

A phylogenomic look into the systematics of oceanic squids (order Oegopsida)

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Oceanic squids of the order Oegopsida are ecologically and economically important members of the pelagic environment. They are the most diverse group of cephalopods, with 24 families that are divergent morphologically. Despite their importance, knowledge of phylogenetic relationships among oegopsids is less than that among neritic cephalopods. Here, we provide the complete mitogenomes and the nuclear 18S and 28S ribosomal genes for 35 selected oceanic squids, which were generated using genome skimming. We performed maximum likelihood and Bayesian inference analyses that included 21 of the 24 oegopsid families. In our analyses, the architeuthid, chiroteuthid and enoploteuthid family groups, which have been proposed previously based on morphological and natural history characteristics, were retrieved as monophyletic. The morphologically divergent Cranchiidae formed a well-supported clade with families Ommastrephidae and Thysanoteuthidae, with a unique mitochondrial gene order. The family Lycoteuthidae was revealed as paraphyletic and contained Pyroteuthidae. Thus, the two lycoteuthid subfamilies are herein elevated to family level, increasing the number of oegopsid squid families to 25. In order to describe the diversity and evolutionary trends of oegopsid squids accurately, the superfamilies Architeuthoidea, Chiroteuthoidea, Cranchioidea and Enoploteuthoidea are resurrected from the literature, and the superfamilies Cycloteuthoidea, Octopoteuthoidea and Pholidoteuthoidea are proposed. The phylogenetic positions of Gonatidae, Histioteuthidae and Onychoteuthidae were not stable in our phylogenetic analyses and are not assigned to a superfamily. This study supports the utility of genome skimming to solve the phylogenetic relationships of oceanic squids.

ADDITIONAL KEYWORDS: Cephalopoda – open-eyed squids – phylogenomics – taxonomy – mitogenome gene order.

INTRODUCTION

Oceanic squids are important members of the deep scattering layer and important predators of mesopelagic organisms (Villanueva *et al.*, 2017). Mesopelagic ecosystems currently represent the largest known potential fishery resource (St. John *et al.*, 2016). Importantly, oceanic squids occupy multiple trophic levels in mesopelagic food webs (Murphy *et al.*, 2020), but their ecological role remains mostly unexplored

(Hoving *et al.*, 2014). Like fishes and many endangered megafaunal taxa, such as sharks and toothed whales that prey on oceanic squids (e.g. Zylinski & Johnsen, 2011; Galván-Magaña *et al.*, 2013; Foskolos *et al.*, 2020), they represent important drivers of matter and energy in pelagic ecosystems (Young *et al.*, 2013). Oceanic squids can account for huge biomasses, and the handful of commercial flying squid species alone account for half of the total cephalopod fishery landings in the world (Rosa *et al.*, 2013; Arkhipkin *et al.*, 2015).

Taxonomically, oceanic squids contain two sister taxa: the orders Bathyteuthida Lindgren, 2010 and

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Oegopsida d'Orbigny, 1847 (Lindgren *et al.*, 2012; Strugnell *et al.*, 2017). These two groups share a duplication of six mitochondrial genes (Yokobori *et al.*, 2004; Allcock *et al.*, 2011; Strugnell *et al.*, 2017), which form two distinct duplicated gene blocks associated with NADH dehydrogenase subunits 2 and 3 (Yokobori *et al.*, 2004; Fig. 1).

Despite their huge ecological and economic importance, the oceanic lifestyle of these squids hinders their sampling and the subsequent study of many fundamental biological aspects. Therefore, phylogenetic knowledge of cephalopods is biased towards more accessible neritic species. For example, the recent phylogenomic study by Tanner *et al.* (2017) included the same number of terminals for the neritic family Loliginidae Lesueur, 1821 as for the oceanic order Oegopsida. Oegopsida is the most morphologically diverse group of cephalopods at the family level and includes 24 families, accounting for almost as many families as the remaining extant cephalopods together. Until now, the phylogenetic relationships among oegopsid squids have been elusive, in most cases owing to the lack of phylogenetic resolution of the studied molecular markers (Lindgren *et al.*, 2012; Sanchez *et al.*, 2018), with the group even being described as a 'phylogenetic void' (Young *et al.*, 1998). Despite this lack of phylogenetic knowledge, several families have been grouped based on morphological and life-history traits. These groups include the architeuthid, chiroteuthid, enoploteuthid, histioteuthid and lepidoteuthid family groups (Lindgren, 2010; Young & Vecchione, 2019a). The morphological and life-history traits strongly support four of these five family groups, whereas the relationships among the three families that form the lepidoteuthid family group is comparatively weaker: the families Lepidoteuthidae Pfeffer, 1912 and Octopoteuthidae Berry, 1912 share the same type of paralarval tentacular club and the loss of tentacles in subadults and adults (Young *et al.*, 1998), but the relationship of these to Pholidoteuthidae Voss, 1956 is based solely on the presence of skin ornamentation in both Lepidoteuthidae and Pholidoteuthidae. Traditionally, the family Lycoteuthidae Pfeffer, 1908a has been considered a member of the morphologically well-characterized enoploteuthid family group. The

lycoteuthid family comprises two subfamilies, the monotypic Lampadioteuthinae Berry, 1916 and Lycoteuthinae Pfeffer, 1908a, which contains three genera that differ in the number of male genitalia (single or paired), by the presence or absence of sexual dimorphism in the dorsolateral or ventrolateral arms (enlarged in males) and in the assemblage of mantle and tentacle photophores (Vecchione & Young, 2019a). The taxonomic rank of these subfamilies is controversial, and Lampadioteuthinae has been treated at the family or the subfamily level (see Berry, 1916, 1920; Naef, 1922; Voss, 1956, 1962). Also, the morphology and distribution of photophores of members of Pyroteuthidae Pfeffer, 1912, which is also in the enoploteuthid family group, are similar (Herring *et al.*, 1985; Young & Harman, 1998) to those of both Lycoteuthinae and Lampadioteuthinae. Therefore, Pyroteuthidae and Lycoteuthidae are sometimes considered sister taxa. Lindgren (2010) and Lindgren *et al.* (2012) did not recover a sister relationship between these two families. Thus, knowledge of relationships among oegopsid families suffers from many questions that previous attempts have failed to answer.

Genome skimming (Dodsworth, 2015) is a shallow whole-genome sequencing method that allows for the assembly of regions of the genome that are highly represented in whole-genome sequencing projects, such as the mitogenome and the complete nuclear ribosome cluster. It is comparatively cheap to obtain a large nucleotide dataset, and there is no requirement for fresh samples for library preparations. Despite these advantages, this method remains under-used in cephalopod systematics, and only one study so far provides extensive representation of taxa within a cephalopod group (Sanchez *et al.*, 2021). Here, we took advantage of genome skimming to study the phylogenetic relationships of oegopsid squid families.

MATERIAL AND METHODS

SAMPLING, DNA EXTRACTION AND GENOME SKIMMING
Thirty-five selected oceanic squids of the orders Oegopsida and Bathyteuthida were sampled during

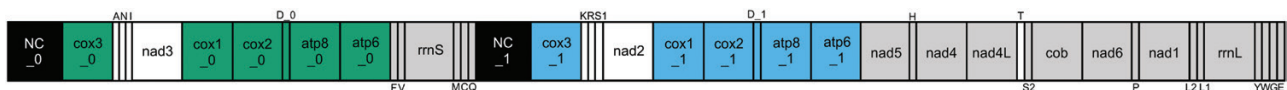


Figure 1. Schematic representation of the mitogenome of oegopsid squids based on the *Watasenia scintillans* (Berry, 1911) mitogenome described by Yokobori *et al.* (2004). The plus (+) strand is represented in the direction 5' → 3'. The duplicated gene blocks associated with NADH dehydrogenase subunit 3 (*nad3*) are coloured in green; the duplicated gene blocks associated with NADH dehydrogenase subunit 2 (*nad2*) are coloured in blue; the non-coding regions are indicated in black; and genes from the minus (-) strand of the mitogenome are coloured in light grey. Squares are not proportional to the size of the genes. See the Material and Methods section for gene abbreviations.

several oceanic cruises around the world. Once collected, a portion of the mantle was excised, fixed in ethanol or RNAlater and preserved at -20 to -80 °C. The whole animals were fixed in formalin and stored in various biological collections as morphological vouchers (Table 1). Samples were selected in order to provide maximum representation of the biodiversity of oegopsid squids at the family level, accounting for 21 out of 24 accepted families.

DNA was extracted according to the phenol–chloroform method. Indexed libraries were prepared using a NEBNext DNA Library Prep Kit (New England Biolabs, Ipswich, MA, USA) following the manufacturer's recommendations and sequenced at 9 Gb per sample in an Illumina NovaSeq 6000 PE150 (Illumina, San Diego, CA, USA). The quality of the reads was assessed through FASTQC (Andrews, 2010). Mitochondrial and nuclear ribosomal DNA were assembled *de novo* using NOVOPLASTY v.3.8.3 (Dierckxsens *et al.*, 2016) using a reference sequence (either the complete mitogenome or the complete nuclear ribosomal gene cluster of a closely related species), and a fragment of cytochrome *c* oxidase subunit I (*cox1*), 12S rRNA or 16S rRNA (for the mitogenomes) or a fragment of 18S or 28S rRNA (for the nuclear markers) as a seed. Owing to the presence of duplicate genes in the mitochondrial genome, NOVOPLASTY usually did not return a circularized genome. Excluding *Octopoteuthis sicula* Rüppell, 1844, *Lepidoteuthis grimaldii* Joubin, 1898 and *Joubiniteuthis portieri* (Joubin, 1916), which were retrieved as unambiguous single contigs, the assembly usually produced the four contigs depicted in Figure 2A–D when *cox1* was used as seed, and the contigs depicted in Figure 2A, B and Figure 2C, D when using 12S RNA and 16S RNA as seeds, respectively. After some manual curation, the combination of the contigs A and D or B and C produce two circular mitogenomes of the same size, including all the genes present in oegopsid and bathyteuthid mitogenomes, but in a different order (Fig. 2E, F). The *nad2* and *nad3* gene blocks could have changed position several times in the evolutionary history of Oegopsida (see Discussion), but we cannot establish this via short-read sequencing; hence, we assumed that our samples had the genome order depicted in Figure 2E, as initially established for *Todarodes pacificus* (Steenstrup, 1880) and *Watasenia scintillans* (Berry, 1911) using long PCR (Yokobori *et al.*, 2004). For mitogenome gene annotations we used MITOS2 (Bernt *et al.*, 2013), with NCBI RefSeq 63 Metazoa database reference and genetic code 5, for invertebrates. Sequence Read Archive (SRA) files downloaded from GenBank for *Architeuthis dux* Steenstrup, 1857a were used to assemble the 18S and 28S rRNA nuclear genes following the same methodology as for our samples. Gene annotations were checked and corrected by hand. Nuclear 18S and

28S rRNA were annotated using RNAMMER (Lagesen *et al.*, 2007). Table 1 summarizes the nucleotide and SRA GenBank accession numbers. All the FASTQ files from this work can be accessed through the GenBank BioProject accession number PRJNA716134.

PHYLOGENETIC ANALYSES

The 13 mitochondrial protein genes were aligned manually. Oceanic squids have five duplicated protein genes that vary little in their sequence (see Yokobori *et al.*, 2004). For those genes (*cox1*, *cox2*, *cox3*, *atp6* and *atp8*), a consensus of both copies was included in the alignment. The mitochondrial 16S and 12S and the nuclear 18S and 28S ribosomal genes were aligned with the MAFFT server (<https://mafft.cbrc.jp/alignment/server/>; Katoh *et al.*, 2009) using the Q-INS-i iterative refinement methods. Conserved blocks were obtained from this alignment through GBLOCKS (Castresana, 2000) using the less restrictive parameters from the GBLOCKS server (http://molevol.cmima.csic.es/castresana/Gblocks_server.html). The edited ribosomal genes were used in the analyses. The dataset includes all mitochondrial protein and ribosomal RNA genes and the nuclear 18S and 28S genes from all the individuals, accounting for a total of 20 561 nucleotides and 17 genes.

A maximum likelihood (ML) analysis was performed through IQTREE v.2.0.7 (Minh *et al.*, 2020), with genes and codons (for protein-coding genes) partitioned, and with the merge option (-m MFP+MERGE) selected such that the 43 initial partitions were reduced automatically to the optimum number. The automatic model selection tool was applied to calculate and implement the best model for each resulting partition based on the Bayesian information criterion (BIC). One hundred bootstrap generations were used to calculate the support of the nodes. A Bayesian inference (BI) analysis was implemented in MRBAYES v.3.2 (Ronquist *et al.*, 2012). Two simultaneous runs were performed with four chains, three hot and one cold. The analysis, which ran for 3 000 000 generations, was sampled every 100 generations, and the first 25% of each run were discarded as burn-in. Stationarity and .p files from each run were checked in TRACER v.1.6 (Rambaut *et al.*, 2003–2009) to ensure that effective sample sizes were > 200 for all parameters. In all analyses, members of the order Bathyteuthida were used as outgroups.

GENE ORDER

Mitochondrial gene order rearrangements were compared using CREX (Bernt *et al.*, 2007), which uses pairwise comparisons to identify possible evolutionary scenarios between two gene orders considering transpositions, reverse transpositions, reversals and tandem-duplication–random-loss events. We used this

Table 1. Summary of the specimens studied in this work, including the voucher, GenBank and Sequence Read Archive accession numbers

Species	Sampling locality	Voucher accession number	Mitogenome GenBank accession number	18S GenBank Accession number	28S GenBank accession number	Sequence Read Archive (SRA)
Outgroups						
Family Bathyteuthidae						
Pfeffer, 1900						
<i>Bathyteuthis inopinata</i>	Atlantic Ocean, 35.64°N, 20.22°W	–	MW255564	MW233760	MW233724	SRR14069311
Judkins <i>et al.</i> (2020)						
Family Chtenopterigidae						
Grimpe, 1922						
<i>Chtenopteryx cf. canariensis</i>	Atlantic Ocean, 3.23°S, 28.43°W	–	MW255568	MW233764	MW233728	SRR14069308
Salcedo-Vargas & Guerrero-Kommritz, 2000						
Ingroup						
Family Ancistrocheiridae						
Pfeffer, 1912						
<i>Ancistrocheirus</i> sp.	Atlantic Ocean, 18.12°N, 20.20°W	–	MW255567	MW233763	MW233727	SRR14069309
Family Architeuthidae Pfeffer, 1900						
<i>Architeuthis dux</i> Steenstrup, 1857a	–	–	FJ429092 (Elliger <i>et al.</i> , unpublished)	MW233782	MW233746	SRX5785089, SRR9006806
Family Brachioteuthidae						
Pfeffer, 1908b						
<i>Brachioteuthis beanii</i> Verrill, 1881	Atlantic Ocean, 48.37°N, 41.33°W	USNM1531159*	MW255575	MW233771	MW233735	SRR14069301
Family Chiroteuthidae Gray, 1849						
<i>Chiroteuthis veranyi</i> (Férussac, 1834)	Mediterranean Sea	ICMC000325†	MW255558	MW233754	MW233718	SRR14069319
<i>Grimalditeuthis bonplandi</i> (Vérany, 1839)	Atlantic Ocean, 30.02°N, 19.83°W	ICMC000123†	MW255577	MW233773	MW233737	SRR14069298
Family Cranchiidae Prosch, 1847						
<i>Bathothauma lyromma</i> Chun, 1906	Atlantic Ocean, 35.35°N, 20.21°W	ICMC000133†	MW255579	MW233775	MW233739	SRR14069296
<i>Egea inermis</i> Joubin, 1933	Atlantic Ocean, 0.26°S, 26.49°W	ICMC000187†	MW255566	MW233762	MW233726	SRR14069310

Table 1. Continued

Species	Sampling locality	Voucher accession number	Mitogenome GenBank accession number	18S GenBank Accession number	28S GenBank accession number	Sequence Read Archive (SRA)
<i>Helicocranchia</i> sp.	Pacific Ocean, 19.50°N, 156.39°W	–	MW255584	MW233780	MW233744	SRR14069289
<i>Leachia atlantica</i> (Degner, 1925)	Atlantic Ocean, 3.23°S, 28.43°W	–	MW255570	MW233766	MW233730	SRR14069306
<i>Megalocranchia</i> cf. <i>oceanica</i> (Voss, 1960)	Atlantic Ocean, 20.90°N, 21.019°W	ICMC000154†	MW255576	MW233772	MW233736	SRR14069299
<i>Taonius pavo</i> (Lesueur, 1821)	Atlantic Ocean, 48.73°N, 40.25°W	USNM1531376*	MW255573	MW233769	MW233733	SRR14069302
<i>Teuthowenia pellucida</i> (Chun, 1910)	Indian Ocean, 35.18°S, 130.69°E	C.500867.001‡	MW255585	MW233781	MW233745	SRR14069290
Family Cycloteuthidae Naef, 1923						
<i>Cycloteuthis sirventi</i> Joubin, 1919	Atlantic Ocean, 30.19°N, 19.99°W	ICMC000127†	MW255578	MW233774	MW233738	SRR14069297
<i>Discoteuthis laciniosa</i> Young & Roper, 1969	Atlantic Ocean, 35.58°N, 20.23°W	ICMC000128†	MW255563	MW233759	MW233723	SRR14069313
Family Gonatidae Hoyle, 1886						
<i>Gonatus fabricii</i> (Lichtenstein, 1818)	Atlantic Ocean, 55.38°N, 23.22°W	ICMC000120†	MW255562	MW233758	MW233722	SRR14069314
Family Histoteuthidae Verrill, 1881						
<i>Stigmatoteuthis arcturi</i> Robson, 1948	Atlantic Ocean, 24.98°N, 21.10°W	–	MW255560	MW233756	MW233720	SRR14069317
Family Joubiniteuthidae Naef, 1922						
<i>Joubiniteuthis portieri</i> (Joubin, 1916)	Pacific Ocean, 19.50°N, 156.39°W	USNM1188444*	MW255583	MW233779	MW233743	SRR14069291
Family Enoplateuthidae Pfeffer, 1900						
<i>Abralia veranyi</i> (Rüppell, 1844)	Mediterranean Sea, 40.81°N, 1.37°E	–	MW255555	MW233751	MW233715	SRR14069288
Family Lepidoteuthidae Pfeffer, 1912						
<i>Lepidoteuthis grimaldii</i> Joubin, 1895	Atlantic Ocean, 40.06°N, 67.45°W	USNM1192539*	MW255582	MW233778	MW233742	SRR14069292

Table 1. Continued

Species	Sampling locality	Voucher accession number	Mitogenome GenBank accession number	18S GenBank Accession number	28S GenBank accession number	Sequence Read Archive (SRA)
Family Lycoteuthidae Pfeffer, 1908a						
<i>Lampadioteuthis megalia</i> Berry, 1916	Atlantic Ocean, 46.75°N, 39.80°W	USNM1531237*	MW255572	MW233768	MW233732	SRR14069303
<i>Selenoteuthis scintillans</i> Voss, 1959	Atlantic Ocean, 3.77°N, 25.18°W	ICMC000312†	MW255571	MW233767	MW233731	SRR14069304
Family Magnapinnidae						
<i>Vecchione & Young, 1998</i>						
<i>Magnapinna</i> sp.	Atlantic Ocean, 30.03°N, 19.76°W	ICMC000146†	MW255565	MW233761	MW233725	SRR14069312
Family Mastigoteuthidae						
Verrill, 1881						
<i>Echinoteuthis atlantica</i> (Joubin, 1933)	Atlantic Ocean, 24.98°N, 21.09°W	ICMC000115†	MW255561	MW233757	MW233721	SRR14069315
Family Neoteuthidae Naef, 1921						
<i>Neoteuthis thielei</i> Naef, 1921	Atlantic Ocean, 2.91°S, 28.44°W	–	MW255569	MW233765	MW233729	SRR14069307
Family Octopoteuthidae Berry, 1912						
<i>Octopoteuthis sicula</i> Rüppell, 1844	Atlantic Ocean, 48.31°N, 38.91°W	USNM1531262*	MW255574	MW233770	MW233734	SRR14069300
Family Ommastrephidae						
Steenstrup, 1857b						
<i>Illex coindetii</i> (Vérany, 1839)	Mediterranean Sea	–	MW255551	MW233747	MW233711	SRR14069322
<i>Dosidicus gigas</i> (d'Orbigny, 1835 [in 1834–1847])	Pacific Ocean	–	EU068697 (Staaf et al., 2010)	KY387931 (Francis WR & Haddock SHD, unpublished)	KY387931 (Francis WR & Haddock SHD, unpublished)	–
<i>Sthenoteuthis pteropus</i> (Steenstrup, 1855)	Atlantic Ocean, 7.27°N, 23.94°W	–	MW255556	MW233752	MW233716	SRR14069321
<i>Todarodes filippovae</i> Adam, 1975	Atlantic Ocean, –34.27°N, 17.62°W	–	MW255557	MW233753	MW233717	SRR14069320
<i>Todarodes sagittatus</i> (Lamarck, 1798)	Mediterranean Sea	–	MW255552	MW233748	MW233712	SRR14069316
<i>Todaropsis eblanae</i> (Ball, 1841)	Mediterranean Sea	–	MW255554	MW233750	MW233714	SRR14069294

Table 1. Continued

Species	Sampling locality	Voucher accession number	Mitogenome GenBank accession number	18S GenBank Accession number	28S GenBank accession number	Sequence Read Archive (SRA)
Family Onychoteuthidae Gray, 1849						
<i>Ancistroteuthis lichtensteini</i> (in Férussac & d'Orbigny, 1835–1848)	Mediterranean Sea	–	MW255553	MW233749	MW233713	SRR14069305
Family Pholidoteuthidae Voss, 1956						
<i>Pholidoteuthis massyae</i> (Pfeffer, 1912)	Gulf of Mexico, 28.0°N, 88.7°W	–	MW255581	MW233777	MW233741	SRR14069293
Family Pyroteuthidae Pfeffer, 1912						
<i>Pyroteuthis margaritifera</i> (Rüppell, 1844)	Atlantic Ocean, 35.60°N, 20.23°W	ICMC000147 [†]	MW255580	MW233776	MW233740	SRR14069295
Family Thysanoteuthidae Keferstein, 1866						
<i>Thysanoteuthis rhombus</i> Troschel, 1857	Mediterranean Sea, 40.76°N, 1.35°E	ICMC000069 [†]	MW255559	MW233755	MW233719	SRR14069318

[†]National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

[‡]Biological Reference Collections (GBR-ICM) of the Institut de Ciències del Mar (ICM-CSIC), Barcelona, Spain (Guerrero *et al.*, 2020).

[§]Australian Museum, Sydney, NSW, Australia.

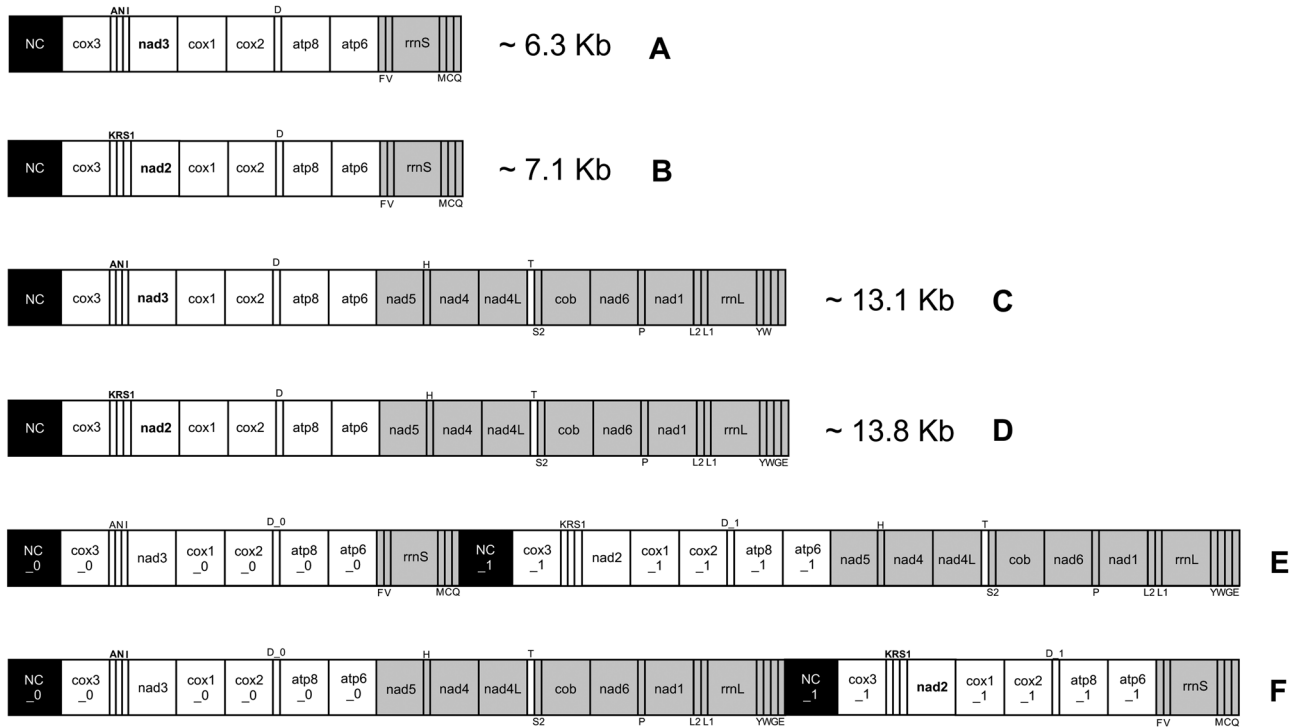


Figure 2. Schematic representation of the contigs usually retrieved from NOVOPLASTY v.3.8.3 (A–D) and the two possible combinations of the same size including all the genes present on oegopsid mitogenomes (E, F). The plus (+) strand is represented in the direction 5′ → 3′. A, contig usually of ~6.3 kb including *nad3*, *rrnS* and transfer RNAs associated with both genes. B, contig usually of ~7.1 kb including *nad2*, *rrnS* and transfer RNAs associated with both genes. C, contig usually of ~13.1 kb including *nad3*, *rrnL* and transfer RNAs associated with both genes. D, contig usually of ~13.8 kb including *nad2*, *rrnL* and transfer RNAs associated with both genes. E, complete mitogenome after manually merging the contigs depicted in A, D. F, complete mitogenome after manually merging the contigs depicted in B, C. The non-coding regions are indicated in black; genes from the minus (–) strand of the mitogenome are coloured in light grey. Squares are not proportional to the size of the genes. See the Material and Methods section for gene abbreviations.

methodology to identify gene order features that can be used as taxonomic characters to characterize oegopsid squid clades. A manually curated mitogenome gene order was prepared for each newly sequenced species except for *Chtenopteryx* cf. *canariensis* Salcedo-Vargas & Guerrero-Kommritz, 2000, which was excluded from the dataset because of problems with assembly of the contigs resulting from duplicated genes. The gene orders of *Architeuthis dux* and *Dosidicus gigas* (d’Orbigny, 1835 [in 1834–1847]) were retrieved from GenBank. Given that the included taxa shared the same duplicated genes (*cox1*, *cox2*, *cox3*, *trnD*, *atp6* and *atp8*) and non-coding regions, both duplications were included using the subindices ‘_0’ and ‘_1’ to identify which copy was lost when that happened. The mitogenome genes are abbreviated as follows: *NC*, non-coding region; *cox1*, cytochrome *c* oxidase subunit 1; *cox2*, cytochrome *c* oxidase subunit 2; *cox3*, cytochrome *c* oxidase subunit 3; *cob*, cytochrome *b* oxidase; *atp6*, ATP synthase subunit 6; *atp8*, ATP synthase membrane 8; *nad1*, NADH dehydrogenase subunit 1; *nad2*, NADH

dehydrogenase subunit 2; *nad3*, NADH dehydrogenase subunit 3; *nad4*, NADH dehydrogenase subunit 4; *nad4L*, NADH dehydrogenase subunit 4L; *nad5*, NADH dehydrogenase subunit 5; *nad6*, NADH dehydrogenase subunit 6; *rrnS*, small mitochondrial ribosomal unit (12S rRNA); *rrnL*, large mitochondrial ribosomal unit (16S rRNA); *trnA*, A, transfer RNA (trn) Alanine; *trnC*, C, trn Cysteine; *trnD*, D, trn Aspartate; *trnE*, E, trn Glutamate; *trnF*, F, trn Phenylalanine; *trnG*, G, trn Glycine; *trnH*, H, trn Histidine; *trnI*, I, trn Isoleucine; *trnK*, K, trn Lysine; *trnL1*, L1, trn Leucine 1; *trnL2*, L2, trn Leucine 2; *trnM*, M, trn Methionine; *trnN*, N, trn Asparagine; *trnP*, P, trn Proline; *trnQ*, Q, trn Glutamine; *trnR*, R, trn Arginine; *trnS1*, S1, trn Serine 1; *trnS2*, S2, trn Serine 2; *trnT*, T, trn Threonine; *trnV*, V, trn Valine; *trnW*, W, trn Tryptophan; and *trnY*, Y, trn Tyrosine. A minus symbol (–) before the gene indicates that the gene is placed in the minus strand of the mitogenome.

Ancestral character reconstructions were performed in MESQUITE v.3.61 (Maddison & Maddison, 2019), coding each gene order as a state within a single

multistate character. *Chtenopteryx cf. canariensis* was removed from the ML consensus tree, and maximum parsimony and maximum likelihood reconstructions of the characters were implemented.

RESULTS

PHYLOGENETIC ANALYSES

The tree topology of ML and BI analyses were congruent with each other (Fig. 3). Oegopsida was fully supported (100% bootstrap/1 posterior probability) and basally split into two main groups: one clade including the families Cranchiidae, Ommastrephidae and Thysanoteuthidae with full support (100%/1); and a group including the remaining families with poor support in the ML (67%)

but high support in BI (0.99) analysis. Within the second group, Chiroteuthidae formed a fully supported clade (100%/1). The family Pholidoteuthidae was the sister taxon to the chiroteuthid family group, forming a clade with high support and full support in the ML and BI analyses, respectively (96%/1). The two remaining lepidoteuthid families, Lepidoteuthidae and Octopoteuthidae, were sister taxa with full support (100%/1), and together were sister to the clade comprising Pholidoteuthidae and the chiroteuthid family group, rendering the lepidoteuthid family group as paraphyletic. This clade comprising families in the chiroteuthid family group plus Pholidoteuthidae, Octopoteuthidae and Lepidoteuthidae was fully supported (100%/1). A clade containing the families Ancistrocheiridae, Enoploteuthidae, Lycoteuthidae

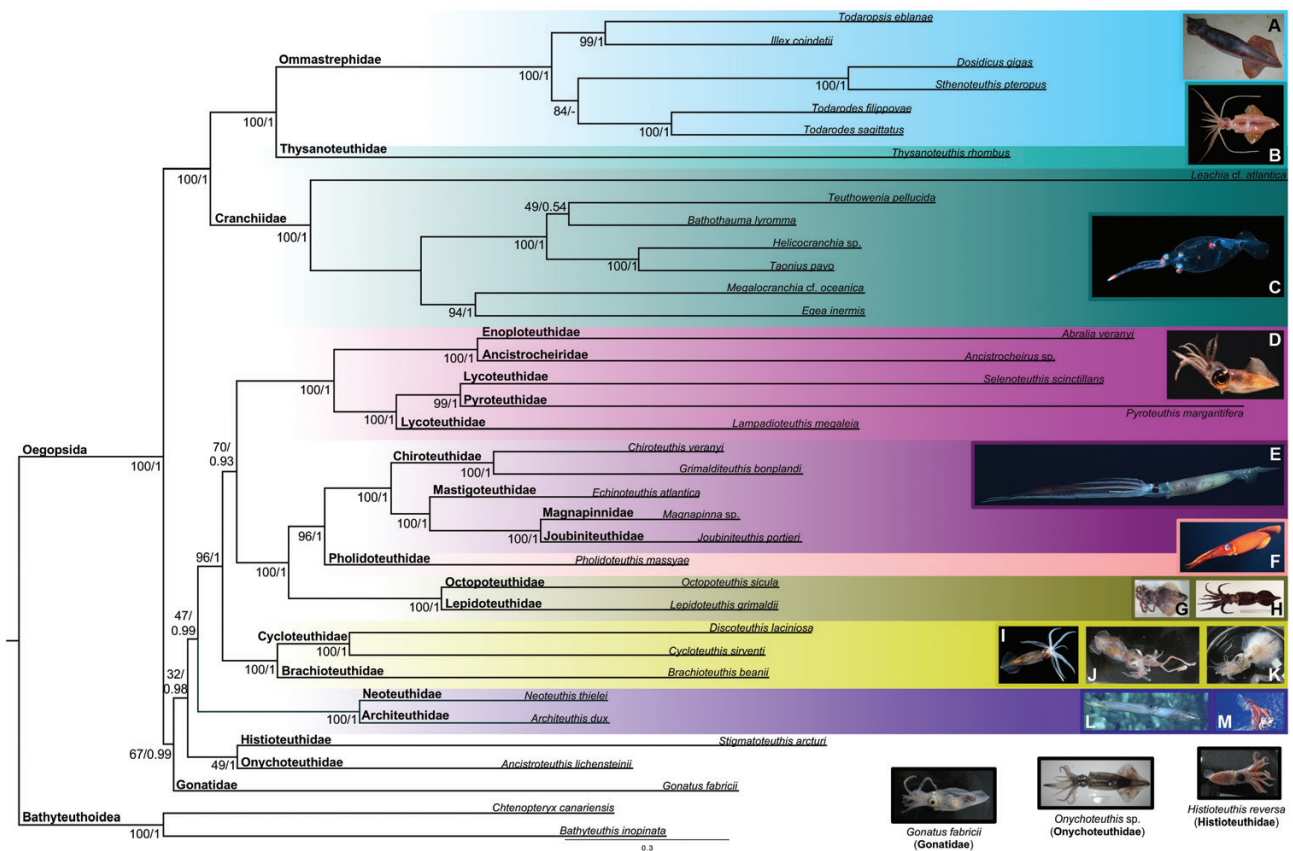


Figure 3. Maximum likelihood phylogenetic tree of oceanic squids constructed with IQTREE v.2. Values on nodes represent bootstrap percentages from the maximum likelihood analysis and posterior probabilities from the Bayesian inference analysis, respectively. A, *Ommastrephes caroli* (Furtado, 1887) (Ommastrephidae). B, *Thysanoteuthis rhombus* (Thysanoteuthidae), modified from Fernández-Álvarez et al. (2021). C, *Leachia* sp. (Cranchiidae). Photograph by Steven Kovacs. D, *Abraliopsis* sp. B (Enoploteuthidae), from Young & Tsuchiya (2014). E, *Chiroteuthis* sp. (Chiroteuthidae), modified from Vecchione (2019). F, *Pholidoteuthis massyae* (Pholidoteuthidae). Photograph by Mark C. Benfield (Louisiana State University). G, *Octopoteuthis sicula* (Octopoteuthidae). H, *Lepidoteuthis grimaldii* (Lepidoteuthidae). Photograph by Alejandro Escánez (University of La Laguna). I, *Brachioteuthis* sp. (Brachioteuthidae). Photograph by David Shale. J, *Cycloteuthis sirventi* (Cycloteuthidae). K, *Discoteuthis laciniosa* (Cycloteuthidae). L, *Neoteuthis theilei* (Neoteuthidae), modified from Vecchione & Young (2019c). M, *Architeuthis dux* (Architeuthidae). Photograph by T. Kubodera, curator emeritus of National Museum of Nature and Science (Tokyo).

and Pyroteuthidae was fully supported (100%/1), but Pyroteuthidae fell among the family Lycoteuthidae [represented by *Selenoteuthis scintillans* Voss, 1959 (subfamily Lycoteuthinae) and *Lampadioteuthis megaleia* Berry, 1916 (subfamily Lampadioteuthinae)], rendering Lycoteuthidae paraphyletic. The enoploteuthid family group clade clustered with the clade ((Lepidoteuthidae + Octopoteuthidae) (Pholidoteuthidae (chiroteuthid family group))). This group received acceptable and poor support in the ML and BI analyses, respectively (70%/0.93). *Discoteuthis laciniosa* Young & Roper, 1969 and *Cycloteuthis sirventi* Joubin, 1919 clustered with full support (100%/1) and formed a clade with the family Brachioteuthidae with full support (100%/1). This clade was sister to the group ((enoploteuthid family group) ((Lepidoteuthidae + Octopoteuthidae) (Pholidoteuthidae(chiroteuthid family group)))). The resulting clade received high and full support in the ML and BI analyses, respectively (96%/1). Architeuthidae and Neoteuthidae clustered together with full support (100%/1). This last clade (Architeuthidae + Neoteuthidae) clustered with the clade ((Brachioteuthidae + Cycloteuthidae) ((Enoploteuthid family group) ((Lepidoteuthidae + Octopoteuthidae) (Pholidoteuthidae(chiroteuthid family group))))) with poor support in the ML analysis but high support in the BI analysis (47%/0.99). The families Histioteuthidae and Onychoteuthidae clustered with one another with poor support in the ML analysis and full support in the BI analysis (49%/1). These two families clustered with the group ((Architeuthidae + Neoteuthidae) ((Brachioteuthidae + Cycloteuthidae) ((Enoploteuthid family group) ((Lepidoteuthidae + Octopoteuthidae) (Pholidoteuthidae(chiroteuthid family group))))) with poor support in the ML analysis and high support in the BI analysis (32%/0.98). Finally, within this large group, the family Gonatidae clustered with all other taxa in the group, with poor support in the ML analysis but high support in the BI analysis (67%/0.99).

GENE ORDER

Most Oegopsida families and our outgroup *Bathyteuthis inopinata* Judkins, Lindgren, Villanueva, Clark & Vecchione, 2020 are characterized by the presence of *trnI* in the *nad3* gene block 'NC_0 cox3_0 trnA trnN trnI nad3' (Fig. 4). Given that this character is present in the sister group of Oegopsida, we consider it as the plesiomorphic state. Both maximum parsimony and maximum likelihood ancestral state reconstructions of mitogenome order support the idea that this arrangement represents the plesiomorphic condition for oegopsid squids (Fig. 4A, B). The proportional likelihoods of all the nodes of the maximum likelihood reconstruction were > 94% and matched those of the maximum parsimony reconstruction. In

Lampadioteuthis megaleia, the position of *trnI* is the same, but the *cox1* and *cox2* copies (normally present as 'nad2 cox1_1 cox2_1 trnD_1 atp8_1 atp6_1') are lost from the *nad2* gene block, resulting in 'nad2 trnD_1 atp8_1 atp6_1' (Fig. 4D). In Histioteuthidae, the position of *trnI* remains the same, but *atp6* is lost from the *nad2* gene block (Fig. 4E). All species within the clade (Cranchiidae (Ommastrephidae + Thysanoteuthidae)) have the same gene order, characterized by the transposition of *trnM* from the *rrnS* to the *rrnL* regions, as follows '-rrnL -trnM -trnY -trnW -trnG -trnE NC_0' (Fig. 4F). In Neoteuthidae and Architeuthidae, there is transposition of the *trnI* from the *nad3* to the *nad2* gene block as follows: 'NC_1 cox3_1 trnK trnR trnI trnS1 nad2' (Fig. 4G, J). In Octopoteuthidae and Lepidoteuthidae, *nad2* is downstream of *rrnL*, and *nad3* is downstream of *rrnS*: '-rrnL -trnY -trnW -trnG -trnE NC_0 cox3_1 trnK trnR trnS1 nad2' and '-rrnS -trnM -trnC -trnQ NC_1 cox3_0 trnA trnN trnI nad3' (Fig. 4H). Only *cox3* is duplicated. In Joubiniteuthidae (Fig. 4I), the relative positions of *nad2* and *nad3* in relationship to *rrnS* and *rrnL* are the same as in Octopoteuthidae and Lepidoteuthidae, one of the copies of *trnD* is lost, and in the space where *cox1* and *cox2* are generally found, smaller non-functional gene-like loci are present.

DISCUSSION

PHYLOGENY OF OEGOPSID SQUIDS AND EVOLUTION OF MITOGENOME GENE ORDER

This is the first phylogenomic study of oegopsid squids with extensive taxon coverage: we included representatives of 21 families of the currently accepted 24 families. We provide the first well-resolved phylogeny of the group at the family level. Several morphologically defined family groups were supported by our phylogeny, such as the architeuthid (Young & Vecchione, 2019b), the chiroteuthid (Young & Vecchione, 2019c) and the enoploteuthid (Young & Vecchione, 2019d) family groups, but this study reveals high support for relationships previously recovered with only low support in molecular phylogenetic studies (Lindgren *et al.*, 2012; Allcock *et al.*, 2015) and never proposed from a morphological perspective (Young *et al.*, 1998), including the relationship between the family Cranchiidae and the clade formed by Ommastrephidae and Thysanoteuthidae and the relationship between Brachioteuthidae and Cycloteuthidae. The morphological support for the relationship between Ommastrephidae and Thysanoteuthidae is weak. They are united by the presence of a modified mantle-funnel locking apparatus with an inverted 'T' and a lazy 'T', respectively, but also by the fact that these are the only two cephalopod families with multiple seminal

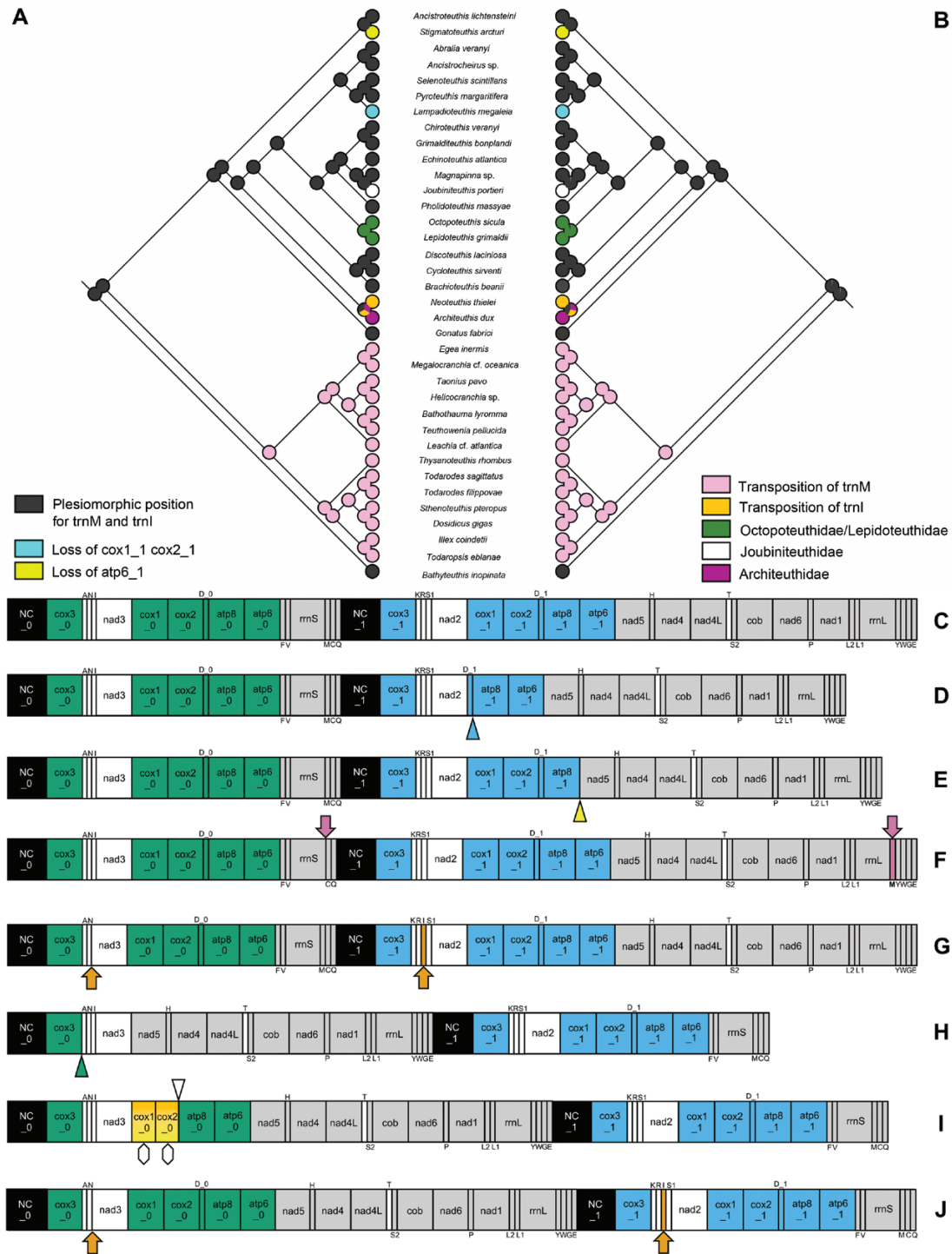


Figure 4. A, B, maximum parsimony (A) and maximum likelihood (B) ancient state reconstruction of the mitogenome gene order of oceanic squids implemented in MESQUITE v.3.61. C, hypothetical mitochondrion including the plesiomorphic positions for *trnM* and *trnI*. D, hypothetical mitochondrial gene order of *Lampidoteuthis megaleia*. E, hypothetical mitochondrial gene order of Histiotuteuthidae. F, hypothetical mitochondrial gene order of Cranchiidae, Ommastrephidae and Thysanoteuthidae. G, hypothetical mitochondrial gene order of Neoteuthidae. H, mitochondrial gene order of Lepidoteuthidae and Octopoteuthidae. I, mitochondrial gene order of Joubiniteuthidae. J, mitochondrial gene order of Architeuthidae based on Winkelmann *et al.* (2013) and the GenBank sequence FJ429092 (Elliger CA, Lebaric ZN, Gilly WF & Robison BH,

receptacles in the buccal membrane (Jereb & Roper, 2010; Fernández-Álvarez *et al.*, 2018b). Additional support is provided by paralarval morphology, because both groups have buccal papillae around the mouth (Wakabayashi *et al.*, 2005; Fernández-Álvarez *et al.*, 2018a). Naef (1922) hypothesized a closer relationship between Ommastrephidae and Thysanoteuthidae based on the lateral displacement of the outer funnel abductor muscles in both taxa and the shape of the funnel pit, neck folds and eyelid. There is no known morphological character shared exclusively between Cranchiidae and the other two families. The Bayesian analysis of Lindgren (2010) found a relationship between Ommastrephidae and Cranchiidae (in Bayesian but not ML analyses), and the phylogenetic analysis of Lindgren *et al.* (2012) recovered Thysanoteuthidae and Ommastrephidae as sister taxa, but with < 50% bootstrap support. Some of the phylogenomic analyses of Lindgren & Anderson (2018) and Anderson & Lindgren (2021) found a relationship between Cranchiidae and Ommastrephidae. However, we found full support in the phylogenetic analyses for this relationship. The shared gene order (*trnM* associated with *rrnL* instead of *rrnS*) among all the species of these three families, unique for this group, constitutes a synapomorphy that provides further molecular support for this clade. The similarities in mitogenome gene order between Ommastrephidae and Thysanoteuthidae have been discussed elsewhere (Tang *et al.*, 2021).

The relationships between Gonatidae, Onychoteuthidae, Histioteuthidae and the clade formed by Architeuthidae and Neoteuthidae were poorly supported in the ML analyses (32–67%), but highly or very highly supported in the BI analyses (0.98–0.99). We prefer to be conservative regarding these positions. However, the relationship between the families Architeuthidae and Neoteuthidae, between Brachioteuthidae and Cycloteuthidae and the relationships among the families previously identified as belonging to the enoploteuthid family group and chiroteuthid family group were fully supported: all received 100% bootstrap support and posterior probabilities of one. Also, the relationship between the cycloteuthid genera was fully supported

(100%/1), in contrast to the results of Lindgren *et al.* (2012). The monophyly of Cycloteuthidae and its sister relationship with Brachioteuthidae was also strongly supported by Lindgren (2010). The lepidoteuthid family group (Vecchione & Young, 2019b) was retrieved as paraphyletic in both analyses, because Pholidoteuthidae clustered with the chiroteuthid family group (96%/1). In spite of the similarity of dermal cushions in *Lepidoteuthis grimaldii* and *Pholidoteuthis adami* Voss, 1956, this group was also recovered as paraphyletic in the Bayesian analysis by Lindgren (2010) and by Lindgren *et al.* (2012). The family Lycoteuthidae was found to be paraphyletic, reinforcing the idea that each lycoteuthid subfamily should be considered at family rank (Berry, 1914, 1920; Voss, 1956). The close relationship of lycoteuthid and pyroteuthid squids is supported morphologically by the similarity of photophore structure and distribution (Herring *et al.*, 1985; Young & Harman, 1998). The resurrection of the family Lampadioteuthidae increases the number of families within Oegopsida to 25.

The positions of *trnI* and *trnM* are the same in Bathyteuthidae and the oegopsid families Ancistrocheiridae, Brachioteuthidae, Chiroteuthidae, Cycloteuthidae, Enoploteuthidae, Histioteuthidae, Gonatidae, *Lampadioteuthismegaleia*, Magnapinnidae, Mastigoteuthidae, Onychoteuthidae, Pholidoteuthidae, Pyroteuthidae and *Selenoteuthis scintillans*. Given that they occur in the same gene blocks in the sister group of Oegopsida, Bathyteuthida, we consider the position of both genes to be the plesiomorphic state within oegopsids. This was supported by our ancestral state reconstruction analyses (Fig. 4A, B). A few variants appear to have arisen from secondary loss of one or more of the duplicated genes, as seen in Histioteuthidae and *Lampadioteuthis megaleia*; these losses can be considered as apomorphic characters. Lastly, the family Joubiniteuthidae and the clade formed by Octopoteuthidae and Lepidoteuthidae show other reorganizations of the mitogenome. One copy of *cox1* and *cox2* appears non-functional and *trnD* is lost in Joubiniteuthidae. In Octopoteuthidae and Lepidoteuthidae, one copy of each of *cox1*, *cox2*, *atp6*, *atp8* and *trnD* is lost. The resulting genome, which

unpublished). In all mitogenomes, the plus (+) strand is represented in the direction 5' → 3'. Arrowheads indicate the points where one or more genes were lost; arrows signal the position of gene transposition (highlighted) and the position of that gene in the plesiomorphic gene order; diamonds signal the position of non-functional copies of genes. The non-coding regions are indicated in black; genes from the minus (–) strand of the mitogenome are coloured in light grey. Squares are not proportional to the size of the genes. See the Material and Methods section for gene abbreviations. Where multiple duplicate genes prevented NOVOPLASTY from returning a single circular contig, we curated the contigs obtained to match the gene order in Figure 2E (see the Material and Methods section). Almost all published oegopsid genomes follow the order depicted in Figure 2E, whereas those reported for *Architeuthis dux* (Winkelmann *et al.*, 2013) and the bathyteuthid *Bathyteuthis abyssicola* Hoyle, 1885 (Kawashima *et al.*, 2013) follow Figure 2F, and our assumption regarding the arrangement of blocks (but not the order of genes within them) could be wrong for some species.

has only one duplicated gene and thus assembled as a circular contig requiring no curation, is identical to the theoretical gene order depicted in [Figure 2F](#), apart from the gene loss. Almost all previously published oegopsid genomes follow the order depicted in [Figure 2E](#), whereas those reported for *Architeuthis dux* and *Bathyteuthis abyssicola* [Hoyle, 1885](#) follow [Figure 2F](#). Our use of [Figure 2E](#) as a reference for contig assembly could be incorrect for some species, and we could therefore be overlooking other important information on gene order. Long-read sequencing would avoid the need for such assumptions and, if used with the analyses developed here, could provide further synapomorphies in this difficult group.

SYSTEMATICS

Here, we review the systematic status at the family level, including super- and subfamilies, of oceanic squids of the order Oegopsida based on this well-resolved phylogeny, and we re-evaluate morphological and molecular features, based mainly on the study by [Young & Vecchione \(2019a\)](#), to provide an accurate and succinct diagnosis for each group. Molecular features have been shown to be useful characters for solving taxonomic problems among morphologically challenging squids ([Fernández-Álvarez *et al.*, 2020](#)) and octopods ([Strugnell *et al.*, 2014](#)). The number of species and genera of each taxon is taken from [MolluscaBase eds \(2021a\)](#), which is based on the number of species currently recognized and named. Some of the groups might include undescribed cryptic biodiversity; hence, the species count provided for each taxon should be taken with caution. The selection of characters for the diagnoses was based on the morphological differences, especially those between families within a superfamily and subfamilies within a family. As a rough estimation, the terms small-, medium-, large- and massive-sized refer to squids of < 100, 100–300, 300–1000 and > 1000 mm in dorsal mantle length, respectively. The term ‘hooks’ refers to suckers developed into hooks.

ORDER OEGOPSIDA [D’ORBIGNY, 1845](#)

(252 SPECIES)

Diagnosis: Squids without a cornea covering the eyes; without suckers on the buccal membrane; without circularis muscles in the arm and tentacle suckers; without accessory nidamental glands; tentacles usually with carpal locking apparatus; gills with branchial canal; with duplications of the mitochondrial genes *atp6*, *atp8*, *cox1*, *cox2*, *cox3* and *trnD*, although lost in some clades.

SUPERFAMILY ARCHITEUTHOIDEA [BERRY, 1920](#)

(FIVE SPECIES)

Diagnosis: Oegopsid with buccal connectives attached to the dorsal margins of ventral arms; without photophores; funnel–mantle locking apparatus straight, reaching the anterior mantle margin; fins without anterior lobes, with anterior fin attachment to mantle rather than gladius; tentacles with numerous carpal suckers; mitochondrial gene *trnI* between *trnR* and *trnS1* in the following sequence: *trnK trnR trnI trnS1 nad2*.

Remarks: The original sense of Architeuthoidea included only the family Architeuthidae ([Berry, 1920](#)).

FAMILY ARCHITEUTHIDAE [BERRY, 1920](#)

(ONE SPECIES)

Diagnosis: Massive adult-sized Architeuthoidea without free posterior fin lobes; long, narrow tentacles, with suckers in four series in manus and dactylus; manus with enlarged suckers in the two medial series; carpal region with six or seven irregular series of suckers with paired knobs.

FAMILY NEOTEUTHIDAE [NAEF, 1921](#)

(FOUR SPECIES IN FOUR GENERA)

Diagnosis: Small to medium adult-sized Architeuthoidea with free posterior fin lobes; more than ten irregular series of suckers on the proximal manus of the tentacular club; tentacle locking apparatus only in the dorsal margin, extending at least in the proximal manus but sometimes also in the tentacle stalk; fins with free posterior lobes.

SUPERFAMILY CRANCHIOIDEA [PROSCH, 1847](#)

(63 SPECIES)

Diagnosis: Small to massive adult-sized Oegopsida with modifications of the funnel–mantle locking apparatus; funnel–mantle locking apparatus reaching the anterior margin of the mantle; with two series of suckers in the arms; tentacle manus suckers usually in four series; mitochondrial gene *trnM* between *rrnL* and *trnY* in the following sequence: *-rrnL -trnM -trnY -trnW -trnG -trnE*.

Synonyms: The superfamilies Ommastrephoidea [Steenstrup, 1857b](#) and Thysanoteuthoidea [Keferstein, 1866](#) were described in a different sense than in the present work: the superfamily Ommastrephoidea included Brachioteuthidae, Ommastrephidae and Thysanoteuthidae according to [Berry \(1920\)](#). However,

owing to our criteria the families Ommastrephidae and Thysanoteuthidae are included within the superfamily Cranchioidea. We therefore consider the names Ommastrephoidea and Thysanoteuthoidea as junior synonyms of Cranchioidea.

FAMILY CRANCHIIDAE [PROSCH, 1847](#)

(37 SPECIES IN 14 GENERA)

Diagnosis: Ammoniacal and muscular Cranchioidea with the head fused to the mantle through the nuchal apparatus and the funnel–mantle locking apparatuses; buccal connectives attached to the ventral borders of ventral arms; tentacles with carpal locking apparatus; with a coelom transformed into a buoyancy chamber filled with ammonium chloride; digestive gland usually spindle shaped; most paralarvae with stalked eyes.

SUBFAMILY CRANCHIINAE [PROSCH, 1847](#)

(12 SPECIES IN FOUR GENERA)

Diagnosis: Small to medium adult-sized Cranchiidae with four or more small ocular photophores; mantle with cartilaginous tubercles dispersed or in strips; ventrolateral arms longest; without tentacle hooks; either left or right ventral arm hectocotylized.

SUBFAMILY TAONIINAE [PFEFFER, 1912](#)

(23 SPECIES IN TEN GENERA)

Diagnosis: Small to massive adult-sized Cranchiidae with one to three ocular photophores; mantle without tubercles except on the funnel–mantle locking apparatus; some species with hooks or hook-like rings in tentacle and/or arm suckers.

FAMILY OMMASTREPHIDAE [STEENSTRUP, 1857B](#)

(25 SPECIES IN 11 GENERA)

Diagnosis: Small to large adult-sized muscular Cranchioidea with funnel–mantle locking apparatus modified into an inverted ‘T’ shape; buccal connectives attached to the dorsal borders of ventral arms; fins short and wide; ‘rhynchoteuthion’ paralarvae, with tentacles fused as a proboscis and with underdeveloped nervous, digestive and respiratory systems and arm crown at hatching relative to other cephalopod hatchlings; spherical, gelatinous egg masses.

SUBFAMILY ILLICINAE [POSSELT, 1891](#)

(FOUR SPECIES IN ONE GENUS)

Diagnosis: Medium adult-sized Ommastrephidae without photophores; funnel groove without foveola or lateral pockets; tentacles without carpal locking apparatus; tentacle club with manus horny sucker

rings smooth or with rounded teeth; eight series of suckers on dactylus; lateral suckers of the paralarva proboscis equal in diameter to the central ones; paralarvae without skin sculpture; adult female without seminal receptacles in the buccal membrane.

SUBFAMILY OMMASTREPHINAE [STEENSTRUP, 1857B](#)

(NINE SPECIES IN FIVE GENERA)

Diagnosis: Small to large adult-sized slightly ammoniacal Ommastrephidae with ocular, mantle and/or visceral photophores or photogenic tissues; funnel groove with foveola and lateral pockets; tentacles with carpal locking apparatus; tentacle club with manus horny rings usually with four larger pointed teeth forming a square; four series of suckers on dactylus; lateral suckers of the paralarva proboscis larger or equal in diameter to the central ones; paralarvae with skin sculpture; adult female with multiple seminal receptacles in the buccal membrane.

SUBFAMILY ORNITHOTEUTHINAE [NIGMATULLIN, 1979](#)

(TWO SPECIES IN ONE GENUS)

Diagnosis: Medium adult-sized Ommastrephidae with ocular photophores and large photophore strip on the ventral midline of viscera (two independent intestinal photophores during paralarval stage); posterior mantle and fins extended into narrow tail; funnel groove with foveola, without lateral pockets; tentacles without carpal locking apparatus; tentacle club with manus horny rings with a homogeneous dentition; four series of suckers on dactylus; lateral suckers of the paralarva proboscis larger in diameter than the central ones; adult female with multiple seminal receptacles in the buccal membrane.

SUBFAMILY TODARODINAE [ADAM, 1960](#)

(NINE SPECIES IN FOUR GENERA)

Diagnosis: Medium to large adult-sized Ommastrephidae without photophores; funnel groove with foveola, without lateral pockets; tentacles without carpal locking apparatus; tentacle club with horny rings of manus suckers with homogeneous dentition; four series of suckers on dactylus; diameter of the lateral suckers of the paralarva proboscis larger than or equal to the central ones; paralarvae with skin sculpture; adult female with multiple seminal receptacles in the buccal membrane.

SUBFAMILY TODAROPSINAE [NIGMATULLIN, 2000](#)

(ONE SPECIES)

Diagnosis: Medium adult-sized Ommastrephidae without photophores; funnel groove without foveola; tentacles without carpal locking apparatus; tentacle

club with manus horny rings with homogeneous dentition; four series of suckers on dactylus; lateral suckers of the paralarva proboscis equal in diameter to the central ones; paralarval development more advanced at hatching than other ommastrephids; paralarvae with skin sculpture; adult female with multiple seminal receptacles in the buccal membrane.

FAMILY THYSANOTEUTHIDAE KEFERSTEIN, 1866

(ONE SPECIES)

Diagnosis: Large adult-sized muscular Cranchioidea with mantle locking apparatus having a modified ('lazy') 'T' shape; anal photophore in juveniles; buccal connectives attached to the ventral borders of ventral arms; nuchal-locking apparatus with two hook-like knobs on mantle component and opposing nuchal knobs and pits; tentacles with carpal locking apparatus; large and wide muscular rhomboidal fins inserted in the dorsolateral surface of the mantle; gladius with vanes projecting anteriorly; with multiple seminal receptacles in the buccal membrane; large, long, cylindrical, gelatinous egg masses; embryos and paralarvae covered by dense chromatophores.

SUPERFAMILY CHIROTEUTHOIDEA GRAY, 1849

(41 SPECIES)

Diagnosis: Ammoniacal and weakly muscled Oegopsida with a secondary adult tentacular club but with primary tentacle club in early stages, with protective membranes on clubs symmetrical or subsymmetrical, without carpal locking apparatus, without keel, without terminal pad; buccal connectives attach ventrally to ventral arms; funnel–mantle locking apparatus usually oval, although sometimes modified by projections (tragus and/or antitragus), reaching the anterior margin of the mantle; fins usually terminal; often with a long tail supported by the secondary conus of the gladius during some stages of development.

Remarks: Tragus and antitragus refer to two protruding knobs found in the funnel–mantle locking apparatus of some Chiroteuthoidea; see Young & Vecchione (2019c) for more information. Adults of the paedomorphic genus *Planctoteuthis* Pfeffer, 1912 retain the primary club; hence, the morphological characters related to the tentacle morphology in this diagnosis do not apply to this genus. The funnel–mantle locking apparatus of *Grimalditeuthis bonplandi* (Vérany, 1839) is fused.

FAMILY BATOTEUTHIDAE YOUNG & ROPER, 1968

(ONE SPECIES)

Diagnosis: Medium adult-sized Chiroteuthoidea with arm suckers in two series and tentacle suckers in six

series, spanning 80% of tentacle length; photophores in aboral surface of ventral arm tips (large in males, small in females); distinctly curved funnel–mantle locking apparatus; long, unadorned tail supported by secondary conus of gladius.

Remarks: Not included in our phylogenetic analyses, but its position within the superfamily is supported provisionally by its morphology (Young & Roper, 1968; Young & Vecchione, 2019c) and the phylogenetic results of Lindgren (2010) and Lindgren *et al.* (2012).

FAMILY CHIROTEUTHIDAE GRAY, 1849

(17 SPECIES IN FIVE OR SIX GENERA)

Diagnosis: Chiroteuthoidea with arm suckers in two series and tentacle suckers in four series or absent; club divided into two or three sections with symmetrical protective membranes; with enlarged ventral arms having expanded lateral membranes modified into sheaths for the tentacles; head with a long neck and usually with a brachial pillar in adults, with an indistinct eyelid sinus, with stalked olfactory organs, without occipital folds; funnel–mantle locking apparatus usually oval and with a series of knobs known as tragus and antitragus; tail with lateral ornamentation, lost in adults of some genera but retained in others; characteristic paralarval type known as 'doratopsis' with an elongated chambered neck and brachial pillar, and with vesicular tissue in the posterior mantle, with vesiculated arms in advanced paralarvae, and with gladius extending beyond the fins and supporting ornamented structures.

Remarks: Adults of the paedomorphic genus *Planctoteuthis* Pfeffer, 1912 retain the primary club; hence, the morphological characters related to the tentacle morphology in this diagnosis do not apply to this genus. The funnel–mantle locking apparatus of *Grimalditeuthis bonplandi* is fused.

FAMILY JOUBINITEUTHIDAE NAEF, 1922

(ONE SPECIES)

Diagnosis: Medium adult-sized Chiroteuthoidea with suckers in six series in dorsal, dorsolateral and ventrolateral arms and four in ventral arms; dorsal, dorsolateral and ventrolateral arms extremely long; tentacle clubs laterally compressed and with five or six basal series increasing in number to the eight to 12 series of the distal club; head with a long brachial pillar; funnel–mantle locking apparatus with an oval depression; without photophores; slender, long tail with membranous appendages.

FAMILY MAGNAPINNIDAE [VECCHIONE & YOUNG, 1998](#)

(THREE SPECIES IN ONE GENUS)

Diagnosis: Chiroteuthoidea with long arms and tentacles having two distinct regions, the basal region thick and bearing normal suckers in two to four series and the distal region slender and with numerous tiny suckers in multiple irregular series; funnel–mantle locking apparatus oval; without photophores; fins terminal and large.

FAMILY MASTIGOTEUTHIDAE [VERRILL, 1881](#)

(16 SPECIES IN SIX GENERA)

Diagnosis: Medium to large adult-sized Chiroteuthoidea with enlarged ventral arms having expanded lateral membranes modified into sheaths for the tentacles; arm suckers in two series; with cylindrical long tentacles on which clubs are covered by multiple irregular series of tiny suckers, sometimes with larger suckers in the proximal end; with oval or ear-shaped funnel–mantle locking apparatus with tragus and antitragus; fins large to very large; short tail present (relatively long in paralarvae).

FAMILY PROMACHOTEUTHIDAE [NAEF, 1912](#)

(THREE SPECIES IN ONE GENUS)

Diagnosis: Chiroteuthoidea with reduced eyes covered by pseudocorneas; with enlarged buccal masses and beaks; arm suckers in two or three series, sometimes more near arm tips; tentacles with thick stalks and with multiple irregular series of suckers; funnel–mantle locking apparatus oval; without photophores; without ink sac and anal flaps; gladius sometimes reduced.

Remarks: Not included in our phylogenetic analyses, but its position within the superfamily is provisionally supported by its morphology ([Roper & Young, 1967](#); [Young & Vecchione, 2019c](#)).

SUPERFAMILY CYCLOTEUTHOIDEA [NAEF, 1923](#)

(11 SPECIES)

Diagnosis: Small to medium adult-sized Oegopsida with buccal connectives attached to the ventral borders of ventral arms; with two series of arm suckers; tentacles with carpal locking apparatus and a broad dorsal keel; manus suckers usually with a large stalk, with three or four series of suckers on the dactylus; terminal pad with dispersed suckers at the end of the tentacle club; gladius with a secondary conus or without a conus.

Remarks: The sister-group relationship between the families Brachioteuthidae and Cycloteuthidae

is strongly supported in our phylogenetic analyses, as in the study by [Lindgren \(2010\)](#). However, the morphological similarities between the two families are few and mostly related to the morphology of the tentacle club. The remaining morphological similarities (number of arm sucker series, presence of a tentacle carpal locking apparatus) most probably represent plesiomorphic characters of Oegopsida. The three analysed species also share the oegopsid plesiomorphic position for *trnM* and *trnI*.

FAMILY BRACHIOTEUTHIDAE [PFEFFER, 1908B](#)

(SEVEN SPECIES IN TWO GENERA)

Diagnosis: Small adult-sized, weakly muscled Cycloteuthoidea with many series of small irregular suckers on proximal manus and four series of larger suckers on distal manus; terminal pad present, with central space lacking suckers; funnel–mantle locking apparatus straight, reaching the anterior margin of the mantle; digestive gland located far posterior to the cephalic cartilage; gladius with a secondary conus; paralarvae with long retractile neck connected with a fluid-filled chamber inside the mantle.

FAMILY CYCLOTEUTHIDAE [NAEF, 1923](#)

(FOUR SPECIES IN TWO GENERA)

Diagnosis: Medium adult-sized ammoniacal Cycloteuthoidea with four series of suckers on the tentacle clubs; with subtriangular funnel–mantle locking apparatus not reaching the anterior margin of the mantle; gladius with secondary conus or without conus.

SUPERFAMILY ENOPLOTEUTHOIDEA [PFEFFER, 1900](#)

(57 SPECIES)

Diagnosis: Oegopsida with eight or the remnants of eight buccal supports, the ventral supports attached to the dorsal margins of ventral arms; with photophores; two series of arms suckers usually with hooks; four series of tentacle suckers in young stages, sometimes reduced in adults; spermatangia usually attached to specialized tissue in the nuchal region.

Remarks: According to [Berry \(1920\)](#), this superfamily included the families Benthoteuthidae [Pfeffer, 1900](#) (= Bathyteuthidae), Enoploteuthidae, Gonatidae, Histioteuthidae, Lampadioteuthidae [Berry, 1916](#), Lycoteuthidae, Octopoteuthidae and Onychoteuthidae. This taxonomic composition does not agree with our phylogenetic results ([Fig. 3](#)).

FAMILY ANCISTROCHEIRIDAE PFEFFER, 1912

(ONE SPECIES)

Diagnosis: Medium to large adult-sized Enoploteuthoidea with photophores embedded in muscles of the tentacles; photophores on the surface of the mantle with two different sizes and geometrical assemblages, the large ones on the ventral and lateral surfaces of the mantle usually following the pattern 4+2+4+2+4+2+4; without visceral and ocular photophores; with hooks on all arms; tentacular clubs with hooks in two series on manus, suckers absent from manus, dactylus reduced, with a terminal pad; nuchal folds present; digestive gland located far posterior to the nuchal cartilage; nidamental glands present, oviducts equally developed; no hectocotylus, but males with additional photophores in ventrolateral arms.

Remarks: Although a single species is currently recognized, our data (F. A. Fernández-Álvarez, pers. obs.) suggest that at least three molecularly divergent species occur within this family. Our specimen, therefore, is currently unidentified at the species level (Table 1).

FAMILY ENOPLOTEUTHIDAE PFEFFER, 1900

(43 SPECIES IN FOUR GENERA)

Diagnosis: Small adult-sized Enoploteuthoidea with photophores on ventral surfaces of mantle, head and arms and with ocular photophores; without visceral and tentacular photophores; with hooks on arms and tentacles; broad tail extending beyond conus of the gladius; without nidamental glands, but oviducal glands enlarged; left or right ventral arm hectocotylized.

FAMILY LAMPADIOTEUTHIDAE BERRY, 1914

(ONE SPECIES)

Diagnosis: Small adult-sized and colourful Enoploteuthoidea with four ocular and five tentacular photophores (the most proximal stalked near the base of the tentacle), plus anal, branchial and posteroabdominal photophores, branchial photophores transversally elongated, without central abdominal photophore; rostrum in gladius; without hooks on arms and tentacles; right ventral arm hectocotylized with enlarged protective membrane in the mid-arm; males with single terminal organ.

Remarks: This group has a complex taxonomic history (see Vecchione & Young, 2019a). Berry (1914) erected this monotypic family, but it was later included as the subfamily Lampadioteuthinae

Berry, 1914 within Lycoteuthidae by Naef (1923). Voss (1956) maintained them as separated families in an initial article. He then considered them to occur within the same family in a subsequent article (Voss, 1962). The results provided here support a family-level treatment.

FAMILY LYCOTEUTHIDAE PFEFFER, 1908A

(FIVE SPECIES IN THREE GENERA)

Diagnosis: Small to medium adult-sized Enoploteuthoidea with five ocular photophores and a variable number of tentacular photophores; anal, branchial, abdominal and posteroabdominal photophores present; usually with sexual dimorphism; without hectocotylus; with one or two terminal organs of male reproductive tract.

Synonym: Thaumtolampadidae Chun, 1903

Remarks: Voss (1962) stated that because the name Thaumtolampadidae had not been used for nearly 50 years this name should not be maintained regardless of possible priority (see also Vecchione & Young, 2019a).

FAMILY PYROTEUTHIDAE PFEFFER 1912

(SEVEN SPECIES IN TWO GENERA)

Diagnosis: Small adult-sized Enoploteuthoidea with ocular photophores in two series, anal, branchial, anterior abdominal, mid-abdominal and posteroabdominal and tentacular photophores, without mantle photophores; secondary buccal connectives attached to ventral margins on dorsal and dorsolateral arms; usually with hooks on dorsal, dorsolateral and ventrolateral arms; four series of tentacle suckers; tentacle-retractor muscle present; occipital folds absent; gladius with small, pointed conus extending beyond the fins, rostrum of gladius absent; fins subterminal with anterior and posterior lobes; oviducts sometimes reduced or absent on one side; right or left arm hectocotylized.

SUPERFAMILY PHOLIDOTEUTHOIDEA VOSS, 1956

FAMILY PHOLIDOTEUTHIDAE VOSS, 1956

(TWO SPECIES IN ONE GENUS)

Diagnosis: Large adult-sized Oegopsida with buccal connectives attached to the ventral borders of ventral arms; with two series of arm suckers; tentacles with long tentacle clubs, carpal locking apparatuses poorly developed or absent; small flaps with short membranes present near the base of lateral tentacle suckers; club

suckers transversally compressed, dactylus poorly defined, with terminal pad; dermal cushions or papillose tubercles present in skin; funnel–mantle locking apparatus straight, reaching the anterior margin of the mantle; without photophores; with primary or secondary conus; digestive gland far posterior to the nuchal cartilage; without hectocotylization.

SUPERFAMILY OCTOPOTEUTHOIDEA [BERRY, 1912](#)

(NINE SPECIES)

Diagnosis: Medium or large adult-sized weakly or strongly muscled ammoniacal Oegopsida with buccal connectives attached to the ventral borders of ventral arms; with two series of arm suckers, some or all of which may be modified into hooks; adults without tentacles; the funnel–mantle locking apparatus straight, reaching the anterior margin of the mantle in some species; with secondary conus in the gladius; paralarval tentacle club characteristic, with small compact clubs with a few small and large suckers arranged in two series; with a characteristic mitogenome lacking the oegopsid duplicated genes *cox1*, *cox2*, *atp6*, *atp8* and *trnD* from the duplicated gene block after *nad3*, with *nad2* associated with *rrnL* as follows: ‘*-rrnL -trnY -trnW -trnG -trnE NC_0 cox3_1 trnK trnR trnS1 nad2*’; and with *rrnS* associated with *nad3* as follows: ‘*-rrnS -trnM -trnC -trnQ NC_1 cox3_0 trnA trnN trnI nad3*’.

FAMILY LEPIDOTEUTHIDAE [PFEFFER, 1912](#)

(ONE SPECIES)

Diagnosis: Large adult-sized Octopoteuthoidea with overlapping dermal scales on mantle; without photophores; males with hooks near the bases of dorsolateral arms; paralarva with brachial pillar and eyes slightly tubular.

FAMILY OCTOPOTEUTHIDAE [BERRY, 1912](#)

(EIGHT SPECIES IN TWO GENERA)

Diagnosis: Medium or large adult-sized Octopoteuthoidea with two series of hooks on most arms; with photophores at the tips of one or more pairs of arms; with large, broad, muscular fins, fin length almost the same as the mantle length, fused together along dorsal midline.

INCERTAE SEDIS

We have not determined the superfamily level for the following families owing to the weak support for their phylogenetic position. Psychroteuthidae [Thiele, 1920](#) was not included in the phylogenetic analyses.

FAMILY GONATIDAE [HOYLE, 1886](#)

(19 SPECIES IN FOUR GENERA)

Diagnosis: Medium adult-sized muscular Oegopsida with buccal connectives attached to the ventral borders of ventral arms; with four series of arm suckers, usually with hooks in the two medial series of dorsal, dorsolateral and ventrolateral arms; tentacles with numerous irregular series of suckers, sometimes with hooks, funnel–mantle locking apparatus straight, reaching the anterior margin of the mantle; usually without photophores; gladius with primary conus; egg masses brooded by females.

Remarks: This family has a wide range of variation within several key characters. The genera *Gonatus* [Gray, 1849](#) and *Eogonatus* [Nesis, 1972](#) have a modified carpal locking apparatus with elongated ridges, suckers and knobs at the base of the manus. The genus *Berryteuthis* [Naef, 1921](#) has no hooks on tentacular clubs, whereas *Gonatopsis* [Sasaki, 1920](#) loses its tentacles in the early juvenile stage. *Gonatus pyrus* [Young, 1972](#) has ocular photophores.

FAMILY HISTIOTEUTHIDAE [VERRILL, 1881](#)

(18 SPECIES IN TWO GENERA)

Diagnosis: Medium to large adult-sized, weakly muscled and ammoniacal Oegopsida with buccal connectives attached to the dorsal borders of ventral arms; with an asymmetrical external and internal morphology, left eye much larger than right counterpart; with two series of arm suckers; tentacles characteristic, with expanded clubs having non-uniform series of suckers, with large suckers with stalks devoid of neck constrictions, carpal locking apparatus in linear series; funnel–mantle locking apparatus straight to slightly curved, reaching the anterior margins of the mantle; ventral surfaces of the head, mantle and arms covered with compound anteriorly directed photophores with red colour filters; posterior end of the gladius with a cupped coil shape, without the *atp6* copy in the duplicated gene cluster associated with *nad2*.

Remarks: In the phylogeny provided here, Histioteuthidae and Onychoteuthidae clustered together with poor support in the ML analysis and high support in the BI analysis. [Young & Vecchione \(2016a\)](#) showed that the morphology of the tentacle suckers of Histioteuthidae and Psychroteuthidae is almost identical and considered it a good taxonomic character. This last relationship also received high support in the multilocus phylogenetic work of [Lindgren \(2010\)](#) and [Lindgren et al. \(2012\)](#). We did not include any Psychroteuthidae in the analysis. We avoid any superfamily designation until the

relationship between Histioteuthidae, Onychoteuthidae and Psychroteuthidae can be confirmed by future phylogenomic analyses.

FAMILY ONYCHOTEUTHIDAE GRAY, 1849

(26 SPECIES IN SEVEN GENERA)

Diagnosis: Small to massive adult-sized muscular Oegopsida with buccal connectives attached to the ventral borders of ventral arms; with two series of arm suckers; tentacle club with two series of hooks, hooks larger in the ventromedial series; usually without dactylus but with terminal pad; carpal locking apparatus formed by a well-defined circular region; funnel–mantle apparatus straight, reaching the anterior margin of the mantle; head with three or more occipital folds; gladius with a primary conus and usually with a prominent rostrum; without hectocotylization.

Remarks: According to MolluscaBase eds (2021b), the superfamily Onychoteuthoidea Gray, 1849 includes Ancistrocheiridae, Architeuthidae, Brachiotheuthidae, Cycloteuthidae, Enoploteuthidae, Gonatidae, Histioteuthidae, Lepidoteuthidae, Lycoteuthidae, Neoteuthidae, Octopoteuthidae, Onychoteuthidae, Pholidoteuthidae, Psychroteuthidae and Pyroteuthidae. This taxonomic composition does not agree with the phylogeny provided here, but this name can be resurrected with a new diagnosis for Histioteuthidae, Onychoteuthidae and Psychroteuthidae if the morphological support provided by Young & Vecchione (2016a) for a relationship between Histioteuthidae and Psychroteuthidae and the weak molecular support provided here for a relationship between Histioteuthidae and Onychoteuthidae is supported in future phylogenetic analyses.

FAMILY PSYCHROTEUTHIDAE THIELE, 1920

(ONE SPECIES)

Diagnosis: Large adult-sized muscular Oegopsida with buccal connectives attached to the dorsal borders of ventral arms; with two series of arm suckers; tentacles characteristic, with expanded clubs having non-uniform series of suckers, with large suckers with stalks devoid of neck constrictions; carpal locking apparatus in linear series; funnel–mantle locking apparatus straight, reaching the anterior margins of the mantle; glandular structures (possibly photophores) present on the tips of the ventrolateral arms in males and the dorsolateral and ventrolateral arms in females; gladius without conus.

Remarks: Not included in our phylogenetic analyses, but its position as sister group of Histioteuthidae is supported provisionally by its morphology (Young &

Vecchione, 2016a) and by the phylogenetic results of Lindgren (2010) and Lindgren *et al.* (2012).

ORDER BATHYTEUTHIDA LINDGREN, 2010

(NINE SPECIES)

Diagnosis: Small adult-sized muscular squids without a cornea covering the eyes; with suckers on the buccal membrane; without circularis muscles in the arm and tentacle suckers; tentacles usually without carpal locking apparatus; tentacle club not divided into manus and dactylus, club suckers in more than seven series; straight funnel–mantle locking apparatus, reaching the anterior margin of the mantle; gladius with a spoon-like conus; oviducts paired; without accessory nidamental glands; gills with branchial canal; with duplications of the mitochondrial genes *atp6*, *atp8*, *cox1*, *cox2*, *cox3* and *trnD*.

Remarks: The clade formed by the families Bathyteuthidae and Chtenopterygidae is commonly referred at the superfamily level (Bathyteuthoidea Pfeffer, 1900; e.g., Young & Vecchione, 2016b; Strugnell *et al.*, 2017) or at the order level, usually referred as order Bathyteuthida (e.g. Allcock *et al.*, 2015; MolluscaBase eds. 2021c). Lindgren (2010) confirmed the sister-taxon relationship of this clade with the order Oegopsida and designated it as the order Bathyteuthoidea. We agree with the treatment of this group at the ordinal level, but we have changed the ordinal suffix from ‘-oidea’ to ‘-ida’. Although Article 29.2 of the International Code of Zoological Nomenclature (ICZN, 1999) states that the suffix for the superfamily level is ‘-oidea’, the code does not regulate ordinal level names. We decided to change the original spelling of Lindgren (2010) by adjusting it to ‘-ida’, the conventional cephalopod ordinal level ending, to avoid further confusion regarding the rank at which this clade should be treated.

FAMILY BATHYTEUTHIDAE PFEFFER, 1900

(SIX SPECIES IN ONE GENUS)

Diagnosis: Bathyteuthida with buccal connectives attaching to the dorsal border of ventral arms; with two sucker series in dorsal, dorsolateral and ventrolateral arms increasing distally to four with ontogeny; with anteriorly oriented semitubular eyes; with small, separated and paddle-like fins having anterior and posterior lobes; sometimes with single photophores at the bases of dorsal, dorsolateral and ventrolateral arms; egg masses brooded by the female.

FAMILY CHTENOPTERYGIDAE GRIMPE, 1922

(THREE SPECIES IN ONE GENUS)

Diagnosis: Bathyteuthoidea with buccal connectives attaching to the ventral border of ventral arms; with

six or more sucker series in dorsal, dorsolateral and ventrolateral arms; with eight or more sucker series in tentacles, with tentacle club ventrally expanded; with accessory nidamental glands; fins long, with muscular ribs attached to the dorsolateral surface of the mantle; distinct paralarva with disc-shape tentacle clubs covered with minute suckers.

CONCLUSIONS

Genome skimming proved to be a good method for solving the phylogenetic relationships among oegopsid squids, a group of cephalopods diverse at the family level with enigmatic evolutionary relationships among the families, although assembly difficulties result from the combination of short-read sequencing and multiple duplicate genes. Three of the previously defined family groups tested (architeuthid, chiroteuthid and enoploteuthid family groups) proved to be monophyletic, whereas the lepidoteuthid family group, whose morphological and natural history trait support was lower, was found to be paraphyletic. A relationship among the families Cranchiidae, Ommastrephidae and Thysanoteuthidae was recovered, and mitochondrial gene order proved to be a suitable taxonomic character in the absence of strong morphological similarities. The relationships of the Gonatidae, Onychoteuthidae, Histiototeuthidae and Psychroteuthidae are still unresolved, and better taxon sampling and additional molecular markers might be required to solve them. Despite this problem, we identified superfamily names from the previous literature to name all the well-supported clades presented, and we proposed the superfamilies Cycloteuthoidea, Octopoteuthoidea and Pholidoteuthoidea in order to describe the evolutionary relationships among oegopsid families accurately. Lastly, the family Lycoteuthidae proved to be paraphyletic because it included Pyroteuthidae; hence, we elevated the lycoteuthid subfamilies to the family level. This taxonomic change increases the number of oegopsid families to 25.

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DATA AVAILABILITY

The data underlying this article are available in the GenBank Nucleotide Database at <https://www.ncbi.nlm.nih.gov/genbank/> and can be accessed with the GenBank accession numbers MW233711–MW233782 and MW255551–MW255585. The FASTQ files can be accessed within the GenBank Nucleotide Database with the BioProject accession number PRJNA716134.

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