species

described from a single layer are conspecific. Also, some taxa might have been so rare or difficult to recognize that the diversity is actually underestimated.

- (ii) Did faunal mixing and condensation occur? What were the sediment accumulation rates?

These are real issues as shown by, e.g., Kidwell (1985) or Kidwell et al (1991). However, even if this explains parts of the species richness, highly diverse ammonoid associations are far too common to make faunal mixing sufficient as the sole explanation.

- (iii) Were some of the cephalopod conchs transported?

This problem was repeatedly discussed and studied using varying approaches. For example, Chamberlain et al. (1981) suggested that the phragmocone of ammonoids may have become flooded quite quickly after the animal's demise and thus may explain a short time span between death and settling on the sediment. By contrast, Chirat (2000) interpreted wide geographical distribution of the nautilid *Aturia* by an extended drift of empty conchs. Wani et al. (2005) experimented with nautilid conchs and found that they became waterlogged rather quickly after their demise. Similarly, Yacobucci (2018) suggested that postmortem drift played a subordinate role in ammonoid conchs.

The observations of occurrences and diving depths of modern sepiids discussed here cannot solve all these problems and contradictions. However, in some respects, these modern coleoids provide valuable information. For example, the specialization in habitat close to the sediment or in the water column as well as in different water depths suggest that the often quite high alpha diversity of extinct cephalopods such as ammonoids may partially root in similar specializations. This is confirmed to some degree by stable oxygen isotopes from ammonoid conchs, suggesting different habitat depths as well as changes through ontogeny (e.g., Cochran et al., 1981; Lécuyer & Bucher, 2006; Lukeneder, 2015; Lukeneder et al., 2010; Moriya et al., 2003). Isotope data from ammonoids are still rare future research will hopefully provide more detail about diving depth. This implies that transport happened vertically, thereby seemingly fusing different habitats.

Does sepiion shape inform about diving in extinct ectocochleates?

We are at the beginning of understanding the construction, function and limitation of cephalopod phragmocones in general. The results presented here, however, reveal gaps in our knowledge concerning extinct coleoids.

Diving depth was often discussed in the context with sutural complexity (e.g., Daniel et al., 1997; Klug & Hoffmann, 2015; Lemanis et al., 2016; Peterman et al., 2021). There is a growing body of evidence that hydrostatic stability was not the primary function of septal frilling. The fact that deeper diving sepiids tend to be smaller and have a more strongly curved chamber wall shows that ammonoid hydrostatics needs to be reconsidered. It is here hypothesized that possibly the whorl expansion rate and relative whorl height as well as septal spacing (Korn et al. in prep.) might play an equally important role to support hydrostatic pressure at greater depths. This can be tested by a combination of morphometry, virtual 3D-models and finite element analyses as well as oxygen isotopes as a measure of depth.

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Authors' contributions

PDW had the idea, wrote most of the text, and produced the figures. JLV wrote parts of the text and provided some data. CK wrote parts of the text, added several references and edited the text. All authors read and approved the final manuscript.

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Availability of data and materials

The sources of all information are provided in the text. All specimens illustrated here are kept in Natural History Museum in London, the South African Museum in Cape Town, the Australian Museum in Sydney, and the Burke Museum, University of Washington.

Declarations

Competing interests

The authors declare no competing interests.

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