# Cephalopod embryonic shells as a tool to reconstruct reproductive strategies in extinct taxa

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## ABSTRACT

An exhaustive study of existing data on the relationship between egg size and maximum size of embryonic shells in 42 species of extant cephalopods demonstrated that these values are approximately equal regardless of taxonomy and shell morphology. Egg size is also approximately equal to mantle length of hatchlings in 45 cephalopod species with rudimentary shells. Paired data on the size of the initial chamber *versus* embryonic shell in 235 species of Ammonoidea, 46 Bactritida, 13 Nautilida, 22 Orthocerida, 8 Tarphycerida, 4 Oncocerida, 1 Belemnoidea, 4 Sepiida and 1 Spirulida demonstrated that, although there is a positive relationship between these parameters in some taxa, initial chamber size cannot be used to predict egg size in extinct cephalopods; the size of the embryonic shell may be more appropriate for this task. The evolution of reproductive strategies in cephalopods in the geological past was marked by an increasing significance of small-egged taxa, as is also seen in simultaneously evolving fish taxa.

*Key words*: embryonic shell, initial chamber, hatchling, egg size, Cephalopoda, Ammonoidea, reproductive strategy, Nautilida, Coleoidea.

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## I. INTRODUCTION

Reconstruction of the evolutionary ecology of extinct animals is always a challenging task because it is based on such incomplete evidence. Reproductive biology is a particularly difficult case, as it largely requires preservation of soft parts. However, cephalopod molluscs, as they have a shell, might be a rare exception to this rule, providing an opportunity to track the evolution of reproductive strategies through geological time. Both ectocochleate and endocochleate cephalopods possess a shell – either outer (ammonoids, nautiloids) or inner (squids, belemnites, cuttlefishes) – that records events chronologically in the life of an individual. These records include anything from daily growth bands on squid gladii,

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to evidence of change of the entire lifestyle documented in changes of ammonite shell coiling pattern, or signs of the last fatal attack of a predator. One of the most important ecological features of the cephalopod lifestyle is the embryonic shell (ES), which is present in most extinct taxa and extant species, as it reflects the egg size and thus parental investment into individual offspring. Throughout their evolutionary history cephalopods exhibit a variety of body plans and ES morphologies. Generally, in most ectocochleate taxa, the ES consists of an initial chamber (IC) sometimes called the 'protoconch' and a few chambers, although in some groups like Ellesmerocerida a distinctive IC is absent (Barskov *et al.*, 2008). In modern coleoids the internal ES represents a structure very similar to that of adults: the sword-like gladius of squid, the broader cuttlebone of Sepiida, the ram's-horn-shaped spiral structure of *Spirula* spp., or paired spindle-like stylets in octopods.

Obviously, there is no ES in cephalopod species that have a rudimentary shell or no shell at all, particularly Octopoda and some Sepiolida, but for the rest of the class, the size of the ES might be a suitable tool to reconstruct historical changes in egg and larval sizes, assuming that larger eggs produce hatchlings with a larger ES. Such an assumption is widely used by palaeontologists, e.g. for Palaeozoic nautiloids (Manda & Frýda, 2010), belemnites (Doguzhaeva *et al.*, 2014*b*), and particularly for ammonites for which the ES 'ammonitella' is considered to be a good proxy for egg size (Landman, Tanabe & Shigeta, 1996). Thus, not only is a positive relationship between egg size and hatchling size assumed (which is likely although not yet proven) but also, without any available evidence, this relationship is assumed to be linear.

Not only ES size but also IC diameter is often used to define tentative reproductive strategy as, in contrast to ES size, these data are relatively easy to obtain. Small IC size [*ca.* 0.5 mm (Nützel, Lehnert & Frýda, 2007; Kröger, Servais & Zhang, 2009) although likely up to 1.6 mm as in some ammonites (Laptikhovsky *et al.*, 2013)] is interpreted as evidence for a small amount of yolk in the eggs, and therefore for hatchlings with a planktotrophic strategy, and *vice versa* [several millimetres (Manda, 2008)]. The fact that any cephalopod hatchling is both lecitotrophic and planktotrophic, and even cephalopods born from the smallest eggs have sufficient yolk reserves to enable them to develop their hunting behaviour (Boletzky, 2003*b*) is largely ignored in such palaeobiological reconstructions.

These widely held beliefs are not based on any analysis of primary data from recent cephalopods, and are not even accompanied by references to any significant amount of information on the relationship between egg size and hatchling shell size. However, in theory, larger eggs do not necessarily result in larger offspring, as the energy from extra yolk could also be used for organogenesis during the embryonic period – so-called embryonisation that could be interpreted as delayed hatching with the accomplishment within the egg of developmental processes otherwise occurring after hatching (Crowson, 1981). On the other hand, under some environmental conditions (usually adverse), cephalopod embryos tend to hatch at earlier stages of development, at smaller sizes but with a large outer yolk sac that either might be dropped or consumed, depending on species (Boletzky, 2003*b*). These processes (embryonisation and de-embryonisation) might potentially have a strong impact on the evolution of the relationship between egg size and hatchling size. Such heterochronies, if they occurred in cephalopods during speciation events, were probably only one of a number of effects, given the likely pleiotropic effects of genes involved in such temporal modifications (Boletzky, 1997).

This review considers all existing data on the relationship between egg size and ES size in recent cephalopods, and aims to verify the assumption that ES size is linearly proportional to egg size. Development of artificial fertilisation and ongoing research in cephalopod culture during recent decades has provided abundant new materials, and to the best of our knowledge this review summarises all existing information on extant cephalopods in which both egg length and ES length at hatching are known. We make similar comparisons between hatchling size (mantle length, ML) and egg size in species with a rudimentary shell, to reveal whether the presence/absence of the shell impacts this relationship. During embryonic development, eggs swell and their volume may increase by more than 150% (Boletzky, 1986; Gomi, Masamichi & Tohru, 1986); thus, in our review we use the size of freshly laid eggs, which is nearly the same as that of unfertilised eggs in oviducts.

Secondly, we aim to determine whether hatchling size (ML) can be predicted from egg size. In practice it is much easier to catch a mature female and to measure the length of ovulated eggs than to measure hatchlings in planktonic samples. Moreover, as cephalopods grow very rapidly, collected paralarvae could be much bigger than at birth: hatchlings of *Sthenoteuthis pteropus* increase fourfold in ML (and hence, ES) in just two weeks (Laptikhovsky, Arkhipkin & Golub, 1993). For this, we used a separate set of data on egg and hatchling size in species that do not possess hard shells, such as octopods and some sepiolids.

The gladius extends exactly from the anterior to the posterior part of the mantle in hatchlings of nearly all Decabrachia, so the ML is effectively the gladius length. There are some rare exceptions that were taken into consideration: in the genus *Idiosepius* a delicate membranous gladius covers only about two-thirds of the ML (Hylleberg & Nateewathana, 1991), in the sepiolids *Rossia* and *Semirossia* the gladius extends for some 70–75% of the ML (Bizikov, 2008), and the cuttlefish genus *Metasepia* have a sepion of half to two-thirds the ML (Grasse, 2014; B. Grasse, personal communication). However, such exceptions are rare. To estimate relationships between egg size and hatchling size we used literature data on embryogenesis of 42 species with an internal shell and 45 species with a rudimentary shell that to the best of our knowledge represents all existing information to date.

Another question we address herein is whether a universal statistically significant relationship exists between IC size and ES size that might allow use of IC, rather than ES, to judge inferred reproductive strategies. For example, although there is abundant information on IC size in the ecologically important Belemnitida, their ES size is poorly known and is reported (as 1.3 mm) only from the genus *Cylindroteuthis* (Hewitt & Jagt, 1999) in which the IC size is ∼0.5 mm (measured from fig. 4 in Hewitt & Jagt, 1999). By analogy with the extant decabrachs *Spirula* and *Sepia,* it was assumed that in the studied belemnites with a IC size of 0.3–1.0 mm the ES might be about 1.5–3 mm (Doguzhaeva *et al.*, 2014*b*) suggesting pelagic offspring.

For this purpose, we used a data set of IC and ES sizes for Ammonoidea and Nautilida from Laptikhovsky *et al.* (2013), as well as available data for other extinct and extant cephalopod taxa based on an extensive literature search. This resulted in paired data (IC *versus* ES) in 235 species of Ammonoidea, 46 Bactritida, 13 Nautilida, 22 Orthocerida, 8 Tarphycerida, 4 Oncocerida, 1 Belemnoidea, 4 Sepiida, and 1 Spirulida. To reconstruct the evolution of cephalopod reproductive strategies this data set was supported by non-paired data of either IC or ES in another 324 species of Ammonoidea, 56 Belemnoidea, 9 Coleoidea, 10 Bactritida, 125 Nautilida, 6 Oncocerida, 34 Orthocerida, 9 Pseudorthocerida and 8 Tarphycerida.

In spite of being heavily biased towards ammonites, as these paired measurements are extremely rare for other groups, the available data set on the relationship between IC and ES size is reasonably complete and sufficient for an initial assessment. For taxonomy we used the reviews of Shevyrev (2006*a*,*b*), Allcock, Lindgren & Strugnell (2014) and Hoffmann (2015).

## II. MORPHOLOGICAL STRUCTURE OF EMBRYONIC SHELLS IN EXTANT AND EXTINCT CEPHALOPODS

All chambered nautiloids and ammonoids share a shell that is divided into two major parts: (*i*) the phragmocone which is divided by septa into separate chambers interconnected *via* the siphuncle; and (*ii*) the body chamber where the animal lives. In endocochleate cephalopods the shell exhibits various degrees of reduction up to complete absence. Hard ESs of extinct and recent cephalopods differ in structure among taxa (Fig. 1). They generally consist of the IC together with several (0–15) chambers of the phragmocone or proostracum combined with the phragmocone.

The boundary between the ES and post-ES in cephalopods can be clearly seen in some clades (i.e. in ammonoids it is marked by a prominent constriction and accompanied by changes in microsculpture), while in others it is poorly known (i.e. belemnoids) or cannot be defined with certainty (some nautiloids *s.l.*). The following features were used for determination of the ES: (*i*) nepionic constriction – some bactritoids and Nautilida are characterised by the presence

of a wide constriction in the early part of the shell; (*ii*) septal approximation (decrease in the distance between septa) – this is known in many nautilids and is commonly used for recognition of the ES (Stumbur, 1959; Shimansky, 1975), but as in recent *Nautilus* the septal approximation lies some one-third of a whorl before the end of the ES (Landman, 1988), such measurements may be slight underestimates; (*iii*) changes in microsculpture are rarely seen in fossil cephalopods as this relies on excellent preservation, but they were recently reported in tarphycerids by Turek & Manda (2016) who also emphasised very high variability in the ES size of the taxa studied; (*iv*) shell thickening as a kind of hatching scar and a shift in the shell axis as in some Belemnoidea (Hewitt & Jagt, 1999); (*v*) the ES of ammonoids, the so-called ammonitella, is finished by a constriction known as the primary constriction, which is accompanied by the nacreous primary varix, indicating appearance of the nacreous layer.

For this study, we tried to use as many features as possible to define ESs, but due to incomplete data about initial shell parts of many taxa, in some cases only a single feature could be used for the determination of ES size.

These ESs can be grouped as follows:

(1) Yanhecerida, Protactinocerida, Iterjocerida (Cambrian – Ordovician) – the earliest cephalopod orders, with few known species. Neither the IC nor the ES is described.

(2) Ellesmerocerida (Cambrian) – the apical initial chamber of the shell is simple, large (∼2–3 mm), conical or bluntly rounded, rather rapidly expanding. The larval shell is cylindrical, with several chambers, and no nepionic constriction or hatching scar to define it (Flower, 1964; Dzik, 1984; Barskov *et al.*, 2008).

(3) Endocerida (Ordovician – Early Silurian) – the largest Early Palaeozoic animals, reaching up to 10 m in length (Teichert & Kummel, 1960), an abundant and common taxon. The ES is large, some 5–60 mm in length, inflated, with a chambered apical part and the IC distinctly separated from the post-larval shell (Dzik, 1984; Kröger, 2013).

(4) Oncocerida (Ordovician – Carboniferous) – the IC of the apical end with a slightly larger septal distance than in the following chambers (Kröger, 2007); its maximum diameter is approximately 0.8–1.5 mm. Chambers 2–5 (particularly 3–4) are shorter than the previous and subsequent ones; in our opinion this might be interpreted as marking the end of embryonic development. ES length is 4–7 mm.

(5) Orthocerida (Ordovician – Triassic, ?Cretaceous) – the ES consists of a spherical IC (0.3–1.7 mm) and a single chamber that made it capable of early access to the pelagic zone, before reaching the phragmocone stage (Barskov *et al.*, 2008). ES length is usually 1–5 mm, up to 12 mm in Triassic *Trematoceras*.

(6) Pseudorthocerida (Ordovician – Triassic) – in contrast to Orthocerida the IC is conical (Barskov *et al.*, 2008) and 0.5–2 mm, the ES varies between 1 and 14 mm.
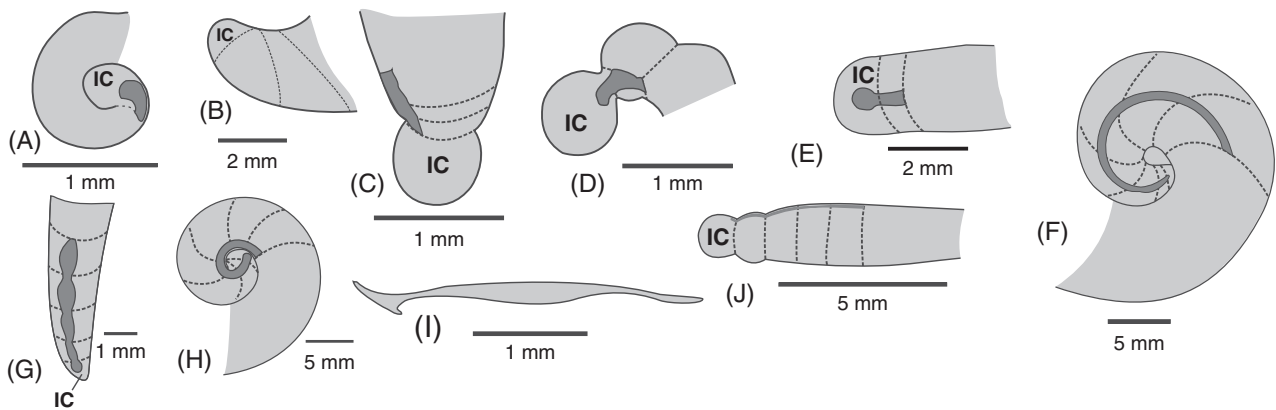
**Fig. 1.** Embryonic shells of extant and extinct cephalopods. IC, initial chamber. (A) Ammonoidea; (B) Neocoleoidea: Sepiida (*Mississaepia*, after Doguzhaeva, Weaver & Ciampaglio, 2014*a*); (C) Coleoidea: Belemnoidea (*Pachybelemnopsis*, after Doguzhaeva *et al.*, 2014*b*); (D) Neocoleoidea: Spiriluda (*Spirula*, after Warnke & Boletzky, 2009); (E) Orthocerida (*Archigeisonoceras*, after Kröger, 2006); (F) Nautilida (*Nautilus*, after Landman, 1988); (G) Oncocerida (after Kröger, 2007); (H) Pseudorthocerida (*Reticycloceras*, after Kröger & Mapes, 2004); (I) Neocoleoidea: Oegopsina (*Onychoteuthis*, after Sweeney *et al.*, 1992); (J) Bactritida (after Mapes, 1979).

(7) Tarphycerida (Ordovician – Devonian) – the IC is large, 1–5 mm, and cup-like on the apical end of the shell; the ES is slightly curved (Turek, 2010), finger-like, and approximately 2.5–16 mm in length.

(8) Lituitida (Ordovician) – the IC is spherical, ∼0.7 mm. The ES is not well defined and is 'a few millimetres' long (Kröger, 2006).

(9) Actinocerida (Ordovician – Carboniferous) – a large initial part of the shell has a conical IC (Barskov *et al.*, 2008) exceeding 10 mm in diameter (Dzik, 1984).

(10) Ascocerida (Ordovician – Silurian) – the apex of the shell is bullet-shaped without a well-defined ES; the IC is approximately 1–2 mm (Kröger, 2007).

(11) Bactritida (Devonian – Triassic) – the IC is bulbous, from 0.3–0.7 to 1.5 mm, situated at the apical end of the phragmocone. The ES is 1–3 mm in length, includes a few chambers, and is separated by a constriction (Fig. 1) from the juvenile shell (Mapes, 1979).

(12) Discosorida (Ordovician – Devonian) – the IC is 0.8–1.5 mm, the ES is cup-like, separated by a circular or elliptical cicatrix with additional radial depressions (Manda & Turek, 2009). The ES length is 4–7 mm.

(13) Nautilida (Devonian – Present) – the ES consists of a coiled calcified phragmocone and is approximately 4–32 mm in diameter; the proostracum is absent; the IC is cup-like, approximately 1–6 mm long.

(14) Ammonoidea: Anarcestida, Tornocerida, Goniatitida, Clymeniida, Ceratitida, Phyllocerida, Lytocerida, Ammonitida (Devonian – Paleogene (Danian)) – the ES (ammonitella) consists of an IC of 0.2–2 mm that may be spherical, barrel- or spindle-shaped and several chambers covering up to an entire whorl, separated from the adult shell by a primary constriction. Total diameter of the ES (ammonitella) is around 0.5–3 mm.

(15) Coleoidea: Boletzkyida (Devonian) – the ES consists of a spherical IC of 0.5–0.9 mm and a single septum. The total ES length is ∼3–4 mm (Bandel, Reitner & Stürmer, 1983).

(16) Coleoidea: Belemnoidea: Aulacocerida, Phragmoteuthida, Donovaniconida, Belemnitida, Hematitida (Devonian – Cretaceous) – the ES consists of a globular IC of 0.3–0.7 mm and several chambers. The total length is about 1.5–3 mm (Hewitt & Jagt, 1999; Doguzhaeva *et al.*, 2014*b*).

(17) Coleoidea: Neocoleoidea: Myopsida, Oegopsida, Bathyteuthida, Sepiolida and Idiosepiida (Paleogene - Present) and Vampyromorpha (Jurassic – Present) – the ES is the gladius (absent in some Sepiolida and reduced in Idiosepiida), a pen-like decalcified chitinous proostracum, sometimes bearing remnants of the phragmocone; the IC is absent (Bizikov, 2008; Fuchs & Iba, 2015; Sutton, Perales-Raya & Gilbert, 2016).

(18) Coleoidea: Neocoleoidea: Sepiida (Paleogene – Present) – the ES is the sepion, consisting of a calcified proostracum and a phragmocone with a siphuncular surface of some 4–10 mm at hatching; IC is ovoid or spherical, approximately 0.6–2 mm in length (Bandel & Boletzky, 1979; Doguzhaeva *et al.*, 2014*a*).

(19) Coleoidea: Neocoleoidea: Spirulida (Jurassic – Present) – the spiralling ram's-horn-like shell consists of a spherical IC of ∼0.7 mm and 2–3 chambers, a cicatrix is absent (Warnke & Keupp, 2005; Lukedener *et al.*, 2008). It is represented by a phragmocone, and lacking a proostracum, with early chambers covered with a thin membrane possibly representing a reduced rostrum (Warnke & Boletzky, 2009; Arkhipkin, Bizikov & Fuchs, 2013).

Some neocoleoid cephalopods, mostly octopods as well as some sepiolids, have a reduced shell. These groups exhibit all possible reproductive strategies from the smallest egg size known for cephalopods (0.6–0.8 mm in *Argonauta* spp.) to the largest (40 mm in *Graneledone boreopacifica*),

which is similar to the studied extinct taxa (from 0.5–0.6 mm in some Orthocerida, Ceratitida, Ammonitida and Lytocerida to 50–68 mm in *Proterovaginoceras belemnitiforme* and *Cameroceras turrisoides* of Endocerida and in some Nautilida). Unfortunately, they cannot be included this study. However, their exclusion is unlikely to be important as these taxa (judging from the relatively rare occurrence of their very characteristic beaks) were never abundant in seas of the Palaeozoic and Mesozoic, the periods of our primary interest.

## III. RELATIONSHIP BETWEEN EGG SIZE, EMBRYONIC SHELL SIZE AND INITIAL CHAMBER SIZE IN EXTANT AND EXTINCT CEPHALOPODS

Analysis of our data on recent cephalopods demonstrated that egg size might be predicted from ES or (in cephalopods with a rudimentary shell) ML size (and *vice versa*) (Tables 1 and 2, Fig. 2). The mean ± C.I. ratio between egg size and hatchling size was $1.09 \pm 0.8$ in shell-bearing cephalopods, significantly higher than the mean of $0.85 \pm 0.07$ in species with a rudimentary shell (Welch two-sample *t*-test, $t = 2.4121$, d.f. $= 97.917$, $P = 0.0177$). These two relationships thus could be used to estimate the ES or ML of hatchlings from egg size regardless of taxon or reproductive strategy (Fig. 2). For fossil materials, the egg size could be estimated from the ES.

No significant relationship predicting ES size from IC size could be established for all cephalopods (Fig. 3A) although correlations did exist at order and subclass levels in Ammonoidea (Pearson product–moment correlation $r^2 = 0.948$, $P < 0.0001$), Bactritida ($r^2 = 0.662$, $P < 0.0001$), Tarphycerida ($r^2 = 0.922$, $P = 0.003$), and possibly Nautilida ($r^2 = 0.590$, $P = 0.056$). The ES to IC ratio is 1.2–2.9 (mean 1.9) in Ammonoidea, 2.7–3.5 (mean 3.1) in Coleoidea (Sepiida, *Spirula*), 1.9–8.1 (mean 4.2) in Bactritida (Nautiloidea), 2.6–22.3 (mean 9.0) in Nautilida, and 1.8–14.9 (mean 6.3) in Orthocerida. Analysis of covariance (Crawley, 2007) demonstrated that ES size is highly influenced by IC size ($F = 1191.6$, $P < 0.0001$), belonging to a particular taxonomic group ($F = 162.2$, $P < 0.0001$) and taxa-specific interactions between IC and ES ($F = 4.9$, $P = 0.02$) (Fig. 3B).

Among the diversity present in Fig. 3, three evolutionary groups can be identified by principal component analysis (Crawley, 2007). One is represented by the subclass Ammonoidea, another group consists of the order Nautilida (Fig. 4), the third unites the subclass Orthoceratoidea and its descendants – the order Bactritida and the subclass Coleoidea. The evolutionary significance of these three groupings is unclear but possibly is related to shell morphology and hatchling ecology. In Nautilida the shell is external and coiled and the hatchlings demersal, in Ammonoidea the shell is external and the hatchlings pelagic, in the other three taxa the shell may be either external or internal, but is usually straight and streamlined with
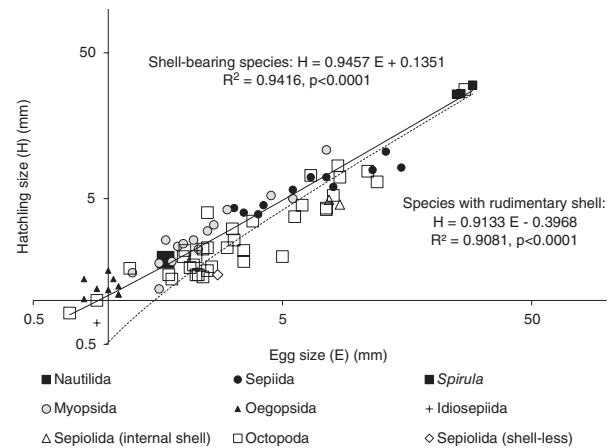


**Fig. 2.** Relationship between egg size and hatchling shell size in cephalopods. Hatchling shell size was measured as embryonic shell (ES) size in shell-bearing cephalopods and mantle length (ML) in those with a rudimentary shell. The southwest Atlantic *Benthoctopus eureka* was excluded from consideration as an 'outlier'.
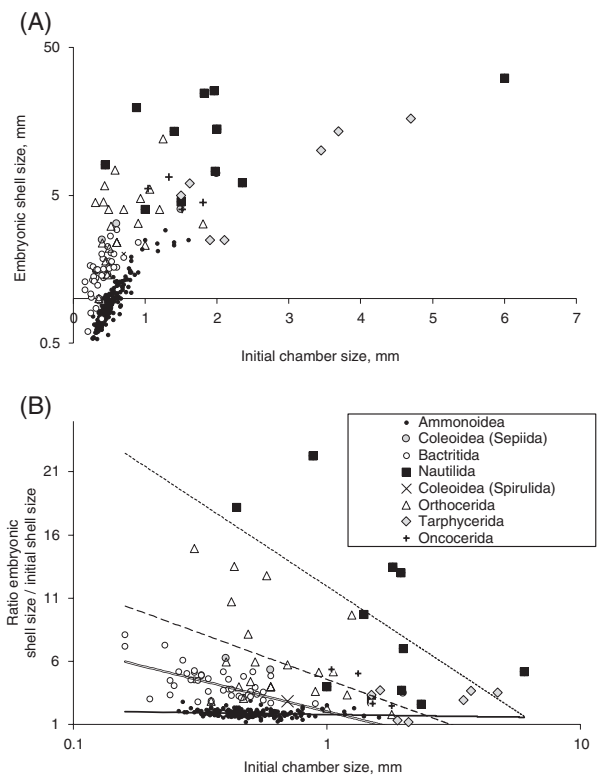


**Fig. 3.** Relationship between (A) initial chamber (IC) size and embryonic shell (ES) size and (B) changes in ES/IC ratio with initial chamber size in extant and extinct cephalopods.

some very rare exceptions, and hatchlings either pelagic or demersal.

A strict isometric linear relationship between egg size and maximum ES size (length of gladius, maximum distance in *Spirula* embryonic crescent, or diameter in spheroid nauta) is probably based on some general patterns of shell formation

Table 1. Relationship between egg size and hatchling size (embryonic shell size, ES) in shell-bearing cephalopods. ML, mantle length

| Species | Egg size (mm) | Source | Max. shell size (mm) | Source |
|---|---|---|---|---|
| **Nautilida** | | | | |
| *Nautilus belauensis* | 29 | J. M. Arnold (personal communication in Hanlon & Messenger, 1998) | 28.2–31.8 | Carlson, Awai & Arnold (1992) and Arnold, Landman & Mutvei (2009) |
| *N. macromphalus* | 26 | Willey (1896) | 26.2 | Arnold *et al.* (2009) |
| *N. pompilius* | 25 | Haven (1977) | 23.1–29 | Willey (1902) and Arnold *et al.* (2009) |
| **Spirulida** | | | | |
| *Spirula spirula* | 1.5–1.9 | Sweeney *et al.* (1992) and Warnke & Keupp (2005) | 1.8–2.0 | Sweeney *et al.* (1992) and Lukedener *et al.* (2008) – hatching occurs when shell contains 2–3 chambers; measured in Warnke & Boletzky (2009) |
| **Sepiida** | | | | |
| *Sepia apama* | 15 | Cronin (2000) | 12.4–13.9 | Cronin (2000) and Payne *et al.* (2013) |
| *S.elegans* | 3.7–4.2 | Mangold-Wirz (1963) | 3.9 | Sweeney *et al.* (1992) measured from picture |
| *S. esculenta* | 5–6 | Siqung *et al.* (2010) | 5.1–6.4 | Choe (1966) |
| *S. latimanus* | 11–15 | Okutani (1978) | 10–14 | Dan *et al.* (2012) |
| *Sepia lycidas* (=*S. subaculeata*) | 6.0–7.0 | Luo *et al.* (2014) | <7 | Choe (1966) |
| *S. officinalis* | 6.0–9.0 | Boletzky (1983a) | 6.0–8.0 | Vidal *et al.* (2014) |
| *S. orbygniana* | 7.0–9.0 | Naef (1923) | 6 | Bandel & Boletzky (1979) |
| *S. pharaonis* | 8–15 | Zuev (1971) and Gabr *et al.* (1998) | 7.7–8.0 | Nabhitabhata & Nilaphat (1999) and Nabhitabhata *et al.* (2005) |
| *Sepiella inermis* | 3.0–3.5 | Zuev (1971) | 4.3 | Nabhitabhata *et al.* (2005) |
| *Se. japonica* | 3.5 (measured on picture) | Gomi *et al.* (1986) | 4 | Zheng *et al.* (2010) |
| *Se. maindroni* | 4.0–4.4 | Luo *et al.* (2014) | 4.0–5.0 | Choe (1966) |
| **Sepiolida** | | | | |
| *Rossia macrosoma* | 5.6–9.2 | Laptikhovsky *et al.* (2008) | 5 | Boletzky & Boletzky (1973) |
| *R. pacifica* | 7.9–9.1 | Laptikhovsky *et al.* (2008) | 6.0 | Summers & Colvin (1989) |
| **Idiosepiida** | | | | |
| *Idiosepius* spp. | 0.9 | Boletzky (2003a) | *ca.* 0.7 | Nabhitabhata & Suwanamala (2008) |
| **Myopsida** | | | | |
| *Alloteuthis subulata* | 1.5–1.9 | Hastie *et al.* (2009) | 2.0–3.2 | Hastie *et al.* (2013) |
| *Doryteuthis gahi* | 1.9–3.2 | Guerra *et al.* (2001) and Laptikhovsky & Arkhipin (2001) | 2.6–3.4 | Arkhipkin, Laptikhovsky & Middleton (2000) and Guerra *et al.* (2001) |
| *D. cf. gahi* (Peru) | 1.7–2.1 | Cardozo, Baltazar & Bautista (2005) | 1.9–2.8 | Cardozo *et al.* (2005) |
| *D. opalescens* | 2.0–2.5 | Fields (1965) | 2.5–2.7 | McGowan (1954), Sweeney *et al.* (1992) and Vidal *et al.* (2002) |
| *D. pealei* | 1.6 | Hanlon *et al.* (2013) | 1.8 | Hanlon *et al.* (2013) |
| *D. sanpaulensis* | 1.2–1.3 | Vidal, Marian & Martins (2013) | 1.4–1.7 | Vidal *et al.* (2013) |
| *Heterololigo bleekeri* | 2.6–2.7 | Baeg, Sakurai & Shimazaki (1992) | 3.0–3.5 | Ikeda *et al.* (2005) and Sweeney *et al.* (1992) |
| *Loligo reynaudi* | 2 | Sauer *et al.* (2013) | 2.3–2.6 | Vidal, Roberts & Martins (2005) and Martins *et al.* (2010) |
| *L. vulgaris* | 1.8–2.7 | Moreno *et al.* (2013) and ICES (2015) | 2.2–3.3 | Sweeney *et al.* (1992), Sen (2004) and ICES (2015) |
| *L. forbesi* | 3.06 | Rocha & Guerra (1996) | 3.5–4.9 | Sweeney *et al.* (1992) and ICES (2015) |
| *Uroteuthis duvauceli* | 1.3–1.9 | Choi (2008) and Neethu, Anil & Rohini Krishna (2015) | 1.1–1.3 | Nabhitabhata *et al.* (2005) and Choi (2008) |
| *Lolliguncula brevis* | 1.8 | Hall (1970) | 1.7–2.0 | Perez & Zaleski (2013) |

Table 1. Continued

| Species | Egg size (mm) | Source | Max. shell size (mm) | Source |
|---|---|---|---|---|
| *Sepioteuthis australis* | 5–10 | Pecl (2001) | 4.3–7.3 | Steer, Pecl & Moltschaniwskyj (2003) |
| *S. lessoniana* | 3–6 | Zuev (1971), Mhitu, Mgaya & Ngoile (1999) and Deepak & Patterson (2002) | 3.5–7.0 | Choe (1966), Lee *et al.* (1994), Nabhitabhata *et al.* (2005) and Vidal *et al.* (2014) |
| *S. sepioidea* | 5–6 | Zuev (1971) | 5 | Sweeney *et al.* (1992) |
| **Oegopsida** | | | | |
| *Dosidicus gigas* | 1.1 | Rosa *et al.* (2013) | 0.9–1.3 | Rosa *et al.* (2013) |
| *Ommastrephes bartrami* | 1.1 | Sakurai *et al.* (1995) | 1.0–1.5 | Sakurai *et al.* (1995) (measured from picture) and Yatsu & Mori (2000) |
| *Sthenoteuthis oualaniensis* | 0.84 | Sakurai *et al.* (1995) | 1.4 | Sakurai *et al.* (1995) (measured from picture) |
| *Illex argentinus* | 1 | Rodhouse *et al.* (2013) | 1.6 | Rodhouse *et al.* (2013) |
| *I. coindeti* | 0.8–1.3 | Gonzalez & Guerra (2013) | 1.4 | Gonzalez & Guerra (2013) |
| *I. illecebrosus* | 0.9–1.1 | O'Dor & Dawe (2013) | 1.1–1.25 | O'Dor & Dawe (2013) |
| *Todarodes pacificus* | 0.8 | Watanabe *et al.* (1996) | 0.95–1.1 | Bower & Sakurai (1996), Watanabe *et al.* (1996) and Sakurai *et al.* (2013) |
| *Abralia trygonura* | 0.9 | Young & Mangold (1994) | 1.2 | Bigelow (1992) |
| *Thysanoteuthis rhombus* | 1.0–1.2 | Sabirov *et al.* (1987) | 0.9–1.3 | Sabirov *et al.* (1987) |
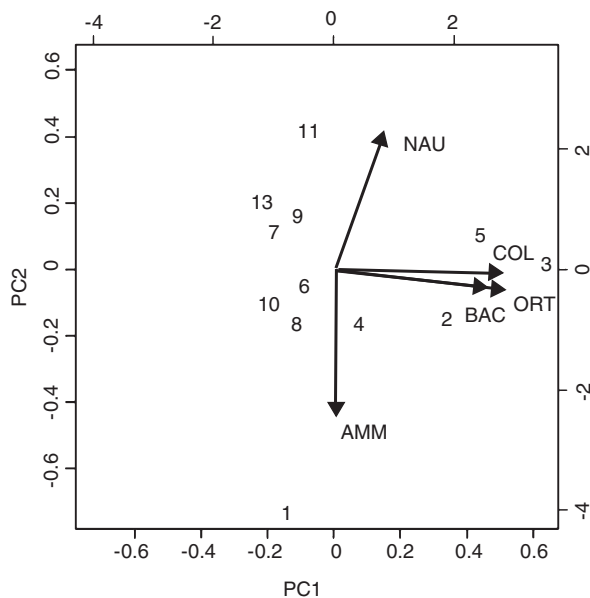


**Fig. 4.** Principal component analysis of the ratio between embryonic shell size and initial chamber size (ES/IC). Numbers define observed ES/IC ratio calculated to the nearest number below (e.g. 1 corresponds to the range from 1.0 to 1.9999). AMM, Ammonoidea; BAC, Bactritida; COL, Coleoidea; ORT, Orthocerida; NAU, Nautiloidea.

during embryogenesis that are shared by all cephalopods. One possible explanation is the expression of the *engrailed* gene universal in all molluscs for delimiting the boundaries of shell-forming fields during embryogenesis, although in cephalopods also involved in the production of evolutionary novelties such as the tentacles, eyes and funnel (Baratte, Andouche & Bonnaud, 2007). The presence of a shell possibly affected the ratio between egg size and hatchling size, which is higher in shelled species as detailed above.

A strong correlation between ES (= hatchling) size and egg length in cephalopods (Fig. 2) is consistent with observations from gastropods that lack adelphophagy (intra-capsular cannibalism), in which the shell length of hatchlings is correlated with egg length (Ito, 1997; Collin, 2003). This might be caused by scaling of the ectoderm invagination in proportion to yolk volume at shell formation. Unfortunately, there is no information available to support this suggestion. Despite the conservation of the early shell-forming developmental program across molluscan classes, little is known about the underlying fine-scale cellular or molecular processes (Hohagen & Jackson, 2013). The initial contact between endoderm and dorsal ectoderm that precedes shell gland invagination has been observed in representatives of Gastropoda, Bivalvia, Scaphopoda and Cephalopoda. In species with a rudimentary shell, shell gland development ceases during dorsal ectoderm invagination, and the shell field never forms. In cephalopods with an internal shell, the shell gland is also internalised forming a 'shell sac', whereas *Nautilus* retains an external shell throughout embryogenesis (Kniprath, 1981; Tanabe & Uchiyama, 1997; Hohagen & Jackson, 2013). However, cephalopod eggs differ from those of other molluscs in the presence of large yolk stocks, strongly impacting embryonic development, therefore there might be underlying cephalopod-specific developmental patterns.

Hatchlings of the deep-sea Southwest Atlantic *Benthoctopus eureka* have very small ML of 3 mm but hatch from eggs of a final size of 23–25 mm (Laptikhovsky, 2001). Initial

Table 2. Relation between egg size and hatchling size (mantle length, ML) in cephalopods with a rudimentary cartilaginous shell

| Species | Egg size (mm) | Source | Hatchling ML (mm) | Source |
|---------|---------------|--------|-------------------|--------|
| **Octopoda** | | | | |
| *Argonauta argo* | 0.6−0.8 | Sweeney *et al.* (1992) | 0.75−0.9 | Sweeney *et al.* (1992) |
| *A. hians* (= *A. boettgeri*) | 0.7−1.1 | Sweeney *et al.* (1992) | <1−1.25 | Sweeney *et al.* (1992) |
| *Amphioctopus aeguina* | 3.0−3.3 | Ignatius & Srinivasan (2006) | 3.1 | Ignatius & Srinivasan (2006) |
| *A. burryi* | 2.2−2.5 | Sweeney *et al.* (1992) | 1.5 | Sweeney *et al.* (1992) |
| *Bathypolipus bairdii* | 11 | Wood, Kenchington & O'Dor (1998) | 7.7 | Wood *et al.* (1998) |
| *Benthoctopus eureka* | 20−30 | Laptikhovsky (2001) | 3 | Laptikhovsky (2001) |
| *Bolitaena pygmaea* | 2 | Young (1972) | 2 | Young (1972) |
| *Callistoctopus macropus* | 2.5 | Voight (1998) | 4 | Villanueva & Norman (2008) |
| *Eledone cirrhosa* | 6.0−9.0 | Sweeney *et al.* (1992) | 3.7−4.5 | Mangold, Boletzky & Frösch (1971) and Sweeney *et al.* (1992) |
| *Enteroctopus dofleini* | 6.0−8.0 | Sweeney *et al.* (1992) | 3.0−5.5 | Villanueva & Norman (2008) |
| *E. megalocyathus* | 8.35 | Uriarte *et al.* (2014) | 8.38 | Ortiz, Ré & Màrquez (2006) |
| *Graneledone boreopacifica* | 15−32 | Robison, Seibel & Drazen (2014) and Voight & Drazen (2004) | 23−30 | Voight & Drazen (2004) |
| *Hapalochlaena lunulata* | 2.5−3.5 | Sweeney *et al.* (1992) | 2.3 | Sweeney *et al.* (1992) |
| *Macroctopus maorum* | 5.0−8.0 | Sweeney *et al.* (1992) | 6.7−7.6 | Villanueva & Norman (2008) |
| *Macrotritopus defilippi* | 1.5−2.1 | Sweeney *et al.* (1992) | 1.3−1.5 | Sweeney *et al.* (1992) |
| *Octopus bimaculatus* | 2.5−4.0 | Sweeney *et al.* (1992) | 2.6 | Sweeney *et al.* (1992) |
| *O. briareus* | 10.0−14.0 | Jereb *et al.* (2014) | 5.5−7.5 | Mangold *et al.* (1971) and Jereb *et al.* (2014) |
| *O. chierchiae* | 3.8 | Rodaniche (1984) | 3.5 | Rodaniche (1984) |
| *O. cyanea* | 2.0−3.0 | Sweeney *et al.* (1992) | 1.2−2.0 | Sweeney *et al.* (1992) |
| *O. fitchi* | 4.0−6.0 | Sweeney *et al.* (1992) | 2 | Sweeney *et al.* (1992) |
| *O. hubbsorum* | 1.66 | Alejo-Plata & Alejo (2014) | 1.22 | Alejo-Plata & Alejo (2014) |
| *O. insularis* | 2.13 | Lenz *et al.* (2015) | 1.68 | Lenz *et al.* (2015) |
| *O. jubini* | 6 | Mangold *et al.* (1971) | 4.5 | Mangold *et al.* (1971) |
| *O. laqueus* | 2.6 | Kaneko, Oshima & Ikeda (2006) | 1.7 | Kaneko *et al.* (2006) |
| *O. ornatus* | 2.0−3.0 | Sweeney *et al.* (1992) | 2.3 | Sweeney *et al.* (1992) |
| *O. rubescens* | 3.0−4.0 | Sweeney *et al.* (1992) | 1.7−2.0 | Sweeney *et al.* (1992) |
| *O. salutii* | 5.2−6.0 | Sweeney *et al.* (1992) | 3.5−4 | Villanueva & Norman (2008) |
| *O. tetricus* | 2.4 | Sweeney *et al.* (1992) | 1.3−1.6 | Sweeney *et al.* (1992) |
| *O. vulgaris* | 1.5−2.7 | Sweeney *et al.* (1992) | 1.5−2.0 | Sweeney *et al.* (1992) |
| *O. maya* | 6−17 | Van Heukelem (1976, 1983) | 7 | Van Heukelem (1983) and Sweeney *et al.* (1992) |
| *O. mimus* | 2.03 | Warnke (1999) | 2.0−2.4 | Warnke (1999) |
| *Paroctopus digueti* | 6.0−10.0 | Sweeney *et al.* (1992) | 4.5−6 | Jereb *et al.* (2014) |
| *Robsonella australis* | 2.0−2.8 | Sweeney *et al.* (1992) | 2.2−2.3 | Sweeney *et al.* (1992) |
| *R. fontaniana* | 3.1−3.8 | Uriarte *et al.* (2009) | 2.2 | Uriarte *et al.* (2010) (from graph) |
| *Scaeurhus patagiatus* | 2.0−2.5 | Sweeney *et al.* (1992) | 21.5 | Sweeney *et al.* (1992) |
| *Scaeurhus unicirrhus* | 2.0−2.5 | Sweeney *et al.* (1992) | 2 | Sweeney *et al.* (1992) |
| *Tremoctopus violaceus* | 1.5−2.0 | Laptikhovsky & Salman (2003) | 1.5 | Sweeney *et al.* (1992) |
| **Sepiolida** | | | | |
| *Sepiola atlantica* | 2.5−3.0 | Yau & Boyle (1996) and Jones & Richardson (2010) | 1.1−1.9 | Jones & Richardson (2010) and Rodrigues, Guerra & Troncoso (2011). |
| *Euprymna berryi* | >2 | Choe (1966) | 2.4−2.8 | Choe (1966) |
| *Euprymna scolopes* | 2 | Arnold, Singley & Williams-Arnold (1972) | 1.6−1.9 | Hanlon *et al.* (1997) |
| *Sepietta obscura* | 2.1−2.5 | Deickert (2009) | 2.0−3.0 | Deickert (2009) |
| *Sepietta neglecta* | 1.4−2.8 | Lefkaditou & Kaspiris (1998) | 2.0−2.7 | Boletzky *et al.* (1971, figure 1) |
| *Sepiola rondeletii* | 2.5−3 | Mangold-Wirz (1963) | 3.5−4.5 | Boletzky *et al.* (1971, figure 1) |
| *Sepiola ligulata* | 2.6 | Naef (1928) | 1.9−2.7 | Boletzky *et al.* (1971, figure 1) |
| *Sepiola robusta* | 2.2−2.4 | Boletzky (1983*b*) | 2.0−2.6 | Boletzky *et al.* (1971, figure 1) |

egg size in this species is 17–19 mm (Gleadall *et al.*, 2010). This species has unusually long arms of about 2.5 times the mantle length; in other octopods arm length is about the same as mantle length or less, with marked similarity in body proportions between hatchlings of pelagic and merobenthic octopods (Boletzky, 1997). The very small mantle length relative to body size in *B. eureka* might be a heterochrony that resulted in accelerated phenotypic expression of adult features (see Boletzky, 1997). Appearance of this heterochrony could result from inactivity of *engrailed* with respect to the determination of ML from shell size, as the shell is reduced in octopods. It is difficult to judge whether such heterochronies might be possible in other cephalopods. There are examples of the opposite process: partial reduction of the shell not affecting the final hatchling size, with the mantle extending well beyond the skeletal elements (in *Metasepia*, *Idiosepius*, *Rossia*, *Semirossia*). This evolutionary direction could presumably lead to the eventual disappearance of the internal shell. In such 'half-shelled' cephalopods the soft-body size, rather than shell size, might be predicted more accurately from the egg size, with the use of ES measurements to predict egg size leading to slight underestimates.

The size of the IC cannot be used to predict ES size (Fig. 3), although significant correlations were observed within some orders and subclasses, as well as in some gastropods (in which the ES is termed the protoconch II) (Nützel *et al.*, 2007). The relationship between IC size and ES size (and hence egg size) differed among different cephalopod taxa (see above). Further measurements of these variables in a wider range of species will hopefully allow the establishment of a statistical correlation between IC and ES with appropriate uncertainty estimates (confidence intervals or credible intervals) to allow the estimation of egg size in extinct cephalopod taxa.

## IV. EVOLUTIONARY HISTORY OF CEPHALOPOD REPRODUCTIVE STRATEGIES DERIVED FROM EMBRYONIC SHELL SIZE

The evolutionary history of Palaeozoic and Mezozoic cephalopod life forms and lifestyles has been reviewed in detail elsewhere (e.g. Barskov *et al.*, 2008; Kröger *et al.*, 2009; Wani, 2011; Ritterbush *et al.*, 2014; Servais *et al.*, 2016). However, these reviews considered only the evolution of adult life forms. The life forms of cephalopod hatchlings and early juveniles can be very different from those of adults (Nesis & Nigmatullin, 2003) and their evolution could involve entirely different processes. For example, octopods of the family Octopodidae, with nearly identical adult lifestyles, can produce either small eggs with paralarval hatchlings that spend up to four months in the pelagic layers (e.g. *Enteroctopus dofleini*), or large eggs with 'crawl-away' demersal young (Sweeney *et al.*, 1992; Villanueva & Norman, 2008).

Egg size reflects numerous adaptations. It is usually inversely related to fecundity (see Vance, 1973*a*,*b*) as well as to offspring survival and hence population

dynamics. Cephalopods with smaller hatchlings (and thus smaller eggs) have broader latitudinal distribution ranges (Villanueva *et al.*, 2016). The reproductive strategies of most marine invertebrate taxa cover an adaptive range from relatively highly fecund species with small eggs to relatively low-fecundity species with large eggs. Within this range, two more or less separate categories of small- and large-egged species exist. The mathematical model of Vance (1973*a*,*b*) predicted only the extremes of the range of egg size and method of nutrition (i.e. planktotrophy, lecithotrophy) to be evolutionarily stable. This model was developed further (Christiansen & Fenchel, 1979; Roughgarden, 1989), confirming that intermediate egg sizes are at a disadvantage.

A recent review by Villanueva *et al.* (2016) found the mean ± S.D. ML of planktonic hatchlings to be 2.5 ± 1.5 mm (range 0.6–8.4 mm), and that of benthic hatchlings to be 6.5 ± 4.6 mm (range 1.5–28 mm). Eggs of intermediate size are relatively rare among cephalopods and generally are produced by either small-sized species with large eggs (e.g. *Octopus micropyrsus*) or large species with relatively small eggs (e.g. *Enteroctopus magnificus*, *E. dofleini*) (Sweeney *et al.*, 1992; Boletzky, 2003*a*). Given that hatchling size is roughly equivalent to egg size, to a first approximation we can assume that taxa with eggs of <4–5 mm are characterised by planktonic early stages, whereas cephalopods with larger eggs produce benthic offspring.

Analysis of egg sizes across a wide range of cephalopod taxa potentially allows exploration of the evolution of reproductive strategies of this class in relation to biotic and abiotic events such as glaciations, global warming events, continental sea expansions and retreats, and appearances and extinctions of competitors and predators. Because of uncertainties in measurement of ES size in Cambrian cephalopods we begin from Ordovician cephalopods following the taxonomy of Sepkoski (2002) as given in the online genus database (http://strata.geology.wisc.edu/jack/).

During the Ordovician planktonic revolution when the proportion of planktonic organisms increased, particularly in the Early to Middle Ordovician (Servais *et al.*, 2016), the adult stages of many cephalopods evolved to live in the pelagic layers (Kröger *et al.*, 2009). The entire life cycles of many such cephalopods became pelagic. Orthocerida were the first to evolve a small spherical chamber (the IC), which might represent a crucial element of assuming a pelagic lifestyle in hatchlings. The IC allowed them to develop a functional hydrostatic apparatus before reaching the phragmocone stage, and thus to inhabit open waters earlier (Barskov *et al.*, 2008), presumably immediately after hatching. This reproductive pathway was followed later by Ammonoidea, Bactritida, Belemnoidea and some other groups.

Early Ordovician cephalopods were represented mostly by large-egged species (*K* strategists): Ellesmerocerida, Endocerida, and Actinocerida, likely with demersal hatchlings as large pelagic eggs would be easily predated. Small-egged *r*-strategist Orthocerida and Pseudorthocerida represented 5–15% of genus diversity in the early Ordovician, increasing to 30–40% in the second half of the period (Fig. 5).
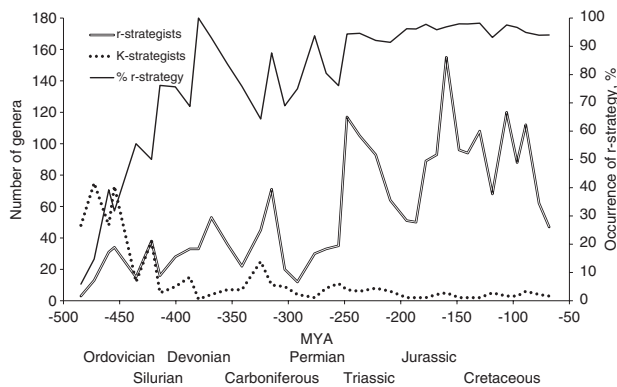
**Fig. 5.** The occurrence of reproductive strategies in cephalopods over geological time expressed as number of genera with either small (*r*-strategists) or large (*K*-strategists) eggs.



**Fig. 6.** Trends in embryonic shell (ES) size in Orthocerida. The fitted trend line is a quintic polynomial.

The occurrence of large eggs both in number of genera and in percentage occurrence of *K* strategists decreased steadily from the early Ordovician through the Silurian and Devonian, mostly due to the demise of archaic large-egged taxa such as Actinocerida and Oncocerida and the simultaneous emergence of pelagic hatchlings. The *r* strategy of pelagic spawning of small eggs peaked in terms of percentage occurrence in the late Devonian with the first appearance of Ammonoidea, and large-egged taxa reduced to just four genera. During the Devonian, evolutionary trends toward tighter coiling and some reduction of ES size occurred in several lineages of ammonoids (Bogoslovsky, 1969; De Baets *et al.*, 2012; see also fig. 1 in Laptikhovsky *et al.*, 2013).

A gradual decline in prevalence of the small-egged *r* strategy during the early Palaeozoic was coincident with the evolution of armoured predators: the Placodermi, joined in the Devonian by cartilaginous and bony fishes (Friedman & Sallan, 2012). Agile sharks and bony fishes could forage in both pelagic and benthic environments, whereas heavy and slow-moving armoured fishes were restricted to a benthic lifestyle. Therefore, immobile food sources like carrion and benthos (including benthic eggs) would represent important food sources. Placodermi were declining in the Late Devonian, and eventually became extinct at the onset of the Carboniferous (Friedman & Sallan, 2012).

In the late Palaeozoic (Carboniferous – Permian) large-egged cephalopods became increasingly common due to the evolution of the new large-egged taxon Nautilida, as well as an increase in egg size in Orthocerida, some of which shifted from a small-egged *r* to a large-egged *K* strategy (Fig. 6). We know nothing about egg envelopes in early Palaeozoic cephalopods, but recent *Nautilus* spp. might provide insights into these features. Their hard egg capsule has a ridged surface, and retains its shape even when dry (Willey, 1896). To the best of our knowledge, the only predator of nautilus eggs is *Nautilus* itself, although this was observed only in captivity (Arnold, Awai & Carlson, 1993), possibly arising as an artefact of stress. Large-egged species of fish became abundant and diverse (e.g. up to 25 genera
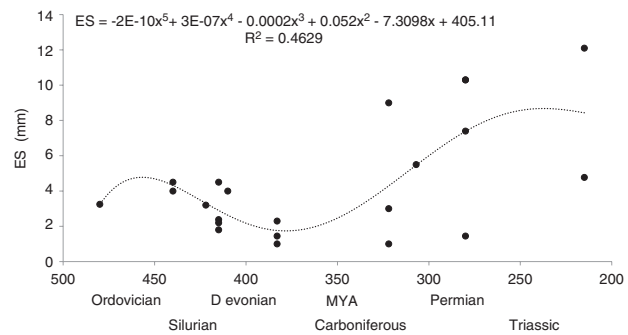
of elasmobranchs), particularly in the mid to late Carboniferous and late Permian (the age of sharks). The biodiversity of fishes *sensu lato* (Agnatha, Acanthodii, Chondrichthyes and Teleostei), the main competitors of cephalopods and occupying the same broad adaptive zone (Packard, 1972), declined during the Carboniferous to reach its lowest level in the Permian, possibly leading to an increase in *K* strategists investing more into each individual egg.

After the catastrophic end-Permian extinction, large-egged cephalopods never again reached their former levels of diversity, with the number of genera fluctuating between two and eight from the Mesozoic era onwards, and those present having a similar lifestyle to modern *Nautilus* spp. (Schlögl *et al.*, 2011). The number of small-egged genera varied between 90 and 120 from the Triassic to the Cretaceous, declining to 50–64 genera in the late Triassic – early Jurassic. This decline (mirrored in general cephalopod biodiversity) coincided with an explosion of diversification of teleost fish from the middle Triassic onwards (Romano *et al.*, 2016). Intensive competition with teleosts, particularly Holostei and 'Subholostei' that became predominant in marine habitats from the mid-Triassic (Romano *et al.*, 2016) might underlie this decline.

Both fishes *sensu lato* and cephalopods diversified from the late Cambrian onwards, their ecology and biodiversity reacting to similar environmental and biotic factors. A general trend in both taxa is a gradual shift from the production of large eggs to the production of smaller eggs. Small-egged species predominated among cephalopods from the Devonian, and by the Triassic, the number of large-egged species represented only 3–9% of genus richness (Fig. 5). By contrast, early fishes such as Agnatha, Placodermi, Chondrichtyes and archaic Osteichthyes that produced huge eggs (Smith, 1986; Johanson & Trinajstic, 2014), predominated until the end of Permian. The Acanthodii (about which we have no information on reproduction) were not sufficiently diverse to impact this pattern. A small-egged *r* strategy became increasingly important from the mid-Triassic, but until the end-Cretaceous extinction, teleost and elasmobranch fishes had similar genus richness (Friedman & Sallan, 2012). However, a large-egged *K* strategy may have shown greater resilience to catastrophic environmental change within cephalopods (Laptikhovsky

*et al.*, 2013); while Nautilida and Sepiida survived into Cainozoic seas, only a few small-egged ammonite genera were still found in the Danian (Surlyk & Nielsen, 1999; Landman *et al.*, 2014) and rapidly became extinct thereafter.

It is difficult to reconstruct the evolution of cephalopod reproductive strategies after the end-Cretaceous extinction as archaic coleoids with large adult shells like Belemnoidea became extinct, being succeeded in the Paleogene by Neocoleoidea that are poorly represented in the fossil record, due to shell morphology and rarity. This group includes Decabrachia (squid and cuttlefish) and Octobrachia (octopuses and vampyromorphs) as well as the enigmatic Ostenoteuthidae. Neocoleoidea existed from the Permian, but throughout the Mesozoic were represented by only ~40–45 genera (Doguzhaeva & Mapes, 2015; Tanabe, Misaki & Ubukata, 2015; Young, Vecchione & Fuchs, 2015), meaning that they were relatively uncommon compared to the 1,201 other cephalopod genera listed by Sepkoski (2002) for the Mesozoic era. Data on IC and ES sizes, where they are known (e.g. in the Mesozoic *Groenlandibelus*, *Ceratisepia*, and early Paleogene *Belemnosis* and *Mississaepia* IC = 0.6–1.5 mm; see Doguzhaeva *et al.*, 2014*a*,*b*), do not allow firm conclusions regarding reproductive strategy, and possibly this group may have exhibited both *r* and *K* reproductive strategies, as in extant species.

Recent coleoid cephalopods have exclusively small eggs in all myopsid squids (with the exception of *Sepioteuthis*) (~50 species) and oegopsid squids (~250 species), *Vampyroteuthis*, and some sepiolids (~50 species); large eggs are produced by cuttlefishes (~120 species), Rossiinae (Sepiolida) (~20 species) and cirrate octopods (~45 species). Species of incirrate octopods (at least 350 species) may lie at either end of the reproductive continuum, with small-egged species predominating (Laptikhovsky, 1998, 2006). A similar pattern occurs in Cainozoic fishes, with a predominance in terms of species numbers of small-egged Acanthopterygii and Petromyzontiformes (Agnatha) over large-egged Myxini (Agnatha), Coelacanthimorpha and Chondrichthyes (Friedman & Sallan, 2012).

## V. CONCLUSIONS

(1) We demonstrate that the maximum dimension of a cephalopod embryonic shell (ES) at hatching is approximately equal to egg size, regardless of shell morphology and taxon-specific patterns of embryogenesis. Therefore, the size of the ES can be used to reconstruct the egg size of extinct species.

(2) In modern cephalopods with a reduced shell, the mantle length (ML) of hatchlings is approximately equal to the initial egg size before embryogenesis-induced egg swelling.

(3) The size of the initial chamber (IC) in extant and extinct cephalopods is related to ES size by different ratios in different taxa. The IC size could still be used to predict whether extinct species exhibited small-egged or large-egged strategies.

(4) The evolution of reproductive strategies in both cephalopods and fishes can be shown to have similar general patterns, with a gradual increase in occurrence of small-egged *r* strategies in both taxa. Both small- and large-egged strategies are common among cephalopods with some predominance in diversity of taxa producing small eggs and offspring.

## VI. ACKNOWLEDGEMENTS

## VII. REFERENCES

Alejo-Plata, M. & Alejo, S. H. (2014). First description of eggs and paralarvae of green octopus *Octopus hubbsorum* (Cephalopoda: Octopodidae) under laboratory conditions. *American Malacological Bulletin* **32**, 132–139.

Allcock, L., Lindgren, A. & Strugnell, J. M. (2014). The contribution of molecular data to our understanding of cephalopod evolution and systematics: a review. *Journal of Natural History* **49**, 1373–1421.

Arkhipkin, A. I., Bizikov, V. A. & Fuchs, D. (2013). Vestigial phragmocone in the gladius points to a deepwater origin of squid (Mollusca: Cephalopoda). *Deep Sea Research Part I: Oceanographic Research Papers* **61**, 109–122.

Arkhipkin, A. I., Laptikhovsky, V. V. & Middleton, D. A. J. (2000). Adaption for cold water spawning in loliginid squid *Loligo gahi* in Falkland waters. *Journal of Molluscan Studies* **66**, 551–564.

Arnold, J. M., Awai, M. & Carlson, B. A. (1993). Speculation and comments on predation of *Nautilus* on egg capsules of other *Nautilus*. *Journal of Cephalopod Biology* **2**, 47–50.

Arnold, J. M., Landman, N. H. & Mutvei, H. (2009). Development of the embryonic shell of *Nautilus*. *Topics in Geobiology* **6**, 373–400.

Arnold, J. M., Singley, C. T. & Williams-Arnold, L. D. (1972). Embryonic development and post-hatching survival of the sepiolid squid *Euprymna scolopes* under laboratory conditions. *The Veliger* **14**, 361–365.

Baeg, G.-H., Sakurai, Y. & Shimazaki, K. (1992). Embryonic stages of *Loligo bleekeri* Keferstein (Mollusca: Cephalopoda). *The Veliger* **35**, 234–241.

Bandel, K. & Boletzky, S. V. (1979). A comparative study of the structure, development and morphological relationships of chambered cephalopod shells. *The Veliger* **21**, 313–353.

Bandel, K., Reitner, J. & Stürmer, W. (1983). Coleoids from the Lower Devonian Black Slate ("Hunsrück-Schiefer") of the Hunsrück (West Germany). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **165**, 397–417.

Baratte, S., Andouche, A. & Bonnaud, L. (2007). Engrailed in cephalopods: a key gene related to the emergence of morphological novelties. *Development Genes and Evolution* **217**, 353–362.

Barskov, I. S., Boiko, M. S., Konovalova, V. A., Leonova, T. B. & Nikolaeva, S. V. (2008). Cephalopods in the marine ecosystems of the Paleozoic. *Paleontological Journal* **42**, 1167–1284.

Bigelow, K. A. (1992). Age and growth in paralarvae of the mesopelagic squid *Abralia trigonura* based on daily growth increments in statoliths. *Marine Ecology Progress Series* **82**, 31–40.

Bizikov, V. A. (2008). *Evolution of the Shell in Cephalopoda*. VNIRO Publishing, Moscow.

Bogoslovsky, B. I. (1969). Devonskie ammonoidei I. Agoniatitidy. *Trudy Paleontologicheskogo Instituta* **124**, 1–328 (in Russian).

Boletzky, S. v. (1983a). *Sepia officinalis*. In *Cephalopod Life Cycles, Vol. I – Species Accounts* (ed. P. R. Boyle), pp. 31–52. Academic Press, London.

Boletzky, S. v. (1983b). *Sepiola robusta*. In *Cephalopod Life Cycles, Vol. I – Species Accounts* (ed. P. R. Boyle), pp. 53–67. Academic Press, London.

Boletzky, S. v. (1986). Encapsulation of cephalopod embryos: a search for functional correlations. *American Malacological Bulletin* **4**, 217–227.

Boletzky, S. v. (1997). Developmental constraints and heterochrony: a new look at offspring size in cephalopod molluscs. *GEOBIOS* **21**, 267–275.

Boletzky, S. v. (2003a). A lower limit to adult size in coleoid cephalopods: elements of a discussion. *Berliner Paläobiologische Abhandlungen* **3**, 19–28.

Boletzky, S.v. (2003b). Biology of early life stages in Cephalopod molluscs. *Advances in Marine Biology* **44**, 143–203.

Boletzky, S.v. & Boletzky, M.v. (1973). Observations on the embryonic and early post-embryonic development of *Rossia macrosoma* (Mollusca, Cephalopoda). *Helgoländer Wissenschaftliche Meeresuntersuchungen* **25**, 135–161.

Boletzky, S. v., Boletzky, M. v., Frösch, D. & Gätzi, V. (1971). Laboratory rearing of Sepiolinae (Mollusca: Cephalopoda). *Marine Biology* **8**, 82–87.

Bower, J. R. & Sakurai, Y. (1996). Laboratory observations on *Todarodes pacificus* (Cephalopoda: Ommastrephidae) egg masses. *American Malacological Bulletin* **13**, 65–71.

Cardozo, F., Baltazar, P. & Bautista, J. (2005). The early development of the Patagonian squid *Loligo gahi* d'Orbigny, 1835 in Peruvian Waters (Cephalopoda: Loliginidae). *Revista Peruana de Biología* **12**, 369–376.

Carlson, B. A., Awai, M. L. & Arnold, J. M. (1992). Hatching and early growth of *Nautilus belauensis* and implications on the distribution of the genus *Nautilus*. *Proceedings of the Seventh International Coral Reef Symposium*, Vol. 1, pp. 587–592. Guam.

Choe, S. (1966). On the eggs, rearing, habits of the fry, and growth of some Cephalopoda. *Bulletin of Marine Science* **16**, 330–348.

Choi, K. S. (2008). *Reproductive biology and ecology of the loliginid squid*, Uroteuthis (*Photololigo*) duvauceli (*Orbigny, 1835*), *in Hong Kong waters*. MPhil thesis, University of Hong Kong.

Collin, R. (2003). Worldwide patterns in mode of development in calyptraeid gastropods. *Marine Ecology Progress Series* **247**, 103–122.

Christiansen, F. B. & Fenchel, T. M. (1979). Evolution of marine invertebrate reproductive patterns. *Theoretical Population Biology* **16**, 267–282.

Crawley, M. J. (2007). *The R Book*. John Wiley & Sons Ltd, Chichester.

Cronin, E. R. (2000). *Morphology, respiration and energetics of the eggs of the giant cuttlefish*, Sepia apama. Doctoral dissertation: Department of Environmental Biology, University of Adelaide.

Crowson, R. A. (1981). *The Biology of the Coleoptera*. Academic Press Inc, London.

Dan, S., Hamasaki, K., Yamashita, T., Oka, M. & Kitada, S. (2012). Age-based life cycle traits of the broadclub cuttlefish *Sepia latimanus* confirmed through release–recapture experiments. *Aquatic Biology* **17**, 181–195.

De Baets, K., Klug, C., Korn, D. & Landman, N. H. (2012). Early evolutionary trends in ammonoid embryonic development. *Evolution* **66**, 1788–1806.

Deepak, V. S. & Patterson, J. (2002). Intercapsular embryonic development of the big fin squid *Sepioteuthis lessoniana* (Loliginidae). *Indian Journal of Marine Sciences* **31**, 150–152.

Deickert, A. (2009). Reproductive mode in the genus *Sepietta* (Cephalopoda: Sepiolidae). *Bolletino Malacologico* **45**, 87–94.

Doguzhaeva, L. A. & Mapes, R. H. (2015). Arm hooks and structural features in the Early Permian Glochinomorpha Gordon 1971, indicative of its coleoid affiliation. *Lethaia* **48**, 100–114.

Doguzhaeva, L. A., Weaver, P. G. & Ciampaglio, C. N. (2014a). A unique late Eocene coleoid cephalopod *Mississaepia* from Mississippi, USA: new data on cuttlebone structure, and their phylogenetic implications. *Acta Palaeontologica Polonica* **59**, 147–162.

Doguzhaeva, L. A., Weis, R., Delsate, D. & Marioti, N. (2014b). Embryonic shell structure of Early–Middle Jurassic belemnites, and its significance for belemnite expansion and diversification in the Jurassic. *Lethaia* **47**, 49–65.

Dzik, J. (1984). Phylogeny of the Nautiloidea. *Palaeontologia Polonica* **45**, 1–219.

Fields, W. G. (1965). The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. *Fishery Bulletin* **131**, 1–108.

Flower, R. H. (1964). The nautiloid order Ellesmeroceratida (Cephalopoda). *New Mexico Bureau of Mines and Mineral Resources Memoir* **12**, 1–233.

Friedman, M. & Sallan, L. C. (2012). Five hundred million years of extinction and recovery: a phanerozoic survey of large-scale diversity patterns in fishes. *Palaeontology* **55**, 707–742.

Fuchs, D. & Iba, I. (2015). The gladiuses in coleoid cephalopods: homology, parallelism, or convergence? *Swiss Journal of Palaeontology* **134**, 187–197.

Gabr, H. R., Hanlon, R. T., Hanafy, M. H. & El-Etreby, S. (1998). Maturation, fecundity and seasonality of reproduction of two commercially valuable cuttlefish, *Sepia pharaonis* and *S. dollfusi*, in the Suez Canal. *Fisheries Research* **36**, 99–115.

Gleadall, I. G., Guerrero-Kommritz, J., Hochberg, F. G. & Laptikhovsky, V. V. (2010). The inkless octopuses (Cephalopoda: Octopodidae) of the Southwest Atlantic. *Zoological Science* **27**, 528–553.

Gomi, F., Masamichi, Y. & Tohru, N. (1986). Swelling of egg during development of the cuttlefish, *Sepiella japonica*. *Zoological Science* **3**, 641–645.

Gonzalez, A. & Guerra, A. (2013). *Illex coindeti*, broadtail shortfin squid. In *Advances in Squid Biology and Fisheries (Part II. Oegopsid Squids)* (eds R. Rosa, R. O'Dor and G. Pierce), pp. 49–72. Nova Biomedical, New York.

Grasse, B. (2014). The biological characteristics, life cycle, and system design for the flamboyant and paintpot cuttlefish, *Metasepia* sp., cultured through multiple generations. *Drum and Croaker* **45**, 58–71.

Guerra, A., Rocha, F., Gonzalez, A. F. & Bückle, L. F. (2001). Embryonic stages of the Patagonian squid *Loligo gahi* (Mollusca: Cephalopoda). *The Veliger* **44**, 109–115.

Hall, J. R. (1970). Description of egg capsules and embryos of the squid, *Lolliguncula brevis*, from Tampa Bay, Florida. *Bulletin of Marine Science* **20**, 762–768.

Hanlon, R. T., Buresch, K., Moustahfidh, H. & Staudinger, M. (2013). *Doryteuthis pealei*, Longfin inshore squid. In *Advances in Squid Biology and Fisheries (Part I. Myopsid Squids)* (eds R. Rosa, R. O'Dor and G. Pierce), pp. 159–204. Nova Biomedical, New York.

Hanlon, R. T., Claes, M. F., Ashcraft, S. E. & Dunlap, P. V. (1997). Laboratory culture of the sepiolid squid *Euprymna scolopes*: a model system for bacteria-animal symbiosis. *Biological Bulletin* **192**, 364–374.

Hanlon, R. T. & Messenger, J. B. (1998). *Cephalopod Behaviour*. Cambridge University Press, Cambridge.

Hastie, L. C., Allcock, L. A., Jereb, P., Lefkaditou, E., Moreno, A., Oesterwind, D. & Pierce, G. J. (2013). *Alloteuthis subulata*, European common squid. In *Advances in Squid Biology and Fisheries (Part I. Myopsid Squids)* (eds R. Rosa, R. O'Dor and G. Pierce), pp. 109–122. Nova Biomedical, New York.

Hastie, L. C., Nyegaard, M., Collins, M. A., Moreno, A., Pereira, J. M. F., Piatkowski, U. & Pierce, G. J. (2009). Reproductive biology of the loliginid squid, *Alloteuthis subulata*, in the north-east Atlantic and adjacent waters. *Aquatic Living Resources* **22**, 35–44.

Haven, N. (1977). The reproductive biology of *Nautilus pompilius* in the Philippines. *Marine Biology* **42**, 177–184.

Hewitt, R. A. & Jagt, J. W. M. (1999). Maastrichtian *Ceratisepia* and Mesozoic cuttlebone homeomorphs. *Acta Palaeontologica Polonica* **44**, 305–326.

Hoffmann, R. (2015). The correct taxon name, authorship, and publication date of extant ten-armed coleoids. *Paleontological Contributions* **11**, 1–4.

Hohagen, J. & Jackson, D. J. (2013). An ancient process in a modern mollusc: early development of the shell in *Lymnaea stagnalis*. *BMC Developmental Biology* **13**, 1–13.

Hylleberg, J. & Nateewathana, A. (1991). Redescription of *Idiosepius pygmaeus* Steenstrup, 1881 (Cephalopoda: Idiosepiidae), with mention of additional morphological characters. *Phuket Marine Biological Center Research Bulletin* **55**, 33–42.

ICES (2015). *Cephalopod Biology and Fisheries in Europe: II. Species Accounts*, ICES Cooperative Research Report 325 (eds P. Jereb, A. L. Allcock, E. Lefkaditou, U. Piatkowski, L. C. Hastie and G. J. Pierce), pp. 1–375. ICES, Copenhagen.

Ignatius, B. & Srinivasan, M. (2006). Embryonic development in *Octopus aegina* Gray, 1849. *Current Science* **91**, 1089–1092.

Ikeda, Y., Sakurazawa, I., Ito, K., Sakurai, Y. & Matsumoto, G. (2005). Rearing of squid hatchlings, *Heterololigo bleekeri* (Keferstein 1866) up to 2 months in a closed seawater system. *Aquaculture Research* **36**, 409–412.

Ito, K. (1997). Egg-size and -number variations related to maternal size and age, and the relationship between egg size and larval characteristics in an annual marine gastropod, *Haloa japonica* (Opisthobranchia; Cephalaspidea). *Marine Ecology Progress Series* **152**, 187–195.

Jereb, P., Roper, C. F. E., Norman, M. D. & Finn, J. K. (eds) (2014). *Cephalopods of the World. An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date. 3. Octopods and Vampire Squids*. FAO Species Catalogue for Fishery Purposes 4, FAO, Rome.

Johanson, Z. & Trinajstic, K. (2014). Fossilised ontogenies: the contribution of placoderm ontogeny to our understanding of the evolution of early gnathostomes. *Palaeontology* **57**, 505–516.

Jones, N. J. E. & Richardson, C. A. (2010). Laboratory culture, growth, and the life cycle of the little cuttlefish *Sepiola atlantica* (Cephalopoda: Sepiolidae). *Journal of Shellfish Research* **29**, 241–246.

Kaneko, N., Oshima, Y. & Ikeda, Y. (2006). Egg brooding behavior and embryonic development of *Octopus laqueus* (Cephalopoda: Octopodidae). *Molluscan Research* **26**, 113–117.

Kniprath, E. (1981). Ontogeny of the molluscan shell field: a review. *Zoologica Scripta* **10**, 61–79.

Kröger, B. (2006). Early growth-stages and classification of orthoceridan cephalopods of the Darriwillian (Middle Ordovician) of Baltoscandia. *Lethaia* **39**, 129–139.

Kröger, B. (2007). Concentrations of juvenile and small adult cephalopods in the Hirnantian cherts (Late Ordovician) of Porkuni, Estonia. *Acta Palaeontologica Polonica* **52**, 591–608.

Kröger, B. (2013). The cephalopods of the Boda Limestone, Late Ordovician, of Dalarna, Sweden. *European Journal of Taxonomy* **41**, 1–110.

Kröger, B. & Mapes, R. H. (2004). Lower Carboniferous (Chesterian) embryonic orthoceratid nautiloids. *Journal of Paleontology* **78**, 560–573.

Kröger, B., Servais, T. & Zhang, Y. (2009). The origin and initial rise of pelagic cephalopods in the Ordovician. *PLoS ONE* **4**(9), e7262.

LANDMAN, N. H. (1988). Early ontogeny of Mesozoic ammonites and nautilids. In *Cephalopods Present and Past* (eds J. WIEDMANN and J. KULLMANN), pp. 215–228. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

LANDMAN, N. H., GOOLAERTS, S., JAGT, J. M. W., JAGT-JAZYKOVA, E. A., MACHALSKI, M. & YAKOBUCCI, M. M. (2014). Ammonite extinction and nautilid survival at the end of the Cretaceous. *Geology* **42**, 707–710.

LANDMAN, N. H., TANABE, K. & SHIGETA, Y. (1996). Ammonoid embryonic development. In *Ammonoid Paleobiology* (eds N. H. LANDMAN, K. TANABE and A. DAVIS), pp. 343–405. Plenum Press, New York.

LAPTIKHOVSKY, V. V. (1998). Differentiation of reproductive strategies within a taxon, as exemplified by octopods. *Ruthenica* **8**, 77–80.

LAPTIKHOVSKY, V. V. (2001). Fecundity, egg masses and hatchlings of *Benthoctopus* spp (Octopodidae) in the Falkland waters. *Journal of Marine Biological Association of the U.K.* **81**, 267–270.

LAPTIKHOVSKY, V. V. (2006). Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. *Marine Ecology* **27**, 7–14.

LAPTIKHOVSKY, V. V. & ARKHIPKIN, A. I. (2001). Oogenesis and gonad development in the cold water loliginid squid *Loligo gahi* (Cephalopoda: Myopsida) on the Falkland shelf. *Journal of Molluscan Studies* **67**, 475–482.

LAPTIKHOVSKY, V. V., ARKHIPKIN, A. I. & GOLUB, A. A. (1993). Larval age, growth and mortality in the oceanic squid *Sthenoteuthis pteropus* (Cephalopoda, Ommastrephidae) from the eastern tropical Atlantic. *Journal of Plankton Research* **15**, 375–384.

LAPTIKHOVSKY, V. V., NIGMATULLIN, C. M., HOVING, H. J. T., ONSOY, B., SALMAN, A., ZUMHOLZ, K. & SHEVTSOV, G. A. (2008). Reproductive strategies in female polar and deep-sea bobtail squid genera *Rossia* and *Neorossia* (Cephalopoda: Sepiolidae). *Polar Biology* **31**, 1499–1507.

LAPTIKHOVSKY, V. L., ROGOV, M. A., NIKOLAEVA, S. V. & ARKHIPKIN, A. A. (2013). Environmental impact on ectocochleate cephalopod reproductive strategies and the evolutionary significance of cephalopod egg size. *Bulletin of Geosciences* **88**, 83–93.

LAPTIKHOVSKY, V. & SALMAN, A. (2003). On the reproductive strategies of the epipelagic octopods of the superfamily Argonautoidea (Cephalopoda: Octopoda). *Marine Biology* **142**, 321–326.

LEE, P. G., TURK, P. E., YANG, W. T. & HANLON, R. T. (1994). Biological characteristics and biomedical applications of the squid *Sepioteuthis lessoniana* cultured through multiple generations. *Biological Bulletin* **186**, 328–341.

LEFKADITOU, E. G. & KASPIRIS, P. (1998). Distribution and reproductive biology of *Sepietta neglecta* (Naef, 1916) (Cephalopoda: Sepioidea) in the North Aegean Sea (Eastern Mediterranean). *The Veliger* **41**, 239–242.

LENZ, T. M., ELIAS, N. H., LEITE, T. S. & VIDAL, E. A. G. (2015). First description of the eggs and paralarvae of the tropical octopus, *Octopus insularis*, under culture conditions. *American Malacological Bulletin* **33**, 101–109.

LUKEDENER, A., HARZHAUSER, M., MÜLLEGGER, S. & PILLER, W. E. (2008). Stable isotopes ($\delta^{18}$O and $\delta^{13}$C) in *Spirula spirula* shells from three major oceans indicate developmental changes paralleling depth distributions. *Marine Biology* **154**, 175–182.

LUO, J., JIANG, X.-M., LIU, M.-H., TANG, F. & PENG, R.-B. (2014). Oogenesis and ovarian development in *Sepia lycidas*. *Acta Hydrobiologica Sinica* **38**, 1107–1116 (in Chinese).

MANDA, Š. (2008). Palaeoecology and palaeogeographic relations of the Silurian phragmoceratids (Nautiloidea, Cephalopoda) of the Prague Basin (Bohemia). *Bulletin of Geosciences* **83**, 39–62.

MANDA, Š. & FRÝDA, J. (2010). Silurian–Devonian boundary events and their influence on cephalopod evolution: evolutionary significance of cephalopod egg size during mass extinctions. *Bulletin of Geosciences* **85**, 513–540.

MANDA, Š. & TUREK, V. (2009). A Silurian oncocerid with preserved colour pattern and muscle scars (Nautiloidea). *Bulletin of Geosciences* **84**, 755–766.

MANGOLD, K., BOLETZKY, S.v. & FRÖSCH, D. (1971). Reproductive biology and embryonic development of *Eledone cirrosa* (Cephalopoda: Octopoda). *Marine Biology* **8**, 109–117.

MANGOLD-WIRZ, K. (1963). Biologie des cephalopodes bentiques et nectoniques de la Mer Catalane. *Vie et Milieu, Supplement* **13**, 1–285.

MAPES, R. H. (1979). Carboniferous and Permian Bactritoidea (Cephalopoda) in North America. *University of Kansas Paleontological Contributions* **64**, 1–75.

MARTINS, R. S., ROBERTS, M. J., VIDAL, E. A. G. & MOLOONEY, C. L. (2010). Effects of temperature on yolk utilization by chokka squid (*Loligo reynaudii* d'Orbigny, 1839) paralarvae. *Journal of Experimental Marine Biology and Ecology* **386**, 19–26.

MCGOWAN, J. A. (1954). Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at La Jolla, California. *California Fish and Game* **40**, 47–54.

MHITU, H. A., MGAYA, Y. D. & NGOILE, M. A. K. (1999). Growth and reproduction of the big fin squid, *Sepioteuthis lessoniana*, in the coastal waters of Zanzibar. In *Marine Science Development in Tanzania and Eastern Africa: Proceedings of the 20th Anniversary Conference on Advances in Marine Science in Tanzania, 28 June-1 July 1999, Zanzibar, Tanzania* (eds M. D. RICHMOND and J. FRANCIS), pp. 289–300. Dar es Salaam University, IMS/WIOMSA, Dar-Es-Salaam.

MORENO, A., BOAVIDA-PORTUGAL, J., PIMENTEL, M., PEREIRA, J. & ROSA, R. (2013). *Loligo vulgaris*, European squid. In *Advances in Squid Biology and Fisheries (Part I. Myopsid Squids)* (eds R. ROSA, R. O'DOR and G. PIERCE), pp. 3–32. Nova Biomedical, New York.

NABHITABHATA, J. & NILAPHAT, P. (1999). Life cycle of cultured pharaon cuttlefish, *Sepia pharaonis* Ehrenberg, 1831. *Phuket Marine Biological Center Special Publication* **19**, 25–40.

NABHITABHATA, J., NILAPHAT, P., PROMBOON, P., JAROONGPATTANANON, P., NILAPHAT, G. & TEUNRENG, A. (2005). Performance of simple cephalopod culture system in Thailand. *Phuket Marine Biological Center Research Bulletin* **66**, 337–350.

NABHITABHATA, J. & SUWANAMALA, J. (2008). Reproductive behaviour and cross-mating of two closely related pygmy squids *Idiosepius biserialis* and *Idiosepius thailandicus* (Cephalopoda: Idiosepiidae). *Journal of the Marine Biological Association of the United Kingdom* **88**, 987–993.

NAEF, A. (1923). Die Cephalopoden (Systematik). *Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Monographia* **35**, 1–863.

NAEF, A. (1928). Die Cephalopoden (Embryologie). *Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Monographia* **35**, 1–357.

NEETHU, R. P., ANIL, M. K. & ROHINI KRISHNA, M. V. (2015). Studies on egg morphology, availability and hatching of four species of cephalopods along Vizhinjam Coast, Kerala. *International Journal of Innovative Research and Development* **4**, 209–214.

NESIS, K. N. & NIGMATULLIN, C. M. (2003). Life form and the possibilities of using this notion to analyze life cycles and evolutionary strategies. *Zhurnal Obschej Biologii* **64**, 227–237 (in Russian).

NÜTZEL, A., LEHNERT, O. & FRÝDA, I. (2007). Origin of planktotrophy: evidence from early molluscs: a response to Freeman and Lundelius. *Evolution & Development* **9**, 313–318.

O'DOR, R. K. & DAWE, E. G. (2013). *Illex illecebrosus*, Northern short-finned squid. In *Advances in Squid Biology and Fisheries (Part II. Oegopsid Squids)* (eds R. ROSA, R. O'DOR and G. PIERCE), pp. 73–108. Nova Biomedical, New York.

OKUTANI, T. (1978). Studies on early life history of decapodan Mollusca-VII. Eggs and newly hatched larvae of *Sepia latimanus* Quoi & Gaimard. *Venus* **37**, 245–248.

ORTIZ, N., RÉ, M. & MÀRQUEZ, F. (2006). First description of eggs, hatchlings and hatchling behaviour of *Enteroctopus megalocyathus* (Cephalopoda: Octopodidae). *Journal of Plankton Research* **28**, 881–890.

PACKARD, A. (1972). Cephalopods and fish: the limits of convergence. *Biological Reviews* **47**, 241–307.

PAYNE, N. L., SNELLING, E. P., SEMMENS, J. M. & GILLANDERS, B. M. (2013). Mechanisms of population structuring in Giant Australian Cuttlefish *Sepia apama*. *PLoS ONE* **8**, e58694.

PECL, G. (2001). Flexible reproductive strategies in tropical and temperate *Sepioteuthis* squids. *Marine Biology* **138**, 93–101.

PEREZ, J. A. A. & ZALESKI, T. (2013). *Lolliguncula brevis*, Western Atlantic brief squid. In *Advances in Squid biology and Fisheries (Part I. Myopsid Squids)* (eds R. ROSA, R. O'DOR and G. PIERCE), pp. 301–321. Nova Biomedical, New York.

RITTERBUSH, K. A., HOFFMANN, R., LUKENEDER, A. & DE BAETS, K. (2014). Pelagic palaeoecology: the importance of recent constraints on ammonoid palaeobiology and life history. *Journal of Zoology* **292**, 229–241.

ROBISON, B., SEIBEL, B. & DRAZEN, J. (2014). Deep-sea octopus (*Graneledone boreopacifica*) conducts the longest-known egg-brooding period of any animal. *PLoS ONE* **9**, e103437.

ROCHA, F. & GUERRA, A. (1996). Signs of an extended and terminal spawning in the squids *Loligo vulgaris* Lamarck and *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae). *Journal of Experimental Marine Biology and Ecology* **207**, 177–189.

RODANICHE, A. F. (1984). Iteroparity in lesser Pacific striped octopus *Octopus chierchiae* (Jatta, 1889). *Bulletin of Marine Science* **35**, 99–104.

RODHOUSE, P. G. K., ARKHIPKIN, A. I., LAPTIKHOVSKY, V., NIGMATULLIN, C. & WALUDA, C. M. (2013). *Illex argentines*, Argentine shortfin squid. In *Advances in Squid Biology and Fisheries (Part II. Oegopsid Squids)* (eds R. ROSA, R. O'DOR and G. PIERCE), pp. 109–148. Nova Biomedical, New York.

RODRIGUES, M., GUERRA, A. & TRONCOSO, J. S. (2011). The embryonic phase and its implication in the hatchling size and condition of Atlantic bobtail squid *Sepiola atlantica*. *Helgoland Marine Research* **65**, 211–216.

ROMANO, C., KOOT, M. B., KOGAN, I., BRAYARD, A., MINIKH, A., BRINKMANN, W., BUCHER, H. & KRIWET, J. (2016). Permian–Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution. *Biological Reviews* **91**, 106–147.

ROSA, R., YAMASHIRO, C., MARKAIDA, U., RODHOUSE, P. G. K., WALUDA, C. M., SALINAS-ZAVALA, C. A., KEYL, F., O'DOR, R., STEWART, J. S. & GILLY, W. F. (2013). *Dosidicus gigas*, Humboldt squid. In *Advances in squid biology and fisheries (Part II. Oegopsid squids)* (eds R. ROSA, R. O'DOR and G. PIERCE), pp. 169–206. Nova Biomedical, New York.

ROUGHGARDEN, J. (1989). The evolution of marine life cycles. In *Mathematical Evolutionary Theory* (ed. M. W. FELDMANS), pp. 270–300. Princeton University Press, Princeton.

SABIROV, R. M., ARKHIPKIN, A. I., TSYGANKOV, V. Y. & SCHETINNIKOV, A. S. (1987). Egg laying and embryonal development of diamond-shaped squid, *Thysanoteuthis rhombus* (Oegopsida, Thysanoteuthidae). *Zoologicheskyi Zhurnal* **66**, 1155–1163.

SAKURAI, Y., KIDOKORO, H., YAMASHITA, N., YAMAMOTO, Y., UCHIKAWA, K. & TAKAHARA, H. (2013). *Todarodes pacificus*, Japanese common squid. In *Advances in Squid Biology and Fisheries (Part II. Oegopsid Squids)* (eds R. ROSA, R. O'DOR and G. PIERCE), pp. 249–272. Nova Biomedical, New York.

SAKURAI, Y., YOUNG, R. E., HIROTA, J., MANGOLD, K., VECCHOINE, M., CLARKE, M. R. & BOWER, J. (1995). Artificial fertilization and development through hatching in the oceanic squids *Ommastrephes bartramii* and *Sthenoteuthis ouananiensis* (Cephalopoda: Ommastrephidae). *The Veliger* **38**, 185–191.

SAUER, W. H. H., DOWNEY, N. J., LIPINSKI, M., ROBERTS, M. J., SMALE, M. J., SHAW, P. & MELO, Y. (2013). *Loligo reynaudi*, Chokka squid. In *Advances in Squid Biology and Fisheries (Part I. Myopsid Squids)* (eds R. ROSA, R. O'DOR and G. PIERCE), pp. 33–72. Nova Biomedical, New York.

SCHLÖGL, J., CHIRAT, R., JOACHIMSKI, M., HUDÁČKOVÁ, N. & QUILLÉVÉRÉ, F. (2011). Aturia from the Miocene Paratethys: an exceptional window on nautilid habitat and lifestyle. *Palaeogeography, Palaeoclimatology, Palaeoecology* **308**, 330–338.

SEN, H. (2004). A preliminary study on the effects of salinity on egg development of European squid (*Loligo vulgaris* Lamarck, 1798). *The Israeli Journal of Aquaculture – Bamidgeh* **56**, 93–99.

SEPKOSKI, J. J. JR. (2002). A compendium of fossil marine genera. *Bulletins of American Palaeontology* **363**, 1–560.

SERVAIS, T., PERRIER, V., DANELIAN, T., KLUG, C., MARTIN, R., MUNNECKE, A., NOWAK, H., NÜTZEL, A., VANDENBROUCKE, T. R. A., WILLIAMS, M. & MAC ØRUM RASMUSSEN, C. (2016). The onset of the 'Ordovician Plankton Revolution' in the late Cambrian. *Palaeogeography, Palaeoclimatology, Palaeoecology* **458**, 12–28.

SHEVYREV, A. A. (2006a). The cephalopod macrosystem: a historical review, the present state of knowledge, and unsolved problems: 2. Classification of nautiloid cephalopods. *Paleontological Journal* **40**, 46–54.

SHEVYREV, A. A. (2006b). The cephalopod macrosystem: a historical review, the present state of knowledge, and unsolved problems: 3. Classification of Bactritoidea and Ammonoidea. *Paleontological Journal* **40**, 150–161.

SHIMANSKY, V. N. (1975). Cretaceous Nautiloidea. *Trudy Paleontologicheskogo Instituta* **150**, 1–208 (in Russian).

SIQUNG, C., CHANGLIN, L., ZHIMENG, Z., WENPING, J., SUN, J., GUANCHENG, Y., FENG, L. & XIAOHUA, W. (2010). Study on embryonic development of *Sepia esculenta*. *Advances in Fisheries Science* **5** (in Chinese). Available online at http://www.cnki.com.cn/Article/CJFDTOTAL-HYSC201005002.htm. Accessed on 12.05.2016.

SMITH, M. M. (1986). Latimeriidae. In *Smiths' Sea Fishes* (eds M. M. SMITH and P. C. HEEMSTRA), pp. 152–153. Springer-Verlag, Berlin.

STEER, M. A., PECL, G. T. & MOLTSCHANIWSKYJ, N. A. (2003). Are bigger calamary *Sepioteuthis australis* hatchlings more likely to survive? A study based on statolith dimensions. *Marine Ecology Progress Series* **261**, 175–182.

STUMBUR, H. A. (1959). On the embryonic shells of some Ordovician Tarphyceratida. *Paleontologicheski Zhurnal* **2**, 25–29 (in Russian).

SURLYK, F. & NIELSEN, J. M. (1999). The last ammonite? *Bulletin of the Geological Society of Denmark* **46**, 115–119.

SUMMERS, W. C. & COLVIN, L. J. (1989). On the cultivation of *Rossia pacifica* (Berry, 1911). *Journal of Cephalopod Biology* **1**, 21–32.

SUTTON, M., PERALES-RAYA, C. & GILBERT, I. (2016). A phylogeny of fossil and living neocoleoid cephalopods. *Cladistics* **32**, 297–307.

SWEENEY, M. J., ROPER, C. F. E., MANGOLD, K. M., CLARKE, M. R. & BOLETZKY, S. v. (eds) (1992). "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology* **513**, 1–282.

TANABE, K., MISAKI, A. & UBUKATA, T. (2015). Late Cretaceous record of large soft-bodied coleoids based on lower jaw remains from Hokkaido, Japan. *Acta Palaeontologica Polonica* **60**, 27–38.

TANABE, K. & UCHIYAMA, K. (1997). Development of the embryonic shell structure in Nautilus. *The Veliger* **40**, 203–215.

TEICHERT, C. & KUMMEL, B. (1960). Size of endocerid cephalopods. *Breviora* **128**, 1–7.

TUREK, V. (2010). Embryonic shells in some lechritrochoceratids (Nautiloidea, Barrandeocerina). In *Cephalopods – Present and Past* (eds K. TANABE, Y. SHIGETA, T. SASAKI and H. HIRANO), pp. 85–92. Tokai University Press, Tokyo.

TUREK, V. & MANDA, Š. (2016). Early ontogeny, anomalous growth, and healed injuries in the Silurian nautiloid *Ophioceras* Barrande – implications for hatching and autecology of the *Tarphicerida*. *Bulletin of Geosciences* **91**, 331–366.

URIARTE, I., ESPINOZA, V., GUTIÉRREZ, R., ZÚÑIGA, O., OLIVARES, A., ROSAS, C., PINO, S. & FARÍAS, A. (2014). Key aspects of egg incubation in Patagonian red octopus (*Enteroctopus megalocyathus*) for cultivation purposes. *Aquaculture* **424–425**, 158–166.

URIARTE, I., HERNÁNDEZ, J., DÖRNER, J., PASCHKE, K., FARÍAS, A., CROVETTO, E. & ROSAS, C. (2010). Rearing and growth of the octopus *Robsonella fontaniana* (Cephalopoda: Octopodidae) from planktonic hatchlings to benthic juveniles. *Biological Bulletin* **218**, 200–210.

URIARTE, I., ZÚÑIGA, O., OLIVARES, A., ESPINOZA, V., CERNA, V., FARÍAS, A. & ROSAS, C. (2009). Morphometric changes and growth rate during embryonic development of *Robsonella fontaniana*. *Vie et Milieu* **59**, 315–323.

VANCE, R. R. (1973a). More on reproductive strategies in marine benthic invertebrates. *American Naturalist* **107**, 353–361.

VANCE, R. R. (1973b). On reproductive strategies in marine benthic invertebrates. *American Naturalist* **107**, 339–352.

VAN HEUKELEM, W. F. (1976). *Growth, bioenergetics and life-span of* Octopus cyanea *and* Octopus maya. Doctoral dissertation: University of Hawaii, Honolulu.

VAN HEUKELEM, W. F. (1983). *Octopus maya*. In *Cephalopod Life Cycles, Vol. 1: Species Accounts* (ed. P. R. BOYLE), pp. 311–323. Academic Press, London.

VIDAL, E. A. G., DIMARCO, F. P., WORMUTH, J. H. & LEE, P. G. (2002). Influence of temperature and food availability on survival, growth and yolk utilization in hatchling squid. *Bulletin of Marine Science* **71**, 915–931.

VIDAL, E. A. G., MARIAN, J. E. A. R. & MARTINS, R. S. (2013). *Doryteuthis sanpaulensis*, Sao Paolo squid. In *Advances in Squid Biology and Fisheries (Part I. Myopsid Squids)* (eds R. ROSA, R. O'DOR and G. PIERCE), pp. 257–300. Nova Biomedical, New York.

VIDAL, E. A. G., ROBERTS, M. J. & MARTINS, R. S. (2005). Yolk utilization, metabolism and growth in reared *Loligo vulgaris reynaudii* paralarvae. *Aquatic Living Resources* **18**, 385–393.

VIDAL, E. A., VILLANUEVA, R., ANDRADE, J. P., GLEADALL, I. G., IGLESIAS, J., KOUETA, N., ROSAS, C., SEGAWA, S., GRASSE, B., FRANCO-SANTOS, R. M., ALBERTIN, C. B., CAAMAL-MONSREAL, C., CHIMAL, M. E., EDSINGER-GONZALES, E., GALLARDO, P., et al. (2014). Cephalopod culture: current status of main biological models and research priorities. *Advances in Marine Biology* **67**, 1–98.

VILLANUEVA, R. & NORMAN, M. D. (2008). Biology of the planktonic stages of benthic octopuses. *Oceanography and Marine Biology: An Annual Review* **46**, 105–202.

VILLANUEVA, R., VIDAL, E. A. G., FERNANDEZ-ÁLVAREZ, F. Á. & NABHITABHATA, J. (2016). Early mode of life and hatchling size in cephalopod molluscs: influence on the species distributional ranges. *PLoS ONE* **11**, e0165334.

VOIGHT, J. R. (1998). An overview of shallow-water octopus biogeography. In *Systematics and Biogeography of Cephalopods, Smithsonian Contributions to Zoology, Vol. 586* (Volume **II**, eds N. A. VOSS, M. VECCHIONE, R. B. TOLL and M. J. SWEENEY), pp. 549–560. Smithsonian Institution Press, Washington.

VOIGHT, J. R. & DRAZEN, J. C. (2004). Hatchlings of the deep-sea octopus *Graneledone boreopacifica* are the largest and most advanced known. *Journal of Molluscan Studies* **70**, 400–402.

WANI, R. (2011). Sympatric speciation drove the macroevolution of fossil cephalopods. *Geology* **39**, 1079–1082.

WARNKE, K. (1999). Observations on the embryonic development of *Octopus mimus* (Mollusca: Cephalopoda) from Northern Chile. *The Veliger* **42**, 211–217.

WARNKE, K. & BOLETZKY, S. v. (2009). The "ventral rib" of the shell in *Spirula* (Cephalopoda, Coleoidea): a cryptic rostrum? *Berliner Paläobiologische Abhandlungen* **10**, 357–359.

WARNKE, K. & KEUPP, H. (2005). *Spirula*—a window to the embryonic development of ammonoids? Morphological and molecular indications for a palaeontological hypothesis. *Facies* **51**, 60–65.

WATANABE, K., SAKURAI, Y., SEGAWA, S. & OKUTANI, T. (1996). Development of the ommastrephid squid *Todarodes pacificus*, from fertilized egg to the rhynchoteuthion paralarva. *American Malacological Bulletin* **13**, 73–88.

WILLEY, A. (1896). The oviposition of *Nautilus macromphalus*. *Proceedings of the Royal Society* **60**, 467–471.

WILLEY, A. (1902). *Contribution to the Natural History of the Pearly Nautilus*. Cambridge University Press, Cambridge.

WOOD, J. B., KENCHINGTON, E. & O'DOR, R. K. (1998). Reproduction and embryonic development time of *Bathypolypus arcticus*, a deep-sea octopod (Cephalopoda: Octopoda). *Malacologia* **39**, 11–19.

YATSU, H. & MORI, J. (2000). Early growth of the autumn cohort of neon flying squid, *Ommastrephes bartramii*, in the North Pacific Ocean. *Fisheries Research* **45**, 189–194.

YAU, C. & BOYLE, P. R. (1996). Ecology of *Sepiola atlantica* (Mollusca: Cephalopoda) in the shallow sublittoral zone. *Journal of Marine Biological Association of the U.K.* **76**, 733–748.

YOUNG, R. E. (1972). Brooding in a bathypelagic octopus. *Pacific Science* **26**, 400–404.

YOUNG, R. E. & MANGOLD, K. M. (1994). Growth and reproduction in the mesopelagic-boundary squid *Abralia trigonura*. *Marine Biology* **119**, 413–421.

YOUNG, R. E., VECCHIONE, M. & FUCHS, D. (2015). Octopodiformes Berthold & Engeser, 1987. Vampire Squid and Octopods. Version 11 October 2015 (under construction). http://tolweb.org/Octopodiformes/19405/2015.10.11. Accessed 16.04.2016.

ZHENG, X., LIN, X., WANG, Z., YU, R., TIAN, C. & LI, Q. (2010). Studies on life cycle of cultured spineless cuttlefish *Sepiella japonica*. *Transactions of Oceanology and Limnology* **3**, 24–28 (in Chinese).

ZUEV, G. V. (1971). Golovonogie mollyuski severo-zapadnoi chasti Indiiskogo okeana [*Cephalopod Molluscs of the Northwestern Indian Ocean*]. Naukova Dumka, Kiev (in Russian).