

THE MOLECULAR PHYLOGENY OF CIRRATE OCTOPODS (CEPHALOPODA: OCTOPODA: CIRRATA) USING COI AND 16S SEQUENCES

TRISTAN JOSEPH VERHOEFF

Invertebrate Zoology, Tasmanian Museum and Art Gallery, Winkleigh Place, 7018, Rosny Park, Australia
 (e-mail: tristan.verhoeff@utas.edu.au);  <https://orcid.org/0000-0001-5103-8592>

ABSTRACT: Contrasting accounts of taxonomic relationships between finned octopod (Octopoda: Cirrata) taxa complicate species identification and generate nomenclatural instability. A comprehensive analysis based on both 16S and COI mitochondrial gene phylogenies is presented, using all currently accepted genera and approximately 27 putative species (including type species for all genera excepting *Grimpoteuthis*). The goal of this is to stabilise the concepts of genera and families and identify areas needing further systematic research. Four well supported clades are consistent with families Cirroteuthidae, Cirroctopodidae, Grimpoteuthidae, and Opisthoteuthidae across both 16S and COI phylogenies. Family Stauroteuthidae resolves as a sister clade to Cirroteuthidae in some analyses of the COI gene. Combined molecular and morphological similarities suggest that the Cirrata comprises two superfamily level clades, for which Cirroteuthoidea (for Cirroteuthidae and Stauroteuthidae) and Opisthoteuthoidea (for Cirroctopodidae, Grimpoteuthidae, and Opisthoteuthidae) are proposed. The paraphyletic *Cirrothauma* (Cirroteuthidae) contains at least three species, while within the Grimpoteuthidae, *Cryptoteuthis* and *Luteuthis* form clades within a paraphyletic *Grimpoteuthis* clade, indicating a need for further taxonomic assessment. Intra-clade structure within *Opisthoteuthis* is better resolved with COI than 16S data. At least one potentially undescribed *Opisthoteuthis* occurs in the northwestern Pacific, and northeastern Pacific specimens are tentatively referred to *O. bruuni*, representing a significant range expansion. Lastly, using the dates of fossil stem-Octobranchians and fossil cirrates for approximate calibration, a timetree estimated from COI gene data suggests that these cirrate families and most cirrate genera arose within the Late Cretaceous, possibly as part of the Mesozoic marine revolution, between 124–62 million years ago.

KEY WORDS: biodiversity; Cirromorpha; deep-sea; evolution; marine invertebrates, Mollusca; phylogenetics; systematics; taxonomy

INTRODUCTION

Finned octopods (variously attributed to the sub-order Cirrata (Cirrini) [Grimpe, 1916](#)) are generally regarded to be a sister clade to the non-finned octopods (sub-order Incirrata). These two groups have been alternatively elevated to the level of order, Cirroctopoda and Octopoda ([YOUNG 1989](#)) or Cirromorphida and Octopodida ([SANCHEZ et al. 2018](#)). Cirrates retain a robust internal gladius that supports paired mantle fins, and paired cirri that flank the suckers along each of the eight arms – features shared with Jurassic and Cretaceous stem-Octobranchia including *Proteroctopus ribeti* [Fischer et Riou, 1982](#) ([KRUTA et al. 2016](#)), teu-

dopseids ([FUCHS & LARSON 2011a](#)), and relic vampyroteuthids ([ROWE et al. 2022](#)).

Cirrates are far less active and have a more protracted lifestyle than their incirrate relatives. To feed on small benthic invertebrates or planktonic prey, the cirrate's webbing between the arms is extensively developed, and this coordinates with cirri in feeding ([HUNT 1999](#), [GOLIKOV et al. 2023](#)); their radula and salivary glands are reduced or even lost; and the ink sac and gill branchial canal are lost. The loss of the right oviduct and continuous spawning strategy reflect a longer life cycle and reduced reproductive po-



tential (COLLINS & VILLANUEVA 2006, LINDGREN et al. 2012). Rapid movement is achieved in part by fins (e.g., in *Grimpoteuthis*; VILLANUEVA et al. 1997) and in part by medusoid locomotion of arms and webbing (especially in *Opisthoteuthis*; HUNT 1999), with cirroteuthids also relying on passive drifting via the umbrella-like webbing along with gentler medusoid movements (VILLANUEVA et al. 1997). The greatly reduced mantle musculature and smaller pallial opening reduce the effectiveness of jet propulsion (VILLANUEVA et al. 1997, COLLINS & VILLANUEVA 2006).

The classification of cirrates has been the subject of intense systematic revision over recent decades by a variety of authors, the revisions of which have operated from local to regional or global scales, and been based on a variety of molecular techniques and morphological characters and their states (NESIS 1987, VOSS 1988, VOIGHT 1997, O'SHEA 1999, PIERTNEY et al. 2003, PARDO-GANDARILLAS et al. 2021, ZIEGLER et al. 2021) (see Table 1). Consequently, nomenclature at the family and genus level has been quite unstable, aggravated by the poor condition and delicate nature of many specimens, loss or effective disintegration of types, specimen rarity, lack of genetic samples, and disagreement regarding taxonomically informative traits.

The doctoral thesis of HUDELLOT (2000), upon which the work of PIERTNEY et al. (2003) is largely

based, was the first comprehensive molecular appraisal of relationships among cirrate taxa, the authors electing to use the 16S mitochondrial gene for this task. The four families recognised in these studies (Cirroteuthidae Keferstein, 1866, Opisthoteuthidae Verrill, 1896, Grimpoteuthididae O'Shea, 1999, and a new family later named Cirroctopodidae Collins et Villanueva, 2006) were reviewed in the most-recent revision of the suborder by COLLINS & VILLANUEVA (2006), wherein the Stauroteuthidae Grimpe, 1916 and Luteuthididae O'Shea, 1999 were considered to be junior synonyms of the Cirroteuthidae and Grimpoteuthididae, respectively. Conflicting systematic appraisals are provided by HOCHBERG et al. (2014) and VECCHIONE et al. (2016), who inexplicably recognised Stauroteuthidae but refused to recognise Grimpoteuthididae (even though the former had far less molecular support than the latter).

With more sequence data for more species and genes, including for the COI gene which has never been thoroughly investigated for the cirrates, a more comprehensive appraisal of relationships among cirrate octopods is possible. Results provide a more stable nomenclature for cirrate taxonomy, and through estimating divergence times allow for more detailed evolutionary studies. Further research that is required to better understand relationships between these deep-sea octopods is identified.

Table 1. Historical treatments of cirrate octopod genera in family level clades. NESIS (1987) is used as a starting point. Genera currently synonymized are given in parentheses below the accepted genus. Abbreviations: CirroT – Cirroteuthidae, CirroC – Cirroctopus, Grimp – Grimpoteuthididae, Lut – Luteuthididae, Opis – Opisthoteuthidae, Stauro – Stauroteuthidae

Genus	NESIS (1987)	VOSS (1988)	O'SHEA (1999)	PIERTNEY et al. (2003); COLLINS & VILLANUEVA (2006)	HOCHBERG et al. (2014); VECCHIONE et al. (2016)	PARDO-GANDARILLAS (2021)	ZIEGLER et al. (2021); Herein
<i>Cirroteuthis</i>	CirroT	CirroT	CirroT	CirroT	CirroT	CirroT	CirroT
<i>Cirrothauma</i>	CirroT	CirroT	CirroT	CirroT	CirroT	CirroT	CirroT
<i>Stauroteuthis</i> (<i>Chunioteuthis</i>)	CirroT	Stauro	NA	CirroT	Stauro	CirroT	CirroT**
<i>Grimpoteuthis</i> (<i>Enigmatiteuthis</i>)	CirroT	Opis	Grimp	Grimp	Opis	Opis	Grimp
<i>Cryptoteuthis</i>	NA	NA	NA	Grimp	Opis	Opis	Grimp
<i>Luteuthis</i>	NA	NA	Lut	Grimp	Opis	Opis	Grimp
<i>Opisthoteuthis</i> (<i>Cirroteuthopsis</i>)	Opis	Opis	Opis	Opis	Opis	Opis	Opis
<i>Cirroctopus</i> *	NA	NA	Opis	CirroC	CirroC	CirroC	CirroC

Incertae cedis and notes: *Froekenina* Hoyle, 1904 – possible synonym of *Stauroteuthis* (see VERHOEFF 2023).

Laetmoteuthis Berry, 1913 – taxonomic placement never satisfactorily investigated.

* *Cirroctopus* was synonymized under *Grimpoteuthis* (as *G. mawsoni*) until resurrected by O'SHEA (1999).

** As discussed later, *Stauroteuthis* does resolve as family Stauroteuthidae in one analysis, but not consistently.

MATERIAL AND METHODS

Abbreviations: 16S – 16Svedberg ribosomal RNA (ribonucleic acid) mitochondrial gene; BI – Bayesian Inference; BIC score – Bayesian Information Criterion score; COI – cytochrome c oxidase subunit I mitochondrial gene; Ma – million years ago; ML – maximum likelihood; MP – maximum parsimony; NJ – neighbour joining; NIWA – National Institute of Water & Atmospheric Research Ltd. (New Zealand); NMNS – National Museum of Natural Science (Taichung, Taiwan).

ACQUISITION OF MOLECULAR SEQUENCES AND ISSUES WITH SEQUENCE IDENTITIES

All available cirrate 3'-end 16S and COI mitochondrial sequences were sourced from GenBank and BOLD databases. For whole mitochondrial sequences, aforesaid gene sequences were isolated, the 16S and COI genes being antisense to each other. Sequences, species identifications, and capture localities are detailed in Table 2 (16S) and Table 3 (COI).

In all cases, excepting the following, existing identifications are uncritically accepted. GenBank sequence AF487303 from offeastern Brazil (RV *Thalassa* station E-522, 13°30.495–29.472'S, 38°38.977–37.943'W, 1,044–1,275 m, per MINCARONE *et al.* 2014) is provisionally attributed to *O. agassizii* Verrill, 1883, the type species of *Opisthoteuthis*, because this is the only local species (VILLANUEVA *et al.* 2002a). Other sequences identified to *Opisthoteuthis* sp. are referred to *O. calypso* Villanueva, Collins, Sánchez *et Voss*, 2002 (a) (AJ315374), *O. massyae* (Grimpe, 1920) (AY557515, AF377961), given their clustering with known sequences in early tree constructions, and *O. dongshaensis* Lu, 2010 (AJ315375) given that this is from the *Opisthoteuthis* tissue sample given by C.C. Lu for inclusion in HUDELLOT (2000) and from specimens later described by LU (2010) as *O. dongshaensis*. Genbank sequence AJ315377 of HUDELLOT (2000) referred to *L. dentatus* O'Shea, 1999 was based on a sample sent by O'Shea in mid-1999 from (almost certainly) NIWA 103765 (collected March 1999) – a specimen figured by O'SHEA & LU (2002: fig. 4). PIERTNEY *et al.* (2003) erroneously referred to this sample as *L. shuishi* O'Shea *et Lu*, 2002 (NMNS 002157-00088). Many COI sequences attributed to *Cirroctopus* sp. are herein attributed to *C. mawsoni* (Berry, 1917) given that they were collected from George V Land (Antarctica) close to the type locality (within the adjacent Adélie Land) (CEAMARC V3 voucher specimens; UNDHEIM *et al.* 2010).

PHYLOGENETIC INFERENCE

Alignment, trimming, and phylogenetic tree construction was conducted in MEGA X (KUMAR *et al.* 2018). Sequencing data alignment utilised MUSCLE with settings for non-coding DNA for 16S rRNA gene data and protein coding DNA for COI. For COI, alignment was further checked by manually examining the translated amino acid sequence (ensuring no internal stop codons). Phylogenetic trees were inferred using maximum-likelihood (ML), neighbour-joining (NJ), maximum-parsimony (MP), and Bayesian inference (BI) methods. For ML trees, the substitution model and settings for rates among sites were estimated using MEGA X's inbuilt 'Model Selection' tool (substitution type = nucleotide, and gaps/missing data treatment set as per trees defined later), selecting the model with the lowest (most ideal) BIC score. For each gene the final trees generally agreed with each in topology and approximate branch lengths (none being obviously more 'accurate'), with two trees (ML and MP) combined as an illustration, and with the Bayesian inference (BI) trees illustrated separately. For both 16S and COI analyses, *Octopus vulgaris* Cuvier, 1797 (a generic incirrate octopus) was selected as an outgroup, as the Incirrata have been shown to be a sister group to all Cirrata (e.g., TAITE *et al.* 2023).

All phylogenies other than Bayesian inference (ML, MP, and NJ) for both 16S and COI were tested with the bootstrap method (using 1,000 replications). Bayesian inference (BI) analyses used BEAST (Bayesian Evolutionary Analysis Sampling Trees) v1.10.4 (SUCHARD *et al.* 2018), set to run 10 million generations of MCMC (Markov Chain Monte Carlo), sampling log parameters every 1,000 generations, and discarding the first million generations as burn-in. Tracer v1.7.2 (RAMBAUT *et al.* 2018) was used to confirm the effective sampling size (ESS) and tree likelihood values, and FigTree v1.4.4 (RAMBAUT 2016) was used to illustrate BI trees.

16S GENE ANALYSIS

For 16S rRNA gene analyses the final alignment used was 538 bp (140 bp parsimony informative, or 26.0%). ML analysis was conducted with gaps/missing data treatment set to 'partial deletion', and with site coverage cut-off = 90% (i.e., considering sites present in at least 90% of sequences). This analysis included 440 sites (bp positions) in the final dataset, and the HKY+G+I model was used (Hasegawa–Kishino–Yano model; discrete gamma distribution to model evolutionary rate differences among sites, 5



Table 2. The 16S rRNA partial sequences used in this study. * – whole mitochondrial sequence. ** – sequences with regions of poor-quality (excluded from phylogenetic trees). † – ON367806 and MT725732 were both extracted from the same specimen (NIWA 95257) with the former being used herein. Abbreviations: N – north, NE – northeast, NW – northwest, S – south, SW – southwest.

Species	Location	GenBank / BOLD ID	Registration / voucher IDs
<i>Cirroteuthis muelleri</i>	NE Atlantic N Atlantic, Mid-Atlantic Ridge	AF487284 ON367802*	Discovery 13945 Bigelow 2009 Stn. 28, a200023
<i>Cirrothauma magna</i>	N Atlantic, Charlie Gibbs fracture zone	ON367803*	Bigelow 2009 Stn. 27, a200026
<i>C. murrayi</i>	N Atlantic, Charlie Gibbs fracture zone	ON367801*	Bigelow 2009 Stn. 29, a200019
<i>Cirrothauma</i> sp. <i>Stauroteuthis syrtensis</i>	NE Atlantic	AF487282	Discovery 13945
	NE Atlantic	AF487283	Discovery 13924
	NE Pacific, Gorda Ridge	ON367804*	FMNH 309245
	N Atlantic	DQ280042	
	NE Atlantic	AF487290	Scotia 404
	NE Atlantic	AF487289	Scotia 411b
	NE Atlantic	AF487288	Scotia 406a
	NE Atlantic	AF487287	Scotia 411a
	NE Atlantic	AF487286	Discovery 13919b
	NE Atlantic	AF487285	Discovery 13919a
	NW Atlantic	AJ252769	
	NE Atlantic, N Rockall Trough	ON367808*	a201565
	N Atlantic	AF487296**	Bahia II e537
	SW Atlantic, South Georgia	AY545102	AGSG 97-21-9
<i>S. gilchristi</i>	SW Atlantic	AF487295	AGSG21-10
<i>Grimptoteuthis discoveryi</i>	NE Atlantic	AF487294	AGSG21-8
		AF487293	AGSG21-15
		AF487292	AGSG21-11
		AF487291	AGSG21-1
		AF487312	Discovery 11908 68c
		AF487311	Discovery 12930 60
		AF487310	Challenger 134 6a
		AF487309	Challenger 134 6b
		AF487308	Discovery 13925c
		AF487307	Discovery 133692b
<i>G. imperator</i> <i>G. sp.</i>	NW Pacific	MW575539	ZMB MOLL 240160
	NE Atlantic, N Hebrides Terrace	ON367810*	S200183
	NE Atlantic	MT435502	Discovery 13960b
<i>Cryptoteuthis brevibracchiata</i>	NE Atlantic	ON367809*	NIWA 50746
<i>Luteuthis dentatus</i>	SW Pacific, New Zealand	ON367806*/ MT725732†	NIWA 95257
<i>Cirroctopus glacialis</i> <i>C. mawsoni</i> <i>C. hochbergi</i> <i>Opisthoteuthis agassizii</i> <i>O. bruuni</i>	Antarctica, SW Atlantic S Indian Ocean, Heard Island SW Pacific, New Zealand W Atlantic, eastern Brazil SE Pacific, off Chile	AJ315377	NIWA 103765
		AF487304	
		ON367800*	a200013
		AJ315376	NIWA (?)
		AF487303	<i>Thalassa</i> E-522
<i>O. bruuni</i>	SE Pacific, off Chile	MT725734	MNHNCL 300139
		MT725733	MNHNCL 300138



Table 2 continued

Species	Location	GenBank / BOLD ID	Registration / voucher IDs
<i>O. sp. 'Monterey'</i>	NE Pacific, Monterey Bay	ON367811* AF110100.2	USNM 1660928 USNM, same specimen as COI AF075419.1 (ANDERSON 2000)
<i>O. californiana</i>	NW Pacific, Bering Sea	AJ315373 ON367799*	a200005
<i>O. calypso</i>	Mediterranean Sea, Sardinian Channel	FJ403541	Haplotype 9 specimens (CUCCU et al. 2009)
		FJ403542	
<i>O. chathamensis</i>	SE Atlantic, off Namibia	AJ315374	B-PCHH2001
	SW Pacific, New Zealand	MT216982	NZP22
<i>O. depressa</i>	NW Pacific, off Japan	AB191117	
<i>O. dongshaensis</i>	NW Pacific, Taiwan	AJ315375	NCHU
	NE Pacific, California	AJ252768	
<i>O. grimaldii</i>	NE Atlantic, N Hebrides Terrace	ON367812*	BMNH 20200402
<i>O. hardyi</i>	SW Atlantic, off Falkland Islands	FJ785404	BMNH 20080844
	SW Atlantic, off Falkland Islands	FJ785403	BMNH 20080845
	SW Atlantic, off South Georgia	AF487302	AGSG-25
<i>O. massyae</i>	NE Atlantic, Scotland	AY545103	00/160C
	NE Atlantic	AF487301	Scotia 402
	NE Atlantic	AF487300	Scotia 414
	NE Atlantic	AF487299	NMSZ199158.077
	NE Atlantic	AF487298	NMSZ199158.076
	NE Atlantic	AF487297	NMSZ199158.001
	NE Atlantic, North Sea	AJ315372	
	NE Atlantic, S Hebrides Terrace	ON367805*	BMNH 20200399
	NE Atlantic, N Hebrides Terrace	ON367807*	a200669
	SE Atlantic, off Namibia	AY616970	2222/880/2
	SE Atlantic, off South Africa	AJ414702	
	SE Atlantic, off Namibia	AJ315371	
	SE Atlantic?	AF299265	2222/880/2
<i>O. mero</i>	SW Pacific, New Zealand	MT216998	NIWA95194
		MT216997	NIWA106093
<i>O. sp. 'JN-2021'</i>	NW Pacific?	MW354513*	JN-2021

Table 2 and Table 3 institutional and voyage acronyms: BMNH – British Museum of Natural History (now Natural History Museum UK); CEAMARC – Collaborative East Antarctic Marine Census, Voyage 3; FMNH – Field Museum of Natural History; LACM – Natural History Museum of Los Angeles County; MBARI – Monterey Bay Aquarium Research Institute; MNHNCL – National Museum of Natural History, Santiago, Chile; NIWA – National Institute of Water and Atmospheric Research; NMSZ – National Museums of Scotland; SBMNH – Santa Barbara Museum of Natural History; USNM – United States National Museum (now Smithsonian National Museum of Natural History); SAM – South African Museum; UCONN – University of Connecticut; ZMB MOLL – Zoologisches Museum Berlin Molluskensammlung

gamma categories, G parameter = 0.6088; allowing evolutionarily invariable sites, 44.97% sites) with BIC score = 6170.1. Per MEGAX, the initial trees for the heuristic search were obtained automatically by applying NJ (and slightly improved 'BioNJ') algorithms to the matrix of pairwise distances (matrix estimated using the maximum composite likelihood method) and selecting topology with a superior log-likelihood value (in this case –2587.6).

For MP analysis tree construction used Subtree-Pruning-Regrafting (SPR) as the MP search method (other tree inference options were default; initial tree

obtained by random addition of sequences in 10 replicates); gaps and missing data treatment was set to 'partial deletion' (site coverage cut-off 90%), 440 positions in final dataset (consistency index = 0.503, retention index = 0.902, composite index = 0.498 for all sites or 0.454 for parsimony-informative sites, most parsimonious tree length = 391).

Neighbour-Joining (NJ) tree analysis used a nucleotide substitution method/model set to p-distance (including transitions and transversions), rates among sites was assumed to be uniform. All positions with < 90% site coverage were eliminated),



Table 3. The COI sequences used in this study. * – whole mitochondrial sequence. ** – specimens with additional data from [CARLINI et al. \(2001\)](#). Abbreviations see [Table 2](#)

Species	Location	GenBank / BOLD ID	Registration / voucher IDs
<i>Cirroteuthis muelleri</i>	N Atlantic, Mid-Atlantic Ridge	ON367802*	Bigelow 2009, a200023
<i>Cirrothauma magna</i>	N Atlantic, Charlie Gibbs fracture zone	ON367803*	Bigelow 2009, a200026
<i>Cirrothauma murrayi</i>	N Atlantic, Charlie Gibbs fracture zone	ON367801*	Bigelow 2009, a200019
	NE Pacific, Pt Conception, California,	AF000034	RV New Horizon, NHI-95-291**
	NW Atlantic	GU145063	UCONN Mo18.1.1
<i>Cirrothauma</i> sp.	NE Pacific, Gorda Ridge	ON367804*	FMNH 309245
<i>Stauroteuthis syrtensis</i>	North Atlantic	AF000067	FV Contender 1995**
	NE Atlantic, Rockall Trough	ON367808*	a201565
<i>S. gilchristi</i>	SW Atlantic, off South Georgia	AY545186	AGSG 97-21-9
<i>Grimpoteuthis imperator</i>	NW Pacific	MW570977	ZMB MOLL 240160
<i>G.</i> sp.	NE Atlantic, N Hebrides Terrace	ON367810*	S200183
<i>Luteuthis dentatus</i>	SW Pacific, New Zealand	ON367809*	NIWA 50746
	SW Pacific, New Zealand	ON367806*	NIWA 95257
<i>Cirroctopus glacialis</i>	SW Atlantic, Antarctic Peninsula	AF377962	USNM**
<i>C. mawsoni</i>	S Indian Ocean, Heard Island	ON367800*	a200013
	Terre Adélie/George V Land, Antarctica	GU073588	CEAMARC V3 voucher 3120
		GU073580	CEAMARC V3 voucher 2773
		GU073579	CEAMARC V3 voucher 2772
		GU073577	CEAMARC V3 voucher 2774
		GU073576	CEAMARC V3 voucher 2742
		GU073575	CEAMARC V3 voucher 2741
		GU073529	CEAMARC V3 voucher 1521
		GU073528	CEAMARC V3 voucher 1520
		GU073525	CEAMARC V3 voucher 1439
		GU073520	CEAMARC V3 voucher 1346
<i>Opisthoteuthis borealis</i>	NW Atlantic, N Labrador Sea	LC573902	GLI001
<i>O. californiana</i>	NW Pacific, Bering Sea	ON367799*	a200005
<i>O. depressa</i>	NW Pacific, Japan	AB191282	
	NW Pacific, Japan	AB860128	ODCOI1
<i>O. grimaldii</i>	NE Atlantic, N Hebrides Terrace	ON367812*	BMNH 20200402
<i>O. massyae</i>	NE Atlantic, off Scotland	AY545187	00/160C
	NE Atlantic, S Hebrides Terrace	ON367805*	BMNH 20200399
	NE Atlantic, N Hebrides Terrace	ON367807*	a200669
	Atlantic (?)	AY557515	SBMNH see LINDGREN et al. (2004)
	SE Atlantic, South Africa (?)	AF377961	SAM, CYV-2001**
<i>O.</i> sp. 'Monterey'	NE Pacific, Monterey Bay	ON367811*	S200351, USNM 1660928
	NE Pacific, Monterey Bay	AF075419	USNM, same specimen as 16S AF110100 see ANDERSON (2000)
	NE Pacific, off Los Angeles	DISA355-18 (BOLD)	LACM, DISCO:4111
	NE Pacific, Monterey Bay	AF377963	MBARI, CYV-2001**
<i>O.</i> sp. 'JN-2021'	NW Pacific (?)	MW354513*	JN-2021

440 positions in final dataset (the optimal NJ tree had a sum of branch lengths = 0.770).

Bayesian Inference (BI) tree analysis used the same HKY+G+I model as the ML analysis, using 4 gamma categories, partitioning into three codon positions, and using UPGMA as a starting tree.

COI GENE ANALYSIS

The same set of analyses (ML, MP, NJ, and BI) was conducted using all available COI data. Final COI alignment comprised 661 bp (of which 227 bp, or 34.3%, were parsimony informative).

ML analysis was conducted generally as for the 16S sequences, except using a GTR+G+I model (General Time Reversible substitution model; discrete gamma distribution, G parameter = 1.051; allowing for invariant sites, 55.74% sites) with lowest BIC score = 9949.4. Gaps/missing data treatment was set to 'partial deletion', site coverage cut-off = 90% (resulting in 612 sites in the final dataset), and all codon positions and noncoding sites were considered in ML analysis (highest log-likelihood for initial replicate tree = -4524.3).

MP analysis of COI was as per the 16S MP tree, but included all codon positions and noncoding sites, again with site coverage cut-off = 90%, with 612 sites in final dataset (consistency index = 0.403, retention index = 0.756, composite index = 0.314 for all sites or 0.304 for parsimony-informative sites, most parsimonious tree length = 909).

NJ analysis was also as for the 16S NJ tree, but considering all codon positions and noncoding sites, and with the optimal tree with sum branch length = 1.216 (612 sites in final dataset).

BI analysis used the same GTR+G+I model as the ML analysis, and otherwise was conducted as per analysis of 16S.

P-DISTANCE CALCULATIONS

For both 16S and COI sequencing data, the extent of sequence similarity and difference between and within putative family level clades (supported by molecular phylogenies) was calculated in order to partly assess robustness of different clades. Distance estimation used P-distance as the method/model (including transitions + transversions as substitutions), rates among sites was set as uniform rates, and gaps/missing data treatment was set to pairwise deletion. Average, minimum, and maximum distances were calculated within each group, and average distance was calculated between each group.

RESULTS

PHYLOGENETIC ANALYSES

Phylogenetic trees (16S and COI) were generated covering all currently accepted cirrate genera and included sequences for type species of all accepted genera other than *Grimpoteuthis*.

Phylogenetic trees using 16S covered a broader range of 26 putative species but had fewer parsimony informative sites and shorter sequences compared with COI (26% of 538 bp sites parsimony informative vs. 34% of 661 sites). The 16S phylogenetic analyses supported four monophyletic families, a ba-

TIMETREE ANALYSIS

To estimate cirrate clade divergence times, a timetree was constructed in MEGA X using the in-built RelTime-ML TimeTree estimation tool (MELLO 2018). Because COI sequences had greater bp coverage than 16S sequences, greater percentage of parsimony informative sites (34% vs. 26%), and considerably greater tree log-likelihood values, COI data were used in timetree estimation.

The previously constructed ML phylogenetic tree with site-coverage cut-off 90% was used (supplying the COI alignment file and a Newick format export of the tree as inputs for the TimeTree tool). For TimeTree parameters the GTR model was used with discrete gamma distribution (G parameter = 1.299), and evolutionarily invariable sites (58.99% of sites). For timetree calibration, previous molecular clock analyses indicated Jurassic or Early Cretaceous (~210–110 Ma) divergence of the Incirrata from the Cirrata (TANNER et al. 2017). However, FUCHS & SCHWEIGERT (2018) hypothesised that Cirrata and Incirrata arose from the Patellocopodidae Fuchs et Schweigert, 2018, represented by the genera *Pearceiteuthis* Hewitt et Jagt, 1999 (Callovian, 166–163 Ma) and *Patelloctopus* Fuchs et Schweigert, 2018 (Kimmerdigian, 157–152 Ma). Secondly, beaks of fossil Cirrata (*Paleocirroteuthis* Tanabe, Trask, Ross et Hikida, 2008) more closely resembling those of cirroteuthids than opisthoteuthids are known from the Cretaceous Santonian (86–84 Ma) and Lower Campanian (84–81 Ma) (TANABE et al. 2008). Therefore, the node for the earliest division of Cirrata was given an upper bound of 164.5 Ma (mid-Callovian) when putative stem-cirrates were apparent, and a lower bound of 85 Ma (mid-Santonian) by which time cirrates resembling cirroteuthids had likely diverged from other cirrates. The calibrated node was set to 'uniform distribution', with the estimated log likelihood value of the resulting timetree being -4543.8.

sal-most Cirroteuthidae (including *Stauroteuthis* sensu COLLINS & VILLANUEVA 2006) (bootstrap support 98% ML, 93% MP, and BI posterior probability (post-prob.) of 1.00), Cirroctopodidae (98–99% ML & MP, BI post-prob. 1.00), Grimpoteuthididae (72% ML, 93% MP, BI post-prob. 1.00), and Opisthoteuthidae (63% ML, 54% MP, Bi post-prob. 1.00). The phylogenetic trees for ML and MP are shown in Figure 1, BI tree in Figure 2. Within Cirroteuthidae, *Stauroteuthis* and *Cirroteuthis* formed clades (97–99% support in ML and MP, 1.00 BI post-prob.) within a consistently polyphyletic *Cirrothauma*. *Stauroteuthis syrtensis* Verrill,

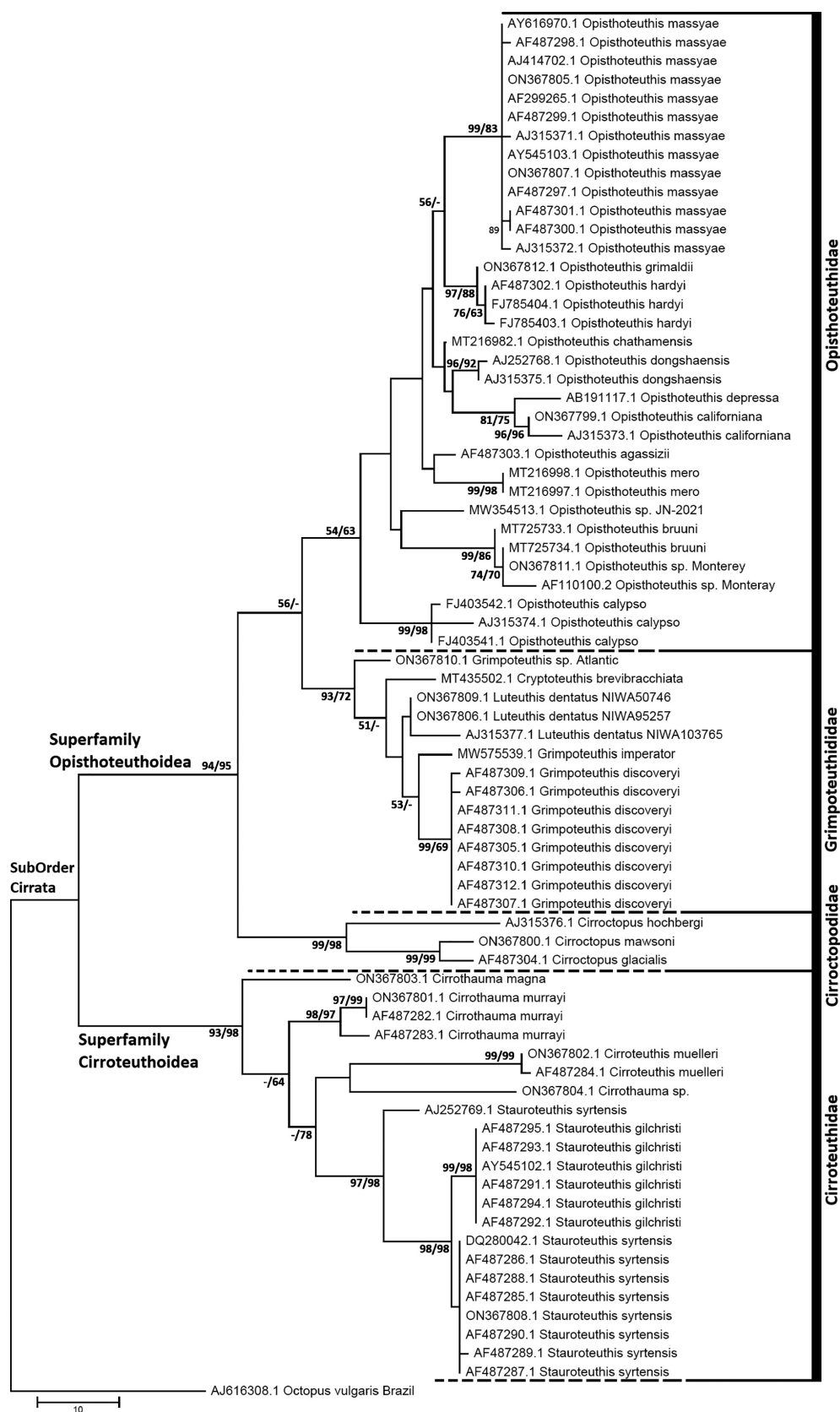
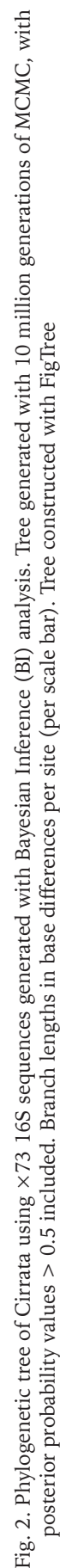


Fig. 1. Phylogenetic tree of Cirrata using $\times 73$ 16S sequences as a combined result for Maximum Likelihood (ML) and Maximum Parsimony (MP) trees, both analyses with a site-coverage cutoff of 90%, tested with 1,000 bootstrap replicates. Topology is that of the MP tree, and bootstrap support values $> 50\%$ are included next to clades in format 'MP value/ML value'. Branch lengths measured in number of substitutions per site (per scale bar). Tree constructed with MEGA X





1879 did not consistently separate from *S. gilchristi* (Robson, 1924) (though this may have been due to one *S. syrtensis* sequence being of poorer quality (AJ252769, and this sequence was excluded from later P-distance calculations). Other than this suspect *S. syrtensis* sequence, both *S. syrtensis* and *S. gilchristi* formed well supported clades, especially with BI (post-prob. values 0.87 and 1.00 respectively). Within Grimpoteuthidae, *Grimpoteuthis* was polyphyletic, with *Grimpoteuthis* sp. being sister to a clade containing *Cryptoteuthis* Collins, 2004, *Luteuthis* O'Shea, 1999, *G. imperator* Ziegler et Sagorny, 2021, and *G. discovery* Collins, 2003. The bootstrap support for Opisthoteuthidae in 16S phylogenies was lower with ML and MP analyses compared to other families, but still had a BI posterior probability of 1.00 (the same as other families). Within Opisthoteuthidae, species generally resolved as clades (many well supported). Interestingly, *O. grimaldii* (Joubin, 1903) and *O. hardyi* Villanueva, Collins, Sánchez et Voss, 2002(a) were very closely related (clade with 88–97% support in ML and MP, 1.00 BI post-prob.), but still resolved as likely separate species (*O. hardyi* forming a clade with 63–76% ML and MP support, 0.99 BI post-prob.) sister to *O. grimaldii*. *Opisthoteuthis bruuni* (Voss, 1982) (southeastern Pacific) and *O. sp.* 'Monterey' (Monterey Bay, northeastern Pacific) were polyphyletic within a well-supported clade, suggesting that they were conspecific, though, as with *O. grimaldii* and *O. hardyi*, some samples did form a well-supported sub-clade, indicating a need for further systematic assessment of eastern Pacific *Opisthoteuthis*. Higher level clades within Opisthoteuthidae were more strongly supported by the BI analysis of the 16S dataset, and two notable clades (BI post-prob. values 0.97–0.99) were one containing 3 species (*O. calypso*, *O. californiana* Berry, 1949, and *O. depressa* Ijima et Ikeda, 1895), and another containing all other species excluding *O. bruuni* / *O. sp.* 'Monterey'.

Clade structure linking the Opisthoteuthidae, Grimpoteuthidae, and Cirrotopodidae varied, and was uncertain in MP and ML analyses (support values < 60%), while in BI analysis the Opisthoteuthidae and Grimpoteuthidae were more closely related (clade with 0.97 post-prob.). These three families formed a well-supported clade with 94–95% support in ML and MP, while in BI this clade had much lower support (0.13 post-prob.).

The NJ tree for 16S data (not shown) produced a topology comparable to that of ML and MP trees, but with increased bootstrap support for many clades. The four families were resolved well: Cirroteuthidae (97%), Cirrotopodidae (99%), Grimpoteuthidae (98%), and Opisthoteuthidae (71%). The latter three families again resolved as a well-supported clade (97% support), and as with MP and ML analyses the

family Opisthoteuthidae had lower support (though still > 70%).

Phylogenetic trees for COI had fewer sequences and covered only 18 taxa but included more parsimony-informative sites (ML and MP see Fig. 3, BI see Fig. 4). These trees produced similar topologies for families and genera, but with several interesting points of similarity and difference to the 16S trees.

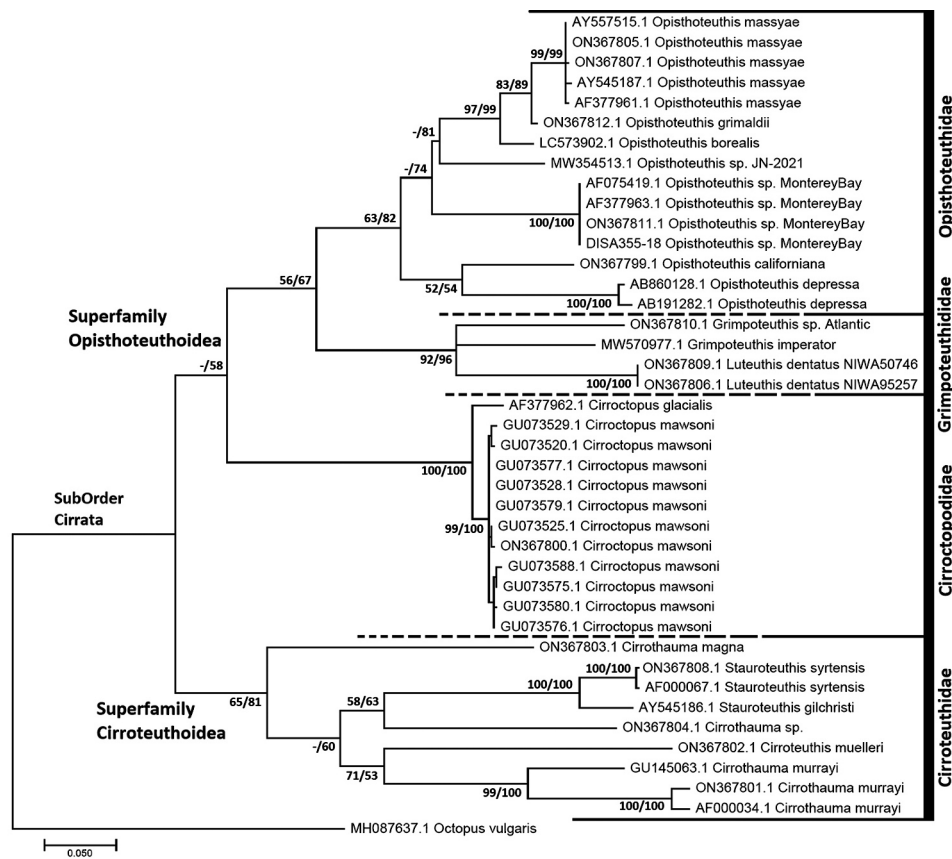
In the ML and MP trees, and NJ tree (not shown), Cirroteuthidae (bootstrap support 65–81%) again resolved as a clade basal to a more weakly-supported clade (55–58%) containing Cirrotopodidae (100% support), Grimpoteuthidae (92–96%), and Opisthoteuthidae (63–82%), the latter two also forming a clade with 56–67% support. Within Cirroteuthidae, *Stauroteuthis* again formed a clade (100% support), while it and *Cirroteuthis* were nested within a polyphyletic *Cirrothauma*. Notably, BI analysis resolved *Stauroteuthis* as a clade sister to one containing both *Cirrothauma* and *Cirroteuthis*, thus supporting two families Stauroteuthidae and Cirroteuthidae. However, while the former had high support (post-prob. 1.00) the latter had very low support (post-prob. 0.31), meaning the separation of these two families was only tentative. BI analysis again resolved Cirrata as two clades with high support (post-prob 0.99–1.00), one containing Cirroteuthidae (including Stauroteuthidae) and the other clade containing the other three families, Grimpoteuthidae, Opisthoteuthidae, and Cirrotopodidae, with these three families all having high BI post-prob. values of 1.00.

Unlike in 16S analyses, *Luteuthis* formed a clade (100% support, post-prob 1.00) but this was again within a polyphyletic *Grimpoteuthis*. Within *Opisthoteuthis*, and unlike in 16S analyses, COI MP, ML, NJ (not shown), and BI analyses consistently resolved clades of species within the genus. *Opisthoteuthis depressa* and *O. californiana* formed a weakly-supported clade (52–54% support, post-prob. 0.99) sister to a clade containing five other species (74% support, post-prob. 1.00), within which *O. borealis* Collins, 2005, *O. grimaldii*, and *O. massyae* formed a clade (97–99% support, post-prob. 1.00).

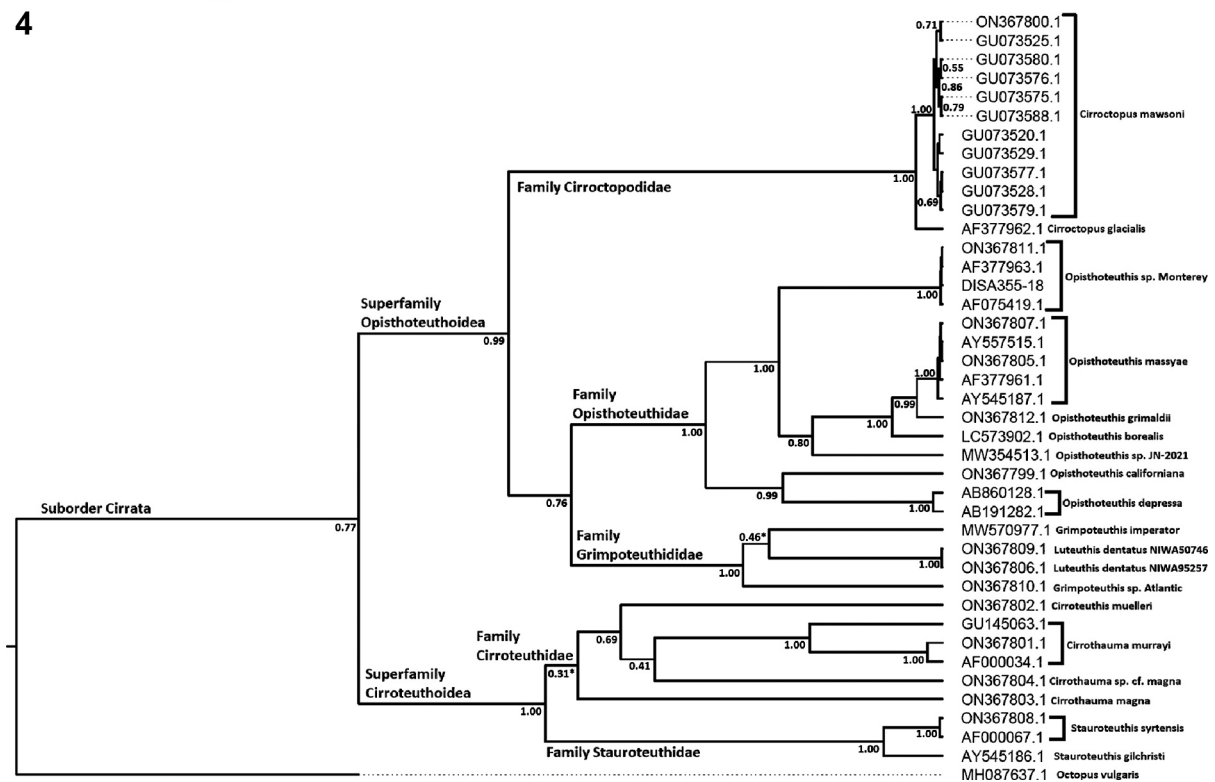
For both the 16S and COI datasets, it was apparent that additional (potentially undescribed) species were present. Notably in the polyphyletic *Cirrothauma*, three species *C. magna* (Hoyle, 1885), *C. sp.*, and *C. murrayi* Chun, 1911 were all well separated from each other, and variable in placement between the different analyses. Even *C. murrayi*, while always forming a well supported clade (97–99% support or post-prob. 0.87–1.00, for 16S and COI analyses) was possibly comprised of two species, with one sequence appearing relatively distinct from the other two (see Figs 1–4). Overall, COI and 16S phyloge-



3



4



Figs 3–4. Phylogenetic trees of Cirrata using $\times 41$ COI sequences: 3 – combined results for ML and MP trees, site-coverage cutoff of 90%, tested with 1,000 bootstrap replicates, topology is that of the ML, and bootstrap support values $> 50\%$ are included next to clades in format ‘MP value/ML value’. Branch lengths in substitutions per site (per scale bar). Tree constructed with MEGA X. 4 – BI tree generated with 10 million MCMC generations, and with posterior probability values > 0.5 included (values below this retained only for comparison and marked with ‘*’). Trees constructed with FigTree



nies suggest underappreciated species diversity in the Cirroteuthidae.

Within (intra)- and between (inter)-group genetic distances (P-distances; pairwise deletion) for the four putative families, for both 16S and COI data, were calculated and are presented in Table 4 (while Stauroteuthidae may have been apparent in the single COI BI analysis, this was the only analysis, and even in this the separation from Cirroteuthidae was weak, thus while Stauroteuthidae may be a valid family, it is not recognised herein). Inter-family genetic distances were consistently greater in COI compared to 16S, the greatest average inter-family genetic distance was for the Cirroteuthidae vs. Cirroctopodidae (15.5% 16S; 18.4% COI). The lowest average distance was between Opisthoteuthidae and Grimpoteuthididae (7.1% 16S; 14.2% COI), though this was comparable to the distance between Opisthoteuthidae and Cirroctopodidae (10.9% 16S; 15.1% COI) and Grimpoteuthididae and Cirroctopodidae (11.2% 16S; 15.9% COI). Average P-distances between Cirroteuthidae and Grimpoteuthididae (12.6% 16S; 18.0% COI) and Opisthoteuthidae (13.1% 16S; 18.3% COI) were between these.

Intra-family P-distances were again higher for COI datasets compared to 16S (with the exception of Cirroctopodidae) (Table 4), and were consistently lower than inter-family distances, except for the intra-Cirroteuthidae distance for COI (14.5% average) which was comparable to the lowest inter-family P-distance for COI (giving some support for Stauroteuthidae as a distinct family – as indicated by the COI BI analysis). For 16S, genetic intra-family P-distances were lowest in Grimpoteuthididae (1.7% average), followed by Opisthoteuthidae (3.6% average), Cirroteuthidae (3.9% average), and Cirroctopodidae (6.3% average); whereas COI intra-family P-distances were lowest in Cirroctopodidae (0.8% average), followed by Opisthoteuthidae (8.3% average), Grimpoteuthididae (9.4% average), and

Cirroteuthidae (14.5% average). Overall, inter- vs. intra-family P-distances were consistent with four families.

SYSTEMATIC PROPOSALS

For both 16S and COI phylogenetic trees (across ML, MP, NJ, and BI trees), robust clades formed at the superfamily level, with Cirroteuthidae (including Stauroteuthidae) forming a sister clade to that containing other cirrate families. These two higher-level clades are consistently reported in other molecular studies that include Cirrata (PIERTNEY et al. 2003, SANCHEZ et al. 2018, PARDO-GANDARILLAS et al. 2021, ZIEGLER & SAGORNY 2021, TAITE et al. 2023). Importantly, the morphology and lifestyle of these taxa also differ. Consequently, the following superfamily level clades are proposed, with the formal recognition of these superfamilies hopefully assisting understanding of cirrate evolutionary relationships and providing a framework for further study:

Superfamily Cirroteuthoidea nov.

Diagnosis. Cirrates with secondary (complex) webbing, elongate cirri (length > 4–10 × maximum sucker diameter), and sepioid gills.

Families. Cirroteuthidae (including Stauroteuthidae).

Remarks. Essentially pelagic or benthopelagic; spending the majority of time in the water column and only briefly contacting the seafloor for feeding (COLLINS & VILLANUEVA 2006, GOLIKOV et al. 2023). Central arm sucker acetabular chamber reduced in *Stauroteuthis*, *Cirroteuthis*, and *Cirrothauma*, with some suckers elevated on fleshy stalks, and for *Stauroteuthis* at least, bioluminescent (ALDRED et al. 1983, JOHNSEN et al. 1999, VERHOEFF 2022). Gill lamellae counts of *Stauroteuthis* are lower than *Cirroteuthis* and *Cirrothauma*, and with increased lamellae branching, but they remain relatively elongate and sepioid (YOUNG & VECCHIONE 2002).

Table 4. P-distances within and between putative family level clades for cirrates from 16S sequences (×72; 538 bp in final alignment) and COI sequences (×40; 661 bp in final alignment), removing all ambiguous positions (pairwise deletion). P-distances are converted to percentages

Comparison	16S 3'-end		COI	
	Average	Min–Max difference	Average	Min–Max difference
Intra Grimpoteuthididae	1.65%	0.00–4.03%	9.40%	0.00–11.66%
Intra Opisthoteuthidae	3.60%	0.00–7.76%	8.31%	0.00–12.69%
Intra Cirroteuthidae	3.94%	0.00–9.21%	14.54%	0.31–18.00%
Intra Cirroctopodidae	6.26%	2.54–8.80%	0.082%	0.00–3.23%
Opisthoteuthidae vs. Grimpoteuthididae	7.09%	4.88–9.98%	14.19%	13.03–16.41%
Opisthoteuthidae vs. Cirroctopodidae	10.90%	8.83–13.48%	15.08%	13.92–16.26%
Grimpoteuthididae vs. Cirroctopodidae	11.18%	9.31–12.67%	15.88%	15.18–16.64%
Grimpoteuthididae vs. Cirroteuthidae	12.57%	9.23–14.90%	17.96%	15.80–19.60%
Opisthoteuthidae vs. Cirroteuthidae	13.07%	9.84–15.08%	18.26%	13.99–20.41%
Cirroctopodidae vs. Cirroteuthidae	15.49%	13.03–17.22%	18.41%	16.41–19.57%

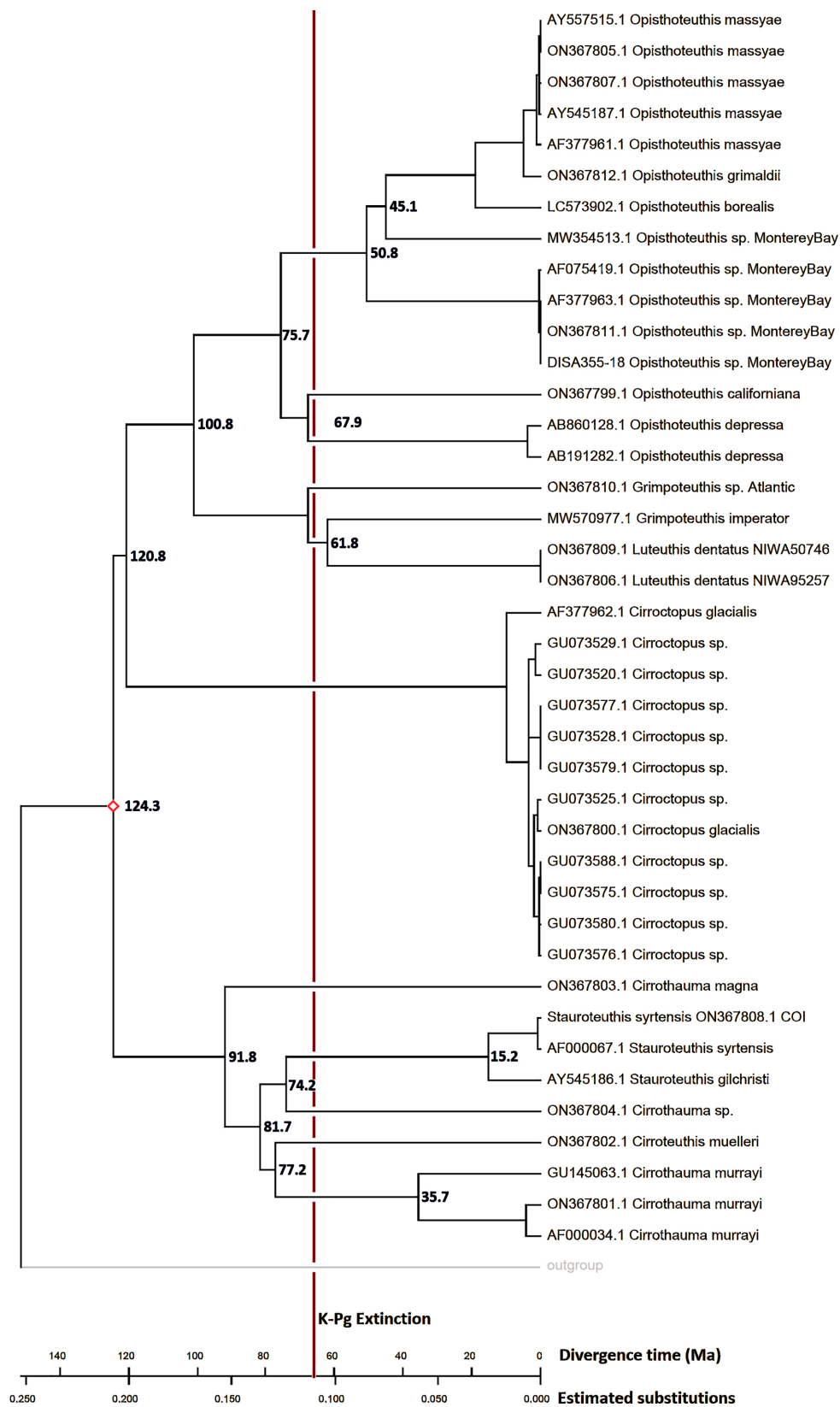


Fig. 5. A TimeTree of cirrates using COI sequences to estimate the divergence times of stem groups (at left) into modern crown groups (at right). Outgroup is marked as the lowermost branch, as is the calibrated node (red diamond) at 164.5–85 million years (Ma). Estimated divergence times in millions of years are included for nodes. Scale bars are provided for millions of years before present with a vertical red bar indicating the Cretaceous-Paleogene mass extinction event. A second scalebar denotes estimated substitutions/sequence change back in time. Tree constructed in MEGA X with the RelTime-ML tool



Superfamily Opisthoteuthoidea nov.

Diagnosis. Cirrates without secondary webbing, with moderate to short cirri (length $< 4 \times$ sucker diameter), and relatively compact gills (semi-sepioid or half orange form).

Families. Opisthoteuthidae, Grimpoteuthididae, and Cirroctopodidae.

Remarks. Primarily benthic, spending time resting on the seafloor, with occasional bursts of fin and medusoid swimming (COLLINS & VILLANUEVA 2006).

DIVERGENCE TIME ESTIMATIONS

An investigation of cirrate divergence times was conducted by constructing a phylogenetic time-tree from the COI sequencing data, calibrating the most-ancestral node between superfamilies Cirro-

teuthoidea and Opisthoteuthoidea at 164.5–85 Ma. The resulting timetree is depicted in Figure 5. This estimation (though limited by the scarcity of cirrate or stem-cirrate fossils) resulted in an estimated divergence of the Cirroteuthoidea and Opisthoteuthoidea at 124 Ma (Early Cretaceous). Within Opisthoteuthoidea, stem-cirroctopodids were estimated to have diverged at 121 Ma, and stem-grimpoteuthidids diverged from stem-opisthoteuthids at 101 Ma. The stem-*Opisthoteuthis* began diversifying in the Late Cretaceous (earliest node at 76 Ma), but most diversification of *Opisthoteuthis* is estimated to have occurred through the Paleogene (nodes within *Opisthoteuthis* having estimated times between 68–45 Ma). Within Cirroteuthidae, stem-*Stauroteuthis*, *Cirroteuthis*, and *Cirrothauma* diverged off from each other between 92–74 Ma (Late Cretaceous).

DISCUSSION

Recent decades have seen conflicting accounts of relationships between cirrate taxa being proposed (O'SHEA 1999, PIERTNEY et al. 2003, COLLINS & VILLANUEVA 2006). The recent work by TAITE et al. (2023) indicated that using many nuclear and mitochondrial genes could be good for interrogating higher-level relationships within octopods, including cirrates, however such sequencing is not yet available for the vast majority of cirrates. Molecular phylogenies using 16S (e.g., PIERTNEY et al. 2003, PARDO-GANDARILLAS et al. 2021) have revealed comparable clade structure to that resolved by TAITE et al. (2023) using whole mitochondrial/nuclear datasets for a much smaller number of species, indicating that smaller numbers of mitochondrial genes are still suitable for analysing higher family-level clades within Cirrata. Furthermore, 16S and COI sequences have the advantage of far greater coverage of species, allowing identification of paraphyletic genera, sub-genus structure, and putative new species (as is done herein). In future, it may be hoped that a much greater number of cirrate taxa will have large mitochondrial and nuclear gene sets sequenced, but this is unlikely to reach comparable species coverage to 16S and COI sequencing anytime soon. Up till now only a single mitochondrial gene (16S) has been widely used, and by combining a phylogenetic analysis of cirrate 16S sequences (including several species never used in such analyses before) with a large set of COI sequences which have never been thoroughly investigated for cirrate octopods, it was anticipated that the molecular phylogeny of Cirrata may be resolved to a far greater degree than possible before.

The most contentious of taxonomic points within cirrate taxonomy has involved the systematic validity of Grimpoteuthididae (whether it was distinct from Opisthoteuthidae), and Stauroteuthidae (whether it was distinct from Cirroteuthidae). HOCHBERG et al. (2014) and VECCHIONE et al. (2016) objected to the recognition of Grimpoteuthididae (synonymising it with Opisthoteuthidae) and synonymising of Stauroteuthidae, while later researchers accepted Grimpoteuthididae (and not Stauroteuthidae) (ZIEGLER et al. 2021) or accepted neither (PARDO-GANDARILLAS et al. 2021). Most molecular studies on Cirrata have relied exclusively on the 16S 3'-end sequence (PIERTNEY et al. 2003, PARDO-GANDARILLAS et al. 2021), with the COI gene being rarely used despite its widespread use in metazoan barcoding (Barcode of Life project or BOLD; RATNASINGHAM & HERBERT 2007) and identification of cephalopod species (e.g., GEBHARDT & KNEBELSBERGER 2015). The first relatively comprehensive molecular phylogeny of cirrates based on the COI gene found support for Cirroteuthidae, Stauroteuthidae, Opisthoteuthidae, and Cirroctopodidae (GOLIKOV et al. 2020); an earlier COI tree of CARLINI et al. (2001) was based on only five taxa. Because COI sequences for *Cirroteuthis* or grimpoteuthidids (other than a species of *Opisthoteuthis* erroneously attributed to *Grimpoteuthis*, discussed later) were unavailable to GOLIKOV et al. (2020), their COI phylogeny could not resolve the monophyly of Cirroteuthidae or validity of Grimpoteuthididae. However, the accumulation of 16S and COI sequence data now permits a much more comprehensive assessment of clade structure using both these mitochondrial genes.

GRIMPOTEUTHIDIDAE

Well-supported clades consistent with four families (Cirroteuthidae, Cirroctopodidae, Grimpoteuthidae, and Opisthoteuthidae) were apparent in both 16S and COI analyses (bootstrap values > 90% or post-prob. values approaching 1.00). Opisthoteuthidae was occasionally more weakly supported in ML/MP, but strongly supported in BI. Such support values were consistent with family level support reported by PIERTNEY *et al.* (2003), but support herein was much stronger for Grimpoteuthidae. Similarly, support across ML and BI analyses for the families was consistent with values reported by PARDO-GANDARILLAS *et al.* (2021) (though these authors did not recognise Grimpoteuthidae, regardless of its high support and did not include *Cryptoteuthis*). While Grimpoteuthidae and Opisthoteuthidae had an average 16S inter-clade P-distance of 7.1%, this difference exceeded that of 16S intra-family genetic distances (including Opisthoteuthidae (3.6%) and Grimpoteuthidae (1.7%)) and was comparable to 16S P-distances between Cirroctopodidae relative to both Opisthoteuthidae and Grimpoteuthidae (10.9% and 11.2%, respectively). COI P-distances between families, which included more parsimony informative sites, provided even greater support for separation of these families, with values between Opisthoteuthidae, Grimpoteuthidae, and Cirroctopodidae ranging from 14.2–15.9%, again far exceeding COI intra-family distances for these three families (0.8–9.4%). While Grimpoteuthidae and Opisthoteuthidae often formed a clade sister to Cirroctopodidae, in some 16S analyses (when using a lower site-coverage cut-off) this clade structure is reversed, and Cirroctopodidae and Opisthoteuthidae formed a clade to which Grimpoteuthidae was sister (see also ZIEGLER & SAGORNY 2021). Similarly, using 18S and 28S nuclear genes, TAITE *et al.* (2023) reported relationships between these three families to be unclear (i.e., a polytomy). Based on morphology, Cirroctopodidae and Opisthoteuthidae appear to be closely related, in that they share branched optic nerve bundles through the white body, have internal shells with tapering wing-ends, and lack a radula and posterior salivary glands. Whereas Grimpoteuthidae differ greatly in having a single optic nerve bundle through each white body (a feature shared with Cirroteuthidae and Stauroteuthidae), internal shells with expanded wing ends, and frequently possess a radula (COLLINS & VILLANUEVA (2006); and personal observations).

Overall, based on clade bootstrap support, comparable inter-family P-distances (especially with COI) between grimpoteuthids, opisthoteuthids, and cirroctopodids relative to low intra-family P-distances, and distinct morphological dif-

ferences, Grimpoteuthidae is at least as valid a family as is the Cirroctopodidae; its synonymy with Opisthoteuthidae is not supported on either morphological or molecular grounds.

CIRROTEUTHIDAE – MONOPHYLY AND NEW TAXA

Herein 16S and COI sequences were analysed for all five recognised cirroteuthid species for the first time (genera *Cirroteuthis*, *Cirrothauma*, and *Stauroteuthis*). Consistent with earlier molecular analyses, the Cirroteuthidae is paraphyletic, in that it contains the mono-generic Stauroteuthidae (i.e., genus *Stauroteuthis*) (PIERTNEY *et al.* 2003, PARDO-GANDARILLAS *et al.* 2021, ZIEGLER & SAGORNY 2021). Accordingly, there is little 16S or COI molecular support to recognise the Stauroteuthidae as discrete from the Cirroteuthidae. *Cirrothauma* is consistently resolved as paraphyletic, although the exact positioning of taxa relative to each other differs in 16S and COI trees. This indicates that further morphological study of this genus is warranted. Furthermore, *Cirrothauma* sp. sequence (ON367804) from the northeastern Pacific (Gorda Ridge) is well separated from *C. magna* (Hoyle, 1885) and *C. murrayi* Chun, 1911 in both 16S and COI trees (resolving as closer to one or the other depending on the analysis), indicating the existence of at least one more *Cirrothauma* species in the northern Pacific. Unfortunately, the ‘known’ *C. magna* sequence (ON367803) is from the North Atlantic, not the type locality in the southern Indian Ocean (though the type locality of the ‘nomen dubium’ *Cirrothauma hoylei* (Robson, 1932) is closer, in the southern Pacific)¹; to determine the sequence of ‘true’ *C. magna*, and assess if *C. hoylei* may be an appropriate name for this third *Cirrothauma* species, will require an integrated molecular and morphological analysis of material from or at least proximal to the type locality. *Cirrothauma murrayi* COI sequences from the North Atlantic (ON367801 & GU145063) and North Pacific (AF000034) resolve as a clade, but the Pacific specimen is sister to the others, and P-distances between these three sequences (8.0%) are greater than within other widely distributed species (e.g., COI sequences for *O. massyae* from north Atlantic and off South Africa had an intra-species P-distance = 0.3%), indicating that *C. murrayi* may comprise more than one species rather than a the single cosmopolitan species reported by ALDRED *et al.* (1983). Cirroteuthids as a family are generally poorly studied, and in addition to the existence of a third (or fourth) species of *Cirrothauma* supported herein, new species of *Cirroteuthis* are likely

¹ See VERHOEFF (2022), this species is assigned to *Cirrothauma* rather than *Cirroteuthis*.

(VERHOEFF 2022), and a new species of *Stauroteuthis* from the southwestern Pacific was recently described (VERHOEFF 2023).

The molecular work of TAITE et al. (2023) indicated that relationships between *Cirroteuthis*, *Cirrothauma*, and *Stauroteuthis* may be better resolved with nuclear 18S and 28S rRNA genes. In their ML phylogeny, *S. syrtensis* was sister to a well-supported clade containing *Cirroteuthis* and *Cirrothauma* (with *Cirroteuthis* in turn a sister taxon to a clade containing the three *Cirrothauma* species). While most analyses of 16S and COI herein failed to recover Stauroteuthidae as a family separate to Cirroteuthidae, this was found in a single analysis (BI analysis of COI, see Fig. 4), though the post-prob. for Cirroteuthidae as a sister clade to Stauroteuthidae was unusually low. Thus, the COI gene may provide better resolution of cirrate family structures than 16S, though only marginally, and nuclear rRNA genes support the separation of the Stauroteuthidae and Cirroteuthidae somewhat better (but these genes are non-sequenced for most cirrate taxa). Regardless, molecular support for considering the Stauroteuthidae as a valid family remains more tenuous than that for recognising the Grimpoteuthididae as a valid family, and recognition of Stauroteuthidae as a family must rely more heavily on morphological differences, notably the U-shaped internal shell which is distinct from the saddle- or butterfly-shaped shell of *Cirroteuthis* and *Cirrothauma* (COLLINS & VILLANUEVA 2006).

NEW SUPERFAMILY DIVISIONS OF CIRRATA

At a higher taxonomic level, multigene phylogenies of cephalopods have revealed monophyly of the Cirrata and Incirrata (LINDGREN et al. 2012, TAITE et al. 2023), as well as potential paraphyly, with Cirroteuthidae (including Stauroteuthidae) forming a basal sister clade to Incirrata and the remaining Cirrata (CARLINI et al. 2001², SANCHEZ et al. 2018) (though paraphyly was doubted by the study authors). This reflects findings presented herein inasmuch as the cirroteuthids (including *Stauroteuthis*) form a distinct clade sister to that containing other cirrate families in both 16S and COI phylogenies (bootstrap and post-prob. support for these two clades is consistently high for 16S and COI). These two clades are also reported in most molecular studies of Octopoda (PIERTNEY et al. 2003, LINDGREN et al. 2012, SANCHEZ et al. 2018, PARDO-GANDARILLAS et al. 2021, TAITE et al. 2023). The consistent phylogenetic separation and strong morphological differences between these two higher-level clades supports the designation of them as superfamilies, the

Cirroteuthoidea nov. (cirroteuthids with secondary webbing, very-elongate cirri, and sepoid gills) and Opisthoteuthoidea nov. (opisthoteuthids, grimpoteuthidids, and cirroctopodids, principally characterised by having a simple web, relatively short cirri, and half-orange/semi-sepoid gills).

OPISTHOTEUTHIDAE & GRIMPOTEUTHIDIDAE – NEW SPECIES AND PARAPHYLETIC GENERA

Presently unidentified, potentially new species are apparent within *Opisthoteuthis* molecular phylogenies. The northwestern Pacific *Opisthoteuthis* sp. ‘JN-2021’ (MW354513) could belong to an already described species, but other North Pacific species (*O. depressa*, *O. californiana*, and *O. dongshaensis* are already represented, though the validity of species assignments to some of these sequences must be questioned). The northeastern Pacific (off Los Angeles and Monterey Bay) *Opisthoteuthis* sp. ‘Monterey’ – a taxon referred to as *Grimpoteuthis* sp. (HUNT 1999, NORMAN 2000: p. 182) and informally as *O. ‘adorabilis’* (Baker, 2015) – forms a well-supported clade, but in the 16S datasets this clade includes sequences for *O. bruuni*, indicating that the two are possibly conspecific or a closely related species complex. Prior to COLLINS (2003), *O. bruuni* was placed in *Grimpoteuthis* (VOSS 1982). HOCHBERG et al. (2014: p. 250) further remarked “... a similar [to *O. bruuni*], or closely related, undescribed species, occurs in the northeastern Pacific Ocean off California.” The attribution of these northeastern Pacific specimens to *O. bruuni* represents a considerable expansion of the recognised distribution of this species (from Chile to Monterey Bay). However such a range is not unusual in *Opisthoteuthis*, and this distribution is comparable in latitudinal extent to the Atlantic ranges of *O. massyae* and *O. calypso* (from the North Sea and Mediterranean to southern Africa) (VILLANUEVA et al. 2002b).

Regarding other *Opisthoteuthis*, AJ252768 (tentatively assigned *O. dongshaensis*) was from a specimen supposedly collected off California (northeastern Pacific), but it forms a clade with a known *O. dongshaensis* sequence (AJ315375) from a specimen collected off Taiwan (HUDELOT 2000, PIERTNEY et al. 2003). Either *O. dongshaensis* is distributed more widely than hitherto recognised, or the locality data or identification of one or both samples is confused.³

COI barcoding sequences confer advantages over 16S 3'-end sequences for resolving cirrate octopod

² Note: the two *Grimpoteuthis* sequences used in this study were actually from *Cirroctopus* and *Opisthoteuthis*.

³ On GenBank AJ252768 is recorded as from the northeast Pacific (matching a SBMNH specimen from HUDELOT 2000) while in PIERTNEY et al. (2003) (supplementary data), there is instead an AJ252769 sequence for *O. n. sp. 3* (from the SBMNH) while AJ252768 is for an *S. syrtensis* (i.e., the sequences were switched).

phylogenies, in that the area amplified contains more parsimony informative sites (34% vs. 26% in 16S sequences). COI may be more appropriate for investigating *intra*-genus structure within *Opisthoteuthis* (or perhaps sub-family or new genus divisions within Opisthoteuthidae) and COI bootstrap support values were higher for clades within *Opisthoteuthis* (compared to 16S). The 16S analysis herein, but only the BI analysis, also revealed some well supported clades as described in results. The species coverage unfortunately differed between COI and 16S analyses, but the relatedness of *O. massyae* and *O. grimaldii* in a well-supported clade was consistent in both. The only other study that published a molecular phylogeny of *Opisthoteuthis* COI sequences only included four species with no support values (GOLIKOV *et al.* 2020), while subgenus structure within *Opisthoteuthis* in 16S analyses herein differed considerably from that revealed by PARDO-GANDARILLAS *et al.* 2021 (though their phylogeny was far less complete, lacking *O. agassizii*, *O. grimaldii*, *O. dongshaensis*, and *O. sp.* 'Monterey'). WAKABAYASHI *et al.* (2012) similarly found that COI was better at resolving genus-level and inter-subfamily level differences in Ommastrephid squids. Collection of COI sequences from more *Opisthoteuthis* species may identify support for new genera or subgenera; O'SHEA (1999: pp. 16–34) recognised three *Opisthoteuthis* 'groups', the systematic validity of which have not been further investigated.

While grimpoteuthidids form a robust clade, *Grimpoteuthis* is paraphyletic (especially in 16S-derived phylogenetic trees) with *Cryptoteuthis* and *Luteuthis* being nested within three different *Grimpoteuthis* species. The identity of the *Grimpoteuthis* sp. sequence (ON367810) is intriguing in that the specimen was collected from the northeastern Atlantic. Because this sequence is distinct from that of *G. discovery*, it may belong to any of *G. boylei* Collins, 2003, *G. challengeri* Collins, 2003, *G. wuelkeri* (Grimpe, 1920), or *G. umbellata* (Fischer, 1884), that have all been described from this region. As discussed in VERHOEFF & O'SHEA (2022), *Grimpoteuthis* may comprise several genera, but the poor condition of the type specimen of *G. umbellata*, the type species of the genus, precludes a detailed comparison. While both *Enigmatiteuthis* O'Shea, 1999 and *Cryptoteuthis* may be available names for species currently grouped in a paraphyletic *Grimpoteuthis*, re-allocating species to either genus (or defining new genera) is premature until *G. umbellata* is redescribed based on material collected from or proximal to the type locality. Grimpoteuthidids are also greatly underrepresented in sequence data, represented by only 4 of 20 species. The nesting of a monophyletic *Luteuthis* clade within a polyphyletic *Grimpoteuthis* is remarkable considering how distinct *Luteuthis* is morphologically from the species classed

as *Grimpoteuthis* (and *Cryptoteuthis*). While *Luteuthis* shares some features in common with other grimpoteuthidids (single optic nerve bundle, internal shell with expanded wing ends, and retained radula) it is readily distinguished by possessing a bilobed digestive gland, more radular teeth per transverse row, palatine teeth on labial palps, extremely short cirri, and strongly crenulated suckers (O'SHEA 1999, O'SHEA & LU 2002, COLLINS & VILLANUEVA 2006). While morphologically distinct, the positioning of *Luteuthis* within otherwise (superficially) similar taxa of *Grimpoteuthis* (and *Cryptoteuthis*) indicates that the family Luteuthidae cannot be supported as distinct from Grimpoteuthidae, but moreover emphasises how unrelated many *Grimpoteuthis* species likely are from one another and how the diversity in this family has been overlooked, perhaps due to evolutionary homeomorphy in the family.

DIVERGENCE TIMES OF CIRRATA

The molecular clock analyses of TANNER *et al.* (2017) indicate that crown coleoids diverged into octopodiforms and decapodiforms in the Late Carboniferous or Permian, with the divergence of stem-Octopoda into the Incirrata and Cirrata occurring within the Jurassic between ~210 Ma and 150 Ma (using CIR clock model). Stem-Octobranchia (superorder) comprised three suborders (Prototeuthidina, Loligosepiina, Teudopseina) in the Mesozoic (FUCHS & WEIS 2008, FUCHS & LARSON 2011a, b), with a robust internal shell, as well as eight arms and cirri (at least in the latter two) being an ancestral condition reflected in the Cirrata. Fossil and recent vampyroteuthids (*Vampyronassa* Fischer *et al.* 2002 and *Vampyroteuthis*, respectively) (ROWE *et al.* 2022), which likely arose from within Loligosepiina (FUCHS & WEIS 2008), also share these ancestral conditions (i.e., cirri and robust internal shell) with Cirrata. The suborder Teudopseina, abundant and diverse within the Jurassic and Cretaceous, likely contains the stem-Octopoda (pre-Cirrata–Incirrata common ancestor) based on gladius morphology. Teudopseids including *Glyphiteuthis* Reuss, 1854 (Trachyteuthidae) had eight arms equipped with cirri (FUCHS & LARSON 2011a), with teudopseids of family Patellocopodidae (superfamily Muensterelloidea) including *Pearceiteuthis* from the Jurassic (Callovian 166–163 Ma) and *Patellocopos* (Kimmerdigian 157–152 Ma) possibly comprising stem-Octopoda, as they display clear reduction and shortening of the median field (restricting the gladius vestige to the mid-posterior mantle alike Cirrata) while retaining expanded lateral fields for fin muscle attachments (FUCHS & SCHWEIGERT 2018). By the Late Cretaceous (Santonian to lower Campanian, ~86–81 Ma) cirrate octopods were already present in



the fossil record with *Paleocirroteuthis haggarti* Tanabe, Trask, Ross et Hikida, 2008 and *P. pacifica* Tanabe, Trask, Ross et Hikida, 2008 beaks resembling modern cirroteuthids (TANABE et al. 2008). Likewise, other Late Cretaceous species including *Palaeoctopus newboldi* (Woodward, 1896), *Keuppia levante* Fuchs, Bracchi et Weis, 2009, and *K. hyperbolaris* Fuchs, Bracchi et Weis, 2009, while still bearing paired mantle fins (at least in *Palaeoctopus*), had a posterior separation of the gladius into two parts, indicating that stem-Incirrata were already diversified (FUCHS et al. 2009). Molecular timetree analysis presented herein indicates that the Cirrata diverged into its basal-most clades ~124 Ma (with stem-cirroteuthids diverging), within the Early Cretaceous, followed by the rapid divergence of stem-cirroctopodids, grimpoteuthidids, and opisthoteuthids (and most genera) within the remainder of the Early and Late Cretaceous.

TANNER et al. (2017) estimated that the incirrate octopods diversified in the mid-late Cretaceous, with stem Decabrachia diversifying into sepiids, and mypopsid and oegopsid squid from the Jurassic to Cretaceous. This diversification was likely part of the Mesozoic Marine Revolution (MMR) (sensu

VERMEIJ 1977), a period of enhanced predator–prey coevolution and ecological shifts over the Jurassic and Cretaceous, possibly furthered by expansion of the Atlantic and Indian Ocean basins in the Early Cretaceous. The herein predicted diversification of Cirrata within the Cretaceous (~124–66 Ma) may also have been part of the MMR. While cirrates and vampyroteuthids are today essentially restricted to the deep sea, late-Mesozoic cirrates likely diversified in shallower shelf waters and were plausibly more active. Unlike modern zooplanktivorous and deep-sea-dwelling *Vampyroteuthis*, fossil vampyroteuthids such as *Vampyronassa rhodanica* Fischer et Riou, 2002 were active predators of shallower regions (ROWE et al. 2022), while potential stem-Octopoda (Cirrata–Incirrata ancestor) *Patelloctopus* were collected from shallow marine deposits (< 100 m depth) (FUCHS & SCHWEIGERT 2018). At the extinction event at the end of the Cretaceous, cirrates and other cephalopods likely survived in the deep-sea (ARKHIPKIN et al. 2012), and while squid and Incirrata re-colonised shallower waters and diversified, the Cirrata and vampyroteuthids did not.

CONCLUSIONS AND FUTURE DIRECTIONS

The Cirrata comprises four well-supported families within two superfamilies, Cirroteuthoidea (for the Cirroteuthidae), and Opisthoteuthoidea (for the Cirroctopodidae, Grimpoteuthididae, and Opisthoteuthidae). While most cirrate genera form clades, *Grimpoteuthis* and *Cirrothauma* are polyphyletic. An integrated morphological and molecular approach is required to assess putative additional *Cirrothauma* and *Opisthoteuthis* species revealed herein, including assessing if historical names (including supposed junior synonyms) are applicable or if these are species new to science, and compare preserved specimens to more-recently collected, presently unidentified material. While COI sequences may be more informative for revealing cirrate phylogenies and taxonomy (because they contain more parsimony informative sites), more sequences for more species, especially the under-represented Grimpoteuthididae, are required. Future directions of study suggested by this research include: 1) systematic review of genera *Grimpoteuthis*, *Cryptoteuthis*, and *Enigmatiteuthis* with

redescription of *Grimpoteuthis* type species *G. umbellata* using new material; 2) sequencing both COI and 16S for a greater number of grimpoteuthidid taxa (though sequencing larger sets including nuclear genes when practical); 3) redescription of North Pacific *Opisthoteuthis* species which may have been historically confused; and 4) increased collection of COI sequences from *Opisthoteuthis* taxa to assess sub-genus structure.

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