A PHYLOGENY OF FOSSIL AND LIVING NEOCOLEOID CEPHALOPODS

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1

Abstract

Coleoid cephalopod phylogeny is well studied via both molecular and morphological data, yet while some agreement has been reached (e.g. that extant Decapodiformes and Octopoda are monophyletic) many details remain poorly resolved. Fossil coleoids, for which much data exists, have hitherto not been incorporated into analyses. Their inclusion is highly desirable both for the support of neontological phylogenies, to better reconstruct character-state histories, and to investigate the placement of the fossil groups themselves. In this study we present and analyse a morphological data matrix including both extinct and extant taxa. Homology assumptions in our data are discussed. Our results are presented both with and without the constraint of a monophyletic Decapodiformes imposed. When analysed with this constraint our results are strikingly congruent with those from molecular phylogeny, for instance placing *Idiosepius* in a basal position within Decapodiformes, and recovering Oegopsida and Bathyteuthoidea (though as grades). Our results support an Octopodiformes clade ('vampire squid' *Vampyroteuthis* as sister to Octopoda) and an octopodiform interpretation for most fossil coleoids. They suggest the fossil sister taxon to the octopods to be Plesioteuthididae. Most fossil higher taxa are supported, although many genera, especially within suborder Teudopseina, appear para- or polyphyletic.

Contents

Introduction

Cephalopod molluscs are a well-studied and important group, both ecologically and economically. Extant cephalopods comprise two diverse groups; the ten-armed Decapodiformes (squid, cuttlefish and relatives) and the eight-armed Octopoda. Only two living cephalopod genera fall outside these groups; the iconic *Nautilus*, and the 'vampire squid' *Vampyroteuthis*. Molluscan phylogeny has been the subject of much recent study and controversy (Kocot *et al.*, 2011; Smith *et al.*, 2011; Stöger *et al.*, 2013; see also Telford and Budd, 2011, Allcock *et al.*, 2014), and no consensus has yet been reached as to the relationships among the molluscan classes. Within the cephalopods, while it is universally agreed that *Nautilus* represents a sister taxon to a monophyletic group comprising all other extant cephalopods (the Neocoleoidea), the internal phylogeny of Neocoleoidea is far from settled. Several morphological (e.g. Young and Vecchione, 1996; Voight, 1997), molecular (e.g. Bonnaud *et al.*, 1997; Carlini and Graves, 1999; Strugnell *et al.*, 2005; Strugnell *et al.*, 2006; Strugnell and Nishiguchi, 2007; Lindgren *et al.*, 2012; see Allcock *et al.*, 2014 for a review) and combined (Lindgren *et al.* 2004) studies have taken a cladistic (i.e. computational phylogenetic) approach. The most fundamental question concerns the position of *Vampyroteuthis*, but even here results from these studies have been far from unambiguous. Non-cladistic morphological classification has long favoured the placement of this eight-armed genus as a sister group to the octopods (see e.g. Engesser, 1988; Bizikov, 2004), the resulting clade being termed Octopodiformes (see Young *et al.*, 2012a). However, while some analyses have placed *Vampyroteuthis* in this position (e.g. Young and Vecchione, 1996; Carlini and Graves, 1999; Strugnell *et al.*, 2005; Lindgren *et al.*, 2012), others (e.g. Bonnaud *et al.*, 1997; Lindgren *et al.*, 2004) have placed it as a sister taxon to Decapodiformes, and still others (e.g. Strugnell and Nishiguchi, 2007) have recovered both positions in different variants of their analysis. Many other details of neocoleoid phylogeny are also under debate; these include the identification of the most primitive extant member of Decapodiformes (see e.g. Lindgren et al., 2004, 2012; Strugnell *et al.*, 2005). The monophyly of extant Decapodiformes *has* however been

recovered from almost all analyses; of the studies cited, only the morphological analysis of Lindgren *et al*. (2004) generated a tree where this group does not form an unambiguous clade.

While many phylogenetic hypotheses for Neocoleoidea have been derived at least in part from palaeontological data (e.g. Doyle *et al*., 1994), all published computationally-derived phylogenies of Neocoleoideaare based exclusively on extant taxa. The cephalopods have an extensive fossil record, and while this is more limited for neocoleoids than for ammonoids and nautiloids, a substantial volume of palaeontological data nonetheless exists. Difficulties in homologizing characters between fossil and extant taxa may be one reason for this exclusion, together with concerns that the relatively low number of determinable character states in fossil taxa would reduce the efficacy of any analysis. We do not, however, consider homology problems to be insuperable (see discussions below). Fossils provide records of extinct character combinations that can, despite their limitations, both increase the resolution of phylogenetic inference and alter topologies – see e.g. Legg *et al*. (2013) for an arthropod example. While the exclusion of fossils from molecular phylogenies cannot be avoided, their incorporation into morphological and total-evidence studies is highly desirable.

This study presents a new cladistic dataset and analysis of Neocoleoidea based for the first time on both living and fossil taxa. It aims to demonstrate that combined palaeontological and neontological morphological data can generate robust phylogenetic results compatible with those obtained from other datasets, and to test and refine existing phylogenetic and taxonomic hypotheses that involve fossil taxa.

Dataset

The current dataset is presented in appendices 3 (print version) and 4 (NEXUS version); it consists of 137 morphological characters and 77 ingroup neocoleoid taxa (31 extant and 46 extinct). While an outgroup consisting of several taxa is preferable in computational cladistics, this was not viable in the current study. Outgroup taxa need to be codeable under the character-set used, and to

demonstrably fall outside the ingroup. Here, therefore, the outgroup must consist of non-coleoid cephalopods, of which only *Nautilus* is extant. There are no fossil candidates for which substantial numbers of characters would have been codeable. *Nautilus pompilius* was hence used as the sole outgroup taxon. Characters have primarily been designed *de novo* for this analysis, although some, especially those relating to rarely-fossilized 'soft tissue' characters, originate from Lindgren *et al*. (2004) or Young and Vecchione (1996). The dataset is designed to facilitate analyses of taxa known from isolated gladii. Character selection reflects this, over 50% of characters relating to shell or gladius morphology. Characters are detailed in appendix 1, which provides full character descriptions. The dataset includes binary, unordered multi-state and ordered (additive) multi-state characters.

Details of the sources used and (where appropriate) assumptions made for each taxon are provided in appendix 2. The taxon-set selected for this study includes 21 extant species of Decapodiformes, selected for both the availability of anatomical data and to provide a breadth of taxonomic (and hence hopefully phylogenetic) coverage. We followed Young *et al*. (2012b) for taxonomic assignments of the decapodiform taxa selected. These comprised three members of order Sepiolida, 13 of order Oegopsida, a spirulid (*Spirula spirula)*, a myopsid (*Doryteuthis* (*Amerigo*) *pealeii*), and three taxa of uncertain order-level affinity (*Bathyteuthis abyssicola*, *Chtenopteryx sicula* and *Idiosepius pygmaeus*). From the extant Octopodiformes, *Vampyroteuthis infernalis,* three cirrate octopods and six incirrate octopods were selected. The latter included two members of the problematic family Amphitretidae. Young *et al*. (2012b) were followed again for taxonomic assignments.

Forty-seven species of Palaeozoic and Mesozoic neocoleoid fossils were also selected. Priority in selection was given to taxa which preserve characterizable soft-tissues, and/or to those in which gladii or homologous structures are well characterized. Taxa that we have excluded from this study are briefly discussed below. Fossils selected for our dataset are three belemnoids, five Mesozoic

octopod species, 23 members of suborder Teudopseina (seven teudopsids, 12 trachyteuthids, three palaeololiginids), six plesioteuthids (representing suborder Prototeuthidina), and six members of suborder Loligoseppiina (two geopeltids, three loligosepiids, and the well-characterised *Leptoteuthis gigas*). These were supplemented by *Vampyronassa rhodanica*, a well-preserved Jurassic 'vampire squid', and species from two genera of uncertain taxonomic status (*Muensterella scutellaris* and *Actinosepia canadensis*). Two single-specimen species from the Carboniferous Mazon Creek Lagerstätte (Selden and Nudds, 2012), *Jeletzkya douglassae* and *Pohlsepia mazonensis*, were also included. While neither *Jeletzkya* nor *Pohlsepia* is especially well characterized, they represent putative first occurrences of Decapodiformes and Octopodiformes repectively.

Fossil taxa known primarily from a mineralised chambered phragmocone, most notably the ammonoids and the nautiloids, are not included in this study. The soft tissues of both groups are very poorly known (though see e.g. Klug *et al.*, 2012), presumably as their buoyant shells militated against the early burial normally required for the preservation of labile tissues. The majority of these taxa also lack a proostracum, and are hence difficult to compare with neocoleoids in the absence of soft-tissue preservation. The Devonian 'coleoids' *Naefiteuthis* and *Boletzkya* (Bandel *et al.*, 1983) possess gladius-like structures as well as chambered phragmocones, but their gladii are poorly characterised. Other exclusions include: the Cretaceous 'spirulids' *Groenlandibelus, Naefia* and *Adygeya* (see Haas, 2003); the Cambrian *Nectocaris*, whose status as a crown-group cephalopod is not well established (see e.g. Smith and Caron, 2010; Smith, 2013; Mazurek and Zatoń, 2011; Kroger *et al.*, 2011); and the unnamed and poorly-known Carboniferous cephalopod described by Allison (1987).

Shell homologies and terminology

The proostracum is an anterior extension of the dorsal wall of the phragmocone's living chamber, and is treated here as homologous with the gladius/stylets/cuttlebone of living Neocoleoidea. In

squid gladii, we exclude the cone and rostrum (if present) from the proostracum (Arkhipkin et al., 2012). All shell-bearing taxa in this study, except *Spirula* and *Nautilus*, possess a proostracum. The cephalopod gladius or proostracum is divided into regions by 'shell asymptotes' (see Figure 1), which are identifiable in most taxa as are more or less distinct lines or ridges diverging between median field (rachis), hyperbolar zone (vane) and lateral field (wing) of the gladius (e.g. Jeletzky, 1966; Bizikov, 1996, 2008; Arkhipkin *et al*., 2012). Some authors (e.g. Fuchs *et al*., 2007a, 2008; Fuchs and Weis, 2008; Fuchs and Larson, 2011a) have preferred the synonymous terms 'inner' and 'outer' asymptotes respectively for the 'median' and 'lateral' asymptotes (see Figure 1). The term 'marginal asymptote' has been also used for living species to delimit the line between wings and cone flags (Bizikov, 2008; Arkhipkin *et al*., 2012). As marginal asymptotes are only present in one taxon under study here (*Vampyrotetuthis*), they are not included in Figure 1 or in our coding scheme. Homology-assumptions for the different parts of the proostracum are discussed below.

Median field = rachis

In Recent teuthids a thickened axis or rachis extends the entire length of the gladius. In many fossil gladii and in the gladius of *Vampyroteuthis* no rachis is present, but typically a 'median field' extends along the entire length (see e.g. Fuchs and Larson, 2011b), delimited laterally by the median asymptotes. Most authors (see e.g. Naef, 1922; Jeletzky, 1966; Fuchs *et al*. 2009) have concluded that the median field and rachis are homologous structures, and we follow this assumption herein.

Hyperbolar zone = vane

We follow the concept of Jeletzky (1966) and Bizikov (2004) in defining the hyperbolar zone as lying between the inner and outer asymptotes (see Figure 1). Hyperbolar zones are thus equivalent to the 'vanes' of extant species. While Bizikov has preferred the term 'lateral plates' (see also Naef, 1922), we consider this term to be synonymous with 'hyperbolar zone' or 'vane'.

Lateral field = wing

We homologize the lateral fields of fossil gladii, the regions outside the lateral asymptotes, with the 'wings' of Recent gladii. This follows Jeletzky (1966), although we consider his term 'parabolar zones' to be a redundant synonym. Naef (1922) used the term 'conus flags' for the lateral fields of many extinct forms. These cannot, however, be homologous to the 'cone flags' or 'conus fields' of extant Neocoleoidea, which sometimes lie outside the wings (e.g. in *Vampyroteuthis*); we hence prefer to use the term 'lateral field'. We also treat the shell rudiments of certain living and fossil octopod species (the 'stylets') as homologues of lateral fields. This concept follows Donovan (1977), who first noted that the gladius of *Palaeoctopus* could be derived from the wings or lateral fields of the Loligosepiina gladius, the median field and hyperbolar zones having been lost. This interpretation has found broad support among other workers; Fuchs *et al*. (2009), for instance, concluded that shell rudiments of *Palaeoctopus* represent mainly the gladius' lateral fields. See further discussion in description of character 13 (appendix 1).

Phragmocone = primary cone

The primary cone (=primary conus) in Recent gladii is normally considered to be a vestige (i.e. a homologue) of the phragmocone (e.g. Jeletzky, 1966; Donovan and Toll, 1988; Arkhipin *et al*., 2012). We follow this homology model here. *Sepia* and close relatives possess a chambered phragmocone in their proostracum. *Spirula* and *Nautilus* have a coiled chambered phragmocone, but lack a proostracum. Definitions of phragmocone and further discussion of homology can be found in our description of character 16 (appendix 1).

Rostrum = guard

Many taxa under consideration here possess a posterior extension of either proostracum or phragmocone – this may be termed either a rostrum or a guard. Detailed homology between such structures is not straightforward to establish, but a broad homology is assumed in our coding scheme. See description of character 14 for further discussion (appendix 1).

Methods

The dataset was analysed using TNT v.1.1 (Goloboff *et al*., 2008b), using both equal-weights and implied-weights (Goloboff, 1993) methodologies. The latter provides a means for determining the most parsimonious tree-topology for a dataset by downweighting highly homoplastic characters without the need for arbitrary *a-priori* weighting decisions, or *a-posteriori* weighting approaches that suffer from logical circularity. See Goloboff *et al*. (1993, 2008a) and Legg *et al*. (2013) for a more complete discussion of the rationale behind the selection of this methodology.

As discussed above, the most consistent result from molecular phylogenetic analyses of cephalopods (e.g. Lindgren *et al*. 2004, 2012; Strugnell and Nishiguchi, 2007; Allcock *et al*., 2011, Kocot *et al*., 2011, see also Kröger *et al*., 2011) is that Decapodiformes is a clade (i.e. is monophyletic). Our unconstrained analyses, in common with prior morphological analyses by other authors (e.g. Lindgren *et al*., 2004), do not consistently recover this topology. Instead they place Decapodiformes as a basal grade within Neocoleoidia, although in the equal-weights analysis a restricted decapodiform clade (excluding *Sepia, Heteroteuthis*, *Rossia*, *Idiosepius, Spirula* and *Gonatus*) does emerge within this grade. These results not only contradict inferences from molecular data, but are also highly stratigraphically incongruent, placing extant forms at the base of the tree, and the majority of Mesozoic fossils as more derived than most extant decapodiforms. The recovery of these topologies is likely an artefact; for this reason we also performed analyses in which a constraint of monophyly was imposed for extant Decapodiformes. These latter analyses are referred to as 'constrained' below. This constraint of monophyly was applied only to living Decapodiformes, the position of all fossil taxa being left unconstrained.

For both constrained and unconstrained cases, equal-weights (EW) and implied-weights (IW) analyses were undertaken. The latter were performed using a range of concavity-constant (k) values (2, 3, 4, 5, 7 and 10) to investigate the effect of character weighting on hypotheses of relationship. We use an informal naming scheme for these analyses herein, suffixing analyses with C for constrained or F for free (unconstrained); hence EWC (equal-weights constrained), IW3F (implied

weights k=3, free) etc. Fourteen analyses were hence performed. All were carried out using the TNT 'New Technology' driven-search command, using 500 initial addition sequences, Parsimony Ratcheting, Sectorial Searches, Tree Drifting and Tree Fusing. Other settings were left at their defaults. Synapomorphies (Figure 2) were mapped using TNT optimise/list synapomorphies for the strict consensus tree from our IW3C analysis.

Results

Appendix 5 provides the full set of strict consensus trees from our analyses, and appendix 6 summarises the occurrences of some of the more important groupings and topologies from these trees.

Extant Decapodiformes

Unconstrained IW analyses produce a decapodiform grade where *Spirula* and *Gonatus* are basal, and *Idiosepius* derived. As discussed above, we do not consider this to be a plausible phylogenetic model; these topologies are not discussed further for extant Decapodiformes.

Our 'raw' analysis (EW) does not recover a monophyletic Decapodiformes, placing *Spirula, Heteroteuthis*, *Rossia*, *Sepia*, *Gonatus* and *Idiosepius* within a basal polytomy. It does, however, recover a clade containing all other extant decapodiform taxa. This corresponds to the Bathyteuthoidea and Oegopsida, except that it excludes *Gonatus* and includes the myopsid *Doryteuthis* within Oegopsida. The two bathyteuthoids under consideration (*Bathyteuthis* and *Chtenopteryx*) form a basal grade to Oegopsida.

Constrained analyses necessarily resolve the Decapodiformes as a clade. Within that clade, all resolve *Idiosepius* as the most basal decapodiform. *Sepia* and the sepiolid *Heteroteuthis* are in all cases the next most basal taxa (sister taxa in IW2C-IW10C), although the sepiolid *Rossia* only occurs near these taxa in EWC. The remainder of Decapodiformes forms a clade whose topology varies substantially, and few consistent patterns are recoverable. The Oegopsida + Bathyteuthoidea clade

described above is recovered also in EWC; a similar clade (but including also *Spirula*, *Gonatus* and *Rossia*) is recovered in IW2C-IW10C, where again the bathyteuthoids consistently resolve together but as a grade basal to a derived *Spirula, Gonatus* and *Rossia* clade. In IW3C-IW5C the Oegopsida + Bathiteuthoidea clade excludes the myopsid *Doryteuthis*, which resolves as its sister taxon.

Other consistent results from all analyses (constrained and unconstrained) include: a clade comprising *Cycloteuthis*, *Mastigoteuthis*, *Octopoteuthis*, *Lepidoteuthis* and *Cranchia*; sister-taxon relationships between (a) *Onychoteuthis* and *Ommastrephes,* and (b) the two species of *Histioteuthis*; a close relationship (sister-taxon or adjacent positions in a grade) between (a) *Thysanoteuthis* and *Abralia*, and (b) *Spirula* and *Gonatus.*

Fossil Decapodiformes

All our analyses resolve belemnoids as a monophyletic group, and all except EWF resolve them as crown-group decapodiforms. All IW analyses recover a clade comprising the belemnoids, *Sepia*, *Heteroteuthis* and *Jeletzkya* (EW analyses are compatible with but not indicative of this topology). Unconstrained implied-weights analyses (which produce a paraphyletic Decapodiformes) place this clade in a relatively derived position, while all constrained analyses place it basally in a position, derived only with respect to *Idiosepius.*

The genera *Jeletzkya* and *Pohlsepia* represent putative early (Carboniferous) representatives of the Decapodiformes and Octopodiformes respectively. All our analyses (except the poorly resolved EWF) place *Jeletzkya* within the decapodiform crown-group, in a position near the belemnoids (see above) and *Sepia*. However *Pohlsepia* never appears within the octopodiform crown; in both EW analyses and all constrained IW analyses it forms part of a basal polytomy within the ingroup, while in all unconstrained IW analyses it represents a sister taxon to Octopodiformes.

The fossils *Eoteuthoides* and *Marekites* always occur within the 'Oegopsida + Bathyteuthoidea' clade (or grade). *Eoteuthoides* is sister to *Bathyteuthis* in most IW analyses, but to *Thysanoteuthis* in EW analyses and in IW10C. *Marekites* varies more in position, but typically occurs close to *Abralia*.

In our IW2 and IW2C analyses the fossil genera *Parabelopeltis* and *Palaeololigo* occur relatively basally within Decapodiformes. In all other analyses these taxa fall within Octopodiformes or are placed in an unresolved basal polytomy (EW analyses).

Extant Octopodiformes

All our analyses recover a monophyletic Octopoda split into cirrate and incirrate sister clades. All IW analyses also recover a monophyletic Octopodiformes clade (*Vampyroteuthis* as sister to Octopoda). Within the incirrates, in all cases, the Amphitretids *Japetella* and *Amphitretus* occur basally, as either a clade or a grade, and Argonautoidea (*Argonauta, Ocythoe, Haliphron*) is a clade.

Fossil Octopodiformes

Most fossil taxa in our analyses resolve within Octopodiformes where that clade occurs (i.e. in all analyses except EWF). Exceptions are discussed under fossil decapodiforms above. While variation among analyses exists, many consistent results emerge.

In all IW analyses the loligosepids, *Leptoteuthis* and the plesioteuthids form successive stem-group plesions to crown-group Octopoda. In both EW analyses the same relationship among the loligosepids, *Leptoteuthis* and the plesioteuthids occurs, but with crown-group Octopoda removed. In all analyses both the loligosepids and plesioteuthids are monophyletic, as are all genera within them for which we analysed multiple species (*Loligosepia*, *Boreopeltis* and *Plesioteuthis*).

In all analyses a trachyteuthid / teudopsid / *Vampyroteuthis* clade occurs, which we term Teudopseina herein for convenience, despite the inclusion of *Vampyroteuthis*. In all analyses except EW, Teudopseina is the sister group to total-group Octopoda (in EWF it forms part of a basal polytomy). It includes the Jurassic *Vampyronassa* (in all cases as sister to *Vampyroteuthis*), all

trachyteuthids, all teudopsids (except as below), all palaeloliginids (except as below), and the genera *Actinosepia* and *Muensterella*. Note that *Eoteuthoides* (Kostak, 2002) and *Marekites* (Kostak, 2002; Fuchs and Larson, 2011b) were originally described as a teudopsid and palaeololiginid respectively, but that their consistent association with Decapodiformes rather than Octopodiformes strongly suggests that these familial assignments are untenable. Only the IW2 analyses provide further discrepancies; here the teudopsid *Teudopsis bunelli* and the palaeololiginid *Rachiteuthis* occur as a basal plesion to total-group Octopoda, while the palaeololiginid *Palaeololigo* occurs within Decapodiformes (see above), and the geopeltid *Geopeltis simplex* occurs within Teudopseina in IW2C (in IW2 it falls outside Octopodiformes).

The internal phylogeny of Teudopseina differs radically in EW and IW analyses. In the former, *Vampyroteuthis* and *Vampyronassa* are sister to the remainder of the clade, palaeololiginids and teudopsids are derived, and trachyteuthids are relatively basal. In the latter, palaeololiginids and (most) teudopsids are basal, and trachyteuthids are derived, with *Vampyroteuthis* and *Vampyronassa* nesting within the trachyteuthids. Details differ subtly among IW variants. No clades emerge consistently from all analysis other than *Vampytoteuthis* + *Vampyronassa.* However *none* of our analyses recover monophyly for either palaeololiginids, trachyteuthids or teudopsids, or indeed for any genera within those groups for which multiple species were included.

The geopeltids (*Geopeltis* and *Parabelopeltis*) are relatively mobile taxa in our analyses, and do not always occur together. They occur in basal polytomies of the neocoleoids (EWF and EWC), in a basal polytomy of the octopodiforms (EWC), as sister taxa to the decapodiform *Idiosepius* (IW2 and IW2C), within the trachteuthids (IW2C), and as the most basal taxa in total-group Octopoda (IW3F-IW10F and IW3C-IW10C).

Two species of *Palaeooctopus* were included; in all analyses except EWF these resolve as a grade of stem-group incirrates (crown-group octopods). The two species of *Keuppia* consistently resolve as a clade of crown-group incirrates (more derived than the amphitretid genera *Amphitretus* and

Japatella), except again in EWF. The EWF positions of these taxa are compatible with these placements, but not fully resolved. The genus *Styletoctopus* always resolves as a crown-group incirrate, the sister taxon to *Octopus*.

Discussion

With the constraint of decapodiform monophyly imposed (see above), our results are broadly consistent with the most recently published molecular phylogeny for extant cephalopods (Lindgren *et al*., 2012). There is agreement, for instance, that Octopodiformes are a clade in which *Vampyroteuthis* is the sister to the Octopoda, that Inicirrata and Cirrata are sister clades within Octopoda, and that Argonautoidea is a clade within the incirrates. Within Decapodiformes there is agreement that *Idiosepius* is the most basal taxon (contra to the position of Bonnaud *et al*., 2005), and that Sepiidae is also basal. The recent sequencing of *Idiosepius* (Hall *et al*., 2014) also suggested a close relationship to *Sepia*, and is hence congruent with our position. Within decapodiforms, groupings such as the 'Lepidoteuthid families' (*sensu* Young *et al*. 2012b; here *Lepidoteuthis* and *Octopoteuthis*) and Bathyteuthoidea (*Chtenopteryx* and *Bathyteuthis*) are recovered as monophyletic. Our analysis recovers Oegopsida and Bathyteuthoidea as grades while Lindgren *et al*. (2012) recovered them as clades; nonetheless both phylogenetic analyses agree that these two groups are cohesive and closely related to each other. One quirk of our results is the consistent association of the oegopsid *Gonatus* with *Spirula*; this may reflect the vestigial siphuncle described by Arkhipkin *et al*. (2012) in *Gonatus*, whose discovery postdates previous morphological phylogenies (Young and Vecchione, 1996; Lindgren *et al*., 2004).

While the position of a few 'difficult' genera (e.g. *Rossia*, *Spirula, Gonatus, Japetella*) differs substantially among analyses, the degree of agreement between our results and those of Lindgren *et al*. (2012) is substantially higher than has previously been seen between molecular and morphological cephalopod phylogenies (see e.g. Lindgren *et al*., 2004). We treat this as valuable

confirmatory evidence that the two approaches are converging on a 'correct' solution, but restrict the rest of the discussion below to a consideration of the position of fossil taxa.

The palaeontological "Octopodiformes theory" is an assertion that the vast majority of Mesozoic gladius-bearing cephalopods were more closely related to extant Octopodiformes than to Decapodiformes (see e.g. Young *et al*., 2012a). The alternative position, the "teuthoid theory" or "Decapodiformes theory", holds that these fossils are best treated within the Decapodiformes as close relatives of various extant teuthoids. This latter position was most recently espoused by Bizikov (2008). Our analyses provide strong support for the Octopodiformes theory. In all analyses we find that almost all gladius-bearing taxa under study group with Octopodiformes. *Parabelopeltis* and *Palaeololigo* group with Decapodiformes in implied weights analyses with k=2, but this position is otherwise not recovered and we consider it spurious. Only two gladii under consideration group with Decapodiformes consistently – *Marekites* and *Eoteuthoides*. These genera are genuine candidates for Mesozoic representatives of crown-group Decapodiformes, and their restudy would be timely.

Our analyses consistently place Belemnoidea within the crown-group Decapodiformes. While orthodoxy places these fossils outside the crown-group (see e.g. Kröger *et al*., 2011), their broad relationship to Decapodiformes is not in dispute: they do, for instance, have ten arms of subequal size. Our crown-group position is driven primarily by similarities to the extant *Sepia*, including the presence of calcification, a chambered shell, and a rostrum (the homology issues of the latter structure are discussed in appendix 1). While we do not rule out the possibility that position is an artefact, we are not aware of any fundamental objections to it other than the apparent absence of tentacular arm-modifications in the belemnoids; this may represent a simple reversal. This position for the belemnoids would imply that both Decapodiformes and Neocoleoidea, as traditionally conceived, are paraphyletic. We note, however, that the cladogram presented by Kröger *et al*. (2011) contains a polytomy that implies similar doubts as to the monophyly of Neocoleoidia.

The two Carboniferous-aged genera in our study, *Pohlsepia* and *Jeletzkya*, are both imperfectly known forms with soft tissue preservation, from the Mazon Creek Lagerstätte. *Pohlsepia* was originally described (Kluessendorf and Doyle, 2000) as an 'octobrachian' (=octopodiform), but our results argue against this interpretation (see above), as have other authors (e.g. Fuchs, 2009). We interpret *Pohlsepia* as a basal coleoid of uncertain affinities. *Jeletzkya,* however, remains a viable candidate for the earliest representative of Decapodiformes, resolving within the crown-group in all but one of our analyses. This genus remains poorly characterized, and a restudy using modern techniques is strongly urged.

Our recovery of Teudopseina (comprising Teudopsidae, Trachyteuthidae, Palaeololiginidae and *Muensterella*) is in accordance with traditional taxonomic practice (e.g. Fuchs, 2010a; Fuchs, 2011b). It provides support for the acceptance of this group as a clade, excepting that our analyses suggest that the extant *Vampyrotheuthis* belongs within this group. We do not find any support, however, for the monophyly of any taxonomic groupings within Teudopseina, and Teudopsidae in particular appears to be highly polyphyletic. Loligosepiina (comprising Geopeltidae, Loligosepiidae and *Leptoteuthis*), another grouping from traditional taxonomy (see e.g. Fuchs, 2010b), is also recovered in many of our analyses. Equivocation here results solely from the relative mobility of Geopeltidae; the loligosepiids consistently form a clade that is closely related to *Leptoteuthis*. Where the geopeltids are resolved as related, they are basal to these two taxa. Loligosepiina is, however, in all cases paraphyletic, forming the basal part of the octopod stem-group rather than a clade.

The identification of the fossil sister group to the crown-group Octopoda is a long-standing palaeontological problem. Fuchs (2009) provides a summary of previous proposals. While most recent authors (e.g. Doyle *et al.*, 1994; Haas, 2003; Bizikov, 2004; Fuchs 2009) agree that the closest fossil relatives of octopods are to be found in the Mesozoic gladius-bearing taxa, there has been little agreement as to which one. Donovan (1977) and Doyle *et al.* (1994), for instance, favoured Loligosepiina, while Haas (2002) and Bizikov (2004) suggested teudopsid or trachyteuthid taxa within

Teudopseina. Fuchs (2009) detailed instead three phylogenetic models in which octopods derived from one or both of two other families within Teudopseina (Paleologinidae and Muensterellidae). Our analyses favour the older theories, as most place Loligosepiina in the octopod stem-group, and none place the octopods within Teudopseina. However we consistently recover not Loligosepiina but Plesioteuthididae (the sole family of Prototeuthidina; see Fuchs and Larson, 2011a) as most derived member of the octopod stem-group. Fuchs (2009) explicitly rejected this (and other) groups from consideration on the grounds of their well-developed median fields (the median field is absent in crown-group octopods). In our analysis, however, this single character is outweighed by other characters placing the octopods with the Loligosepiinae/Plesioteuthididae line (see Fig. 2). While we acknowledge that all hypotheses of phylogeny are based on arbitrarily weighted interpretations of character states, we contend that a computational cladistic analysis of multiple characters provides the most rigorous means of assessing and generating such hypotheses. On this basis, Plesioteuthididae is the most likely sister group to the crown-group octopods.

Our analyses strongly suggest that the fossil taxa *Paleooctopus, Keuppia* and *Styletoctopus* are all crown-group octopods on the incirrate line, branching off after the cirrate/incirrate split which defines the base of the crown. *Palaeoctopus* is likely a stem-group incirrate, while *Keuppia* and *Styletoctopus* are crown-group forms. The crown-group position of *Keuppia* however is less secure as it follows from our basal position for Amphitretidae; this is at odds with molecular results (Lindgren *et al.*, 2012) and should be treated with caution.

Our analyses, taken as a whole, provide the first rigorous computational cladistic treatment of a group of important and well-characterized fossils, whose study is clearly vital to any unravelling of the origins of the major extant cephalopod groups. Results are broadly compatible with both molecular phylogenies and high-level taxonomic groupings within the fossil Coleoidea, in as far as any consensus exists on these matters. We take this as indicative evidence for their validity, and hence for the viability of our approach - synthesis of morphological data from fossil and extant taxa -

for the study of coleoid phylogeny. Further, we contend that incorporating fossil evidence is not merely viable but necessary for a full understanding of the evolutionary history of this important group, as fossils record extinct character-state combinations not recoverable from extant taxa alone. We treat this dataset and the results that it generates, however, as a first iteration. Further refinement and expansion to include more taxa and characters is highly desirable, as is the reinvestigation of taxa currently resolved in aberrant or significant positions (e.g. *Jeletzkya, Eoteuthoides, Marekites*).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix 1 – Character descriptions

Appendix 2 – Notes on coding (by species)

Appendix 3 – Data matrix (print-ready)

Appendix 4 – Data matrix (NEXUS format)

Appendix 5 – Consensus trees for all analyses

Appendix 6 – Table summarising groupings within consensus trees

Figure Captions

Figure 1

Homologies for the neocoleoid gladius. Median field, hyperbolar zone, lateral field and phragmocone are treated here as homologous to rachis, vane, wing and primary cone of living Neocoleoidea.

Figure 2

Tree IW3C (Constrained, Implied Weights with k=3), consensus of two equally parsimonious trees (weighted length=58.93), with shell illustrations. This tree topology is identical to that of IW4C and IW5C. Taxa marked * are fossils. Synapomorphies at indicated nodes are as follows. **A** (Decapodiformes): 109 (Funnel free); 110 (Funnel locking apparatus present); 130 (Arm-pair V hectocotylization present). **B**: 51 (ventral median structure on gladius absent); 55 (dorsal median structure on gladius absent). **C**: 7 (septate phragmocone present); 14 (Rostrum or guard present); 27 (phragmocone l/w > 0.5). **D** (Belemnoidia): 13 (lateral fields present); 15 (guard or rostrum strongly developed); 21 (phragmocone wall thickened into a conotheca). **E** (Myopsida, Bathyteuthidae, 'Oegopsida'): 24 (5 < gladius l/w < 10); 34 (1.25 < vane width / rachis width < 2.5); 43 (convex posterior tip of gladius pointed); 45 (anterior tip of gladius pointed); 47 (vane tapers anteriorly and posteriorly); 58 (split dorsal median interruption anteriorly on gladius); 78 (posterior fins terminal). **F** (Bathyteuthidae, 'Oegopsida'): 114 (One-part cornea present). **G** (*Spirula* + *Gonatus*): 7 (septate phragmocone present); 93 (more than three rows of arm suckers proximally); 130 (Arm-pair V hectocotylization present). **H** (Octopodiformes): 13 (lateral fields present); 24 (3 < gladius length/width < 4); 58 (split dorsal median interruption anteriorly on gladius); 80 (four appendage pairs); 81 (appendage pair two reduced to filaments); 82 (modification of appendage into tentacle absent); 87 (cirri or spines on arms present); 115 (statocyst outer capsule present); 118 (Superior buccal lobe adjacent to brain); 124 (nidamental glands absent). **I** (Teudopseina including *Vampyroteuthis*): 19 (primary cone open ventrally); 25 (0.3 < vane length / rachis length < 0.5); 26 (0.3 < wing length / rachis length < 0.5); 45 (convex posterior tip of gladius pointed); 56 (dorsal

interruption of gladius is a keel). **J** (Palaeololiginidae, *Teudopsinia*, *Rachiteuthis*): 76 (fins rhomboidal). **K**: 48 (15˚ < angle between inner/median asymptote and midline < 20˚); 49 (15˚ < angle between outer/lateral asymptote and midline < 20˚). **L** (*Vampyroteuthis* + *Vampyronassa*): 95 (one row of arm suckers distally); 96 (Ink sac absent). **M** (total-group Octopoda): 30 (0.5 < Rachis width at vane / total wing width < 0.75); 44 (anterior tip of gladius flat). **N** (Geopeltidae): 39 (Rachis width at vane insertion / rachis width 2/3 anteriorly < 1). **O**: 25 (Vane length / rachis length > 0.9); 46 (strong/sharp inflexion in gladius outline where lateral asymptote intersects margin); 49 (5˚ < angle between outer asymptote and midline < 10˚); 56 (median dorsal interruption in gladius is a rib). **P** (Loligosepiidae): 26 (Wing length / rachis length > 0.9); 31 (Wing length / vane length > 1.1); 34 (Vane width / rachis width at vane insertion < 0.25). **Q**: 22 (Cone flags present); 48 (angle between inner asymptote and midline <5˚). **R** (Plesioteuthida + Octopoda): 12 (Hyperbolar zones absent). **S** (Plesioteuthididae): 24 (5 < gladius length / gladius width < 10). **T** (crown-group Octopoda): 2 (shell restricted to posterior half); 11 (median field absent); 16 (phragmocone absent); 24 (gladius length/width < 2); 79 (arms longer than gladius). **U** (Cirrata): 95 (one row of suckers distally); 96 (ink-sac absent); 106 (horizontal arm septa in arm muscles); 109 (funnel locking apparatus); 121 (Posterior salivary gland proximal to buccal mass); 122 (branchial canal absent); 125 (right oviduct present); 131 (sperm-packets). **V** (total-group Incirrata): 10 (prostracum split into two units); 36 (constriction of lateral fields). **W** (crown-group Incirrata): 74 (fins absent). **X**: 41 (posterior margin of lateral field concave). **Y** (*Octopus* + *Styletoctopus*): 45 (posterior tip pointed). **Z** (Argonautoidea): 109 (funnel free); 110 (funnel locking apparatus present).