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Molecular phylogenetics of snailfishes (Cottoidei: Liparidae) based on MtDNA and RADseq genomic analyses, with comments on selected morphological characters

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Abstract

Phylogenetic relationships of snailfishes of the family Liparidae were analyzed on the basis of two sets of molecular sequence data: one from the mitochondrial DNA cytochrome *c* oxidase subunit one gene (COI) and another from restriction-site associated genome-wide sequences (RADseq). The analysis of COI sequence data from at least 122 species of 18 genera from the Pacific, Atlantic, and Southern oceans resulted in a moderately well-resolved phylogeny among the major clades, albeit with significant polytomy among central clades. *Nectoliparis* was the sister of all other members of the family, followed by *Liparis*. *Liparis*, *Careproctus,* and *Paraliparis* were paraphyletic. *Liparis* was recovered in two closely related clades, with *L. fucensis* sister of all other liparids except *Nectoliparis*, and both *Careproctus* and *Paraliparis* were each recovered among at least three widely separated clades. The RADseq analysis of 26 species of 11 genera from the eastern North Pacific strongly confirmed the overall results of the COI analysis, with the exception of the paraphyly of *Liparis* due to the absence of *L. fucensis*. Our results show that the pelvic disc has been independently lost multiple times and the pectoral-fin girdle has been independently reduced in multiple lineages.

Key words: Teleostei, molecular, morphology, *Liparis*, *Careproctus*, *Paraliparis*, phylogeny

Introduction

Snailfishes of the family Liparidae are a well-defined group of diverse cottoid fishes characterized most prominently by their scale-less, typically naked, elongate bodies, and by the development of a sucking disk formed by highly modified pelvic fins. The family is bipolar in distribution and is one of the four most-rapidly speciating clades of marine fishes, all found in high-latitudes (Rabosky *et al.* 2018). The Liparidae comprises over 430 species (Eschmeyer & Fong 2017) allocated to about 32 genera (Chernova *et al.* 2004; Orr 2004; Balushkin 2012; Stein 2015; Eschmeyer *et al.* 2017). Two of its most diverse genera, *Careproctus* and *Paraliparis*, are recognized in both the Northern Hemisphere (northern species) and the Southern Hemisphere (southern species), while a third, *Liparis*, is restricted to the north. Presently, 214 species are known from the north, primarily the North Pacific, whereas 262 species are recorded from the south, primarily the Southern Ocean, and many new species continue to be described both north and south (e.g., Chernova 2005ab, 2014; Stein 2006, 2012, 2016; Orr 2102, 2016; Eschmeyer & Fong, 2017). Liparids are particularly diverse in North Pacific waters, especially off Alaska where over 85 species have either been described or are known but as yet undescribed (Mecklenburg *et al.* 2002; Orr 2004; Orr & Busby 2006; Orr & Maslenikov 2007; Orr 2012, 2016; Orr *et al.* 2015; Orr, unpublished). They are abundant as well as diverse, as documented in trawl surveys conducted throughout a wide range of depths, especially in surveys of the Aleutian Islands (Raring *et al.* 2016) and upper continental slope of the eastern Bering Sea (Hoff 2016).

While bipolar in distribution, and essentially limited to cool-temperate and cold waters, liparids are widely distributed from the shallowest waters of the intertidal region to near the deepest parts of the ocean. The recently described Mariana Snailfish, *Pseudoliparis swirei*, has been documented at depths to 8178 m and is now recognized as the deepest dwelling vertebrate thus far confirmed (Linley *et al.* 2016; Gerringer *et al.* 2017a; JAMSTEC 2017). In addition, although not yet captured and thus not formally described, the Ethereal Snailfish was filmed in the Mariana Trench at a depth of 8,145 m, only 33 m shallower (Linley *et al.* 2016; Gerringer *et al.* 2017a). Most species are demersal or benthic, but many species are found also in the midwater. Their precise contributions to marine ecosystems are unclear, but liparids are important as prey and as predators in many ecosystems (Bansode *et al.* 2014;

Gerringer *et al.* 2017b; Whitehouse *et al.* 2017). Among their unusual behavioral characteristics, species of *Careproctus* are known to lay their eggs within the carapace of lithodid king crabs (Stein 1980; Gardner *et al.* 2016).

Phylogenetic status. Historically placed within the Scorpaeniformes among the sculpins (Nelson *et al.* 2016), the Liparidae was recently reallocated to the perciform suborder Cottoidei by Smith & Busby (2014; = infraorder Cottales of Betancur-R *et al.* 2017). Its close relationship with the Cyclopteridae, as originally proposed by Peter Artedi (1738; see also Walbaum, 1792), followed later by Cuvier (1817) and Garman (1892), has been unchallenged, and both families are unquestionably monophyletic (Near *et al.* 2012; Smith & Busby 2014). While systematic progress has been made with the Cyclopteridae (Kai *et al.* 2015; Oku *et al.* 2017; Stevenson *et al.* 2017), the phylogenetic relationships of the far more diverse Liparidae are poorly understood (Smith & Busby 2014) and the monophyly of major genera within the family has been questioned (Andriashev 1986; Knudsen & Møller 2007; Balushkin 2012). Previous studies have been limited primarily by inadequate taxon sampling of this morphologically diverse and species-rich group, as well as by the challenges of working with the morphology of these poorly ossified, reductive, and easily damaged fishes.

Early works focused on the few species known at the time and gave only general ideas of their evolution and relationships: Garman (1892) provided the first detailed anatomical descriptions and reviewed all 18 known species in the three genera—*Liparis*, *Careproctus*, and *Paraliparis*—recognized at the time; Goode & Bean (1896) reviewed 10 deep-sea species in five genera; and Jordan & Evermann (1898) included all 39 species known among 10 genera in North American waters. Burke's (1930) monumental revisionary work on the family summarized all that was known at the time about the family, its 114 species in 13 genera, and its evolution. As in the works of previous authors, Burke described the family as being closely related to the Cyclopteridae and more distantly to the broadly defined Cottidae, supporting the early consensus about evolution within the group: that is, their evolution from shallow-water, large-disc species of *Liparis*, through disc reduction among deeper dwelling *Careproctus*, to the complete loss of the pelvic disc among deeper dwelling and semi-pelagic species of *Paraliparis* and related genera. Thus, genera were arranged in phylogenetic order from least to most derived, with those more basal bearing a disc (i.e., *Liparis* and *Polypera*, *Careproctus* and *Temnocora*, *Crystallichthys* and *Crystallias*, and *Gyrinichthys*) and those more derived lacking or having a highly reduced disc (i.e., *Elassodiscus*, *Paraliparis*, *Rhinoliparis*, *Acantholiparis*, *Nectoliparis*, and *Lipariscus*).

Overall, later analyses supported these general patterns, but some notable exceptions were demonstrated. Especially as the full diversity of the Liparidae has become more clearly understood, wide gaps in our understanding of the phylogenetics have been revealed. Several modern phylogenetic analyses have been published based on morphological and molecular data (Figs. 1–7). As in other complex groups, analyses have moved from those using strictly morphological data, to combined analyses including both molecular and morphological data, and most recently to strictly molecular data. Taxon and individual sampling have generally increased among species and genera with each analysis.

The earliest analyses used morphological characters exclusively. In the first modern phylogenetic analysis, Kido (1988; Fig. 1) examined 60 species in about nine genera using osteology and external morphology, focusing on species of Japanese waters augmented by selected species from the North Atlantic. In challenging aspects of Kido's (1988) results, particularly the position of *Nectoliparis* as sister of all other liparids, Balushkin (1996; Fig. 2) attempted to describe the relationship of his new monotypic genus, *Palmoliparis,* among the other 26 known liparid genera. While preliminary and supported by only seven osteological and external characters, his analysis was the first attempt to place all known genera within a cladistic scheme based on well-recognized character transformations and current interpretations of liparid evolution (Andriashev 1998; Andriashev & Stein 1998). In both of these morphological analyses, *Liparis* was monophyletic and *Careproctus* was paraphyletic (in the reanalysis of Kido's 1988 data by Knudsen *et al.* 2007). *Paraliparis* was also paraphyletic in Kido's (1988) analysis; its status was not examined by Balushkin (1996).

The first phylogenetic analysis to use molecular data was that of Knudsen *et al.* (2007; Fig. 3), who conducted a combined analysis of two mitochondrial DNA (mtDNA) datasets of over 1000 bp with morphological data, based on 24 species in nine North Atlantic and North Pacific genera. With this limited taxon sampling, they found all genera except *Paraliparis* to be monophyletic.

More recent species-level analyses have used only mitochondrial sequence data, primarily the cytochrome *c* oxidase subunit I gene (COI), and have focused on the identification of species. As collections of tissues have increased, numbers of species, genera, and individuals have grown with each analysis.

Steinke *et al.* (2009; Fig. 4) analyzed sequence divergences in a 650 bp alignment of COI of 78 tissues of 19 species of eight Canadian Pacific genera. Their goal was to evaluate the utility of COI for distinguishing species, although misidentifications hampered the accuracy of their species-level conclusions. In their neighbor-joining tree, *Liparis* was monophyletic and both *Paraliparis* and *Careproctus* were paraphyletic. Similarly, Duhamel *et al.* (2010; Fig. 5) focused on Antarctic species and significantly increased the overall number of species and geographic scope sampled by analyzing 157 tissues of 46 species in nine genera. With much new material of Antarctic species and 103 COI sequences 668 bp in length from other geographic areas taken from online databases, their Bayesian analysis found not only *Paraliparis* and *Careproctus* to be paraphyletic but, for the first time, *Liparis* as well.

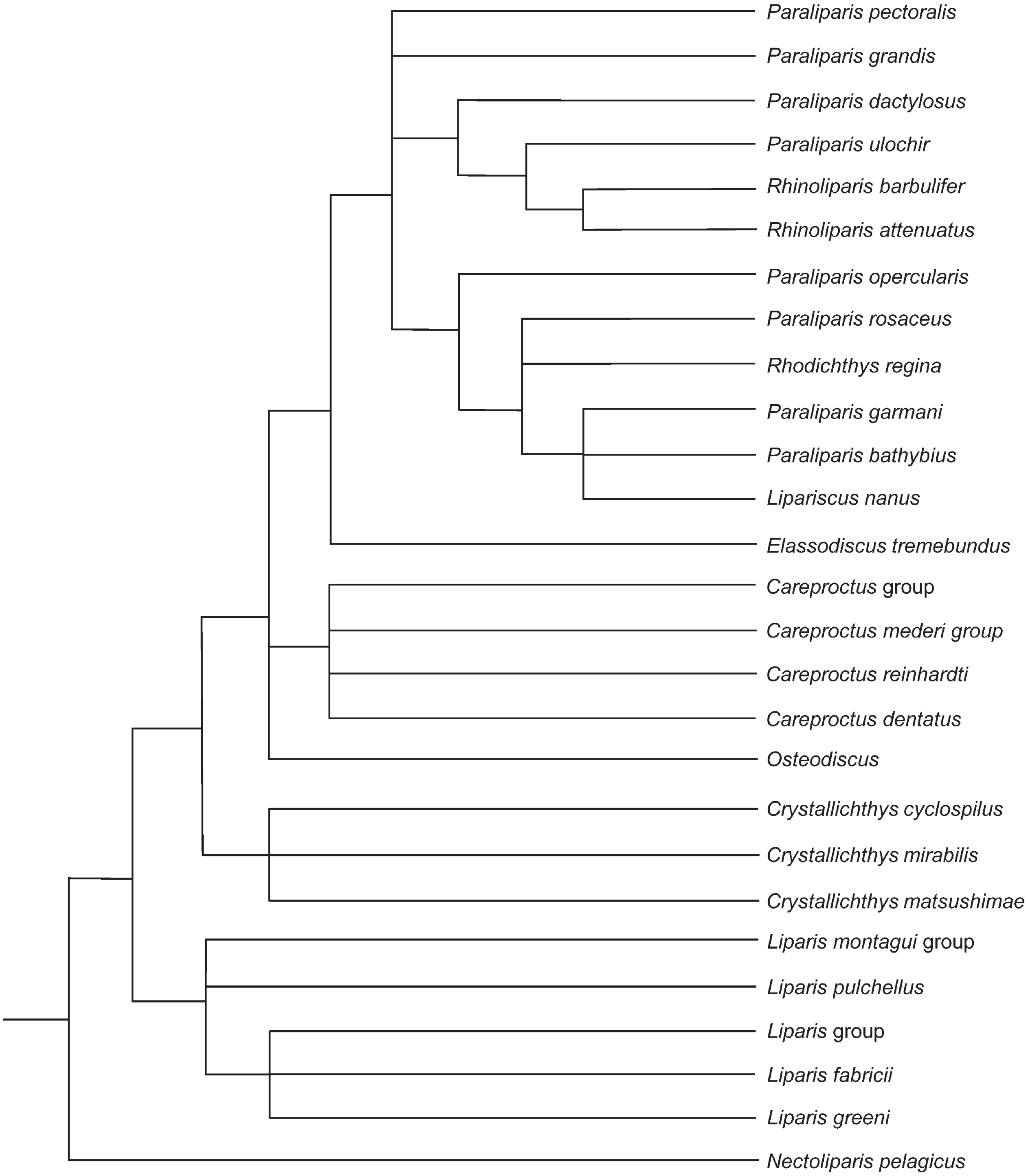

FIGURE 1. Phylogenetic hypothesis of Kido (1988, after fig. 20), derived from a maximum parsimony analysis of morphological data, using 34 osteological and external characters, for 60 liparid species.

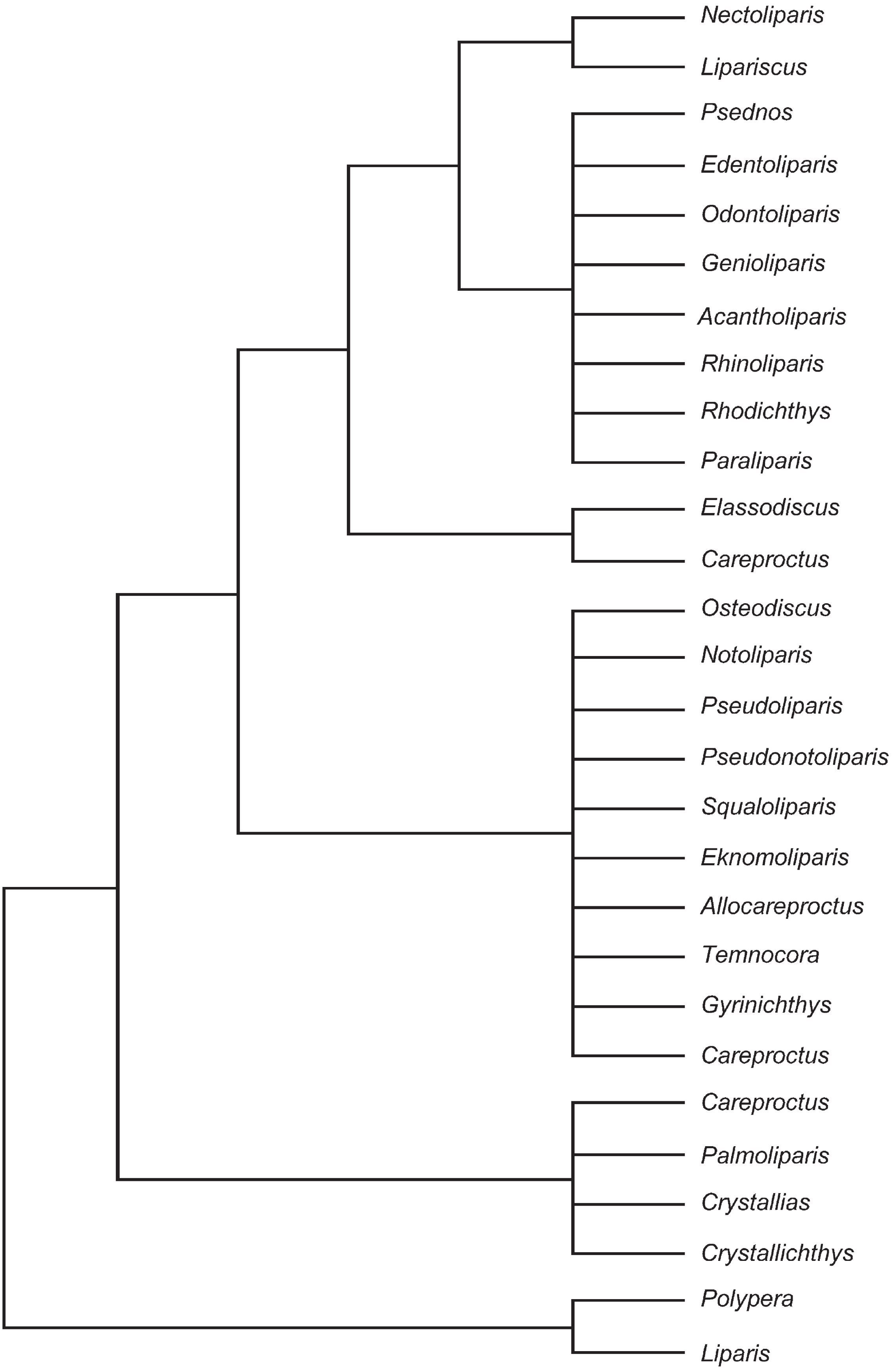

FIGURE 2. Phylogenetic hypothesis of Balushkin (1996, after fig. 4), derived from a manual cladistic analysis of morphological data, including seven osteological and external characters, for 26 liparid genera.

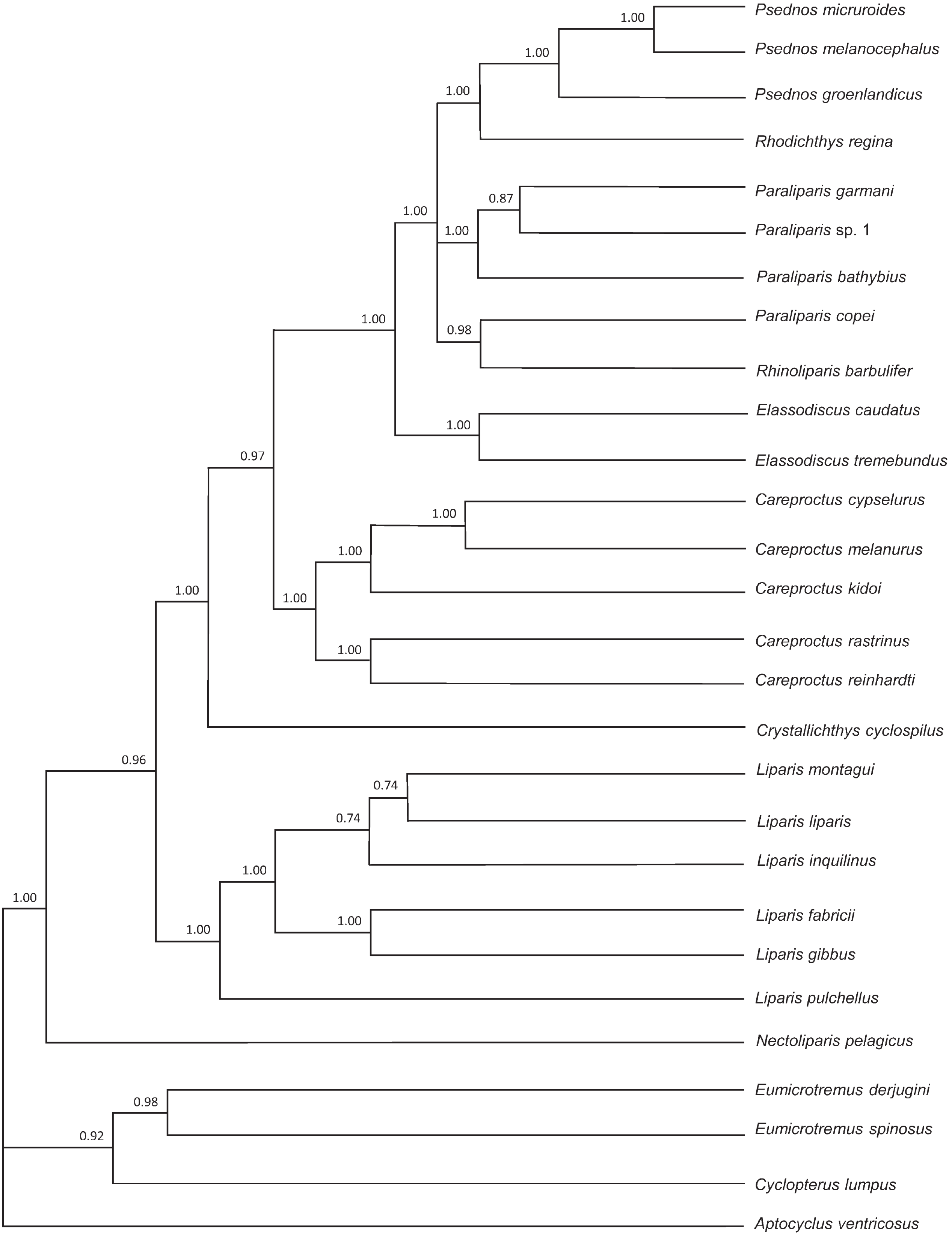

FIGURE 3. Majority-rule (50%) consensus tree of Knudsen *et al.* (2007, after fig. 3), derived from a Bayesian analysis of three combined datasets composed of mitochondrial DNA (16S and cytochrome *b*) and morphological data for 24 liparid species. Tree is rooted with species of the Cyclopteridae. Posterior probabilities are above branches.

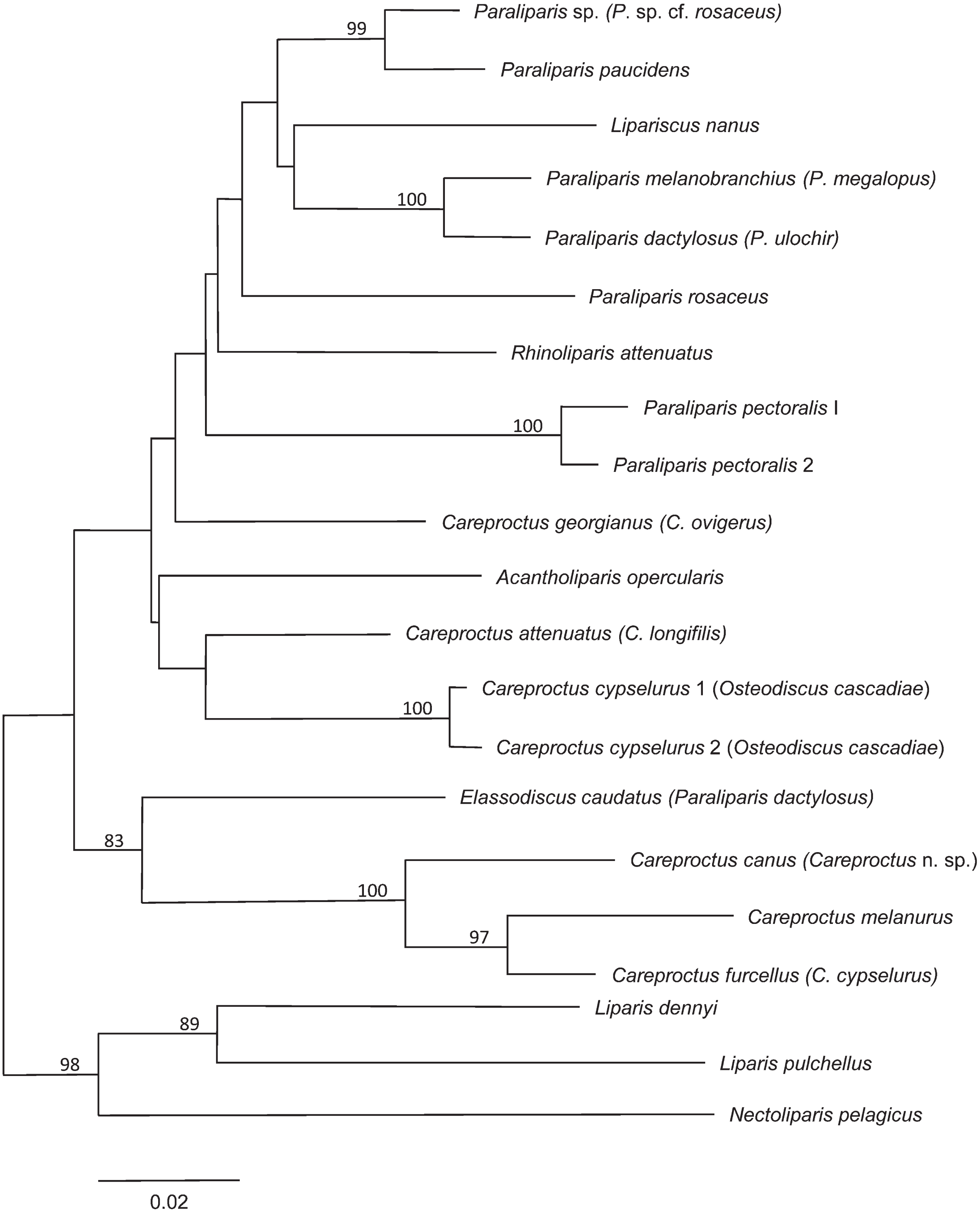

FIGURE 4. Unrooted neighbor-joining tree of Steinke *et al.* (2009, after fig. 4), derived from cluster analysis of a 650 bp alignment of cytochrome *c* oxidase subunit 1 gene (COI) sequences for 78 samples of 19 liparid species. Bootstrap values >80 are above branches leading to multiple species. Corrected identifications based on our study are in parentheses.

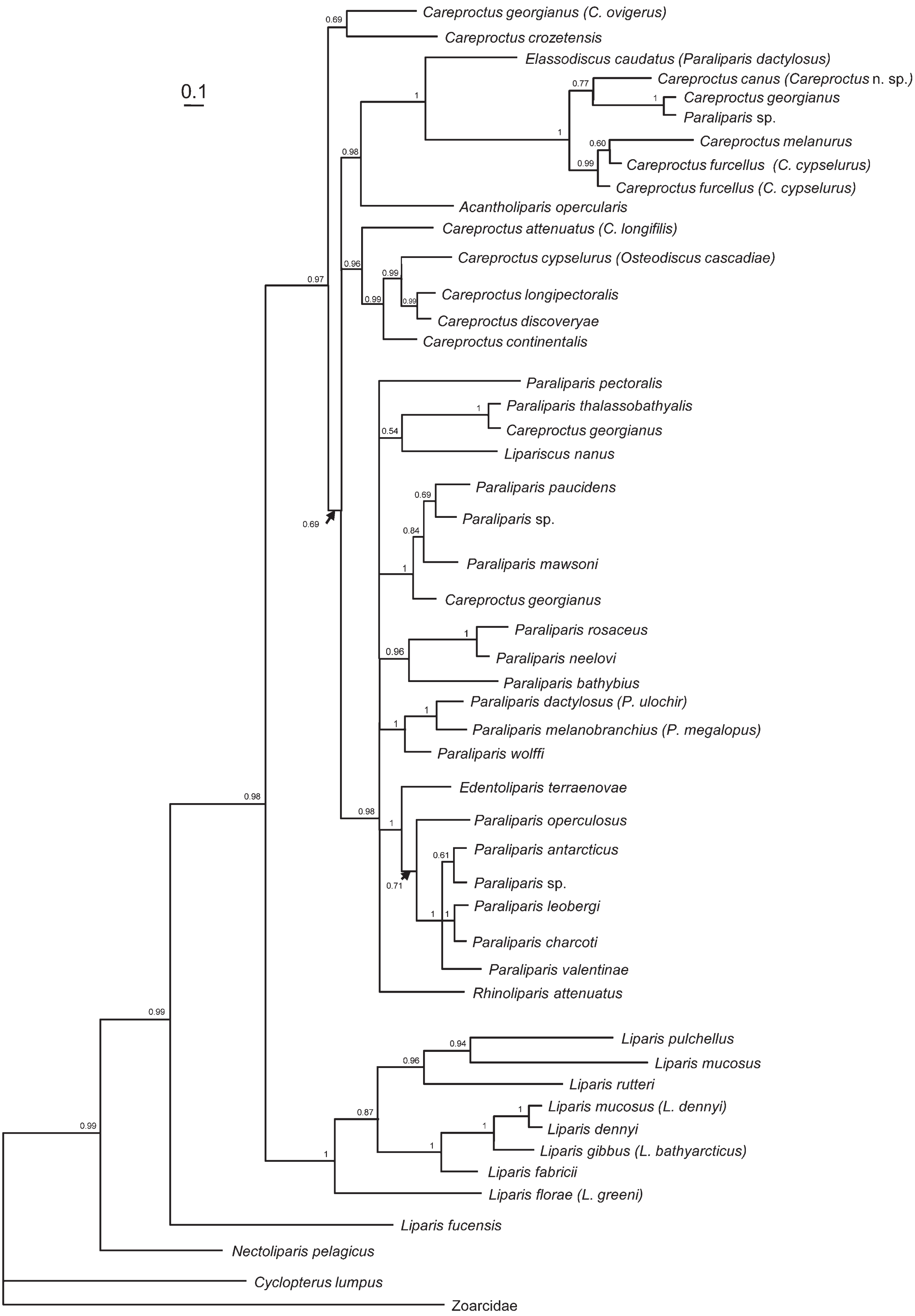

FIGURE 5. Consensus phylogenetic tree of Duhamel *et al.* (2010, after fig. 3), derived from Bayesian and maximum parsimony analyses of a 668 bp alignment of cytochrome *c* oxidase subunit 1 gene (COI) sequences for 157 samples of 46 liparid species. Bayesian posterior probabilities are above branches that lead to multiple species. Tree is rooted with species of the Cyclopteridae and Zoarcidae. Corrected identifications based on our study are in parentheses.

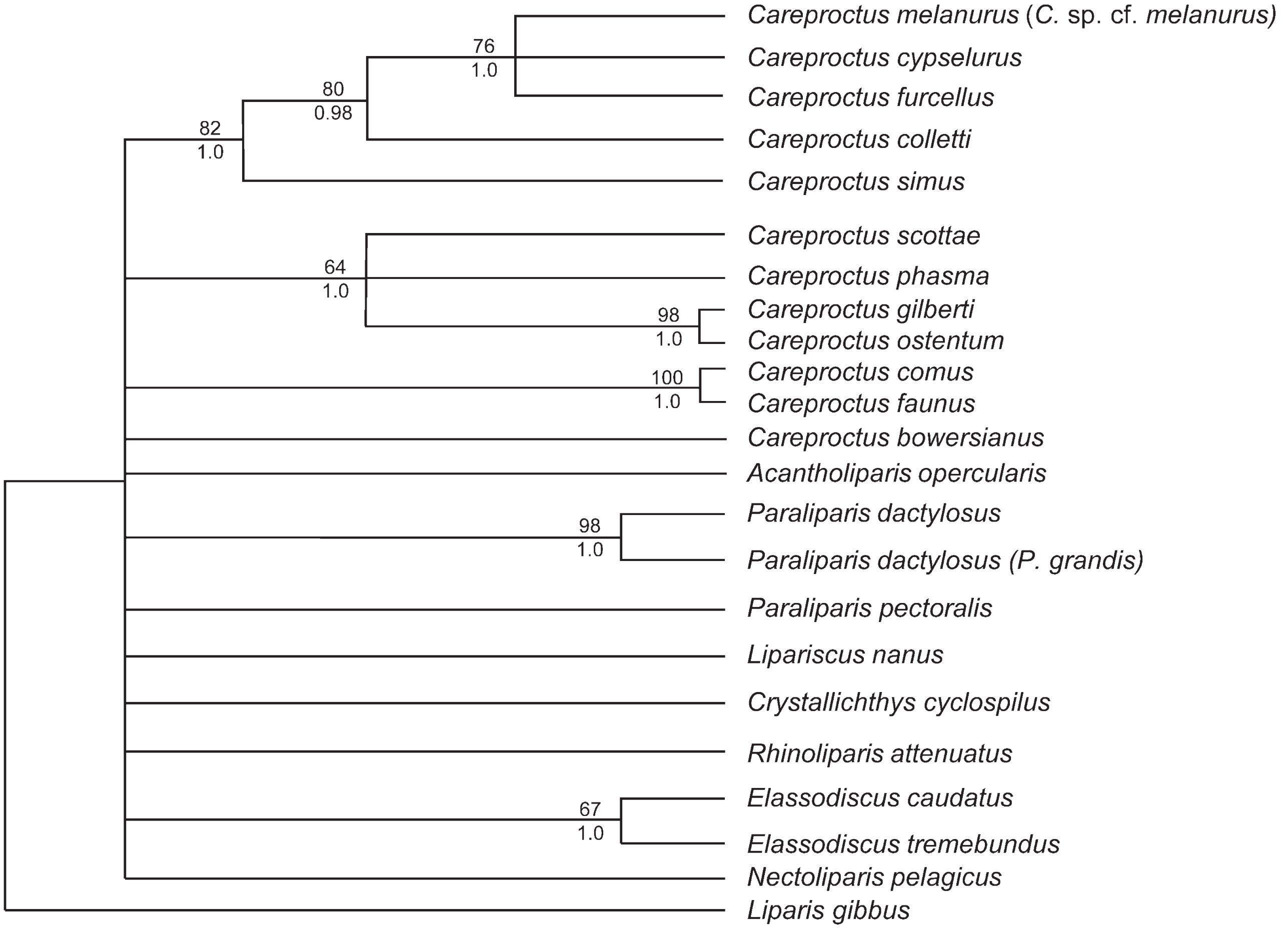

FIGURE 6. Majority rule (50%) consensus phylogenetic tree of Gardner *et al.* (2016, after fig. 4), derived from Bayesian inference and maximum parsimony analysis of a 492 bp alignment of cytochrome *c* oxidase subunit 1 gene (COI) sequences of 492 bp for 128 samples of 23 liparid species. Bootstrap values are above and Bayesian posterior probabilities are below branches that lead to multiple species. Tree is rooted with *Liparis gibbus*. Corrected identifications based on our study are in parentheses.

Primarily concerned with identifying eggs of snailfishes found within lithodid crabs, Gardner *et al.* (2016; Fig. 6) conducted a Bayesian analysis of 429 bp of COI data for 23 species and nine genera of 53 liparid adults from the Bering Sea, Aleutian Islands, and eastern North Pacific Ocean. In their analysis, multiple clades of *Careproctus* and *Paraliparis*, as well as other genera, were placed in an unresolved polytomy of their consensus tree.

Most recently, Shen *et al.* (2017; Fig. 7) published the full mitochondrial genome of an undescribed deep-water liparid and attempted to place the species phylogenetically through the analysis of mtDNA data, including COI, taken from online databases. In analyses with the 16S and Cytb mtDNA data, their overall results were unsurprisingly similar to those of Knudsen et al. (2007), the primary source of their data. With the COI data alone for 440 bp of 83 species in nine genera, they produced a tree that resolved all three major genera as paraphyletic.

Methodological approach. Despite these many previous efforts, the phylogenetic relationships of liparids remain poorly understood and increasing evidence reveals incongruence between liparid taxonomy and its phylogenetic history. The explosion of readily available molecular data, especially the wide use of COI sequence data stored in public databases, and the development of new next-generation DNA sequencing techniques, which incorporate more data than typically employed by Sanger sequencing techniques and encompass a greater range of sites throughout the genome, have provided new resources and tools for phylogenetic research (e.g., Leaché *et al.* 2015). The time is thus ripe for more extensive molecular phylogenetic analyses.

The mitochondrial COI gene is relatively easy to sample and because of widespread efforts to routinely sample species to capture biodiversity information, copious data are available from public databases, such as the Barcode of Life Database (BOLD; Ratnasingham & Hebert 2007) and GenBank (Benson *et al.* 2005). However, the gene may have insufficient phylogenetic signal to resolve deeper evolutionary divergences in many groups (Hajibabaei *et al.* 2006, 2007). Coupled with limited taxon sampling, it may also be positively misleading because of homoplasy and long branch lengths among diverse taxa (Felsenstein 1978; Anderson & Swofford 2004).

To overcome some of the limitations of using COI alone, we complemented our analysis with data derived from restriction-site associated DNA sequencing, or RADseq (Baird *et al.* 2008), which describes a range of related techniques that use restriction enzymes to target for sequencing a subset of genomic regions flanking the cut sites. The target regions are barcode-tagged, isolated, pooled, and amplified, and next-generation sequencing techniques are used to generate DNA sequence data from flanking regions adjacent to restriction enzyme cut sites. Targeted regions include coding and non-coding loci from throughout the genome and, because restriction cut-sites are generally conserved, individuals of the same or closely related species typically share most loci (Andrews *et al.* 2016). Although taxon sampling may be limited because more intensive effort and higher quality DNA is required than in a single-gene approach, RADseq utilizes hundreds more loci than could previously be surveyed in single- or multi-gene approaches and generates a wealth of useful data for phylogenomics. It therefore has the potential to create more fully resolved and better supported phylogenetic hypotheses, as well as better estimates of historical divergence times, than are possible with traditional studies (Eaton & Ree 2013; Cruaud *et al.* 2014; Longo & Bernardi 2015; Tariel *et al.* 2016).

RADseq has been successfully applied to a wide variety of species and for a variety of uses. A single RADseq library can be used for a wide range of applications by filtering the data at appropriate levels. Like whole-genome sequencing, its uses range from genome mapping (Baxter *et al.* 2011) to population identification (Davey & Blaxter 2010), analyses of genetic diversity, and phylogenetics (Cruaud *et al.* 2014). Additionally, RADseq is advantageous over whole-genome sequencing because it produces many independent amplifications of the target regions, yielding a greater depth of coverage, which is important to distinguish sequence errors from sequence variants (Sims *et al.* 2014), and because it is relatively inexpensive, allowing more samples to be sequenced without requiring prior information on the genomes of interest (Andrews *et al.* 2016). Although generally not considered feasible for higher-level, broad scale phylogenetics, RADseq has been successfully used to analyze family-level relationships (Longo & Bernardi 2015).

Objectives. In this study, our objectives were, first, to infer the phylogenetic relationships of a large number of species of liparids, with multiple individuals when possible, using readily available and easily obtained sequence data from the mitochondrial COI gene. New sequence data were obtained from species collected and identified from the eastern North Pacific and augmented with data from species in the BOLD and GenBank public databases to provide insight into global interrelationships. Second, we attempted to infer a more robust phylogeny for a select group of eastern North Pacific species for which we could obtain an appropriate quality of data by using the more intensive techniques of RADseq analysis to survey hundreds of genome-wide restriction-site associated loci.

Materials and methods

Sample collection. Specimens were collected primarily during survey operations conducted in the eastern North Pacific from Alaska to California by the Resource Assessment and Conservation Engineering (RACE) Division of the U.S. National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC). Additional specimens from the Salish Sea were obtained from the field collections conducted by the Washington Department of Fish and Wildlife and University of Washington. Tissue samples were taken from fresh whole specimens at sea or from frozen specimens in the laboratory and preserved in 95% ethanol for storage at -80°C. Most whole specimens serving as vouchers were fixed in 10% formalin and stored in 70% ethanol; some whole specimens were fixed and stored in 95% ethanol. Right-side pectoral girdles, from specimens fixed in 10% formalin and preserved in 70% ethanol, were dissected, cleared, and counter stained following Potthoff (1984). Institutional codes follow Sabaj (2016). All specimens and tissues were archived at the Burke Museum of Natural History and Culture, University of Washington Fish Collection (UW; Appendix Tables 1–3).

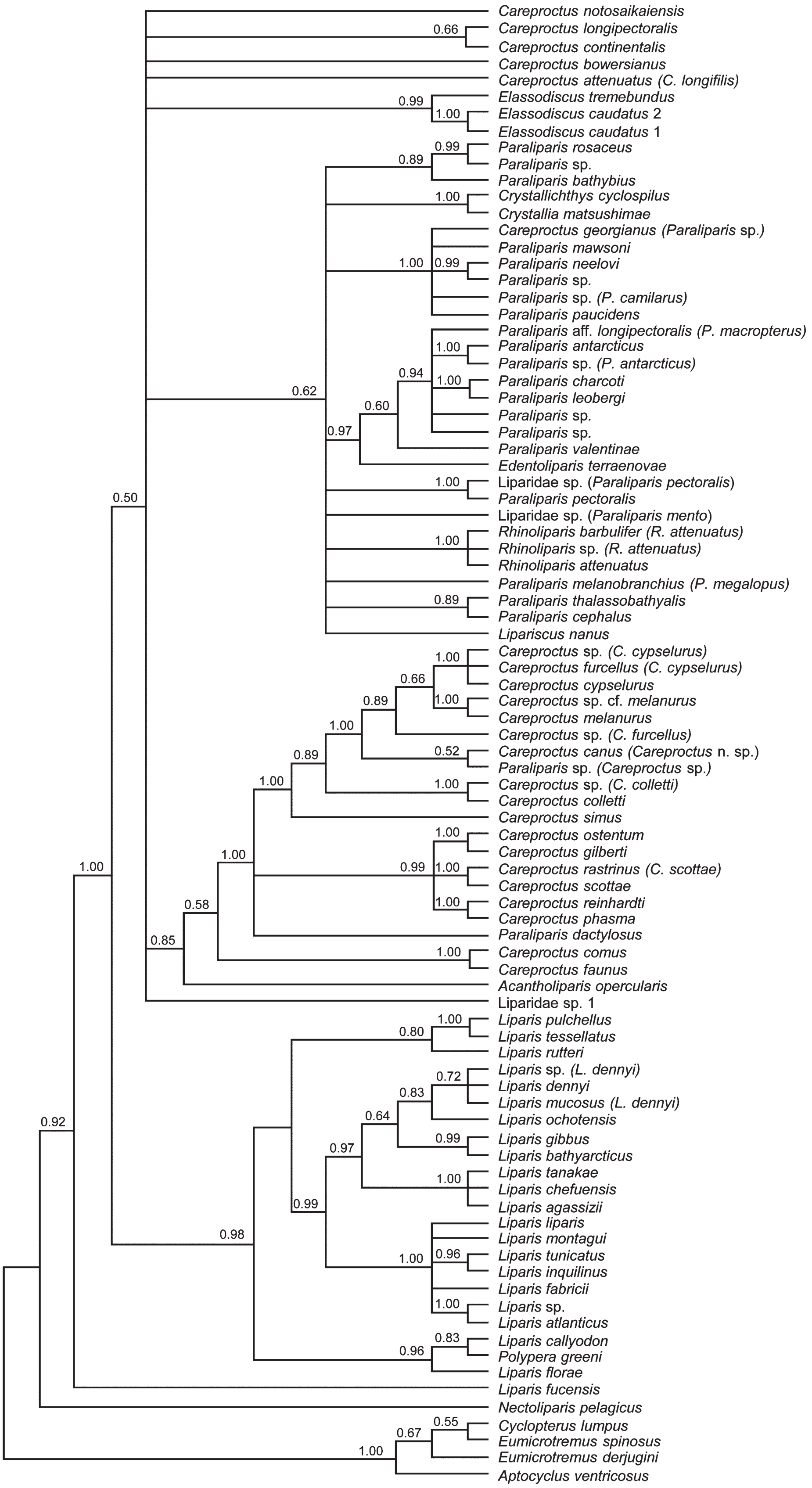

FIGURE 7. Majority-rule (50%) consensus phylogenetic tree of Shen *et al.* (2017, after fig. S6), derived from a Bayesian inference of a 440 bp alignment of cytochrome *c* oxidase subunit 1 gene (COI) sequences for 84 samples of 83 liparid species. Bayesian posterior probabilities are above branches. Tree is rooted with species of the Cyclopteridae. Corrected identifications based on our study are in parentheses.

Cytochrome *c* oxidase subunit I sequences. We attempted to collect sequence data for species never before analyzed as well as for species used in previous molecular phylogenetic or barcoding analyses. With the exception of *Psednos*, we included representatives of all valid genera and all species in these genera used in previous broad-scale analyses (i.e., Knudsen *et al.* 2007; Rock *et al.* 2008; Steinke *et al.* 2009; Duhamel *et al.* 2010; Gardner *et al.* 2016; Shen *et al.* 2017). We used a total of 268 sequences of at least 122 species among 18 genera plus two outgroup taxa for the COI phylogeny (Appendix Table 1). In deciding which data to use, we evaluated over 773 sequences derived from 247 tissues of new specimens collected primarily from across the North Pacific and 526 sequences from the public online databases BOLD and GenBank (Appendix Tables 1 and 2). Only sequences among species that were complete and not identical were included in the dataset used in the phylogenetic analysis. Other sequences surveyed and identical to those used in the analysis are listed in the Appendix Table 2. Additionally, for clarity in figures, monophyletic species clades were collapsed, except when notable sequence divergences were evident—these are discussed in the text. Illustrated branch tips are thus often supported also with specimens representing multiple haplotypes. Total numbers of sequences are in parentheses following taxa on the tree and each sequence is listed in Appendix Tables 1 and 2.

We used sequences from public databases with special caution because misidentifications among snailfishes are common within them. These data were used only when we were able to confirm identifications by verifying sources from vouchered specimens or their photographs, by comparison with our new data, or by accepting published identifications. A complete list of material with corrected identifications is provided in Appendix Tables 1 and 2. Our corrections to identifications in historical trees (Figs. 1–7) are presented in parentheses following the names as originally published. Institutional abbreviations are those provided by Sabaj (2016), unless otherwise indicated.

To obtain new sequence data, we extracted DNA using a QIAGEN DNeasy blood and tissue kit (Valencia, CA, USA) in single column format. We used primers HCO2198 and LCO1490 to amplify a 710 bp segment of the COI gene via the polymerase chain reaction (PCR) in 25 µl volume, as described in (Folmer *et al.* 1994). PCR products were sequenced in both forward and reverse directions with Sanger sequencing using the PCR primers at the High Throughput Genomics Unit at the University of Washington (Seattle, WA, USA), with the exception of *Prognatholiparis ptychomandibularis* (UW 116036), *Careproctus candidus* (UW 156091-1, UW 156091-2), *C. staufferi* (UW 155711, UW 119196-1), *Paraliparis penicillus* (UW 119192), and *P. ulochir* (UW 119776-1), which were sequenced at MCLAB (San Francisco, CA, USA). Contigs were assembled, checked manually with their chromatograms using Sequencher (2011, version 5.0, Gene Codes Corporation, Ann Arbor, MI), and aligned using BioEdit version 7.2.6 (Hall 1999). Forward and reverse sequences were obtained from all 247 new samples. A fragment of 490 bp was used for analysis after trimming ends with low sequencing quality. New sequences were deposited in BOLD or GenBank. BOLD sequence identification numbers and GenBank accession numbers are given in Appendix Tables 1 and 2.

Restriction-site Associated DNA sequences. We used tissues from 44 individuals of 28 species among 10 genera of liparids, plus four individuals of the cyclopterid *Eumicrotremus orbis*, to generate the phylogenetic tree from RADseq data (Appendix Table 3). All sequences were generated from samples taken from whole specimens from the eastern North Pacific archived at the University of Washington (Appendix Table 3). DNA was extracted using the same methodology as for COI sequencing. DNA was quantified using the Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen Inc., Carlsbad, CA), and GEN5 software (BioTek, Winooski, VT). DNA extraction produced low yields, eliminating some species (e.g., *Liparis fucensis*), which we suspect was due to the presence of excessive mucopolysaccharides in snailfishes (Jeong 2008). We designated species groups (Appendix Table 3) in the DNA library. Some species groups were represented by four individuals; many by only one. DNA of the selected samples was concentrated using a vacuum concentrator to 6.25 ng/µl in a 20 µl volume. Preparation of pooled RAD-tagged fragments (*Sbf*I restriction enzyme digestion, adapter ligation, shearing, and PCR) was performed following the methods of Baird *et al.* (2008) and Hohenlohe *et al.* (2011). Following DNA digestion with *SbfI*, P1 adapters were ligated and a unique 6-nucleotide barcode was assigned to each individual pooled into a single library. DNA was randomly sheared to a target size of 300-500 bp using a Qsonica Q800R DNA sonicator (Qsonica, LLC, Newtown, CT). Size selection was performed using Agencourt AMPure XP magnetic beads (Agencourt Bioscience Corp., Beverly, MA). A second set of adapters (P2) was then added using blunt-end ligation. The base-pair target length of libraries (200–400 bp), concentration, and quality were assessed with a 2100 Bioanalyzer and DNA 1000 kit (Agilent Technologies, Santa Clara, CA). Single-read next-generation sequencing was performed as a single library in one direction at 150 bp target length (SR150) on a HiSeq 4000 at the University of Oregon Genomics Core Facility (https://gc3f.uoregon.edu/).

The Stacks software package v. 1.44 (Catchen *et al.* 2011, 2013) was used to filter raw genetic data to distinguish sequencing errors from nucleotide polymorphisms within samples and to identify orthologous loci across taxa. The restriction site overhang (6 bp) and unique barcode identifier (6 bp) were removed from raw reads, which were then trimmed to 94 bp (due to low quality scores on the 3' end of reads) and quality filtered using the program *process_radtags*. To avoid genotyping errors associated with variable coverage, individuals with fewer than 100,000 filtered reads were dropped from downstream analyses while the maximum number of filtered reads per individual was capped at 2,000,000. The program *denovo_map.pl* pipeline in Stacks was used to call loci in individuals and then build a catalog of loci from across all individuals. The minimum stack depth (–m) was five, the number of mismatches allowed between loci within an individual (–M) was two, and the number of mismatches allowed between loci among individuals when building the catalog (–n) was 10. Datasets with various amounts of missing data were generated by running multiple iterations of the Stacks program *populations* by altering filter parameters for the minimum number of species (–p) and the percentage of individuals within each species (–r) required to retain the locus. Complete RADseq loci were exported for each individual and concatenated into supermatrices using *FASconCAT-G* (Kück & Longo 2014) with the most frequent option (–c) used for generating consensus sequences. The RADseq dataset of quality filtered reads was submitted to the National Center for Biotechnology Information (NCBI) sequence read archive (SRA) at https://www.ncbi.nlm.nih.gov/sra under accession number SUB4307188; SRA sample numbers are provided in Appendix Table 3.

Zoogeographic sampling. Our COI dataset included a wide geographic range of species but was dominated by samples from the eastern North Pacific (Appendix Tables 1 and 2), while our RADseq dataset (Appendix Table 3) was made up entirely of specimens from the eastern North Pacific. Samples with COI data from the North Pacific were primarily from verified vouchers, although some were from online databases and not verified, as were most from the North Atlantic. All sequence data from the Southern Hemisphere, including species of *Careproctus* and *Paraliparis* (with *Edentoliparis*), were taken from online databases with accepted identifications from the literature, limiting a more detailed interpretation of our results. Of the more than 127 species with COI data, 53% of the species included in the analysis were from the eastern North Pacific and Bering Sea, 24% from the Southern Hemisphere, 17% from the western North Pacific, and 10% from the North Atlantic. While about half the known species of the Northern Hemisphere were sampled, only about 12% of Southern Hemisphere species were available. Our North Atlantic material was similarly limited, but reflective of the lower diversity of the region, with 13 species representing four of the six genera in the region—*Liparis*, *Careproctus*, *Paraliparis*, and *Rhodichthys*—and about half the species. The 21 western North Pacific species sampled represent nearly half of the described liparids from the region (Nakabo & Kai 2013).

Phylogenetic inference. Phylogenetic analyses of both the COI and RADseq datasets were performed under both maximum likelihood and Bayesian optimality criteria. The maximum likelihood analyses were conducted in R version 3.4.1 (R Core Team 2017) using the packages *APE* 4.1 (Paradis *et al.* 2004) and *phangorn* 2.2.0 (Schliep 2011); the Bayesian analysis was conducted with MrBayes v3.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). The *modelTest* function in the *phangorn* package was used to determine the most appropriate nucleotide substitution model for both data sets. In both cases, the model with both the greatest log likelihood score and the lowest AIC score was a generalized time reversible (GTR) model with gamma-distributed rate variation across sites and invariant sites (GTR + G + I).

For the COI data set, we included at least 122 liparid species plus 10 individuals identified only to genus in the analysis, as well as two cyclopterid outgroup species (*Eumicrotremus orbis* and *Cyclopterus lumpus*) to root the trees (Appendix Table 1). The final data matrix included 270 sequences, 490 bp in length. For the maximum likelihood analysis, parameters of the GTR + G + I model were optimized using the *optim.pml* function of the *phangorn* package with nearest neighbor interchange (NNI) rearrangement, and 1,000 bootstrap replicates of the data set were created using the *bootstrap.pml* function of *phangorn*. Bootstrap support was mapped to the optimized tree using the *plotBS* function of *phangorn*, and the tree was rooted using the *root* function of *APE*. For the Bayesian analyses, posterior probability distributions were generated by running four Markov chains, under the default of three heated chains and one cold. After 10 million generations, the average standard deviation of split frequencies was well below 0.01, potential scale reduction factor (PSRF) scores were either 1.000 or 1.001 for all parameters, and minimum effective sample size (ESS) values were all well over 200, indicating that the runs had converged. Sampling frequency was 1,000 generations. The initial 2,500 samples were discarded as burn-in, and the remaining 7,500 samples were used to estimate tree topology and posterior probabilities.

For the RADseq data set, we included 25 liparid species in the analysis, as well as two specimens of the cyclopterid outgroup species *Eumicrotremus orbis* (Appendix Table 3). The final data matrix included 40 sequences 33,370 bp in length from 355 RADseq markers, each 94 bp after trimming and concatenation. Procedures for both the maximum likelihood analysis and the Bayesian analysis were the same as for the COI data set, except that satisfactory convergence diagnostics for the MrBayes run (as noted above) were achieved in 4 million generations. Thus, the initial 1,000 samples were discarded as burn-in, and the remaining 3,000 samples were used to estimate tree topology and posterior probabilities.

Results

COI sequences. High levels of diversity were found among individuals with confirmed identifications of *Careproctus melanurus*, *C. phasma*, *E. caudatus*, and *P. pectoralis.* In each of these "species" at least two distinct monophyletic taxa are evident. Some of this diversity had been recognized in the past (Steinke *et al.* 2009; Orr *et al.* 2015; Gardner *et al.* 2016), while other examples were newly discovered here after being compared with correctly identified specimens. Our reidentifications based on vouchered specimens, either by physical examination of specimens or of photos, are listed in Appendix Tables 1 and 2.

With few exceptions, all species were reciprocally monophyletic (Figs. 8–11). While we reidentified many records from online databases, exceptions were likely because of simple misidentifications of specimens in on-line databases, or previously unidentified cryptic variation, for which we could not verify identifications. Previously unidentified cryptic variation may also be responsible. The exceptions to monophyly occur among five groups of species:

(1) Within the clade of *Liparis agassizii, L. tanakae*, and *L. chefuensis* (Fig. 9), we verified the identification of one specimen of *L. tanakae* (FAKU 135637), which differed from all others in this group by at least two base pairs. While identified in BOLD as *L. agassizii, L. tanakae*, or *L. chefuensis,* all other sequences were identical, except for that of a specimen of *L. tanakae* (ABJF123), which alone differed by a single base pair.

(2) All specimens of *L. fabricii* were recovered with *L. bristolensis* in a polytomy basal to other Arctic and North Atlantic species.

(3) Some specimens of *Careproctus reinhardti, C. lerikimae*, and *C. phasma* were recovered in a polytomy (Fig. 10). Among several individuals identified as these species, sequences are identical, although most specimens of each species differ from all other species.

(4) One individual of *Paraliparis "bathybius"* collected from the Southern Ocean (ANTFI351-06) was nested in a clade phylogenetically distant (Fig. 11) from 11 individuals of *P. bathybius* collected from the North Atlantic. Although listed with a pending species identification of *P. thalassobathyalis* (BOLD, 5 Jan 2018), it was distant also from the *P. thalassobathyalis* used in our analysis.

(5) Three specimens of *Paraliparis neelovi* identified by Duhamel *et al.* (2010; MNHN 2008-2630, -2631, -2632) are apparently not the same species as specimens identified by Stein (2012; NMNZ P.42667 and P.42304). These specimens differ by 6.5–6.7 % sequence divergence (Fig. 11) as well as in the number of proximal pectoral radials (Duhamel *et al.* 2010; Stein 2012).

Among species, uncorrected sequence divergences ranged from 0 to 21 %, with an overall mean of 11.5%. With the exceptions noted above, 0% divergence was found among species of *Paraliparis* recently described from the Ross Sea (Stein 2012): among *P. nullansa* and *P. plicatus, P. ekaporus, P. epacrognathus, P. posteroporus*, and *P. mentikoilon* (Fig. 11). No divergence was also found between *P. camilarus*, *P. longicaecus,* and the previously described *P. stehmanni* Andriashev 1986; between *P. andriashevi* Stein and Thompkins 1989 and *P. valentinae* Andriashev and Neyelov 1984; and between *Paraliparis* sp. (FOAG559) and *P. neelovi* Andriashev 1982 (MNHN 2008-2631) (Fig. 11). The lack of sequence divergence among these species, despite described morphological differences (Stein 2012), indicates that the COI gene may not be not useful to distinguish among them (Smith *et al.* 2012). Eliminating these 0% divergences, the lowest divergence was 0.2%, which was characteristic of many within-species comparisons throughout the Liparidae, as well as among other species of the Ross Sea. In addition to the cases listed above, intraspecific divergences above 1% were from largest to smallest within *Liparis bathyarcticus, Paraliparis pectoralis, Liparis dennyi, Lipariscus nanus*, and *P. cephalus*.

TABLE 1. Summary of mean uncorrected pairwise sequence divergence estimates (in %), within and among genera, for the mitochondrial COI gene for taxa included in this study (Appendix Tables 1–2). Pairwise comparisons of identical sequences (0% divergence) not included; number of unique sequences in parentheses; NA = within-genus distance not calculated for genera for which only one specimen was sequenced.

		Within genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	*Allocareproctus* (10)	2.3																
2	*Liparis* (67)	8.6	14.7															
3	*Crystallichthys* (2)	0.2	12.9	12.9														
4	*Nectoliparis* (4)	0.3	13.0	14.6	15.9													
5	*Lipariscus* (11)	0.8	11.4	13.8	9.6	15.3												
6	*Elassodiscus* (8)	4.7	12.6	15.8	11.2	17.3	11.0											
7	*Rhinoliparis* (3)	4.7	11.1	13.4	8.7	14.1	8.0	11.6										
8	*Acantholiparis* (1)	NA	9.5	13.1	9.3	14.1	7.9	9.7	9.5									
9	*Paraliparis* (68)	6.9	11.1	13.5	8.8	14.9	7.6	11.0	8.2	8.8								
10	*Rhodichthys* (1)	NA	10.7	12.3	8.2	14.7	7.2	9.9	7.3	8.7	5.7							
11	*Lopholiparis* (1)	NA	11.0	14.3	10.5	15.5	11.3	14.0	12.4	9.4	10.9	10.2						
12	*Prognatholiparis* (1)	NA	10.5	13.9	11.3	15.0	9.2	10.8	11.0	7.3	9.8	8.9	11.6					
13	*Careproctus* (73)	9.1	11.4	14.6	10.8	14.7	11.2	11.9	11.9	9.5	10.9	10.9	10.7	10.1				
14	*Osteodiscus* (3)	0.5	8.8	13.0	8.4	13.9	8.7	9.9	9.4	7.2	8.8	8.7	9.7	7.2	9.1			
15	*Notoliparis* (2)	0.8	9.3	10.8	8.6	13.0	8.7	9.7	8.8	7.5	8.3	7.1	9.8	8.1	9.4	6.9		
16	*Pseudoliparis* (2)	0.2	9.3	10.7	8.4	12.9	8.7	9.4	8.8	7.4	8.3	7.0	9.5	8.4	9.4	7.2	0.5	
17	*Squaloliparis* (1)	NA	11.0	13.3	4.8	14.3	7.8	10.6	7.6	8.1	7.6	7.5	10.2	9.4	9.6	7.0	6.9	7.4

Within genera, uncorrected sequence divergences ranged from 0.2 to 9.1 %, with a mean of 4.0% (Table 1). In genera with multiple species represented, divergences ranged from 0.8% in *Notoliparis* to 9.1% in *Careproctus*. In genera represented by single species with multiple specimens, divergences ranged from 0.2% in *Crystallichthys* and *Pseudoliparis* to 0.8% in *Lipariscus*. In the three major genera, sequence divergence was highest within *Careproctus* (9.1%), followed by *Liparis* (8.5%) and *Paraliparis* (6.9%). Eliminating species of *Paraliparis* placed in distant clades (i.e., *P. dactylosus*, *P. grandis*, and *P. penicillus*), the sequence divergence within *Paraliparis* was reduced to 6.6%.

Among genera, uncorrected sequence divergences ranged from 0.5 to 17.3 %, with a mean of 10.5% (Table 1). The smallest divergence was between *Pseudoliparis* and *Notoliparis* at 0.5%, followed by *Squaloliparis* and *Crystallichthys* at 4.8%, and *Rhodichthys* and *Paraliparis* at 5.7%. The largest divergence was between *Nectoliparis* and *Elassodiscus*, followed by that between *Nectoliparis* and *Crystallichthys, Lopholiparis, Lipariscus*, and *Prognatholiparis*, all over 15% divergence.

RAD sequences. The number of filtered reads per individual ranged from 2,597 to 38,478,039, although for downstream analyses, filtered reads were capped at 2,000,000 and individuals with fewer than 100,000 were dropped. Of 47 individuals originally sampled, seven failed to yield the minimum number of quality filtered reads (< 100,000) and were removed from further analyses: *Careproctus bowersianus* (UW 119291), *C. candidus* (UW 156091-02), *C. staufferi* (UW 155711), *C. melanurus* (UW 150589), *Crystallichthys cyclospilus* (UW 119187), *Paraliparis dactylosus* (UW 152008), and *Eumicrotremus orbis* (UW 151223). This left 30 species groups for 40 individuals (Appendix Table 3). Maximum likelihood trees were created using *–p* 26, *–p* 27, and *–p* 28 (the minimum number of species groups in which a locus must be present) and r = 0.5 (the minimum percentage of individuals in a species group required to retain the locus) with the *denovo_map* software subroutine in *Stacks*. The tree with the highest likelihood was *–p* 28 and *–r* 0.5, which was based on 355 phylogenetically informative RADseq markers with length of 94 bp each (for a total of 33,370 bp).

Uncorrected mean sequence divergences among species ranged from ≤ 0.01 to 3.1 %, with a mean of 1.3%. Several species exhibited ≥ 0.01% divergences between individuals: *A. jordani* (0.19%), *A. ungak* (0.03%), *C.* sp. cf. *melanurus* (0.01%), *C. phasma* (0.02%), *C. scottae* (0.01%), and *Elassodiscus* sp. cf. *caudatus* (0.03%).

Within genera for which multiple known species were included, uncorrected sequence divergences ranged from 0.1 to 2.0 %, with a mean of 0.8% (Table 2). Sequence divergence was highest within *Liparis* (2.0%), despite its resolution as a monophyletic genus in this analysis (see below), followed by *Paraliparis* (1.4%) and *Careproctus* (0.44%), both of which were recovered as paraphyletic. *Allocareproctus* exhibited the lowest mean sequence divergence of 0.14%.

Uncorrected sequence divergences among genera ranged from 0.8 to 2.9 %, with a mean of 1.7% (Table 2). The smallest divergence was between *Lopholiparis* and *Careproctus*, followed by *Allocareproctus* and *Careproctus*. The largest was between *Liparis* and *Nectoliparis*, followed by that between both genera and *Lipariscus*.

TABLE 2. Summary of mean uncorrected pairwise sequence divergence estimates (in %), within and among genera, for the RADseq data for taxa included in this study (Appendix Table 3). Number of unique sequences in parentheses; NA = within-genus distance not calculated for genera for which only one specimen was sequenced.

		Within genus	1	2	3	4	5	6	7	8	9	10
1	*Allocareproctus* (4)	0.1										
2	*Careproctus* (15)	0.4	0.8									
3	*Crystallichthys* (2)	0	1.2	1.3								
4	*Elassodiscus* (4)	< 0.1	1.0	1.1	1.2							
5	*Liparis* (4)	2.0	2.3	2.5	2.4	2.4						
6	*Lopholiparis* (1)	NA	1.0	0.8	1.5	1.3	2.5					
7	*Paraliparis* (3)	1.4	1.1	1.1	1.3	1.2	2.5	1.3				
8	*Lipariscus* (1)	NA	1.5	1.7	1.5	1.6	2.6	1.8	1.4			
9	*Nectoliparis* (1)	NA	2.2	2.3	2.2	2.2	2.9	2.5	2.4	2.6		
10	*Prognatholiparis* (1)	NA	0.9	1.1	1.1	0.9	2.3	1.2	1.2	1.5	2.1	
11	*Rhinoliparis* (1)	NA	1.4	1.6	1.3	1.5	2.6	1.7	1.4	1.3	2.5	1.4

COI phylogeny. The 50% majority rule consensus tree resulting from the Bayesian analysis (Figs. 8–11) was characterized by a high level of support at shallow nodes but significant polytomies, especially among non-*Liparis* species, at deeper intermediate nodes. Nodes at the basal portions of the tree were well supported, with posterior probabilities > 0.9. Although nearly all nodes with high Bayesian posterior probabilities also had high bootstrap values calculated in the maximum likelihood analysis, the significant exception being the basal node at the divergence of *L. fucensis* from other liparids, many clades that were recovered in the consensus tree were not well supported by bootstrap values.

In a conservative assessment of this tree, the three major liparid genera—*Liparis, Careproctus*, and *Paraliparis*—are paraphyletic. *Liparis* is represented by two clades, *Careproctus* by at least four, and *Paraliparis* by three or more, if *Edentoliparis* and *Rhodichthys* are recognized as valid. All other genera with multiple species or individuals are monophyletic, including *Allocareproctus*, *Elassodiscus* and *Rhinoliparis*, as well as the monotypic *Lipariscus* and *Nectoliparis*. Our phylogeny infers many relationships that differ from previously published discussions of liparid relationships and of names applied to species groups. Table 3 lists all taxa used in our molecular analysis and the names we have applied. We did not attempt to place all species of the Liparidae within the classification, although we include some discussion about other species when warranted.

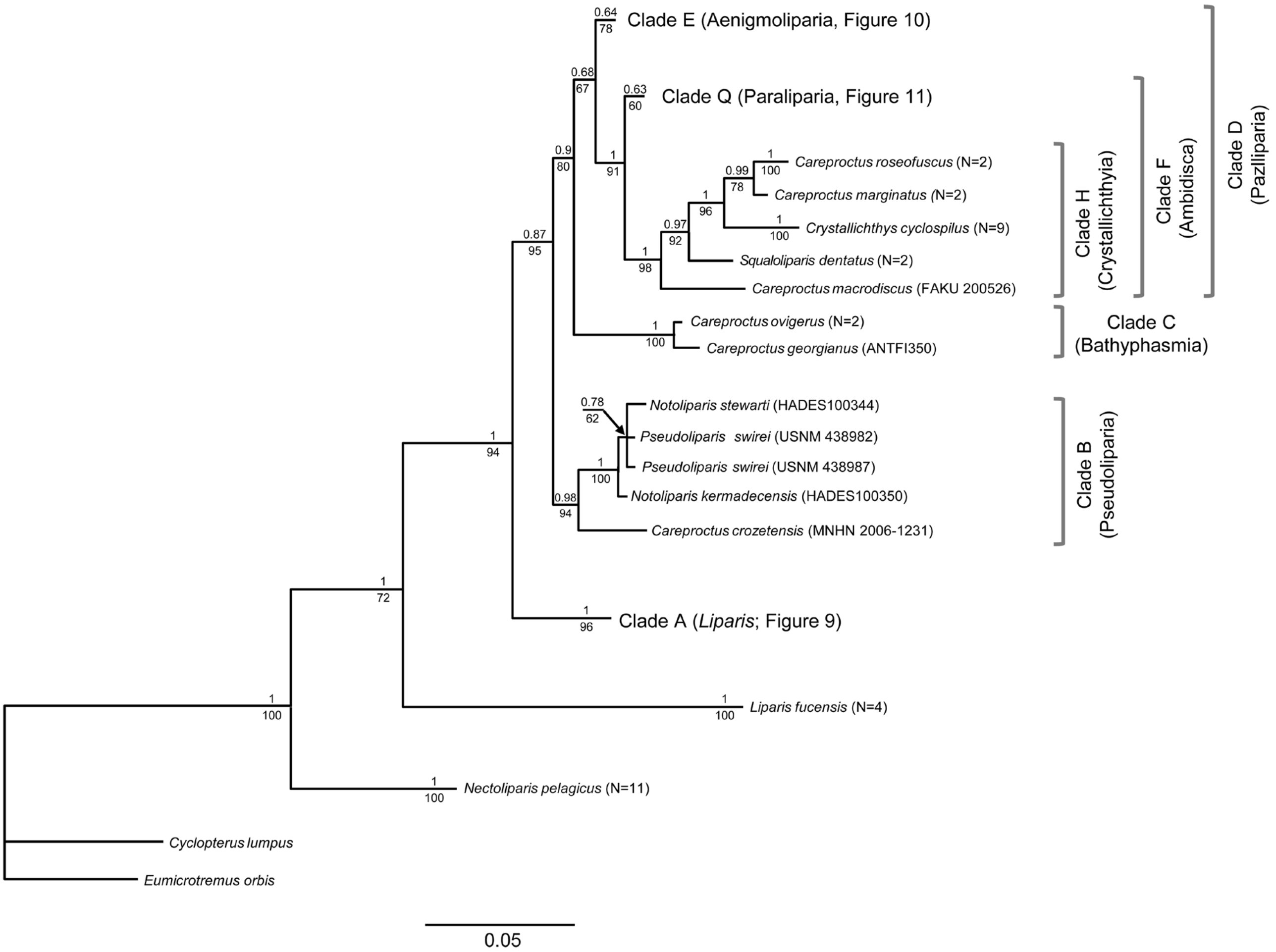

FIGURE 8. Phylogeny of the Liparidae. Majority rule (50%) consensus tree from the Bayesian inference of a 490 bp alignment of 270 cytochrome *c* oxidase subunit one gene (COI) sequences. Nodal values represent Bayesian posterior probabilities and bootstrap values from the maximum likelihood analysis (above and below, respectively). Species names are followed by a catalog number or BOLD "Sequence ID" number when represented by a sequence from a single specimen in our dataset. N indicates number of sequences, when multiple sequences support a branch tip. Only unique sequences were subjected to the analyses (Appendix Table 1); other identical sequences surveyed are listed in Appendix Table 2. Clades *Liparis*, Aenigmoliparia, and Paraliparia are depicted in Figures 9, 10, and 11, respectively.

The inferred phylogeny from the COI dataset included a clade of individuals of *Nectoliparis pelagicus* recovered as the sister of all other liparids (Fig. 8). *Nectoliparis* is followed by *Liparis fucensis,* sister of all other liparids and with the consequence of rendering *Liparis* paraphyletic, a node with a posterior probability of 1.0 but with low bootstrap support. *Liparis fucensis* is followed by a clade of all remaining species of *Liparis* (Clade A). Among these species of *Liparis* are four major clades (Fig. 9). A clade of *L. florae* + *L. greeni* + *L. callyodon* + *L. curilensis* is sister of all other *Liparis*. A polytomy follows containing a clade of *L. punctulatus* + *L. rutteri*; a clade of *L. mucosus* + *L. tessellatus* + *L. pulchellus*; *L. cyclopus* in a separate lineage; and a fourth clade containing all remaining *Liparis*. The three smaller clades of this polytomy all consist of North Pacific species. The large remaining clade of this polytomy includes *L. ochotensis* alone as the sister of two larger clades. One includes several Arctic and North Atlantic species (*L. fabricii, L. liparis, L. tunicatus, L. inquilinus, L. bristolensis, L. atlanticus,* and *L. montagui*); the other is composed of a polytomy with a clade of western North Pacific species (*L. tanakae, L. agassizii*, and *L. chefuensis)*; a clade of *L. bathyarcticus;* and a clade of *L. dennyi* + *L. gibbus*. While most relationships are well supported, the positions of *L. mucosus, L. montagui, L. greeni, L. dennyi*, and *L. fabricii* are not, and monophyly of both *L. dennyi* and *L. fabricii*, although not rejected, is not strongly supported.

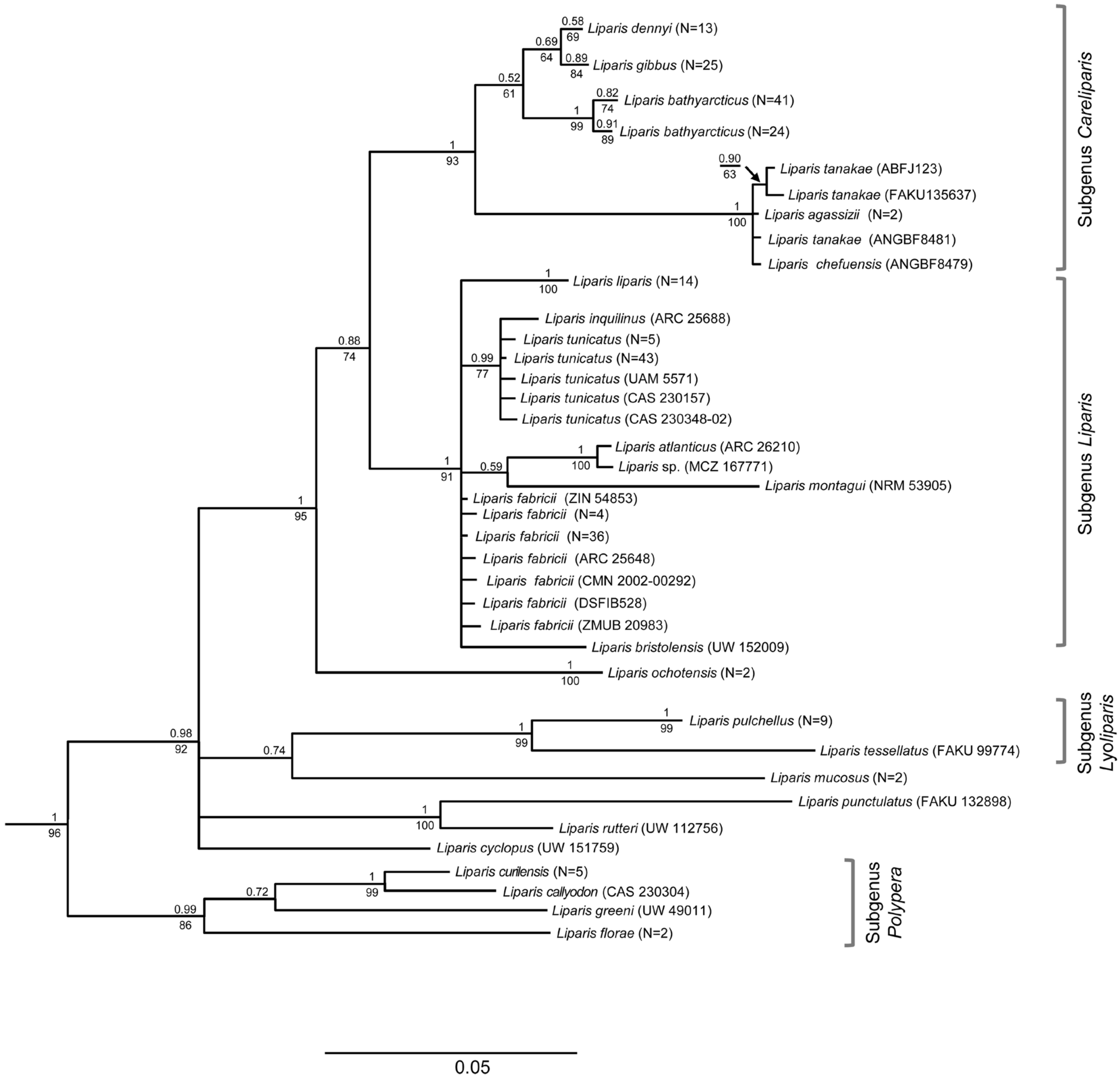

FIGURE 9. Phylogeny of the genus *Liparis*, excluding *L. fucensis* depicted in Figure 8, from the majority rule (50%) consensus tree from the Bayesian inference of a 490 bp alignment of 270 cytochrome *c* oxidase subunit one gene (COI) sequences. Nodal values represent Bayesian posterior probabilities and bootstrap values from the maximum likelihood analysis (above and below, respectively). Species names are followed by a catalog number or BOLD "Sequence ID" number when represented by a sequence from a single specimen in our dataset. N indicates number of sequences, when multiple sequences support a branch tip. Only unique sequences were subjected to the analyses (Appendix Table 1); other identical sequences surveyed are listed in Appendix Table 2.

Following the *Liparis* clade (Fig. 8), a clade of *Careproctus crozetensis* and the hadal *Pseudoliparis* + *Notoliparis* (Clade B in Fig. 8) is followed by a clade of the eastern North Pacific *C. ovigerus* and Antarctic *C. georgianus* (Clade C in Fig. 8). Both clades are highly supported.

A large clade (Clade D in Fig. 8) follows and includes the two major clades E and F. Clade E has both low posterior probability and low bootstrap support and is composed of a large polytomy of several small clades and the large and highly supported Clade G (Fig. 10). The polytomy comprises *Acantholiparis*, *Allocareproctus*, and *Prognatholiparis, C. longifilis,* and *Paraliparis penicillus;* a clade of three Antarctic species of *Careproctus* with the eastern North Pacific *Osteodiscus cascadiae;* a clade of undescribed North Pacific *Careproctus* with *C. canus;* a clade of *Elassodiscus* with *C. bowersianus*, *C. notosaikaiensis,* and *C. cyclocephalus;* a clade of *Careproctus candidus* + *C. comus* + *C. faunus* + *C. iacchus* + *C. staufferi*; and the large Clade G. Clade G is composed of *Lopholiparis* as the sister of three well-supported clades of *Careproctus* with a clade of two North Pacific species of *Paraliparis* (*P. dactylosus* and *P. grandis*) among them. Clade N contains the North Pacific *C. colletti* + *C. cypselurus* + *C. furcellus* + *C. melanurus* plus a clade of two unidentified southern *Careproctus* with an undescribed (Orr, unpublished) northern *Careproctus*, and is the sister of a clade of the North Pacific *C. simus* and Arctic Atlantic *C. micropus* and *C. kidoi.* Clade O contains three lineages: the *C. rastrinus* species group (*C. rastrinus* + *C. scottae* + *C. acanthodes* + *C. trachysoma* + *C. pellucidus)*; the *C. gilberti* species group (*C. ostentum* + *C. gilberti)*; and the *C. reinhardti* species group (*C. phasma* + *C. lerikimae* + *C. reinhardti)*. Clade P encompasses both *P. dactylosus* and *P. grandis*, recovered in a polytomy with clades N and O.

Clade F has high posterior probability and high bootstrap support and includes two well-supported clades. The first contains *Crystallichthys, Squaloliparis,* and western Pacific species of *Careproctus*: *C. macrodiscus, C. marginatus*, and *C. roseofuscus* (Clade H). The second clade (Clade Q), which is larger and more poorly supported, includes nearly all derived species that lack a pelvic disc (excepting only *Acantholiparis opercularis,* and three members of *Paraliparis—P. penicillus, P. dactylosus,* and *P. grandis*).

Within Clade Q, *Paraliparis pectoralis* is sister of all other *Paraliparis*, although the position is not well supported (Fig. 11). *Lipariscus*, *Rhinoliparis*, and six clades of *Paraliparis,* including *Rhodichthys* and *Edentoliparis* embedded within, arise from a large polytomy. *Rhinoliparis* and *Lipariscus* are both monophyletic and well supported. Other species of *Paraliparis* form five highly supported clades arising from the polytomy: *P. wolffi* + *P. megalopus* (reidentified from "*P. melanobranchus")* + *P. ulochir* (Clade I); *P. "neelovi"* + *P. copei* + *P. rosaceus* + *P. "bathybius"* (an Antarctic specimen likely misidentified) (Clade J); *P. cephalus* + *P. mento* (Clade K); *Rhodichthys* + *P. operculosus* + *P. charcoti* + *P. antarcticus* + *P. leobergi* + *P. valentinae* + *P. andriashevi* + *P. macropterus* + *Paraliparis* (=*Edentoliparis*) *terraenovae* (Clade L)*;* and *P. garmani* + *P. paucidens* + *P. mawsoni* + *P. bathybius* plus recently described *Paraliparis* from the Ross Sea and unidentified *Paraliparis* of the eastern North Pacific (Clade M). A sixth lineage of *Paraliparis* is represented by *P. thalassobathyalis*.

RAD phylogeny. Bayesian and maximum likelihood topologies of the RAD tree of the individual consensus sequences of eastern North Pacific species (Fig. 12) were identical. In contrast with the COI phylogeny (Figs. 8–11), all but three nodes of the RAD tree were well supported with Bayesian posterior probabilities of 1.0, and all but five nodes were supported with bootstrap values higher than 80. In this tree (Fig. 12), *Nectoliparis* was recovered as the sister of all other liparids. *Liparis* is monophyletic (although the analysis did not include *L. fucensis*, because of problematic extractions), followed by a clade that includes *Crystallichthys* first, followed by a ladder arrangement of *Rhinoliparis*, *Paraliparis ulochir*, and *Lipariscus*. *Prognatholiparis* is the sister of a clade containing *Elassodiscus* and *Paraliparis penicillus*, a monophyletic *Allocareproctus*, and a clade of *Careproctus* with its sister group *Lopholiparis* followed by a ladder arrangement of *C. staufferi, C. candidus, C. faunus,* and *C. comus*. Its sister clade comprises the *Careproctus melanurus* group, with the *C. melanurus/C.* sp. cf. *melanurus* clade sister of *C. cypselurus* and *C. furcellus; Paraliparis dactylosus;* and the *C. rastrinus* group (*C. scottae, C. gilberti*, and *C. phasma*). The position of *Lopholiparis* has a high posterior probability (1.0) but low bootstrap support (76%). Although with posterior probability of less than one (0.97), the internal nodes of the *Careproctus rastrinus* clade are also well supported. The position of *Paraliparis dactylosus* as sister of the *C. rastrinus* complex has a 1.0 posterior probability but among the lowest bootstrap support within the tree. *Careproctus* and *Paraliparis* are paraphyletic, with species of both genera found in three clades. Three nodes have a posterior probability < 1.0 and low bootstrap support: within *E. caudatus*, within *C. melanurus*, and between *C. gilberti* and the clade of two individuals of *C. phasma.*

Discussion

General classification. Our phylogenetic results support the integrity of some elements of current classifications, although *Liparis*, *Careproctus*, and *Paraliparis* appear to be paraphyletic. While our results suggest a paraphyletic *Liparis*, the low support for the relationship leads us to reject recognizing multiple genera within *Liparis* without additional molecular or morphological evidence. Although as currently understood, *Paraliparis* is paraphyletic, a core component of species likely forms a monophyletic *Paraliparis*, with *Edentoliparis* and *Rhodichthys* in synonymy. However, three species of *Paraliparis* were recovered among species of *Careproctus*. In addition, other genera were uncertainly recovered within the major polytomy within *Paraliparis*. *Careproctus* is certainly paraphyletic but recognizing multiple clades of the current *Careproctus* at the generic level is likely to lead to instability because of incomplete taxon sampling and the lack of support for many of the nodes that would lead to generic reassignments.

Therefore, to encourage stability and to facilitate communication of information about clades we propose the classification detailed in Table 3 and illustrated in Figures 8–12. For the species we examined among the Liparidae, we used as appropriate the few published genus-group names and otherwise created new informal clade and species-group names for highly supported clades recovered in both our COI (Table 3) and RADseq analyses (Table 4). Other than allocating some species to available genus-group names, we propose no formal nomenclatural actions here.

Paraphyly of *Liparis*. The paraphyly of *Liparis* with the inclusion of *L. fucensis* was a somewhat surprising result of our analysis. This arrangement has been reported in other analyses of COI data based on a single sample of *L. fucensis* from BOLD (Duhamel *et al.* 2010; Shen *et al.* 2017). We verified the identification of the voucher of that sample and included several additional individuals in our analysis, as well as many other species and individuals of *Liparis* (Appendix Tables 1 and 2). In our analysis, *Liparis fucensis* was monophyletic, with all specimens clustering together, and was the sister group of all other liparids except *Nectoliparis*. However, bootstrap support for this paraphyletic relationship was weak and additional data should be incorporated before drawing strong taxonomic conclusions. No adult morphological characters have been identified that would suggest this primitive position outside of other species of *Liparis*, and most recently Chernova (2008) placed it among other species in the subgenus *Neoliparis,* with *L. bikunin, L. tarticus,* and *L. cyclopus*, of which only *L. cyclopus* was included in our analysis. However, larvae of *L. fucensis* have a bubble-morph morphology (Marliave & Peden 1989), a derived character unknown in other species of *Liparis*. A similar, but different, larval morphology has been recorded in *Nectoliparis pelagicus* (M. S. Busby, pers. comm., 30 Jan 18) as well as in psychrolutid sculpins (Marliave & Peden 1989).

Polypera Burke is a generic name originally erected for *Liparis greeni* (Burke 1912) and has also included *Liparis simushirae* (Chernova *et al.* 2004; Parin *et al.* 2014). Recently, the genus has been considered valid (Chernova *et al.* 2004; Parin *et al.* 2014) or synonymous with *Liparis* (Kido 1988; Mecklenburg *et al.* 2002; Pietsch & Orr 2015). In our analysis, *Liparis greeni* is placed within a well-supported clade that includes *L. florae*, *L. curilensis*, and *L. callyodon*, providing no support for the validity of the genus, at least when conceived as containing *L. greeni* alone.

Subgenera of *Liparis*. Eight valid genus-group names have been proposed for *Liparis* (Chernova *et al.* 2004; plus *Polypera*), and Chernova (2008) recently reallocated species of *Liparis* among five of the subgenera. Of these, *Liparis*, *Careliparis* Garman, *Lycocara* Gill, and *Lyoliparis* Jordan and Evermann may accurately reflect aspects of the phylogeny of the genus; *Neoliparis* Steindachner is paraphyletic.

Among the species allocated to the subgenus *Liparis* (Chernova 2008), with type species *L. liparis*, we included *L. bristolensis, L. liparis*, and *L. tunicatus* in our analysis. All were resolved in a polytomy with individuals of *L. fabricii* (Fig. 9), which had been placed in the subgenus *Lycocara* with *L. koefoedia*, the type species, and *L. laptevi* (Chernova 2008), for which we had no material. Also in the polytomy were species previously placed in *Neoliparis* (Chernova 2008; *L. montagui, L. atlanticus*, and *L. inquilinus*). Future resolution of this polytomy, by including presently omitted species or additional support from morphological or new molecular data, may recover a monophyletic subgenus *Liparis* that does not include *Lycocara* (*L. fabricii*). We recommend incorporating *L. bristolensis, L. tunicatus, L. montagui, L. atlanticus*, and *L. inquilinus* with *L. liparis* into the subgenus *Liparis* and retaining *Lycocara* for *L. fabricii*.

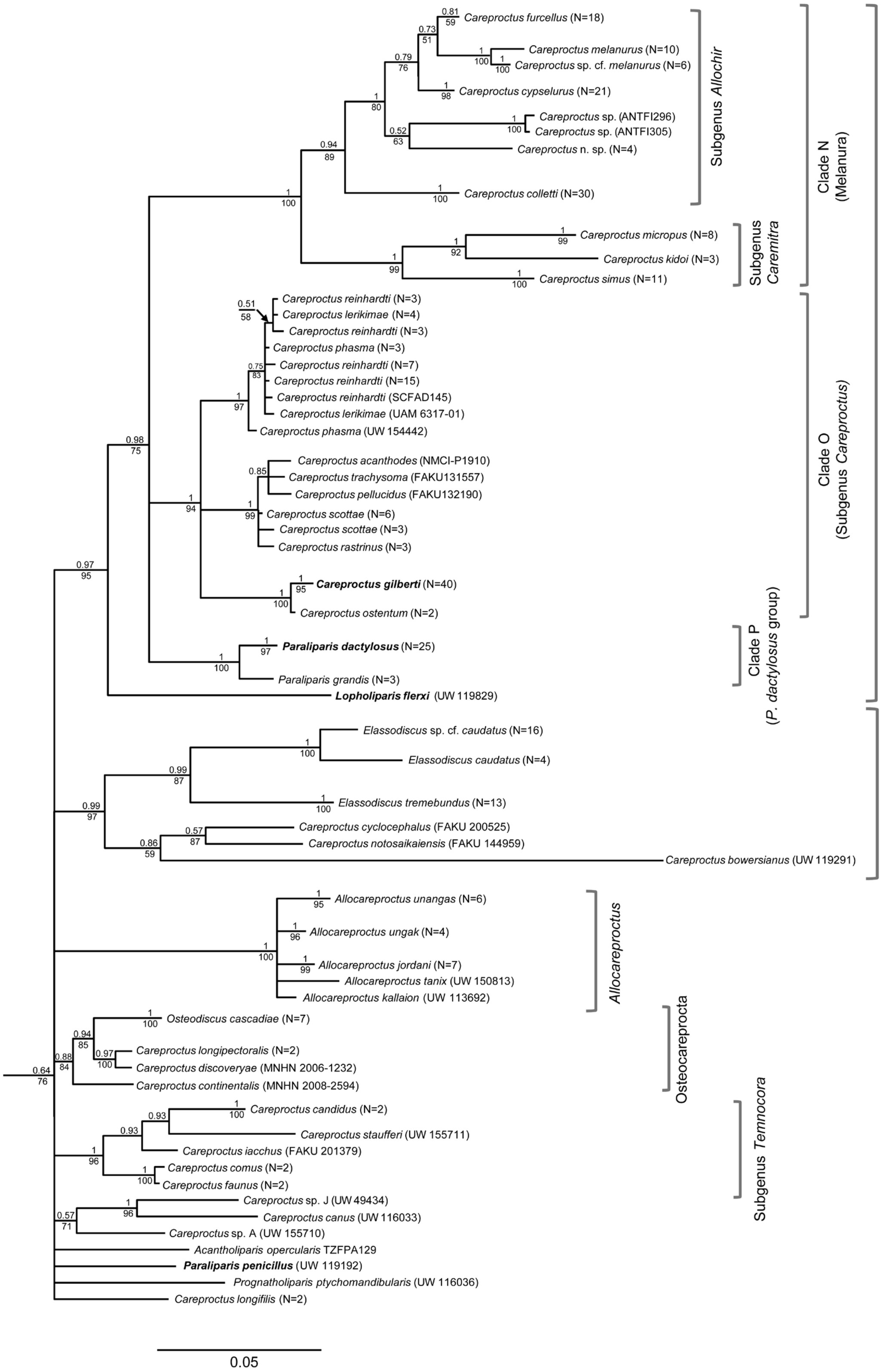

FIGURE 10. Phylogeny of the liparid clade Aenigmoliparia from the majority rule (50%) consensus tree from the Bayesian inference of a 490 bp alignment of 270 cytochrome *c* oxidase subunit one gene (COI) sequences. Nodal values represent Bayesian posterior probabilities and bootstrap values from the maximum likelihood analysis (above and below branches, respectively). Species names are followed by a catalog number or BOLD "Sequence ID" number when represented by a sequence from a single specimen in our dataset. N indicates number of sequences, when multiple sequences support a branch tip. Boldface species names indicate species placed in different positions in COI and RADseq trees. Only unique sequences were subjected to the analyses (Appendix Table 1); other identical sequences surveyed are listed in Appendix Table 2.

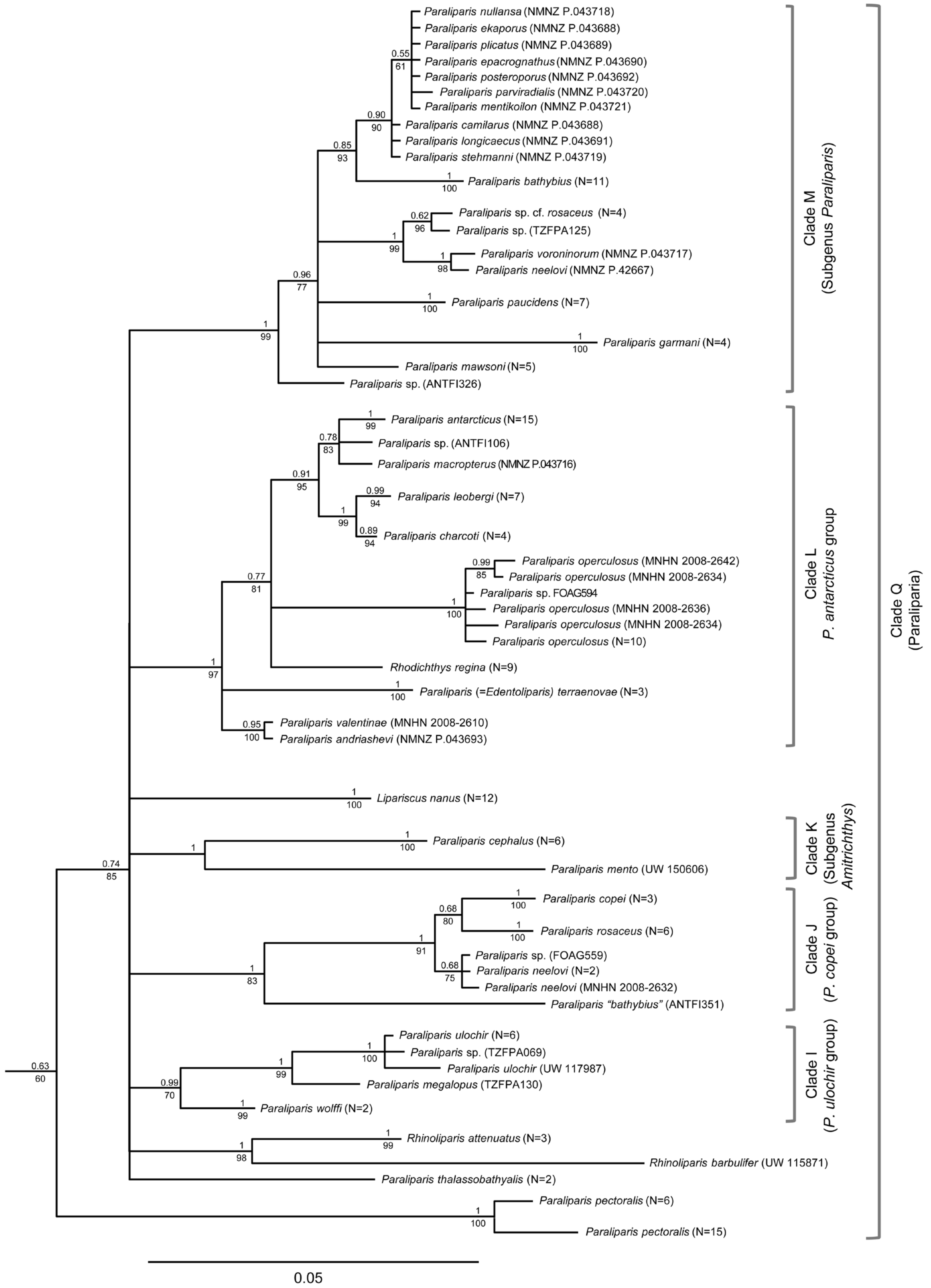

FIGURE 11. Phylogeny of the liparid clade Paraliparia from the majority rule (50%) consensus tree from the Bayesian inference of a 490 bp alignment of 270 cytochrome *c* oxidase subunit one gene (COI) sequences. Nodal values represent Bayesian posterior probabilities and bootstrap values from the maximum likelihood analysis (above and below, respectively). Species names are followed by a catalog number or BOLD "Sequence ID" number when represented by a sequence from a single specimen in our dataset. N indicates number of sequences, when multiple sequences support a branch tip. Only unique sequences were subjected to the analyses (Appendix Table 1); other identical sequences surveyed are listed in Appendix Table 2.

Careliparis, as defined by Chernova (2008), is not fully supported here. Rather, the seven species included in that subgenus formed three groups: *L. ochotensis*; *L. tessellatus* (as sister of *L. pulchellus*); and *L. dennyi, L. gibbus*, and *L. bathyarcticus* plus a clade of *L. agassizii* (the type species), and *L. tanakae*. The latter five species form a well-supported clade with *L. chefuensis* (placed in *Neoliparis* by Chernova 2008; Fig. 9). We use the subgenus *Careliparis* in a more restrictive sense than Chernova and apply it only to this latter clade of six species.

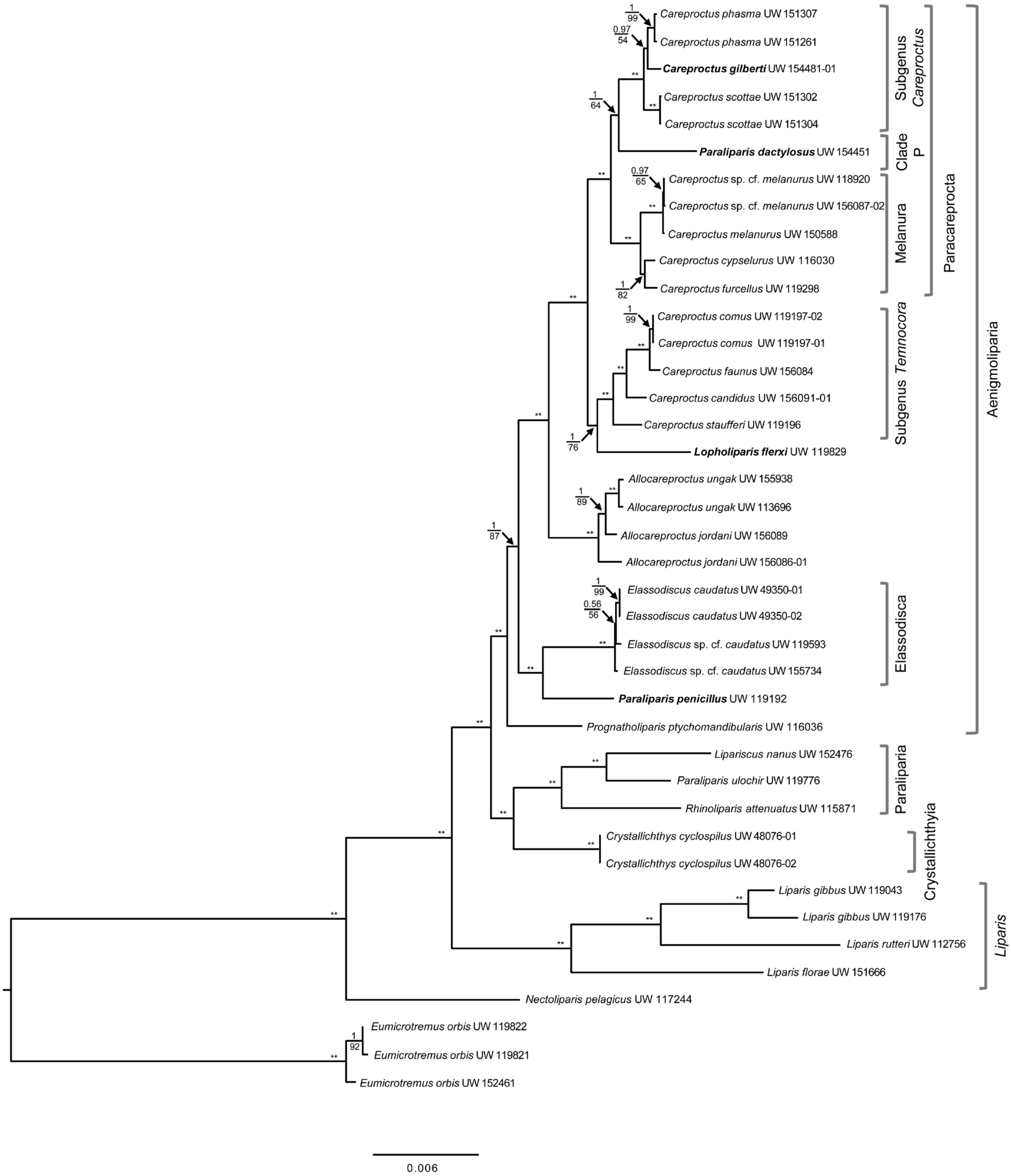

FIGURE 12. Phylogeny of selected eastern North Pacific liparids inferred using genome-wide restriction-site associated DNA sequences (RADseq; *–p* 28, *–r* 0.5) with maximum likelihood and Bayesian methods. Majority rule (50%) consensus tree of individual sequences. Nodal values represent Bayesian posterior probabilities and bootstrap values from the maximum likelihood analysis (above and below branches, respectively); double asterisks denote Bayesian posterior probabilities of 1 and bootstrap support of 100%. Species names are followed by the University of Washington Fish Collection catalog number for the specimen. Boldface species names indicate species placed in different positions in COI and RADseq trees.

Lyoliparis was erected by Jordan and Evermann (1896) as a monotypic subgenus for *Liparis pulchellus*, a distinctive elongate species with the caudal fin nearly entirely joined to the dorsal and anal fins. *Liparis tessellatus* is thought to have a convergent general morphology (Chernova 2008), but these data suggest rather that it is closely related to *L. pulchellus* despite some morphological differences (Chernova 2008).

The subgenus *Neoliparis* as presently understood (Chernova 2008) is paraphyletic in our analysis, as species previously included in *Neoliparis* were placed among multiple clades. The type of the subgenus is *L. mucosus*, a species relatively unrelated to *L. fucensis* and other species assigned to *Neoliparis* (Chernova 2008); it alone of *Neoliparis* is placed as the sister species of the *Lyoliparis* clade. In addition, *Liparis fucensis* was placed as the sister of all other liparids, rendering *Liparis* paraphyletic. Among other species, a clade of North Atlantic *Liparis* assigned to *Neoliparis* (Chernova 2008; *L. atlanticus* and *L. montagui*) was distantly placed in a derived position among species of the subgenera *Liparis* and *Lycocara*.

In our analysis, four species form a well-supported clade that is sister of all other *Liparis*, except *L. fucensis*: *Liparis greeni, L. florae, L. callyodon*, and *L. curilensis* (Fig. 9). We propose the subgenus *Polypera*, with type species *L. greeni*, for this clade.

Paraphyly of *Careproctus*. Our analysis confirms that *Careproctus* is paraphyletic and will eventually require extensive taxonomic revision. However, because many intermediate nodes of our tree are polytomies with several clades of *Careproctus* mixed with clades of other genera, we choose to retain a paraphyletic *Careproctus* for convenience and propose several informal names for clades, in some cases resurrecting older generic or subgeneric names. Also, four clades were composed of multiple genera including species allocated to *Careproctus*: the Pseudoliparia (Fig. 8), with *C. crozetensis* the sister of *Notoliparis* and *Pseudoliparis*; the Crystallichthyia (Fig. 8), with *Crystallichthys* and *Squaloliparis* recovered within a clade of western Pacific *Careproctus*, and the Osteocareprocta (Fig. 10), with *Osteodiscus* recovered within a clade of southern *Careproctus*. For each of these clades, formal taxonomic treatments will be required when their relationships with other clades and genera are clarified with additional species and data in future analyses.

Subgenera of *Careproctus*. Several genus-group names have been synonymized with *Careproctus* and are available. However, none precisely reflects our present understanding of liparid phylogenetics based on these results. Two subgenera erected by Andriashev (2003) and further elaborated upon by Chernova (2005ab, 2014, 2015) have been recently diagnosed morphologically: *Careproctus* with 22 species and *Careproctula* with 46 species, each found in both Northern, nearly all in the Arctic and Atlantic oceans, and Southern hemispheres (Chernova 2005ab; Chernova 2014). Most species of *Careproctus* of the North Pacific have not previously been assigned to subgenera, which were often erected as genera or subgenera for single species at the time of their original description (e.g., *Allochir* Jordan & Evermann 1896 for *C. melanurus*, *Prognurus* Jordan & Gilbert 1898 for *C. cypselurus*, *Temnocora* Burke 1930 for *C. candidus*, *Allinectes* Jordan & Evermann 1898 for *C. ectenes*, and *Caremitra* Jordan & Evermann 1896 for *C. simus*).

We refer Clade O (including the members of the *C. rastrinus* species group of Orr *et al.* 2015; the *C. gilberti* species group; and the *C. reinhardti* species group) to the subgenus *Careproctus* (Figs. 10, 12). Chernova (2005ab, 2014, 2015) assigned 14 northern species of the North Atlantic and Arctic to the subgenus *Careproctus*, with the northern type species *C. reinhardti.* Included in the subgenus are also seven southern species, following Andriashev's (2003) concept of the subgenus. In our analysis, all members of this clade are northern species; none of the seven southern species was available for this analysis. Chernova (2005ab) further argued for the division of northern members from southern members of the subgenus on the basis of the long lower pectoral-fin lobe ("long-finned careprocts"; Chernova 2005a), among other characters, which also characterizes nearly all members of the *C. rastrinus* and *C. gilberti* species groups. Among northern species of the subgenus *Careproctus,* Chernova (2005a) also informally recognized two or more groups, including the long-finned "slit-eyed careprocts." None of the species in these groups was available for our analysis. Chernova (2005b) also placed *Careproctus furcellus* (= *Cyclopterus gelatinosus* Pallas of Chernova 2005b) in the subgenus, although it is not closely related according to our analysis (Figs. 10, 12).

Careproctus reinhardti likely represents a species complex as suggested by Chernova (2005b), who clarified the morphological characters of the type of *C. reinhardti* and the confusion promulgated by successive authors based on misidentifications. Orr *et al.* (2015) described *C. lerikimae* as a new species based on material from the Beaufort Sea; sequences of some specimens are identical to that of other specimens identified as *C. reinhardti*. These specimens of *C. reinhardti* are likely misidentified, as paratypes of *C. lerikimae* had previously been identified as

C. reinhardti in the BOLD database (e.g., DSFIB 768-11, DSFAL600-09, DSFIB63-11; Orr *et al.* 2015; Appendix Tables 1–2). In addition, the illustration associated with *C. reinhardti* in Mecklenburg *et al.* (2016) is clearly not the species diagnosed by Chernova (2005b) and is more similar to several other species recently described by others (Chernova 2005ab, 2014; Orr *et al.* 2015). Nearly identical sequence data were extracted from other specimens that may represent additional species; and a specimen of *C. phasma* collected in the Gulf of Alaska (UW 154442) may represent a species different from *C. phasma* of the Bering Sea (Orr *et al.* 2015).

We refer some members of Clade N (Clade Melanura) to the subgenus *Allochir* with type species *C. melanurus* (Jordan & Evermann 1896): *C. melanurus, C. colletti, C. cypselurus, C. furcellus*, an undescribed species originally labeled as "*C. canus"* in BOLD from British Columbia, and an unidentified southern *Careproctus.* Two subgeneric names, plus subgenus *Careproctus* for *C. furcellus*, have previously been proposed for two species of this group: the senior name *Allochir* was erected for *C. melanurus* and the junior name *Prognurus*, for *C. cypselurus*. We refer other members of Melanura, previously considered as members of the subgenus *Careproctula*, to the subgenus *Caremitra*.

The subgenus *Careproctula* Andriashev is thought to include 46 species that are each restricted to either the Northern or Southern hemisphere (Andriashev 2003; Chernova 2005b; Chernova 2014, 2015). The type species is *C. fedorovi*, a southern species that was not included in our material. Of the 46 species originally assigned to *Careproctula* (Chernova 2014), our material included only five species. Three were among the 37 species of the southern group (Chernova *et al.* 2004; Chernova 2014): *C. continentalis, C. longipectoralis*, and *C. georgianus*. These southern species were resolved into two clades distant from the northern clade and from one another (Figs. 8, 10). The clade comprising the southern species *C. continentalis*, *C. longipectoralis,* and *C. discoveryae* also includes the eastern Northern Pacific *Osteodiscus cascadiae* (*C. cypselurus* I and II of Steinke *et al.* 2009). To avoid creating a paraphyletic *Careproctula,* and rather than recognizing *Osteodiscus cascadiae* as a derived species of *Careproctula* or allocating all species of the clade to the genus *Osteodiscus*, we propose to use the informal name Osteocareprocta for this clade. *Careproctus georgianus* is a member of the Bathyphasmia clade with the eastern North Pacific *C. ovigerus* (Fig. 8), as discussed below.

Nine other species originally assigned to *Careproctula* have been considered part of a northern *Careproctula* group (Chernova 2015). Of these, our material included *Careproctus micropus* and *C. kidoi*, which together formed a highly supported clade with *C. simus* within Clade Melanura (Fig. 10). For the clade containing *C. simus*, *C. micropus*, and *C. kidoi*, we propose the resurrection of the subgenus *Caremitra*, with type species *C. simus* (Jordan & Evermann 1896). In their description of *C. kidoi*, Knudsen and Møller (2008) recognized that the species fit most closely with northern members of *Careproctula* based on several characters, but because of the presence of ribs and two hypural plates, their specimens did not fit the diagnosis, having more affinity with *Careproctus*. However, despite the common name "ribless *Careproctus*", the diagnosis of *Careproctula* (Chernova 2005b) listed pleural ribs as "absent, rare rudimentary ribs present" and six of nine northern members of the subgenus have ribs (Chernova 2015). The type species of the subgenus *Caremitra*, *Careproctus simus,* has rudimentary ribs (Orr, unpublished). Because our material included only five species of the 41 species previously allocated to *Careproctula*, the name *Careproctula* will likely apply to some monophyletic group of the remaining 36 species that includes *C. fedorovi*.

We propose the name Bathyphasmia for the highly supported clade composed of *Careproctus ovigerus* of the North Pacific and *C. georgianus* of the Antarctic (Fig. 8). The genus *Bathyphasma* was erected by Gilbert (1896) for *Careproctus ovigerus*, primarily on the basis of its long, slender, sharp teeth and large pelvic disc. Balushkin (2012), in describing a new species of *Volodichthys*, argued for the resurrection of *Bathyphasma* based on a combination of general characters including canine teeth, a large gill slit, and an unnotched dorsal fin. However, Orr (2012) described two new species, both closely related to *C. ovigerus* on the basis of morphological characters alone and although very similar in other respects were distinguished from it by strongly trilobed teeth. The dorsal fin has a shallow notch in the smallest and largest specimens of *C. ovigerus* (Stein 1978; Orr 2012). *Careproctus georgianus* has a relatively derived pectoral girdle of four equally spaced radials lacking fenestrae (Andriashev 1998), unlike the plesiomorphic girdles of *C. ovigerus*, and its putative relatives *C. lycopersicus* and *C. kamikawai* (Orr 2012), as well as more vertebrae, simple teeth, and a small gill slit (Andriashev & Stein 1998). Because no known shared derived morphological characters diagnose the clade, we do not formally recognize the genus *Bathyphasma*.

For Clade H (Fig. 8), composed of *Careproctus macrodiscus*, *C. marginatus*, *C. roseofuscus*, *Crystallichthys cyclospilus*, and *Squaloliparis dentatus*, we propose the name Crystallichthyia. Balushkin (1996) also recovered this clade in his analysis and noted the plesiomorphic condition of the unfused caudal fin retained by *Careproctus* *roseofuscus*, *C. marginatus*, and *S. dentatus*, and characteristic also of *Crystallichthys cyclospilus* (Kido 1988), noting that further work is needed to identify morphological synapomorphies of the group.

Within Clade E (Fig. 10), we recognize the subgenus *Temnocora* with type species *C. candidus* for the clade comprising *Careproctus comus, C. faunus, C. iacchus*, *C. staufferi,* and *C. candidus*. The genus *Temnocora* was originally erected for *C. candidus* alone because of its anterior dorsal-fin lobe and slit-like pupil (Burke 1930). While only *C. candidus* among these species has a distinctly notched dorsal fin, all except *C. comus* and *C. faunus* have similar slit-like pupils. Although recovered in the COI tree as the sister species of all other members of the Paracareprocta, *Lopholiparis flerxi* may be closely related, with its lobed dorsal fin and slit-like pupil, having been recovered as the sister of the *Temnocora* clade in the RADseq analysis, albeit with only moderate bootstrap support (Fig. 12). Tissues of other "slit-eyed" species of Chernova (2005a, 2014, 2015) were not available to us but these species are likely more closely related to members of the subgenus *Careproctus*.

Paraphyly of *Paraliparis*. Our analysis confirms that *Paraliparis* is paraphyletic and will require some taxonomic revision. With the type species *P. bathybius*, a core derived component of species forms a monophyletic *Paraliparis*, and if extended to the clade including *Edentoliparis* and *Rhodichthys* would place these genera in synonymy. Otherwise, *Rhodichthys* would be available for the clade including these genera.

Within clade Paraliparia, *Paraliparis terraenovae* and *Rhodichthys regina* are both placed within a well-supported clade of southern *Paraliparis* (Fig. 11: Clade L). Although *P. terraenovae* was allocated to the monotypic genus *Edentoliparis* by Andriashev (1990), a genus also later considered valid by him and others (Duhamel 1992; Andriashev 1998, 2003; Chernova *et al.* 2004), the genus was synonymized by Duhamel *et al.* (2010) on the basis of COI data, a conclusion supported as well by our analysis. The validity of *Rhodichthys* had been questioned by Andriashev (1986) and Kido (1988) but was reaffirmed with the description of a new species in the genus (Andriashev & Chernova 2011) and not examined by Duhamel *et al.* (2010). Based on our results, *Rhodichthys* should be synonymized with *Paraliparis*. Alternatively, if *Rhodichthys* is retained as a distinct genus, a new name will be required to accommodate species of the *P. antarcticus* species group.

We are unable to firmly place *Rhinoliparis* and *Lipariscus* precisely among clades of *Paraliparis* because of a lack of resolution in the COI tree and lack of additional species of *Paraliparis* in the RADseq tree. Both genera were synonymized with *Paraliparis* by Kido (1988) because they were recovered among species of *Paraliparis* in his cladogram of 60 species (Fig. 1), similar to our results. However, in our COI analysis, these genera are uncertainly placed in the large polytomy with most other clades of *Paraliparis* (Fig. 11). Thus, our evidence neither supports nor explicitly rejects their synonymization with *Paraliparis* as proposed by Kido (1988) and, conservatively, we retain their generic status.

The confirmation in this molecular analysis of the position of the *Paraliparis dactylosus* species group (*P. dactylosus* and *P. grandis*) among clades of *Careproctus* and other species with a complete pelvic disc (Fig. 10) is counterintuitive. However, earlier workers considered the species atypical of the genus (Stein 1978; Andriashev 1986), and Stein (1978) stated that *P. dactylosus* was "not closely related" to species of *Paraliparis* known at the time. *Paraliparis dactylosus* may be unique among species of *Paraliparis* in having strongly trilobed teeth, although *P. challengeri* also has some teeth that have "well-developed lateral shoulders" (Chernova 2003, unnumbered figure). In addition to its trilobed teeth, it has high counts of pyloric caeca, like many species of *Careproctus*. Most specimens of *P. dactylosus* we examined also clearly have a pair of pleural ribs, unknown in other *Paraliparis* except *P. grandis*. *Paraliparis grandis* itself was considered an "aberrant" *Paraliparis* by Andriashev (1986), and he eliminated several characters of the species from his generic description, including its unique pectoral fin and its high counts of pectoral-fin rays, pyloric caeca, and vertebrae. In addition, it has two pairs of pleural ribs, which are absent in nearly all other species of *Paraliparis* (Kido 1988; Stein *et al.* 2001). Among these characters, the presence of pleural ribs, as well as high counts of pectoral-fin rays and pyloric caeca, are more typical for *Careproctus* than for *Paraliparis*. While many species of *Careproctus* bear the plesiomorphic condition of relatively strong ribs (Andriashev 1998; Chernova 2014, 2015), species of clade Melanura have one or two pairs of small, slender ribs (Orr, unpublished), unlike most species of the subgenus *Careproctus*, in which species of the *C. rastrinus* and *C. reinhardti* species groups have two or three strong, saber-like ribs (Chernova 2005b; Orr *et al.* 2015). Therefore, we suggest that *Paraliparis dactylosus* and *P. grandis* should both be considered derived species of *Careproctus*, closely related to the Melanura clade, and characterized by the independent loss of the pelvic disc.

Paraliparis penicillus was recovered in the basal polytomy of clade Aenigmoliparia in the COI analysis (Fig. 10) and sister of *Elassodiscus* in the RADseq analysis (Fig. 12). In both analyses it was distant from *P. ulochir*, the only other species of *Paraliparis* included in the RADseq data.

Subgenera of *Paraliparis*. As Stein noted in 1978, none of the subgenera of *Paraliparis* erected by earlier authors reflect the relationships as he understood them and with few exceptions (e.g., Chernova & Prut'ko 2011) later authors have declined to name groups of species. This uncertainty is evident in our analysis. Within *Paraliparis*, seven valid genus-group names have been formally proposed (Chernova *et al.* 2004). Of these we consider only the nominotypical subgenus *Paraliparis* and subgenus *Amitrichthys* to be appropriate for clades resolved in our study.

The subgenus *Paraliparis* (Fig. 11: Clade M) includes species from nearly the entire geographic range of the Liparidae. The type species *P. bathybius* (Collett 1879) and *P. garmani* are from the North Atlantic. The 15 other species comprising the clade include *P. paucidens* and an undescribed species from the eastern North Pacific, and several southern species, including those recently described from the Ross Sea (Stein 2012).

Jordan & Evermann (1896) erected *Amitrichthys* for the type species *P. cephalus*. We propose to use this name for the clade composed here only of *P. cephalus* and *P. mento* (Fig. 11, Clade K). *Paraliparis mento* was also included by Jordan & Evermann (1896) in *Amitrichthys*, along with the distantly related *P. rosaceus*, *P. copei*, and *P. dactylosus*.

Other names available for use as subgenera of *Paraliparis* include *Amitra* Goode 1881 (*Monomitra* Goode 1883 is an unneeded replacement name; Eschmeyer *et al.* 2017) and *Hilgendorfia* Goode & Bean 1896. *Amitra* was a genus erected for *Paraliparis liparinus*, but the characters of *P. liparinus* are poorly known, based on a scant original description and an inadequate illustration of the holotype (Andriashev 1998; Chernova 2003). No other species have been proposed as closely related other than the almost equally rare *P. challengeri*, and neither species was included in our analysis. The genus *Hilgendorfia* was erected for the type species *P. membranaceus* Günther 1887 from off Chile. Although the original description and illustration were excellent, only the holotype is known and one other species from off Chile may be related to it (Stein 2005). Neither were available for our analysis. While Jordan & Evermann (1896) later allocated *P. ulochir* to *Hilgendorfia*, they provided no evidence to justify its closer relationship to *P. membranaceus* than to any other species.

We propose the following informal species group names for other highly supported clades of *Paraliparis*. The *Paraliparis copei* species group (Chernova & Prut'ko 2011) includes *P. copei* and *P. rosaceus*, as well as specimens questionably identified as *P. neelovi* and *P. "bathybius"* from the Antarctic (Fig. 11, Clade J). The *Paraliparis antarcticus* species group includes *P. antarcticus, P. macropterus, P. leobergi, P. charcoti, P. operculosus, Paraliparis* (= *Rhodichthys*) *regina, P. valentinae, P. andriashevi*, and *P. terraenovae* (Fig. 11, Clade L). The *Paraliparis dactylosus* species group includes *P. dactylosus* and *P. grandis* (Fig. 10, Clade P) and appears to be distantly related to the other species of *Paraliparis*. The *Paraliparis ulochir* species group includes *P. ulochir*, *P. megalopus,* and *P. wolffi* (Fig. 11, Clade I).

Consensus between COI and RAD trees. Both COI and RADseq analyses supported similar topologies and conclusions about the phyletic integrity of major taxa. *Allocareproctus* was monophyletic. *Careproctus* and *Paraliparis* were paraphyletic, each split into at least three clades. *Nectoliparis* was the sister of all other liparids, followed by species of a monophyletic *Liparis* (except for *L. fucensis*, which was not available for the RADseq analysis).

Significantly, both COI and RADseq analyses support the position of the *Paraliparis dactylosus* species group within and among otherwise highly supported clades of *Careproctus*. We eliminated the possibility of misidentification of these species by using multiple specimens that either shared the same COI haplotype or differed slightly but were placed within the same clade. In both trees, the relationship of the clade to either subgenus *Allochir* or subgenus *Careproctus* is unresolved—its position as sister of the subgenus *Careproctus* is marginally supported in the RADseq tree and it is in the polytomy with *Allochir* and subgenus *Careproctus* in the COI tree.

Also, the fully resolved RADseq tree placed *Crystallichthys* as the sister of a clade comprising the disc-less *Rhinoliparis*, *Lipariscus*, and one member of *Paraliparis*. In the COI tree, *Crystallichthys* is placed within a highly supported clade of western Pacific *Careproctus* and *Squaloliparis*, which is sister of a large polytomy of clades of nearly all disc-less species we analyzed—a position that is highly supported.

Incongruence between COI and RAD trees. The makeup of more derived clades and the relationships of several less diverse or monotypic taxa differed primarily because of the lack of resolution in the COI tree or the lack of comparative samples in the RADseq tree. Four clear conflicts are evident between the trees. *Lopholiparis* is sister of the *Temnocora* clade, composed of *C. staufferi, C. candidus, C. comus*, and *C. faunus* in the RADseq tree (Fig. 12); in the COI tree (Fig. 10), it is sister of the large, primarily northern, Clade Paracareprocta that includes the subgenera *Allochir* and *Careproctus* and the *P. dactylosus* species group. Its position is highly supported in the COI tree and is at least moderately supported in the RADseq tree. Within *Temnocora*, *C. staufferi* is sister of all other members in the RADseq tree, while it is in a derived position as sister of *C. candidus* in the COI tree. In another apparent incongruity, *Careproctus gilberti* was placed between *C. scottae* and *C. phasma* in the RADseq tree (Fig. 12), but in a separate clade with *C. ostentum* in the COI tree (Fig. 10); RADseq data were not available for *C. ostentum*. The position of *C. gilberti* is strongly supported in both trees. Finally, *Paraliparis penicillus* is recovered in a clade with *Elassodiscus caudatus* in the RADseq tree (Fig. 12); but in the COI tree (Fig. 10), it is in the large polytomy of Clade Aenigmoliparia outside the *Elassodiscus* clade, within which *P. penicillus* is replaced with *C. bowersianus*, a species unavailable for RADseq.

In addition to incongruences due to the lack of comparable samples, other differences in positions are apparent due to lack of resolution in the COI tree. In particular, *Prognatholiparis* is the sister of the remaining members of the Liparidae in the RADseq tree (Fig. 12), including an *Elassodiscus/Paraliparis penicillus* clade; in the COI tree (Fig. 10), it is in the large polytomy of Clade Aenigmoliparia with clades of *Careproctus*, *Allocareproctus,* the *Elassodiscus* clade (with *C. bowersianus*), and *P. penicillus*. Similarly, *Allocareproctus* is in the same general position in both trees (Figs. 10, 12), although in the same large polytomy of the COI tree.

Comparisons with previous results. Significant published phylogenetic hypotheses are those of Kido (1988; Fig. 1), Balushkin (1996; Fig. 2), Knudsen *et al.* (2007; Fig. 3), Steinke *et al.* (2009; Fig. 4), Duhamel *et al.* (2010; Fig. 5), Gardner *et al.* (2016; Fig. 6), and Shen *et al.* (2017; Fig. 7). In all analyses, all genera were monophyletic except for the three large, diverse genera *Liparis*, *Careproctus*, and *Paraliparis*. *Liparis* was considered monophyletic until recent molecular analyses included *L. fucensis*; the monophyly of *Careproctus* and *Paraliparis* has been suspect in most modern analyses. Our results further support the conclusion that these three genera are paraphyletic and require significant revision.

The first modern phylogenetic analysis was conducted by Kido (1988; Fig. 1), who came to the surprising conclusion that the highly derived *Nectoliparis pelagicus* was the sister species of all other liparids. In all previous analyses, this pelagic snailfish—with its apomorphic characters of pelvic disc absent, gill slit entirely in front of the pectoral fin, and anus in a far anterior position—had been considered nested deeply within the family. Our analyses, as well as the results of other recent authors (Steinke *et al.* 2009; Gardner *et al.* 2016; Shen *et al.* 2017), strongly support Kido's (1988) conclusion, indicating that although highly derived, *Nectoliparis* or its ancestor diverged from the liparid lineage relatively early. In contrast, Balushkin (1996) argued for a more derived position for *Nectoliparis*, as traditionally accepted by previous authors (e.g., Burke 1930).

Other than the position of *Nectoliparis*, Balushkin's (1996; Fig. 2) phylogenetic hypothesis exhibits some broad similarities with the results presented here. His results, based on morphological data, include a basal clade of some species of *Careproctus* and three other genera, including *Crystallichthys*, in a polytomy comparable to our clade Crystallichthyia. In a second more derived clade, nine genera and other species of *Careproctus* are placed in a polytomy basal to a more derived clade comprising more species of *Careproctus* plus *Elassodiscus*, comparable to our clade Elassodisca. Finally, Balushkin (1996) recovered two derived clades of genera united by a highly reduced or absent pelvic disk: an unresolved component of eight genera, including the putatively monophyletic *Paraliparis,* and a clade of *Nectoliparis* and *Lipariscus*. Except for the derived position of *Nectoliparis* and *Lipariscus*, a monophyletic *Paraliparis*, and the inclusion of *Acantholiparis*, the clade is comparable to our Paraliparia.

The first phylogenetic analysis incorporating molecular data was that of Knudsen *et al.* (2007; Fig. 3), who performed a combined analysis of mtDNA and morphological data for 24 species of the North Atlantic and North Pacific. In their final tree, *Nectoliparis pelagicus* was resolved as the sister of the rest of the Liparidae, followed by a monophyletic *Liparis* (again without *L. fucensis*), a monophyletic *Careproctus*, and a paraphyletic *Paraliparis*. Their limited taxon sampling included species of *Careproctus* of only our Paracareprocta clade and species of *Paraliparis* from two distinct clades: the subgenus *Paraliparis* and the *P. copei* species group.

All subsequent analyses of liparid phylogeny (Rock *et al.* 2008; Steinke *et al.* 2009; Duhamel *et al.* 2010; Gardner *et al.* 2016; Shen *et al.* 2017) have been strictly molecular, using mitochondrial DNA sequence data, and in all cases both *Careproctus* and *Paraliparis* have been resolved as paraphyletic. Studies that included *Liparis fucensis* (Duhamel *et al.* 2010; Shen *et al.* 2017) have also resolved *Liparis* as paraphyletic, with *L. fucensis* as sister of all other *Liparis*. Our results concur with these findings, providing more evidence that *L. fucensis* may be inappropriately placed in *Liparis*.

Paraliparis dactylosus has been placed by previous authors in positions different from that presented here. This apparent incongruence is the result of misidentifications of BOLD specimens (Appendix Tables 1 and 3). Steinke *et al.* (2009; Fig. 4) placed *P. dactylosus* with *P. melanobranchus* (incorrectly labeled as "*melanobranchius*"; reidentified as *P. megalopus*) together in a clade with other species of *Paraliparis* and *Lipariscus*. Duhamel *et al.* (2010; Fig. 5) recovered *P. dactylosus* with *P. melanobranchus* (also as "*melanobranchius*") within a large polytomy comparable to our clade Paraliparia of disc-less species. However, the sequence data for this "*dactylosus*" in both publications matches our new sequences of *P. ulochir,* and the photo published in BOLD is readily identifiable as *P. ulochir*. Our analysis recovered the clade of *P. ulochir* in our clade Paraliparia, comprising most species of *Paraliparis*, similar to the placement of "*dactylosus*" in both previous analyses. Shen *et al.* (2017; Fig. 7) used a correctly identified *P. dactylosus* (UW 119893) that was placed in a similar position to ours—among species of *Careproctus*.

Morphology

Among significant characters used for broad-scale phylogenetics in liparids are the absence, presence, and size of the pelvic disc; the detailed morphology of the pectoral girdle; and tooth patterns. Many other characters, such as cephalic pore patterns, meristics, and general morphometrics, are critical for taxonomic analysis and are likely to prove useful for phylogenetic work, especially in more fine-scale analyses of the clades we identified (Stein 1978; Kido 1988; Knudsen *et al.* 2007).

Pelvic disc. Perhaps the most significant character of liparid fishes is the highly modified pelvic fin, which is modified into a sucking disc or lost (Table 3). Our results suggest that the disc was independently lost at least three times: in the evolution of *Nectoliparis*, among members of the large disc-less clade of *Paraliparis* and other genera, and with the evolution of the *Paraliparis dactylosus* clade (Table 3). It was likely lost at other points as well, for instance in *Acantholiparis* and *Paraliparis penicillus,* both of which are placed uncertainly in our tree. When not lost, the disc evolved from the plesiomorphic condition of a large, well-developed disc similar to that found in the cyclopterids and the genus *Liparis* to typically becoming further reduced in more derived groups, as for example to the tiny, but complete, structure in *Careproctus ostentum* and *C. gilberti*. The disc was independently reduced to obsolescence in *Elassodiscus*. The unique skeletal pelvic disc of *Osteodiscus* (Stein 1978) is clearly a derived condition from the large pelvic disc of related species.

Pectoral girdle. The number and size of proximal radials, and notches, fenestrae, and the position of each have been considered important systematic characters of the pectoral girdle (e.g., Andriashev *et al.* 1977; Kido 1988; Andriashev 1998; Andriashev & Stein 1998; Stein *et al.* 2001). Distal radials, first identified in liparids by Orr & Maslenikov (2007), are under-reported but their presence and distribution may prove phylogenetically as well as taxonomically informative (Maslenikov *et al.* 2015). The plesiomorphic condition is a robust girdle with four proximal radials (henceforth, "radials"), notched and relatively evenly spaced in the basipterygium, separated by three large fenestrae dorsally, a condition found in cyclopterid outgroups (Ueno 1970; Maslenikov *et al.* 2015; Fig. 13A, Table 3) and all species of *Liparis* (Andriashev 1986; Andriashev & Stein 1998; Fig. 13C). The more derived character states show a reduction in all elements, ultimately to two round widely separated radials, either one dorsal and one ventral or both dorsal, without fenestrae (Andriashev 1990; Andriashev & Stein 1998; Table 3) or, uncommonly, enlarged evenly spaced radials lacking fenestrae (e.g. *Elassodiscus* and *Acantholiparis*, Fig. 13I). Our results support the idea of independent and convergent reduction in pectoral girdle elements as first hypothesized by Andriashev (1998) for southern species. Although these ideas of the evolution of pectoral girdle morphology are supported in most respects by relationships based on molecular data, pectoral morphology is clearly not as tightly constrained as formerly proposed, and intraspecific variability among pectoral girdle characters is more common than previously expected (Knudsen & Møller 2008; Stein 2012, 2016). The plesiomorphic morphology is present basally in most of the major clades more derived than *Liparis*, including the deep-water clades Pseudoliparia, Bathyphasmia, Ambidisca and its sister group Crystallichthyia, clade Aenigmoliparia and its major clade Paracareprocta. The discussion below pertains nearly exclusively to those species included in our analysis. A more complete picture of pectoral girdle evolution will become clearer with the incorporation of additional species into future phylogenetic analyses.

The sister group of all other members of the Liparidae is *Nectoliparis pelagicus*, a highly apomorphic pelagic species. It possesses a pectoral girdle with three rounded radials in the upper half of the basipterygium while lacking the ventral fourth radial (Fig. 13B)—most similar to derived species of *Paraliparis,* as in *P. ulochir* (Fig. 13O) and especially 12 Australian species described by Stein *et al.* (2001) for which we had no material. Most other species without a ventral radial have one or two dorsal radials (Kido 1988; Andriashev 1986, 1998; Stein *et al.* 2001).

Among the hadal and bathyal *Notoliparis, Pseudoliparis*, and *C. crozetensis*, the pectoral girdle morphology of all except *N. stewarti* includes four round moderately sized radials without fenestrae (Duhamel *et al.* 2016; Stein

TABLE 3. Species of Liparidae and outgroups used to construct a COI phylogenetic tree, listed as clades and species appear in the tree. Letter designations of clades and taxonomic names are referenced in the text and in Figures 8–11. Distribution abbreviations are as follows: Atl = Atlantic Ocean, NAtl = North Atlantic Ocean, eNAtl = eastern North Atlantic Ocean, wNAtl = western North Atlantic Ocean, NPac = North Pacific Ocean, eNPac = eastern North Pacific Ocean, wNPac = western Pacific Ocean, Arc = Arctic, Ant = Antarctic, SO = Southern Ocean, MT = Mariana Trench, KT = Kermadec Trench. Pelvic disc sizes are characterized as follows: large is >25% HL; small, <25% HL; minute, <11% HL; obsolete, reduced to small lobes. Pectoral radial formula follows Andriashev (1998): R = round radial; N = notched radial; f = fenestra present; numbers of radials in parentheses from dorsal to ventral. Source refers to literature or to the catalog number of specimen examined for morphological data. Figure numbers 13A–O following catalog number refer to previously unpublished figures of pectoral girdles.

Lettered clade	Taxa	Distribution	Pelvic disc size	Pectoral radial formula	Tooth shape, pattern	Source
	Cyclopteridae					
	Cyclopterus lumpus	NAtl	large	Nf(3+1)	simple, bands	Ueno 1970
	Eumicrotremus orbis	NPac	large	Nf(3+1)	simple, bands	UW 111284, Fig. 13A
	Liparidae					
	Nectoliparis pelagicus	NPac	absent	R(3+0)	simple, bands	UW 119455, Fig. 13B
	genus *Liparis*		large	Nf(3+1)	trilobed, bands	Kido 1988; Andriashev 1998; Chernova 2006
	Liparis fucensis	eNPac	large	Nf(3+1)	trilobed, bands	"
Clade A						
	subgenus *Polypera*					
	Liparis florae	eNPac	large	Nf(3+1)	trilobed, bands	"
	L. greeni	eNPac	large	Nf(3+1)	simple, bands	"
	L. callyodon	eNPac	large	Nf(3+1)	trilobed, bands	"
	L. curilensis	wNPac	large	Nf(3+1)	trilobed, bands	"
	subgenus *Liparis*					
	L. liparis	eNAtl	large	Nf(3+1)	trilobed, bands	"
	L. bristolensis	eNPac	large	Nf(3+1)	trilobed, bands	"
	L. inquilinus	wNAtl	large	Nf(3+1)	trilobed, bands	"
	L. tunicatus	eNPac, Arc	large	Nf(3+1)	trilobed, bands	"
	L. atlanticus	wNAtl	large	Nf(3+1)	trilobed, bands	"
	L. montagui	eNAtl	large	Nf(3+1)	trilobed, bands	"
	subgenus *Lycocara*					
	L. fabricii	NAtl, Arc	large	Nf(3+1)	trilobed, bands	"
	subgenus *Careliparis*					
	L. dennyi	eNPac	large	Nf(3+1)	trilobed, bands	"

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TABLE 3. (Continued)

Lettered clade	Taxa	Distribution	Pelvic disc size	Pectoral radial formula	Tooth shape, pattern	Source
	L. gibbus	NPac, Arc	large	Nf(3+1)	trilobed, bands	UW 113092, Fig. 13C
	L. bathyarcticus	eNPac, Arc	large	Nf(3+1)	trilobed, bands	Kido 1988; Andriashev 1998; Chernova 2006
	L. agassizii	wNPac	large	Nf(3+1)	trilobed, bands	″
	L. tanakae	wNPac	large	Nf(3+1)	trilobed, bands	″
	L. chefuensis	wNPac	large	Nf(3+1)	trilobed, bands	″
	subgenus *Lyoliparis*					
	L. pulchellus	eNPac	large	Nf(3+1)	trilobed, bands	″
	L. tessellatus	wNPac	large	Nf(3+1)	trilobed, bands	″
	subgenus *Neoliparis*					
	L. mucosus	eNPac	large	Nf(3+1)	trilobed, bands	″
	***Liparis rutteri* species group**					
	L. rutteri	eNPac	large	Nf(3+1)	trilobed, bands	″
	L. punctulatus	wNPac	large	Nf(3+1)	trilobed, bands	″
	Liparis incertae sedis					
	L. cyclopus	NPac	large	Nf(3+1)	trilobed, bands	″
	L. ochotensis	NPac	large	Nf(3+1)	trilobed, bands	″
Clade B	**Clade Pseudoliparia**					
	Careproctus crozetensis	SO	large	R(1+1+1+1)	simple, bands	Duhamel *et al.* 2010
	Notoliparis kermadecensis	KT	large	R(1+1+1+1)	simple, bands	Stein 2016
	Pseudoliparis swirei	MT	small	R(1+1+1+1)	simple, bands	Gerringer *et al.* 2017a
	Notoliparis stewarti	KT	large	R(2+0+1)	simple, bands	Stein 2016
Clade C	**Clade Bathyphasmia**					
	Careproctus ovigerus	eNPac	large	Nf(3+1)	simple, bands	Orr 2012
	Careproctus georgianus	Ant	large	R(1+1+1+1)	simple	Andriashev 1998
Clade D	**Clade Pazlliparia**					
Clade E	**Clade Aenigmoliparia *incertae sedis***					

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TABLE 3. (Continued)

Lettered clade	Taxa	Distribution	Pelvic disc size	Pectoral radial formula	Tooth shape, pattern	Source
	Acantholiparis opercularis	eNPac	absent	R(1+1+1+1)	simple, bands	UW 118624, Fig. 13I
	Prognatholiparis ptychomandibularis	eNPac	large	Nf(3+1)	trilobed, bands	UW 156749, Fig. 13H
	Careproctus longifilis	eNPac	small	unknown	simple, bands	Stein 1978
	Paraliparis penicillus	eNPac	absent	R(3+1)	simple, bands	Baldwin & Orr 2010
	***Careproctus canus* species group**					
	Careproctus sp. A (Orr unpublished)	eNPac	large	unknown	trilobed, bands	Orr unpublished
	Careproctus sp. J (Orr unpublished)	eNPac	large	unknown	trilobed, bands	Orr unpublished
	Careproctus canus	eNPac	large	unknown	trilobed, bands	Kido 1985
	genus *Allocareproctus*					
	Allocareproctus jordani	NPac	large	Nf(3+1)	simple, bands	Orr & Busby 2006
	A. kallaion	NPac	large	Nf(3+1)	simple, bands	″
	A. unangas	NPac	large	Nf(3+1)	trilobed, bands	″
	A. ungak	NPac	large	Nf(3+1)	trilobed, bands	″
	A. tanix	NPac	large	Nf(3+1)	trilobed, bands	″
	subgenus *Temnocora*					
	Careproctus comus	eNPac	large	Nf(3+1)	trilobed, bands	Orr & Maslenikov 2007
	Careproctus faunus	eNPac	large	Nf(3+1)	trilobed, bands	Orr & Maslenikov 2007
	Careproctus iaachus	wNPac	large	Rf(3+1)	trilobed, bands	Kai *et al.* 2018
	Careproctus staufferi	eNPac	large	Nf(3+1)	trilobed, bands	Orr 2016
	Careproctus candidus	eNPac	large	Nf(3+1)	trilobed, bands	Orr & Maslenikov 2007
	Clade Osteocareprocta					
	Careproctus continentalis	Ant	large	R(2+0+1)	simple	Andriashev & Prirodina, 1990; Andriashev & Stein 1998; Duhamel *et al.* 2010
	Careproctus discoveryae	Ant	large	unknown	simple, bands	Duhamel & King 2007
	Careproctus longipectoralis	Ant	large	R?(2+0+1)	simple, bands	Duhamel *et al.* 2010

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TABLE 3. (Continued)

Lettered clade	Taxa	Distribution	Pelvic disc size	Pectoral radial formula	Tooth shape, pattern	Source
	Osteodiscus cascadiae	eNPac	large	R(1+0+1)	simple, bands	RBCM 15941; Kido 1988; Stein 1978
	Clade Elassodisca					
	Careproctus bowersianus	eNPac	large	R(1+1+1+1)	trilobed, bands	Orr & Maslenikov 2007
	Careproctus notosaikaiensis	wNPac	large	R(3+1)	trilobed, bands	Kai *et al.* 2011
	Careproctus cyclocephalus	wNPac	small	unknown	simple, bands	Kido 1988
	Elassodiscus caudatus	eNPac	obsolete	R(1+1+1+1)	trilobed, bands	Pitruk & Fedorov 1993
	Elassodiscus tremebundus	eNPac	obsolete	R(1+1+1+1)	trilobed, bands	Pitruk & Fedorov 1993
Clade G	**Clade Paracareprocta**					
	Lopholiparis flerxi	eNPac	large	Nf(1+1+1+1)	trilobed, bands	UW 113885, disarticulated
Clade P	***P. dactylosus* species group**					
	Paraliparis grandis	NPac	absent	unknown	simple, bands	Kido 1988
	Paraliparis dactylosus	eNPac	absent	Nf(3+1)	trilobed, bands	UW 119673
Clade O	**subgenus *Careproctus***					
	C. *gilberti* species group					
	Careproctus ostentum	eNPac	minute	unknown	simple, bands	Burke 1930
	Careproctus gilberti	eNPac	minute	unknown	simple, bands	Stein 1978
	C.* rastrinus *species group					
	Careproctus rastrinus	wNPac	small	Nf(3+1)	simple, bands	Orr *et al.* 2015
	Careproctus scottae	eNPac	small	Nf(3+1)	simple, bands	"
	Careproctus pellucidus	wNPac	small	Nf(3+1)	simple, bands	"
	Careproctus trachysoma	wNPac	small	Nf(3+1)	simple, bands	"
	Careproctus acanthodes	wNPac	small	Nf(3+1)	simple, bands	"
	C. *reinhardti* species group					
	Careproctus phasma	eNPac	small	Nf(3+1)	simple, bands	"
	Careproctus lerikimae	Arc	small	Nf(3+1)	simple, bands	"
	Careproctus reinhardti	NAtl, Arc	small	Nf(3+1)	simple, bands	Chernova 2005b
Clade N	**Clade Melanura**					
	subgenus *Allochir*					
	Careproctus colletti	NPac	small	Nf(3+1)	simple, bands	UW 117996

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TABLE 3. (Continued)

Lettered clade	Taxa	Distribution	Pelvic disc size	Pectoral radial formula	Tooth shape, pattern	Source
	Careproctus sp. (Orr unpublished)	eNPac	small	unknown	simple, bands	Orr unpublished
	Careproctus sp.	Ant	unknown	unknown	unknown	Rock *et al.* 2008
	Careproctus cypselurus	eNPac	small	Nf(3+1)	simple, bands	UW 119352
	Careproctus melanurus	NPac	small	Nf(3+1)	simple, bands	Orr unpublished
	Careproctus sp. cf. *melanurus*	NPac	small	Nf(3+1)	simple, bands	UW 119240, Fig. 13J
	Careproctus furcellus	NPac	small	unknown	simple, bands	Kido 1985
	subgenus *Caremitra*					
	Careproctus simus	NPac	small	unknown	weakly trilobed, bands	Kido 1985
	Careproctus kidoi	NAtl, Arc	small	R(3+1) or R(1–4+1)	simple, bands	Knudsen & Møller 2008
	Careproctus micropus	eNAtl	small	R(2+0+1)	simple, bands	Chernova 2005b
Clade F	**Clade Ambidisca**					
Clade H	**Clade Crystallichthyia**					
	Careproctus macrodiscus	wNPac	large	R(3+1)	simple, bands	Kido 1988; Kai, unpublished, Fig.13E
	Squaloliparis dentatus	wNPac	large	Nf(3+1)	unique, modified trilobed	Pitruk & Fedorov 1993
	Crystallichthys cyclospilus	NPac	large	Nf(3+1)	trilobed, bands	UW 47840, Fig. 13D; Kai, unpublished
	Careproctus marginatus	wNPac	large	Nf(3+1)	trilobed, bands	Kido 1988; FAKU 144616, Fig. 13F
	Careproctus roseofuscus	wNPac	large	Nf(3+1)	simple, bands	Kido 1988; FAKU 144615, Fig.13G
Clade Q	**Clade Paraliparia**					
	Lipariscus nanus	eNPac	absent	R(2+0+0)	simple, bands	Kido 1988; UW 113883
	Rhinoliparis attenuatus	eNPac	absent	Nf(1+1+1+1)	simple, bands	Stein 1978; UW 113736, Fig. 13L
	Rhinoliparis barbulifer	NPac	absent	R(1+1+1+1)	simple mixed, bands	Kido 1988
	Paraliparis pectoralis	eNPac	absent	Nf(3+1)	simple, bands	Stein 1978; UW 117515, Fig. 13N
	Paraliparis thalassobathyalis	Ant	absent	R(2+0+0)	simple, bands	Andriashev 1986
Clade K	**subgenus *Amitrichthys***					

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TABLE 3. (Continued)

Lettered clade	Taxa	Distribution	Pelvic disc size	Pectoral radial formula	Tooth shape, pattern	Source
	Paraliparis cephalus	eNPac	absent	R(1+1+1+1)	simple, bands	Stein 1978; UW 117542, Fig. 13M
	Paraliparis mento	eNPac	absent	unknown	simple, bands	Burke 1930
Clade I	***P. ulochir* species group**					
	Paraliparis wolfii	Ant	absent	R(2+0+0)	simple, bands	Duhamel & King 2007
	Paraliparis megalopus	eNPac	absent	unknown	simple, bands	Stein 1978
	Paraliparis ulochir	eNPac	absent	R(2+0+0)	simple, bands	Stein 1978; UW 150802, Fig. 13O
Clade J	***P. copei* species group**					
	Paraliparis “bathybius”	Ant	absent	unknown	unknown	ANTFI351-06
	Paraliparis “neelovi”	Ant	absent	R(3+1)	unknown	Duhamel *et al.* 2010
	Paraliparis sp.	Ant	absent	unknown	unknown	FOAG 559
	Paraliparis rosaceus	eNPac	absent	unknown	simple, uniserial to bands	Stein 1978; Busby and Cartwright 2009
	Paraliparis copei	Atl	absent	R(3+1)	simple, uniserial	Andriashev 1986
Clade L	***P. antarcticus* species group**					
	Paraliparis andriashevi	Ant	absent	R(1+1+1+1)	simple, bands	Stein and Tompkins 1989
	Paraliparis valentinae	Ant	absent	R(1+1+1+1)	simple, bands	Andriashev 1986
	Paraliparis terraenovae	Ant	absent	R(2+0+1) or R(1+0+0+1)?	absent	Stein 2012
	Rhodichthys regina	NAtl	absent	Nf(2+0+1) or (3+1) rarely 1 small fenestra	simple, bands	Andriashev & Chernova 2010 (for *R. melanocephalus*)
	Paraliparis operculosus	Ant	absent	R(1+1+1+1)	simple, bands	Andriashev 1986
	Paraliparis charcoti	Ant	absent	R(1+1+1+1+1)	simple, bands	Mattallanas 1999
	Paraliparis leobergi	Ant	absent	R(1+1+1+1)	simple, bands	Andriashev 1986
	Paraliparis macropterus	Ant	absent	R(3+1)	simple, bands	Stein 2012
	Paraliparis antarcticus	Ant	absent	R(2–3+1)	simple, bands	Andriashev 1986; Duhamel *et al.* 2010
Clade M	**subgenus *Paraliparis***					
	Paraliparis sp.	Ant	absent	unknown	unknown	ANTFI326-06

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TABLE 3. (Continued)

Lettered clade	Taxa	Distribution	Pelvic disc size	Pectoral radial formula	Tooth shape, pattern	Source
	Paraliparis mawsoni	Ant	absent	R(2–3+1)	simple, bands	Andriashev 1986; Duhamel *et al.* 2010
	Paraliparis garmani	wNAtl	absent	unknown	simple, uniserial	UW 118897
	Paraliparis paucidens	eNPac	absent	Rf(2+0+1)	simple, uniserial	Orr *et al.* 2005
	Paraliparis neelovi	Ant	absent	R(2+0+1)	simple, uniserial	Andriashev 1986; Stein 2012
	Paraliparis voroninorum	Ant	absent	R(2+0+1) or R(3+1)	simple, uniserial	Stein 2012
	Paraliparis sp.	eNPac	absent	unknown	unknown	TZFPA128, -125, -049
	Paraliparis bathybius	eNAtl, Arc	absent	R(2+0+1)	simple, uniserial	Andriashev 1986
	Paraliparis stehmani	Ant	absent	Nf(3+1) or N(3+1+1)	simple, uniserial	Andriashev 1986; Stein 2012
	Paraliparis longicaecus	Ant	absent	N(3+1)	simple, uniserial	Stein 2012
	Paraliparis camilarus	Ant	absent	Nf(3+1)	simple, uniserial	″
	Paraliparis mentikoilon	Ant	absent	R(2+0+1)	simple, uniserial	″
	Paraliparis parviradialis	Ant	absent	R(2+0+1)	simple, uniserial	″
	Paraliparis posteroporus	Ant	absent	N(3+1)	simple, uniserial	″
	Paraliparis epacrognathus	Ant	absent	N(3+1)	simple, uniserial	″
	Paraliparis plicatus	Ant	absent	R(3+1)	simple, uniserial	″
	Paraliparis ekaporus	Ant	absent	R(3+1)	simple, uniserial	″
	Paraliparis nullansa	Ant	absent	N(2+0+1)	simple, uniserial	″

2016; Gerringer *et al.* 2017a). *Notoliparis stewarti*, recovered in a sister group relationship with *P. swirei*, has only three round radials (Stein 2016). Our results suggest that species of *Notoliparis* Andriashev 1975 may be derived members of *Pseudoliparis* Andriashev 1955, as suggested by Gerringer *et al.* (2017a). Other hadal species and genera will be needed to resolve this question conclusively.

In the Bathyphasmia clade including *C. ovigerus* and *C. georgianus*, pectoral girdles are strikingly different. *Careproctus ovigerus* has a relatively plesiomorphic morphology with three deeply notched radials, with three large fenestrae, separated from the round ventral radial (Orr 2012), while *C. georgianus* has four round evenly spaced radials without fenestrae (Andriashev & Stein 1998), similar to those of the hadal and bathyal clade.

Within the Ambidisca, among members of the clade Crystallichthyia, the sister group of the disc-less Paraliparia that also includes western Pacific species of *Careproctus,* the pectoral girdle morphology is of the plesiomorphic condition of three dorsal radials with one ventral radial. In all but *C. macrodiscus*, in which all radials are round and fenestrae are absent, the dorsal radials are notched and three fenestrae are present (Figs. 13D–G).

Among clades of the Paraliparia, pectoral girdles are simplified and typically reduced. Fenestrae are rare or small when present. Exceptionally, among our included species, *Paraliparis pectoralis* (Fig. 13N) and *P. stehmanni* (Andriashev, 1986) have two small to moderately large fenestrae, and *P. camilarus, Rhodichthys melanocephalus,* and *Rhinoliparis attenuatus* (Fig. 13L) have one small fenestra. Radials are typically round and notched only in those species with fenestrae, or uncommonly notched without fenestrae as in *P. ekaporus, P. epacrognathus, P. longicaecus, P. nullansa,* and *P. posteroporus* (Stein 2012)—all members of the subgenus *Paraliparis*. The likely misidentified "*P. neelovi"* of Duhamel *et al.* (2010) placed in the *P. copei* species group has three dorsal radials, like *P. copei* (Andriashev 1986) but unlike *P. neelovi* of Stein (2012) which has only two dorsal radials, a more derived morphology congruent with this phylogeny. Among the four multiple-species clades for which pectoral-fin morphology is known, all members of the *P. copei* species group have three dorsal radials, while members of the *P. ulochir* species group all have a derived pattern with two dorsal radials (Fig. 13O). Among members of the *P. antarcticus* species group, most have four radials evenly spaced and lacking fenestrae, except for the apomorphic *P. terraenovae* and *Rhodichthys (= Paraliparis)* spp., which both have two dorsal and one ventral radials, and *P. charcoti* that uniquely among the species in our analysis has five radials (Matallanas 1999; although later described with only one or two dorsal radials and one ventral radial by Duhamel *et al.* 2010). Members of the subgenus *Paraliparis* have a range of two or three dorsal radials with one ventral radial, as well as some species having notched radials and fenestrae as noted above. In addition, *Lipariscus nanus* and *P. thalassobathyalis,* both with a highly reduced pattern of two dorsal radials and no ventral radial, and *Rhinoliparis* and *P. cephalus* (Fig. 13M)*,* with the modified simple pattern of four large and equally spaced radials, are placed uncertainly. Further resolution of the Paraliparia polytomy with additional data will likely show that reduced girdles were independently derived from modifications of the plesiomorphic state of four equally spaced radials (Andriashev 1998).

Among clades of the Aenigmoliparia within the large basal polytomy, the pectoral girdle morphology is unknown for several species. In some, a more plesiomorphic condition is evident. In *Allocareproctus* the girdle in all species is very similar to that of *Liparis* with three dorsal radials with notches and a ventral radial (Orr & Busby 2006), as is true also for *Prognatholiparis ptychomandibularis* (Fig. 13H). *Acantholiparis opercularis* (Fig. 13I) and all members of the clade Elassodisca share a simple, derived morphology of four large rounded radials, lacking notches and fenestrae, equally spaced in the basipterygium in all except *C. notosaikaiensis*; the morphology is unknown in *C. cyclocephalus*. The girdle is further derived in the clade Osteocareprocta with members having only two round dorsal radials (Kido 1988; Andriashev & Stein 1998; Duhamel *et al.* 2010). In the subgenus *Temnocora*, some differences are evident between the species: *Careproctus comus, C. faunus*, and *C. candidus* share the configuration of three dorsal and one ventral radials, one or two slightly notched with only two small fenestrae (Orr & Maslenikov 2007), while *C. staufferi* has the same number of radials that are strongly notched with three large fenestrae (Orr 2016). The derived *Paraliparis penicillus* has four small round radials in a basipterygium lacking fenestrae (Baldwin & Orr 2010), a common pattern found among members within the clade Paraliparia.

In the clade Paracareprocta, pectoral girdle morphology is known for 14 of the 21 species. *Lopholiparis flerxi* is placed as the sister of other members of clade Paracareprocta in the COI tree and as the sister of other members of the subgenus *Temnocora* in the RADseq tree. Although its specific position is uncertain, its pectoral girdle is strikingly similar to the plesiomorphic condition of the girdles of *Eumicrotremus* and *Liparis*, having large radials with large fenestrae (Orr unpublished, based on a disarticulated specimen, UW 113885). Among species of the subgenus *Careproctus*, all species have three radials in the dorsal half of the basipterygium widely separated from the ventral fourth, and at least two and usually three fenestrae (Andriashev 1986; Kido 1988; Chernova 2015; Orr *et al.* 2015). All species of the Melanura for which the pectoral girdle morphology is known—*C. melanurus*, *C. colletti, C. furcellus, C. cypselurus*, C. *micropus*, and *C. kidoi*—have a similar pattern of three dorsal and one ventral radials (Chernova 2005b; Knudsen & Møller 2008; Maslenikov *et al.* 2015; Fig. 13J). Each radial is round and the girdle either lacks all fenestrae, as in *C. micropus* and *C. kidoi (*Knudsen & Møller 2008), or has a single fenestra between the scapula and first proximal radial. *Paraliparis dactylosus* also has 3+1 round radials lacking notches and fenestrae except for the most dorsal (Fig. 13K), similar to species of Melanura.

Tooth patterns. Stein (2012) discussed the utility of morphological characters among species of *Paraliparis* and identified tooth patterns, particularly uniserial simple teeth, as possibly having phylogenetic utility. The plesiomorphic condition among liparids is simple teeth (Knudsen *et al.* 2007), as found in cyclopterids and in *Nectoliparis* (Table 3). Among species of *Liparis*, nearly all species have trilobed teeth; the exceptions being the species formerly placed in the genus *Polypera, P. greeni* and *P. shimushirae*, which have mainly simple teeth, some with small lateral lobes (Burke 1930). Outside of *Liparis*, simple teeth are present in all members of the Pseudoliparia, some members of the Bathyphasmia, all members of the Paraliparia, and several members of the Aenigmoliparia (Table 3). Among clades within the Aenigmoliparia, trilobed teeth characterize all members of subgenus *Temnocora* and most members of clade Elassodisca, as well as most members of *Allocareproctus* and species placed *incertae sedis* (Table 3). Likely unique among *Paraliparis*, *P. dactylosus* has trilobed teeth (Table 3).

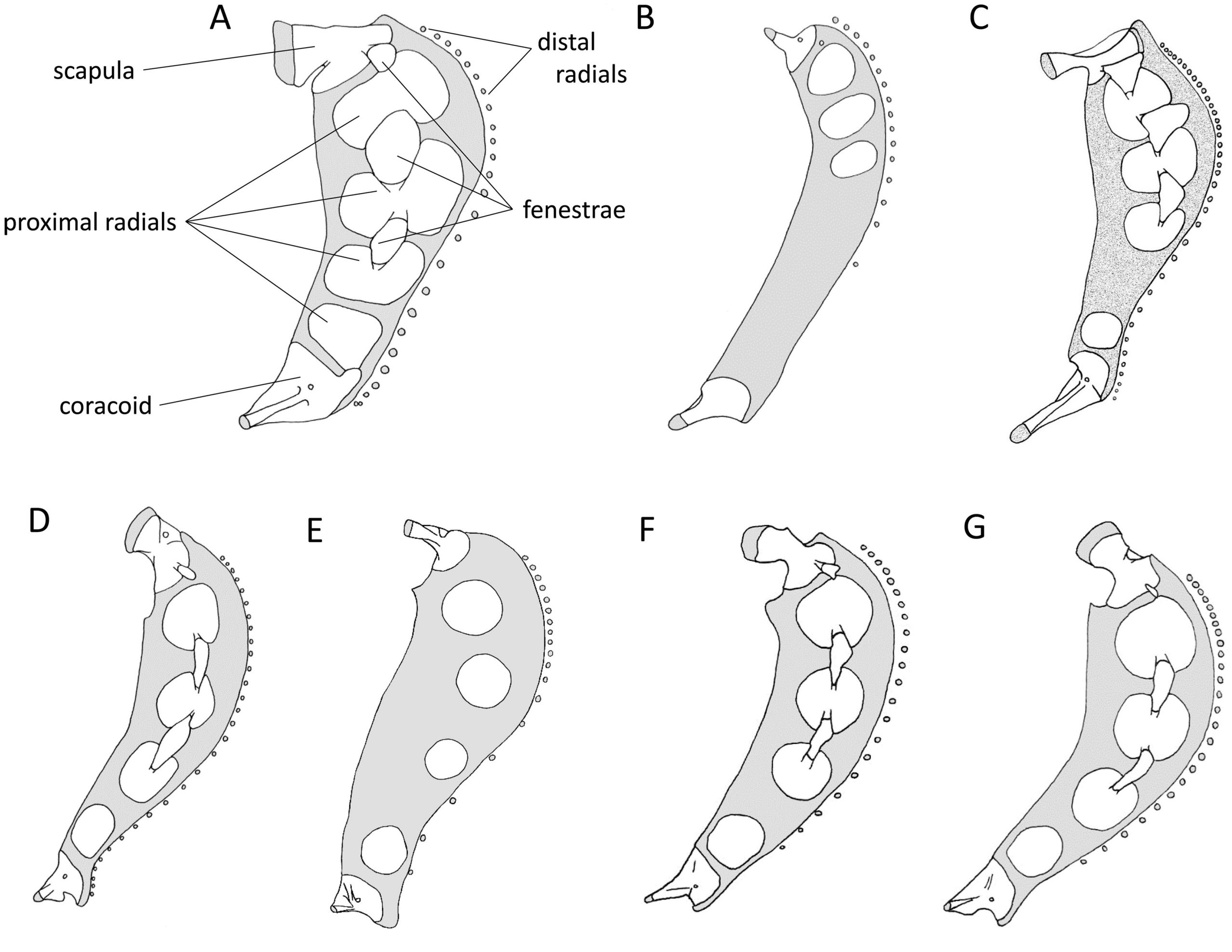

FIGURE 13 A–G. Pectoral girdles of selected species of the Cyclopteridae and Liparidae: A) *Eumicrotremus orbis*, UW 111284; B) *Nectoliparis pelagicus*, UW 119455; C) *Liparis gibbus*, UW 119092; D) *Crystallichthys cyclospilus*, UW 47840; E) *Careproctus macrodiscus*, FAKU 137835; F) *Careproctus marginatus*, FAKU 144616; G) *Careproctus roseofuscus*, FAKU 144615

In most liparids, teeth are aligned in narrow to broad oblique rows on both upper and lower jaws (Burke 1930; Table 3) and are uncommonly in a single series. Of the species Stein (2012, his table 4) identified as having uniserial teeth in the Ross Sea, all were placed within the subgenus *Paraliparis* and most within its derived clade as sister of *P. bathybius*, a North Atlantic species with uniserial teeth. Outside of this clade, species with uniserial teeth in our material are also found in the eastern North Pacific (*P. rosaceus* and *P. paucidens*; Stein 1978; Busby & Cartwright 2009; Orr *et al.* 2005), Atlantic (*P. copei*), and southeast Australia (Stein *et al.* 2001). Of these, *P. rosaceus* and *P. copei* are sister species within the *P. copei* species group, accompanied by three southern species, all presumed to have uniserial teeth and identified as *P. neelovi* (Duhamel *et al.* 2010), *Paraliparis* sp. from Australian Antarctica (FOAG559), and *P. "bathybius"* (Rock *et al.* 2008). *Paraliparis bathybius* is known only from the Arctic and North Atlantic and has numerous small teeth (Andriashev 1954), and many specimens of *P. bathybius* from the North Atlantic were recovered as the sister group of *Paraliparis* from the Ross Sea with uniserial teeth (Fig. 11, Clade M). In contrast, *P.* "*bathybius*" from the Antarctic was included in a clade of species with uniserial teeth from the North Atlantic, North Pacific, and Antarctic (*P. copei*, *P. rosaceus*, and *P. neelovi*, respectively; Fig. 11, Clade J).

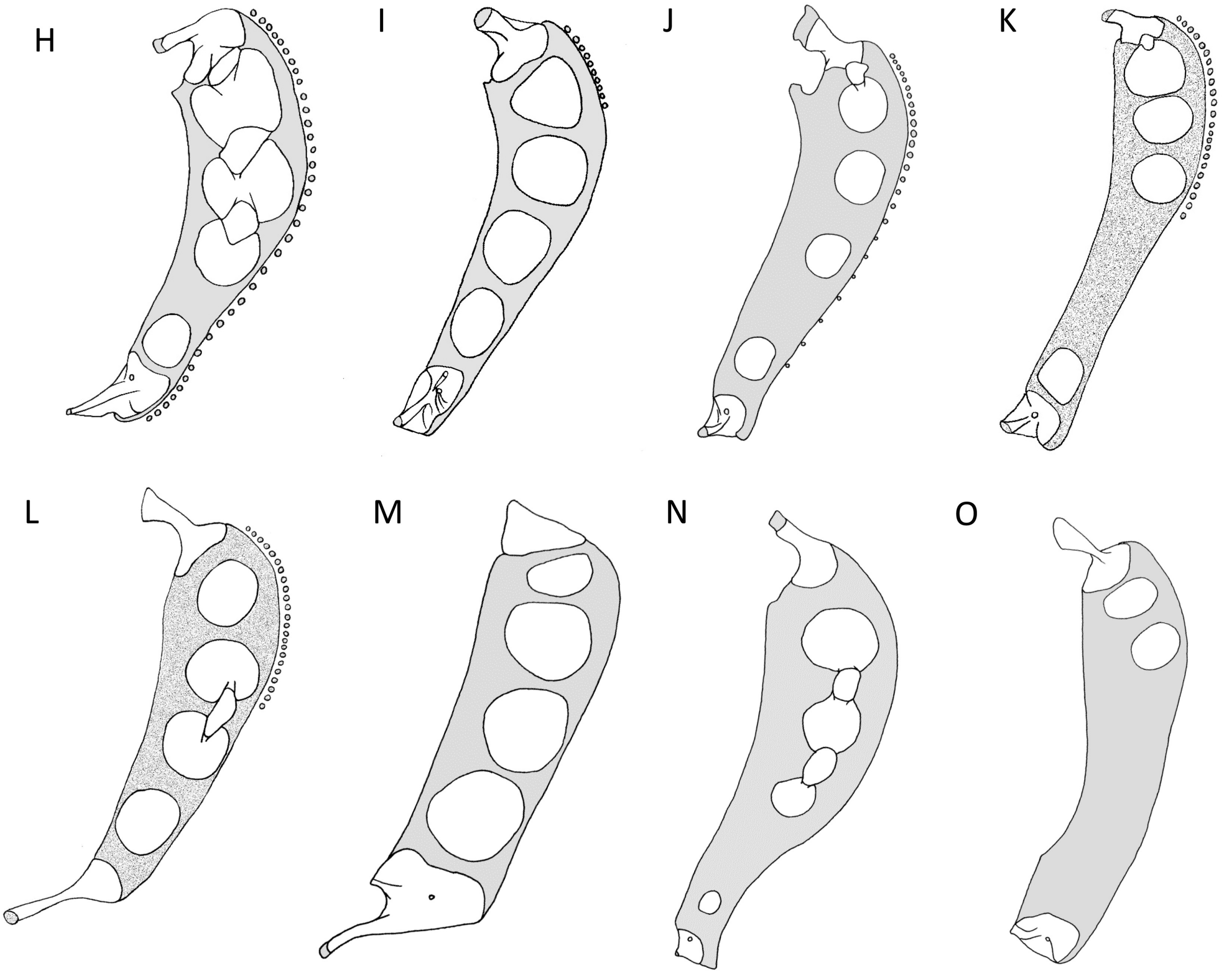

FIGURE 13 H–O. Pectoral girdles of selected species of the Cyclopteridae and Liparidae: H) *Prognatholiparis ptychomandibularis*, UW 156749; I) *Acantholiparis opercularis*, UW 118624; J) *Careproctus* sp. cf. *melanurus*, UW 119240; K) *Paraliparis dactylosus*, UW 116232; L) *Rhinoliparis attenuatus*, UW 113736; M) *P. cephalus*, UW 117527; N) *Paraliparis pectoralis*, UW 117515; O) *P. ulochir*, UW 150802.

Additionally, a species of the eastern North Pacific identified as *Paraliparis* sp. (Steinke *et al.* 2009) with similar morphology to *P. rosaceus* is clearly distinct in COI data (Steinke *et al.* 2009). It was placed within the subgenus *Paraliparis*, as sister of the southern species *P. voroninorum* and *P. neelovi* and near *P. paucidens*, all with uniserial teeth. Exceptionally within this clade is *P. mawsoni*, a species with the plesiomorphic condition of tooth bands (Andriashev 1986), placed uncertainly in the polytomy near the base of the clade (Fig. 11, clade M).

Postorbital cephalic pore. Chernova (2005b) noted for the subgenus *Careproctus* the absence of the postorbital pore in North Atlantic and Arctic species and its presence in Southern Hemisphere species. Among members of the subgenus *Careproctus* in our analysis, Orr *et al.* (2015) suggested that two clades would form the *Careproctus rastrinus* complex of North Pacific and Arctic species based on the presence or absence of the postorbital pore and suggested that *C. acanthodes* may be more distantly related. Our results support the presence of two clades, one with *C. phasma* and *C. lerikimae* closely related to *C. reinhardti* and all lacking the postorbital pore; the other with the five remaining species, including *C. acanthodes*, with postorbital pore present. Members of the third major clade of the subgenus, *C. gilberti* and *C. ostentum*, have a postorbital pore.

Zoogeography and ecology

Distributions of species in trees. The sister groups of all other liparids are species from the North Pacific, including the highly apomorphic *Nectoliparis* and most species of the plesiomorphic *Liparis*, both genera that are limited to the Northern Hemisphere. Among species of *Liparis*, North Pacific species form the sister groups of North Atlantic species. The North Atlantic species *L. atlanticus, L. inquilinus, L. liparis*, and *L. montagui* were recovered in a derived clade among the Arctic species *L. fabricii, L. tunicatus*, and *L. bristolensis*. Among western Pacific species, *L. curilensis* was placed within a clade of the eastern North Pacific species *L. callyodon, L. florae,* and *L. greeni*; *L. punctulatus* with *L. rutteri*; and *L. tessellatus* with *L. pulchellus*, while a clade of *L. agassizii, L. tanakae,* and *L. chefuensis* was the sister of a poorly supported clade of the eastern North Pacific and Arctic species *L. dennyi*, *L. gibbus,* and *L. bathyarcticus*.

Although the relationships among more derived clades are uncertain, the mix of zoogeographic regions represented within most clades indicates multiple invasions of the Southern Ocean from the South Pacific, and the North Atlantic from the Southern Ocean and the North Pacific. Southern species of *Careproctus* were found within four clades placed in several positions among North Pacific or deep-water species.

Among species of the deep-water clade Pseudoliparia, the southern abyssal species *C. crozetensis* is the sister of the deep abyssal and hadal genera *Notoliparis* and *Pseudoliparis* from the Mariana, Kermadec, and Japan trenches. Species of *Notoliparis* are known from the southern Kermadec, Macquarie-Hjort, South Orkney, and Peru-Chile trenches (Andriashev 1975, 1978; Stein, 2005; Stein 2016; Linley *et al.* 2016); *Pseudoliparis* had been known only from the northern Japan and Kuril-Kamchatka trenches (Andriashev 1955, Andriashev & Pitruk 1993) until the recent description of *P. swirei* from the southern Mariana Trench (Gerringer *et al.* 2017a).

In the Bathyphasmia, the southern species *C. georgianus* was sister of the eastern North Pacific *C. ovigerus*. Within the large polytomy of the clade Aenigmoliparia, three southern species—*C. continentalis, C. discoveryae*, and *C. longipectoralis*—formed a clade (subgenus *Careproctula*) with the northern *Osteodiscus cascadiae*. A clade of one or two southern species (both identified as *Careproctus* sp.) was sister of an undescribed northern species (Orr, unpublished) within the subgenus *Allochir*.

The Crystallichthyia, a clade of northern species of *Careproctus* and *Crystallichthys cyclospilus* that are all exclusively from the western North Pacific except for *Crystallichthys*, was the sister group of the clade Paraliparia, the large clade of species and genera that lack a pelvic disc. Although its position was poorly supported in the COI tree, in the RADseq tree it is highly supported. Thus, the derivation of the disc-less clade from the North Pacific is likely.

In contrast with the scattered southern species of *Careproctus*, all southern species of *Paraliparis* were placed within the Paraliparia. Within this clade, southern species were spread over at least four internal clades, plus the single *P. thalassobathyalis*. Three of these clades also included both North Atlantic and North Pacific species; one included a single North Atlantic species. Three other northern species of *Paraliparis*—*P. dactylosus*, *P. grandis*, and *P. penicillus*—were placed among northern species of *Careproctus* within the Aenigmoliparia.

Zoogeography. The Liparidae likely arose in the North Pacific in the late Eocene–early Miocene about 45 to 25 mya (Stein *et al.* 2001; Near *et al.* 2012; results of Shen *et al.* 2017 who estimated 28–10 mya were inappropriately calibrated by a fossil of the derived recent species *Gasterosteus aculeatus* from 13.3 to 13.0 mya), with a burst of rapid speciation that began at about 30 mya (Rabosky *et al.* 2018). Other than a single questionable fossil from the Oligo-Miocene of Belgium (Chernova *et al.* 2004), fossils of liparids are unknown (Andriashev & Stein 1998). Our results indicate that liparids were derived from a shallow-water ancestor in the North Pacific, likely the eastern North Pacific. The highly apomorphic pelagic species *Nectoliparis pelagicus* of the North Pacific diverged early. One, possibly two, lineages of *Liparis* diversified into shallow waters. Following this split, a lineage diverged into deep waters and from this deep-water group all other liparids likely evolved, based on the deep-water group's sister group position to most other liparids and morphological evidence from the plesiomorphic pectoral girdle, among other characters (Andriashev 1978, 1998; Stein 2016). Deep-water groups further diversified throughout the northern and southern Pacific into the relatively cooler shallow waters at the poles, persisting and further diversifying in colder waters as the Miocene climate generally warmed 17–15 mya. Beginning no earlier than about 41 mya, via the opening of the Drake Passage in the Miocene about 41–20 mya (Scher & Martin 2006), liparids dispersed into the South Atlantic in multiple invasions through the Southern Ocean and around Antarctica (Andriashev 1986; Andriashev & Stein 1998; Stein *et al.* 2001). Eastern South Pacific species may also have dispersed into Australian waters (Stein *et al.* 2001).

Clades from both the North Pacific and Southern Hemisphere likely invaded the North Atlantic more recently. *Paraliparis* and perhaps *Careproctus* dispersed north out of the South Atlantic and Southern Ocean (Andriashev 1991, 1997; Andriashev & Stein 1998; Chernova 1999), similar to "ambiguous" patterns evident within the macrourid genus *Coryphaenoides* (Gaither *et al.* 2016). The Antarctic Intermediate Water Mass may have provided a mechanism for this dispersal north (Koslow *et al.* 1994; Stein *et al.* 2001; Probert 2017). Eastern North Pacific species are closely related to Antarctic species in some clades (e.g., Bathyphasmia, *Allochir*, subgenus *Paraliparis*) and members of these clades of bathyal species may have also dispersed across the Central American Seaway over the open Panamanian isthmus (Balushkin 2012), where at its southern extent a complete interchange of Atlantic and Pacific waters at bathyal depths was occurring before 20 mya until 12 mya at the early collision of the American plates (Coates *et al.* 2004). This region shallowed to 200 m or less at 11–10 mya (Sepulchre *et al.* 2014; Montes *et al.* 2015) before its complete closure in the Pliocene 2.76–2.54 mya (Sepulchre *et al.* 2014). Other interpretations visualized a dispersal of North Pacific species along the coast of South America and into the Antarctic and South Atlantic (Andriashev 1987, 1993; Balushkin & Voskoboinikova 2008), as well as to Australia (Stein *et al.* 2001). Examination of molecular and other data of uncommon Pacific South American species will be important to better understand these distributional patterns, especially their relationship to Australian species (Stein *et al.* 2001).

To the north, shallow-water species of *Liparis* and *Careproctus* were also able to invade the North Atlantic since about 7.4–4.8 mya in the upper Miocene, and perhaps earlier in the Middle Miocene during two periods 17–16 mya and 12–11 mya (Sher 1999), across the open but shallow Bering Strait, which has likely never been deeper than 50 m (Marincovich and Gladenkov 2001). This shallow water excluded deep-water liparid genera such as *Paraliparis* from dispersing to the Arctic and North Atlantic via this route (Andriashev 1986, 1991). Movements from the North Pacific into the Arctic and North Atlantic are well-established in the mollusk fossil record (Marincovich & Gladenkov 1999) and through molecular and phylogenetic analyses of many other fish families (e.g., Cottidae: Knope 2013; Scorpaenidae, Sebastinae: Hyde & Vetter 2007; Zoarcidae: Anderson 1994; Møller & Gravlund 2003), although some families, including the cyclopterids (Ueno 1970) and gadids (Coulson *et al.* 2006; Carr & Marshall 2008; Roa-Varón & Orti 2009), may have originated in the Atlantic and diverged into the Pacific.

Reproductive parasitism. All liparid eggs identified to species taken from inside crabs in the Northern Hemisphere have been of species in the Clade Melanura. Gardner *et al.* (2016) previously identified eggs of *Careproctus melanurus*, *C. colletti*, *C. furcellus*, and *C. simus* taken from Golden and Scarlet King Crabs (Lithodidae: *Lithodes aequispinus* and *L. couesi*). Two sequences from GenBank were from eggs deposited in Blue King Crabs (*Paralithodes platypus*; Yanagimoto 2015) and based on our data could be identified as eggs of species of the subgenus *Allochir*: one sequence (LC002654.1) was identical to sequence data of *C. furcellus*; the other (LC002656.1) was identical to sequence data of *C. colletti*. Although Yanagimoto (2015) conducted a GenBank BLAST analysis to identify the eggs, without success, and discounted *C. furcellus* as an identification, sequences labeled as *C. furcellus* in GenBank at the time were based on misidentified specimens of *C. cypselurus* (Appendix Tables 1 and 2), and data for *C. colletti* were not yet publicly available. Yanagimoto's (2015) report is the only published documentation of reproductive parasitism in Blue King Crabs. Other instances of parasitism have been reported from the Southern Hemisphere (citations in Gardner *et al.* 2016) but the only southern species known to deposit eggs in crabs are *C. albescens* (= *C. griseldea*) and *C. falklandicus* (Balbontin *et al.* 1979; Melville-Smith & Louw 1987; Andriashev & Prirodina 1990; Chernova 2014) and neither were available for our analysis.

In contrast to the eggs of *Liparis*, which are commonly found in shallow waters, identified egg masses of deep-water snailfishes are rare and few have been reported outside of crabs (e.g., *C. rastrinus*: Chernova 1992; *Al-*

locareproctus unangas: Busby *et al.* 2006; *Squaloliparis dentatus*: Poltev & Steksova 2010; *C. fulvus*: Chernova 2014; *Elassodiscus tremebundus, Paraliparis rosaceus*: Overdick *et al.* 2014; Gardner *et al.* 2016). Except for eggs identified as *Careproctus* sp. (as either *C. colletti* or *C. melanurus*) that were found in trawls with lithodid crabs (Overdick *et al.* 2014), all species depositing eggs outside crabs, and for which we had molecular data, were outside the Melanura clade. *Careproctus fulvus*, for which we did not have molecular data and which deposits eggs in sponges, is a member of the subgenus *Careproctus* (Chernova 2014).

Conclusions

Our phylogenetic analysis of nearly a third of the species and over half the genera of the Liparidae from both Southern and Northern hemispheres has provided useful insights to continue to build on our understanding of the evolution of the family. However, the relationships of this diverse family of more than 400 species and 32 genera remain in large part unclear. Our results from a single-gene analysis of a wide range of taxa, bolstered by the data-rich and largely congruent genome-wide analysis of North Pacific species, have provided confidence in many nodes of the phylogeny, but several important transitions in liparid evolution remain unresolved.

TABLE 4. Species of Liparidae and outgroups used to construct a RADseq phylogenetic tree, listed as clades and species appear in the tree. Letter designations of clades and taxonomic names are referenced in the text and in Figures 8–12. Species in bold were placed in an alternative position in the COI tree.

Lettered clade	Rank	Species	Position in COI tree
	Cyclopteridae		
		Eumicrotremus orbis	
	Liparidae		
	genus *Liparis*	*Nectoliparis pelagicus*	
Clade Q			
	subgenus *Polypera*		
		Liparis florae	
	subgenus *Careliparis*		
		L. gibbus	
	Liparis rutteri species group		
		L. rutteri	
Clade D	Clade Pazlliparia		
Clade E	Clade Aenigmoliparia		
		Prognatholiparis ptychomandibularis	Aenigmoliparia *incertae sedis*
	Clade Elassodisca		
		Paraliparis penicillus	Aenigmoliparia *incertae sedis*
		Elassodiscus caudatus	
	unnamed clade		
		Allocareproctus* spp. *(A. jordani*, *A. ungak)	Aenigmoliparia *incertae sedis*
	subgenus *Temnocora*		
		Lopholiparis flerxi	Paracareprocta
		Careproctus comus	
		Careproctus faunus	
		Careproctus staufferi	
		Careproctus candidus	

......continued on the next page

TABLE 4. (Continued)

Lettered clade	Rank	Species	Position in COI tree
Clade G	Clade Paracareprocta		
Clade P	*P. dactylosus* species group		
		Paraliparis dactylosus	
Clade O	subgenus *Careproctus*		
	C. *gilberti* species group		
		Careproctus gilberti	
	C. *rastrinus* species group		
		Careproctus scottae	
	C. *reinhardti* species group		
		Careproctus phasma	
Clade N	Clade Melanura		
	subgenus *Allochir*		
		Careproctus cypselurus	
		Careproctus melanurus	
		Careproctus sp. cf. *melanurus*	
		Careproctus furcellus	
Clade F	Clade Ambidisca		
Clade H	Clade Crystallichthyia		
		Crystallichthys cyclospilus	
Clade Q	Clade Paraliparia		
		Lipariscus nanus	
		Rhinoliparis attenuatus	
Clade I	*P. ulochir* species group		
		Paraliparis ulochir	

Although COI has become a widely accepted means for identifying species and describing differences among them, RADseq data contains an order of magnitude more sequence data. It is not unprecedented for RADseq trees and COI trees to differ. In some cases, RADseq trees have been considered an improvement (Razkin *et al.* 2016), the RADseq data providing resolved trees for cases that mtDNA (and nuclear DNA) could not (Diaz-Arce *et al.* 2016), as in the case with liparids. While other work has concluded that reconstruction of recently diverged lineages may still be difficult with RADseq data in some cases (Suchan *et al.* 2017), this is unlikely to be the case for the more distantly related species of our liparid dataset.

While our analysis of COI sequence data successfully resolved many shallow and deep nodes of the global liparid tree, it may be an inadequate source of data for this group because of multiple superimposed nucleotide substitutions in deep phylogenies. Our ability to select loci containing an appropriate level of variation with the RADseq analysis provided a completely resolved tree with high support for a much smaller group of species from the eastern North Pacific—expanding taxon sampling for additional RADseq analyses will be an important avenue for further research. These molecular phylogenies provide a skeleton of proposed relationships that will allow detailed phylogenetically based morphological assessments, leading to taxonomic and nomenclatural clarity.

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APPENDIX TABLE 1. Species, catalog numbers, GenBank accession numbers, BOLD sequence ID numbers, and original identifications in BOLD or GenBank for all COI sequences used in phylogenetic analysis. Sequences are unique for each individual among species. Catalog numbers refer to formal catalog numbers, BOLD's "Museum ID," or "Sample ID" when "Museum ID" was blank. Original identification refers to the identification in BOLD or Genbank as of 31 March 2018 and is listed when it differs from ours in this study. Institutional codes follow Sabaj (2016), with the following additions: AAD = Australian Antarctic Division, BU = Bangor University, DU = Dalhousie University. N/A = Not available. Catalog numbers with asterisks represent specimens newly sequenced for this study.

Species	Catalog number	GenBank Accession	BOLD Sequence	Original Identification
Cyclopterus lumpus	ZMUB F1	AM498313	GBGC5052-08	
Eumicrotremus orbis	UW 119780-1	AB917653	GBGCA12719-15	
Acantholiparis opercularis	RBCM DFO193	FJ164243	TZFPA129-06	
Allocareproctus jordani	UW 113687*	MH882479	SGJWO075-18	
Allocareproctus kallaion	UW 113692*	MH630269	SGJWO003-18	
Allocareproctus tanix	UW 150813*	MH630270	SGJWO002-18	
Allocareproctus unangas	UW 117204*	MH630274	SGJWO004-18	
Allocareproctus unangas	UW 117210*	MH630272	SGJWO005-18	
Allocareproctus unangas	UW 150790*	MH630273	SGJWO006-18	
Allocareproctus unangas	UW 150804*	MH630271	SGJWO007-18	
Allocareproctus ungak	UW 111933*	MH630277	SGJWO009-18	
Allocareproctus ungak	UW 111938*	MH630276	SGJWO010-18	
Allocareproctus ungak	UW 155938*	MH882480	SGJWO076-18	
Careproctus acanthodes	NMCI P1910	LC380018	N/A	
Careproctus bowersianus	UW 119291*	MH630278	SGJWO046-18	
Careproctus candidus	UW 156095*	MH630341	SGJWO067-18	
Careproctus candidus	UW 156094*	MH630340	SGJWO068-18	
Careproctus canus	UW 116033*	MH630279	SGJWO074-18	
Careproctus colletti	FAKU 132433	LC337252	N/A	
Careproctus colletti	FAKU 200528	LC337255	N/A	
Careproctus colletti	UW 117996*	MH630282	SGJWO052-18	
Careproctus colletti	UW 118639*	MH630283	SGJWO051-18	
Careproctus colletti	UW 118684*	MH630284	SGJWO049-18	
Careproctus colletti	UW 118687*	MH630281	SGJWO053-18	
Careproctus colletti	UW 119297*	MH630280	SGJWO050-18	
Careproctus colletti	UW 150595	JQ354031	FMV577-11	*Careproctus* sp.
Careproctus comus	UW 119197*	MH630285	SGJWO060-18	

......*continued on the next page*

APPENDIX TABLE 1. (Continued)

Species	Catalog number	GenBank Accession	BOLD Sequence	Original Identification
Careproctus continentalis	MNHN 2008-2594	HQ712898	EATF525-10	
Careproctus crozetensis	MNHN 2006-1231	N/A	FKCI023-10	
Careproctus cyclocephalus	FAKU 200525	LC337280	N/A	
Careproctus cypselurus	RBCM 006-040-009	FJ164443	TZFPB413-05	*Careproctus furcellus*
Careproctus cypselurus	UW 113569	JQ354028	FMV400-09	
Careproctus cypselurus	UW 116030*	MH630286	SGJWO055-18	
Careproctus cypselurus	UW 116035*	MH630287	SGJWO056-18	
Careproctus cypselurus	UW 117988*	MH630288	SGJWO054-18	
Careproctus cypselurus	UW 150587	JQ354032	FMV573-11	
Careproctus discoveryae	MNHN 2006-1232	N/A	FKCI020-10	
Careproctus faunus	UW 117078*	MH630289	SGJWO061-18	
Careproctus furcellus	FAKU 200774*	LC380015	N/A	
Careproctus furcellus	UW 113817*	MH630290	SGJWO058-18	
Careproctus furcellus	UW 113889*	MH630291	SGJWO057-18	
Careproctus furcellus	UW 150838*	MH630292	SGJWO059-18	
Careproctus georgianus	BU JRAS06-350	EU326327	ANTFI350-06	
Careproctus gilberti	UW 119374*	MH882481	SGJWO077-18	
Careproctus gilberti	UW 151309-02*	MH630294	SGJWO063-18	
Careproctus gilberti	UW 115165	JQ354029	FMV424-09	
Careproctus iacchus	FAKU 201379	LC349295	N/A	
Careproctus kidoi	ZMUC 5893	N/A	GLF269-16	
Careproctus lerikimae	UAM PSR 1956	N/A	DSFAL768-11	*Careproctus reinhardti*
Careproctus lerikimae	UAM 6317-01	N/A	DSFIB092-11	*Careproctus reinhardti*
Careproctus longifilis	RBCM TagG5026	FJ164428	TZFPA103-06	*Careproctus attenuatus*
Careproctus longipectoralis	MNHN 2008-2592	HQ712900	EATF504-10	
Careproctus macrodiscus	FAKU 200526*	LC380008	N/A	
Careproctus marginatus	FAKU 144616	LC337285	N/A	
Careproctus melanurus	UW 115145	JQ354030	FMV419-09	
Careproctus melanurus	UW 150589*	MH630295	SGJWO048-18	
Careproctus sp. cf. *melanurus*	UW 118920*	MH630296	SGJWO047-18	
Careproctus micropus	TMU AL-9299	N/A	DSFNG033-11	

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APPENDIX TABLE 1. (Continued)

Species	Catalog number	GenBank Accession	BOLD Sequence	Original Identification
Careproctus micropus	ZMUB GLF164	N/A	GLF164-14	
Careproctus micropus	ZMUB 22794	N/A	NBMF054-15	
Careproctus notosaikaiensis	FAKU 144959*	LC380012	N/A	
Careproctus ostentum	UW 150925	KU053754	GBMIN119758-17	
Careproctus ovigerus	RBCM TagR5831	FJ164449	TZFPA097-06	*Careproctus georgianus*
Careproctus pellucidus	FAKU 132190*	LC380014	N/A	
Careproctus phasma	UW 117941*	MH630297	SGJWO070-18	
Careproctus phasma	UW 154442	KU053660	SGJWO073-18	
Careproctus rastrinus	FAKU 200415*	LC380017	N/A	
Careproctus reinhardti	UAM PSR 2385-01	N/A	DSFIB356-13	
Careproctus reinhardti	ZMUB 2013-83	N/A	DSFIB538-14	
Careproctus reinhardti	DU SC054	KC015259	SCFAD145-09	
Careproctus reinhardti	ZMUB Vp2013-74	N/A	DSFIB532-14	
Careproctus roseofuscus	FAKU 200516*	LC379999	N/A	
Careproctus roseofuscus	FAKU 144615	LC337284	N/A	
Careproctus scottae	UW 117938-03	KU053659	N/A	
Careproctus scottae	UW 117935-1	KU053656	SGJWO072-18	
Careproctus scottae	UW 117935-2	KU053657	SGJWO071-18	
Careproctus simus	UW 116231*	MH63030	SGJWO064-18	
Careproctus simus	FAKU 201401*	LC380005	N/A	
Careproctus n. sp.	RBCM 15936	FJ164432	TZFPA113-06	*Careproctus canus*
Careproctus sp.	BU JRAS06-296	EU326409	ANTFI296-06	
Careproctus sp.	BU JRAS06-305	EU326326	ANTFI305-06	
Careproctus sp.	UW 49434*	MH630302	SGJWO065-18	
Careproctus sp.	UW 155710*	MH630303	SGJWO066-18	
Careproctus staufferi	UW 155711*	MH630304	SGJWO069-18	
Careproctus trachysoma	FAKU 131557*	LC380016	N/A	
Crystallichthys cyclospilus	UW 117245*	MH630306	SGJWO016-18	
Crystallichthys cyclospilus	UW 151026*	MH630305	SGJWO017-18	
Elassodiscus caudatus	UW 49350-4*	MH630307	SGJWO026-18	
Elassodiscus caudatus	UW 151500	KF918871	FMV698-13	

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APPENDIX TABLE 1. (Continued)

Species	Catalog number	GenBank Accession	BOLD Sequence	Original Identification
Elassodiscus sp. cf. *caudatus*	UW 48021*	MH630308	SGJWO024-18	
Elassodiscus sp. cf. *caudatus*	UW 113896/SIO 06-29	GU440308	MFC394-08	*Elassodiscus caudatus*
Elassodiscus sp. cf. *caudatus*	UW 117993	KU053760	GBMIN119759-17	*Elassodiscus caudatus*
Elassodiscus sp. cf. *caudatus*	UW 119309*	MH882482	SGJWO078-18	
Elassodiscus tremebundus	UW 119440*	MH630310	SGJWO028-18	
Elassodiscus tremebundus	UW 119620*	MH882483	SGJWO079-18	
Liparis agassizii	NSMK PI-000089	HM180655	ANGBF891-12	
Liparis atlanticus	ARC 26210	KC015556	SCFAC642-06	
Liparis bathyarcticus	UW 119176	N/A	DSFIB074-11	
Liparis bathyarcticus	UAM 5996	HQ712565	DSFAL441-08	
Liparis bathyarcticus	UAM 6441	N/A	DSFAL762-11	
Liparis bathyarcticus	ZMUB 22827	N/A	NBMF036-15	
Liparis bathyarcticus	ARC 25596	KC015565	SCFAC570-06	
Liparis bathyarcticus	TMU AL-9234	N/A	DSFNG070-11	
Liparis bathyarcticus	UAM 5506	HQ712569	DSFAL551-09	
Liparis bathyarcticus	UAM 6319	N/A	DSFIB091-11	
Liparis bathyarcticus	ZMUB 19736	N/A	NBMF120-16	
Liparis bristolensis	UW 152009	N/A	DSFIB657-15	
Liparis callyodon	CAS 230304	HQ712548	DSFAL422-08	
Liparis chefuensis	IOCASFY AI001	GU586125	ANGBF8479	
Liparis curilensis	UW 44503-01	KM019338	SDP132012-14	
Liparis cyclopus	UW 151759*	MH630317	SGJWO011-18	
Liparis dennyi	UW 119995	JQ354189	FMV530-11	*Liparis* sp.
Liparis dennyi	UW 119997	JQ354187	FMV532-11	*Liparis* sp.
Liparis dennyi	UW 155549*	MH630318	SGJWO012-18	
Liparis dennyi	UW 112144	JQ354179	FMV231-08	
Liparis dennyi	UW 48801/SIO 05-195	JQ354178	FMV134-08/MFC353-08	
Liparis dennyi	UW 155675*	MH630319	SGJWO014-18	
Liparis dennyi	UW 119994	JQ354188	FMV529-11	*Liparis* sp.
Liparis fabricii	ZMUB Vp2013-66	N/A	DSFIB528-14	
Liparis fabricii	ZMUB 10313	N/A	DSFIB751-16	

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APPENDIX TABLE 1. (Continued)

Species	Catalog number	GenBank Accession	BOLD Sequence	Original Identification
Liparis fabricii	ARC 25648	KC015557	SCFAC361-06	
Liparis fabricii	CMN 2002-00292	N/A	CMNAF020-06	
Liparis fabricii	UAM 5510	HQ712553	DSFAL556-09	
Liparis fabricii	ZIN 54853	HM421735	DSFAL592-09	
Liparis fabricii	ZMUB 20983	N/A	DSFNG060-11	
Liparis florae	SIO 04-103	GU440375	MFC245-08	
Liparis fucensis	UW 112146	JQ354181	FMV399-08	
Liparis fucensis	UW 118573*	MH630320	SGJWO013-18	
Liparis fucensis	UW 151088	KF918880	FMV664-13	
Liparis gibbus	UW 119159	N/A	DSFIB070-11	
Liparis gibbus	CAS 230191	HQ712561	DSFAL266-07	
Liparis gibbus	CAS 228557	HM421805	DSFAL667-09	
Liparis gibbus	CAS 230119	HQ712556	DSFAL183-07	
Liparis greeni	UW 49011	JQ354180	FMV169-08	*Liparis florae*
Liparis inquilinus	ARC 25688	KC015567	SCFAC207-06	
Liparis liparis	MT 2133	KJ204971	BNSF204-11	
Liparis liparis	MT 2136	KJ204975	BNSF207-11	
Liparis liparis	MT 2137	KJ204969	BNSF208-11	
Liparis liparis	MT 2915	KJ204967	BNSF494-12	
Liparis liparis	MT 2627	KJ204965	BNSF573-12	
Liparis liparis	MT 4201	KJ204974	BNSF1006-12	
Liparis liparis	MT 4202	KJ204976	BNSF1007-12	
Liparis montagui	NRM 53905	KJ128532	GBGCA8529-15	
Liparis mucosus	SIO 00-166	GU440377	MFC044-08	
Liparis ochotensis	UAM PSR 2135-01	N/A	DSFIB175-12	
Liparis ochotensis	UAM PSR 2135-02	N/A	DSFIB176-12	
Liparis pulchellus	RBCM NEOCAL07-0036	FJ164724	TZFPA183-07	
Liparis pulchellus	UW 112760	JQ354184	FMV249-08	
Liparis pulchellus	RBCM NEOCAL07-0039	FJ164721	TZFPA186-07	
Liparis pulchellus	UW 110220/SIO 05-200	GU440378	FMV218-08/MFC354-08	
Liparis pulchellus	RBCM NEOCAL07-0032	FJ164725	TZFPA179-07	

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APPENDIX TABLE 1. (Continued)

Species	Catalog number	GenBank Accession	BOLD Sequence	Original Identification
Liparis pulchellus	UW 115849*	MH630321	SGJWO015-18	
Liparis punctulatus	FAKU 132898*	LC380002	N/A	
Liparis rutteri	UW 112756	JQ354186	FMV245-08	
Liparis sp.	MCZ 167771	KF930054	UKBK201-08	
Liparis tanakae	IOCASFY Lt001	GU357851	ANGBF8481-12	
Liparis tanakae	KUSA 1	JF952785	ABJF123-06	
Liparis tanakae	FAKU 135637*	LC380001	N/A	
Liparis tessellatus	FAKU 99774*	LC380003	N/A	
Liparis tunicatus	CAS 230157	HQ712576	DSFAL236-07	
Liparis tunicatus	CAS 230348-02	HQ712580	DSFAL339-07	
Liparis tunicatus	UAM 5571	HM421767	DSFAL629	
Liparis tunicatus	UAM 6391-02	N/A	DSFAL707-11	
Liparis tunicatus	UW 150654	N/A	DSFIB587-14	
Lipariscus nanus	UAM PSR 2144-01	N/A	DSFIB190-12	
Lipariscus nanus	UAM PSR 2144-02	N/A	DSFIB191-12	
Lipariscus nanus	UAM PSR 2144-03	N/A	DSFIB192-12	
Lipariscus nanus	UW 116038/SIO 06-32	GU440371	MFC400-08	
Lipariscus nanus	RBCM 0738-A07	FJ164719	TZFPB861-08	
Lipariscus nanus	UW 49440*	MH630313	SGJWO020-18	
Lipariscus nanus	UW 49441*	MH630315	SGJWO021-18	
Lipariscus nanus	UW 117239-01*	MH630314	SGJWO019-18	
Lipariscus nanus	UW 119179*	MH630316	SGJWO022-18	
Lipariscus nanus	UW 154634-5*	MH630312	SGJWO023-18	
Lipariscus nanus	UW 152476	KU053763	GBMIN119761-17	
Lopholiparis flerxi	UW 119829*	MH630322	SGJWO044-18	
Nectoliparis pelagicus	RBCM NEOCAL07-0049	FJ164905	TZFPA196-07	
Nectoliparis pelagicus	RBCM NEOCAL07-0046	FJ164907	TZFPA193-07	
Nectoliparis pelagicus	RBCM NEOCAL07-0047	FJ164906	TZFPA194-07	
Nectoliparis pelagicus	UW 117244-03*	MH630323	SGJWO018-18	
Notoliparis kermadecensis	HADES 100340	KY659176	N/A	
Notoliparis stewarti	HADES 100344	KY659177	N/A	

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APPENDIX TABLE 1. (Continued)

Species	Catalog number	GenBank Accession	BOLD Sequence	Original Identification
Osteodiscus cascadiae	RBCM 15941	FJ164433	TZFPB101-06	*Careproctus cypselurus*
Osteodiscus cascadiae	RBCM TagG5005	FJ164436	TZFPB133-06	*Careproctus cypselurus*
Osteodiscus cascadiae	RBCM TagG5006	FJ164437	TZFPB134-06	*Careproctus cypselurus*
Paraliparis andriashevi	NMNZ P.043693	JN641083	FNZB196-08	*Paraliparis* sp.
Paraliparis antarcticus	MNHN 2008-2597	HQ713130	EATF398-10	
Paraliparis antarcticus	MNHN 2008-2595	HQ713133	EATF538-10	
Paraliparis antarcticus	NMNZ P.043388	JN641075	FNZB135-08	
Paraliparis bathybius	ZMUB TUNUVI-17	N/A	DSFIB690-15	
Paraliparis bathybius	ZMUB TUNUVI-20	N/A	DSFIB693-15	
Paraliparis "bathybius"	BU JRAS06-351	EU326411	ANTI351-06	
Paraliparis camilarus	NMNZ P.043688	JN641077	FNZB190-08	*Paraliparis* sp.
Paraliparis cephalus	UW 119615*	MH630324	SGJWO035-18	
Paraliparis cephalus	UW 153315	N/A	FMV858-16	
Paraliparis cephalus	UW 153529*	MH630325	SGJWO036-18	
Paraliparis charcoti	MNHN 2008-2613	JN641077	EATF190-10	
Paraliparis charcoti	MNHN 2009-2614	HQ713138	EATF551-10	
Paraliparis copei	ZMUC 9870	N/A	GLF231-14	
Paraliparis copei	UW 118898*	MH630326	SGJWO040-18	
Paraliparis dactylosus	RBCM 0738-A09	FJ164563	TZFPB863-08	*Elassodiscus caudatus*
Paraliparis dactylosus	UW 151505*	MH630328	SGJWO037-18	
Paraliparis dactylosus	UW 119391-02*	MH630327	SGJWO038-18	
Paraliparis ekaporus	NMNZ P.043688	JN641078	FNZB191-08	*Paraliparis* sp.
Paraliparis epacrognathus	NMNZ P.043690	JN641080	FNZB193-08	*Paraliparis* sp.
Paraliparis garmani	ZMUB JYP1630	N/A	GLF279-16	
Paraliparis garmani	UW 118897*	MH630329	SGJWO041-18	
Paraliparis grandis	UW 119304*	MH630330	SGJWO039-18	
Paraliparis leobergi	MNHN 2008-2624	HQ713139	EATF022-10	
Paraliparis leobergi	MNHN 2008-2619	HQ713140	EATF106-10	
Paraliparis leobergi	MNHN 2008-2617	HQ713143	EATF481-10	
Paraliparis longicaecus	NMNZ P.043691	JN641081	FNZB194-08	*Paraliparis* sp.
Paraliparis macropterus	NMNZ P.043716	JN641070	FNZB214-08	*Careproctus* aff. *longipectoralis*

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APPENDIX TABLE 1. (Continued)

Species	Catalog number	GenBank Accession	BOLD Sequence	Original Identification
Paraliparis mawsoni	MNHN 2005-2606	HQ713147	EATF167-10	
Paraliparis megalopus	RBCM TagG5002	FJ164959	TZFPA130-06	*Paraliparis melanobranchus*
Paraliparis mentikoilon	NMNZ P.043721	JN641088	FNZB219-08	*Paraliparis* sp.
Paraliparis mento	UW 150606	JQ354176	FMV582-11	*Paraliparis cephalus*
Paraliparis neelovi	MNHN 2008-2631	N/A	FKC1002-10	
Paraliparis neelovi	MNHN 2008-2632	N/A	FKC1003-10	
Paraliparis neelovi	NMNZ P.42667	JN641069	FNZ965-07	
Paraliparis nullansa	NMNZ P.043718	JN641085	FNZB216-08	*Paraliparis* sp.
Paraliparis operculosus	MNHN 2008-2634	N/A	FKC1005-10	
Paraliparis operculosus	MNHN 2008-2636	N/A	FKC1007-10	
Paraliparis operculosus	MNHN 2008-2639	N/A	FKC1010-10	
Paraliparis operculosus	MNHN 2008-2642	N/A	FKC1013-10	
Paraliparis operculosus	MNHN 2008-2644	N/A	FKC1015-10	
Paraliparis parviradialis	NMNZ P.043720	JN641087	FNZB218-08	*Paraliparis* sp.
Paraliparis paucidens	RBCM Tag0999	FJ164963	TZFPA048-06	
Paraliparis paucidens	RBCM Tag1000	FJ164964	TZFPA049-06	
Paraliparis paucidens	RBCM TagG5048	FJ164965	TZFPA124-06	
Paraliparis pectoralis	RBCM 006-041-001	FJ164969	TZFPB414-05	
Paraliparis pectoralis	RBCM Tag0995	FJ164973	TZFPA044-06	
Paraliparis pectoralis	UW 115765*	MH630332	SGJWO033-18	
Paraliparis pectoralis	UW 117994*	MH630331	SGJWO034-18	
Paraliparis pectoralis	UW 118702*	MH630335	SGJWO030-18	
Paraliparis pectoralis	UW 150597	JQ354177	FMV578-11	*Paraliparis* sp.
Paraliparis pectoralis	UW 153197*	MH630333	SGJWO032-18	
Paraliparis pectoralis	UW 113727/SIO 06-30	GU440448	MFC411-08	
Paraliparis penicillus	UW 119192*	MH630336	SGJWO043-18	
Paraliparis plicatus	NMNZ P.043689	JN641079	FNZB192-08	*Paraliparis* sp.
Paraliparis posteroporus	NMNZ P.043692	JN641082	FNZB195-08	*Paraliparis* sp.
Paraliparis rosaceus	RBCM 006-028-001	FJ164978	TZFPB289-05	
Paraliparis rosaceus	UW 153458	KY570351	FMV877-16	
Paraliparis sp.	BU JRAS06-106	EU326410	ANTFI106-06	

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APPENDIX TABLE 1. (Continued)

Species	Catalog number	GenBank Accession	BOLD Sequence	Original Identification
Paraliparis sp.	RBCM TagG5001	FJ164984	TZFPA125-06	
Paraliparis sp.	AAD SC049646	JN640730	FOAG594-08	
Paraliparis sp.	AAD SC109828	JN640729	FOAG559-08	
Paraliparis sp.	BU JRAS06-326	EU326329	ANTFI326-06	
Paraliparis sp.	RBCM TagR5068	FJ164953	TZFPA069-06	*Paraliparis dactylosus*
Paraliparis sp. cf. *rosaceus*	RBCM INV0712	FJ164981	TZFPA022-06	*Paraliparis* sp.
Paraliparis sp. cf. *rosaceus*	RBCM TagG5001	FJ164985	TZFPA128-06	*Paraliparis* sp.
Paraliparis stehmanni	NMNZ P.043719	JN641086	FNZB217-08	*Paraliparis* sp.
Paraliparis terraenovae	MNHN 2008-2626	N/A	EATF471-10	
Paraliparis terraenovae	MNHN 2008-2628	HQ712980	EATF473-10	
Paraliparis terraenovae	MNHN 2008-2627	HQ712981	EATF548-10	
Paraliparis thalassobathyalis	MNHN 2008-2648	N/A	FKCI019-10	
Paraliparis ulochir	RBCM TagG5009	FJ164958	TZFPA137-06	*Paraliparis dactylosus*
Paraliparis ulochir	UW 117987*	MH630337	SGJWO042-18	
Paraliparis valentinae	MNHN 2008-2610	HQ713151	EATF498-10	
Paraliparis voroninorum	NMNZ P.043717	JN641084	FNZB215-08	*Paraliparis* sp.
Paraliparis wolffi	MNHN 2006-1233	N/A	FKCI021-10	
Paraliparis wolffi	MNHN 2006-1234	N/A	FKCI022-10	
Prognatholiparis ptychomandibularis	UW 116036*	MH630338	SGJWO045-18	
Pseudoliparis swirei	USNM 438982	KY659181	N/A	
Pseudoliparis swirei	USNM 438987	KY659185	N/A	
Rhinoliparis attenuatus	UW 151498	KF918899	FMV697-13	*Rhinoliparis* sp.
Rhinoliparis attenuatus	RBCM 0738-A01	FJ165100	TZFPB855-08	
Rhinoliparis barbulifer	UW 115871	KU053770	SGJWO029-18	*Rhinoliparis attenuatus*
Rhodichthys regina	ZMUB 21001	N/A	DSFNG119-11	
Squaloliparis dentatus	FAKU 144601	LC337282	N/A	

APPENDIX TABLE 2. Species, catalog numbers, Genbank accession numbers, BOLD sequence ID numbers, and original identifications in BOLD or Genbank for additional COI sequences evaluated for phylogenetic analysis. Catalog numbers refer to formal catalog numbers, BOLD's "Museum ID," or "Sample ID" when "Museum ID" was blank. Original identification refers to the identification in BOLD or Genbank as of 31 March 2018 and is provided when it differs from ours in this study. Institutional codes follow Sabaj (2016). AAD = Australian Antarctic Division, BU = Bangor University, DU = Dalhousie University, NRIFS = National Research Institute of Fisheries Science, Japan. N/A = Not available. Catalog number refers either to the formal institutional catalog number or a reference number provided in BOLD or Genbank. Catalog numbers with asterisks were newly sequenced for this study.

Species	**Catalog number**	**Genbank accession**	**BOLD sequence**	**Original identification**
Allocareproctus jordani	UW 112292*	MH715494	N/A	
Allocareproctus jordani	UW 112283*	MH715493	SGJWO001-18	
Allocareproctus jordani	UW 113693*	MH715495	N/A	
Allocareproctus jordani	UW 116018*	MH715497	N/A	
Allocareproctus jordani	UW 116380*	MH715492	N/A	
Allocareproctus jordani	UW 113697-04*	MH715496	N/A	
Allocareproctus jordani	UW 153153-01*	MH715498	N/A	
Allocareproctus jordani	UW 153153-02*	MH715499	N/A	
Allocareproctus unangas	UW 112300*	MH715500	N/A	
Allocareproctus unangas	UW 150777*	MH715501	N/A	
Allocareproctus ungak	UW 113696*	MH630275	SGJWO008-18	
Careproctus colletti	FAKU 144611	LC337286	N/A	
Careproctus colletti	FAKU 144612	LC337287	N/A	
Careproctus colletti	FAKU 136893*	LC337253	N/A	
Careproctus colletti	FAKU 136894*	LC337254	N/A	
Careproctus colletti	FAKU 200529*	LC337256	N/A	
Careproctus colletti	FAKU 200743*	LC337257	N/A	
Careproctus colletti	NRIFS TY2014-FB-A	LC002656	N/A	
Careproctus colletti	UW 112638*	MH715503	N/A	
Careproctus colletti	UW 116381*	MH715504	N/A	
Careproctus colletti	UW 117997*	MH715507	N/A	
Careproctus colletti	UW 119292*	MH715508	N/A	
Careproctus colletti	UW 119305*	MH715509	N/A	
Careproctus colletti	UW 119333*	MH715510	N/A	
Careproctus colletti	UW 119368*	MH715511	N/A	
Careproctus colletti	UW 119384*	MH715512	N/A	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Careproctus colletti	UW 119386*	MH715513	N/A	
Careproctus colletti	UW 117995-01*	MH715505	N/A	
Careproctus colletti	UW 117995-02*	MH715506	N/A	
Careproctus colletti	UW 119446-01*	MH715514	N/A	
Careproctus colletti	UW 119446-02*	MH715515	N/A	
Careproctus colletti	UW 119446-03*	MH715516	N/A	
Careproctus colletti	UW 119446-04*	MH715517	N/A	
Careproctus comus	UW 119700	KU053756	GBMIN95101-17	
Careproctus cypselurus	KU 28299	GU440261	MFC384-08	
Careproctus cypselurus	RBCM 006-028-002	FJ164447	TZFPB290-05	*Careproctus furcellus*
Careproctus cypselurus	RBCM 006-028-003	FJ164446	TZFPB291-05	*Careproctus furcellus*
Careproctus cypselurus	RBCM 006-028-004	FJ164445	TZFPB292-05	*Careproctus furcellus*
Careproctus cypselurus	RBCM 006-029-004	FJ164444	TZFPB312-05	*Careproctus furcellus*
Careproctus cypselurus	RBCM 006-041-005	FJ164442	TZFPB418-05	*Careproctus furcellus*
Careproctus cypselurus	RBCM INV0700	FJ164441	TZFPA010-06	*Careproctus furcellus*
Careproctus cypselurus	UW 113568	KY570326	FMV285-08	
Careproctus cypselurus	UW 113894*	MH715518	N/A	
Careproctus cypselurus	UW 115126	JQ354027	FMV407-09	
Careproctus cypselurus	UW 115127*	MH715519	N/A	
Careproctus cypselurus	UW 115138*	MH715520	N/A	
Careproctus cypselurus	UW 115139*	MH715521	N/A	
Careproctus cypselurus	UW 119289*	MH715522	N/A	
Careproctus cypselurus	UW 150586	JQ354033	FMV572-11	*Careproctus melanurus*
Careproctus faunus	UW 113646	KU053757	N/A	
Careproctus furcellus	UW 113889*			
Careproctus furcellus	UW 113891*	MH715523	N/A	
Careproctus furcellus	UW 117984*	MH715524	N/A	
Careproctus furcellus	UW 118636*	MH715525	N/A	
Careproctus furcellus	UW 118724*	MH715526	N/A	
Careproctus furcellus	UW 119295*	MH715527	N/A	
Species	**Catalog number**	**Genbank accession**	**BOLD sequence**	**Original identification**

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Careproctus furcellus	UW 119298*	MH715528	N/A	
Careproctus furcellus	UW 119365-01*	MH715529	N/A	
Careproctus furcellus	UW 119635-02*	MH715530	N/A	
Careproctus furcellus	UW 119385*	MH715531	N/A	
Careproctus furcellus	UW 119389-01*	MH715532	N/A	
Careproctus furcellus	UW 119389-02*	MH715533	N/A	
Careproctus furcellus	UW 150903	KU053745	GBMIN129897-17	
Careproctus furcellus	NRIFS TY2014-FB-T	LC002654	N/A	
Careproctus gilberti	UW 119373*	MH715535	N/A	
Careproctus gilberti	UW 118715*	MH715534	N/A	
Careproctus gilberti	UW 119457*	MH715536	N/A	
Careproctus gilberti	UW 119716*	MH715537	N/A	
Careproctus gilberti	UW 150926	KU053753	N/A	
Careproctus gilberti	UW 151206*	MH715538	N/A	
Careproctus gilberti	UW 151213*	MH715539	N/A	
Careproctus gilberti	UW 151313*	MH715550	N/A	
Careproctus gilberti	UW 151314*	MH715551	N/A	
Careproctus gilberti	UW 151234-01*	MH715540	N/A	
Careproctus gilberti	UW 151234-02*	MH715541	N/A	
Careproctus gilberti	UW 151308-02*	MH715542	N/A	
Careproctus gilberti	UW 151308-03*	MH715543	N/A	
Careproctus gilberti	UW 151308-04*	MH715544	N/A	
Careproctus gilberti	UW 151308-05*	MH715545	N/A	
Careproctus gilberti	UW 151309-01*	MH715546	N/A	
Careproctus gilberti	UW 151309-03*	MH715547	N/A	
Careproctus gilberti	UW 151309-04*	MH715548	N/A	
Careproctus gilberti	UW 151309-05*	MH715549	N/A	
Careproctus gilberti	UW 152425-01*	MH715552	N/A	
Careproctus gilberti	UW 153160-01*	MH715553	N/A	
Careproctus gilberti	UW 153160-02*	MH715554	N/A	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Careproctus gilberti	UW 153161-01*	MH715555	N/A	
Careproctus gilberti	UW 153161-02*	MH715556	N/A	
Careproctus gilberti	UW 153161-04*	MH715557	N/A	
Careproctus gilberti	UW 153525-04*	MH715558	N/A	
Careproctus gilberti	UW 154452-01*	MH715559	N/A	
Careproctus gilberti	UW 154452-02*	MH715560	N/A	
Careproctus gilberti	UW 154452-03*	MH715561	N/A	
Careproctus gilberti	UW 154452-04*	MH715562	N/A	
Careproctus gilberti	UW 154452-05*	MH715563	N/A	
Careproctus gilberti	UW 154481-02*	MH715566	N/A	
Careproctus gilberti	UW 154481-03*	MH715564	N/A	
Careproctus gilberti	UW 154481-04*	MH715565	N/A	
Careproctus gilberti	UW 154507*	MH715567	N/A	
Careproctus gilberti	UW 154885*	MH715568	N/A	
Careproctus gilberti	UW 154932*	MH715569	N/A	
Careproctus kidoi	CMN 2002-0025.1	N/A	CMNAF009-06	
Careproctus kidoi	ZMUB JYP1637	N/A	GLF285-16	*Careproctus* sp.
Careproctus lerikimae	UAM 6448	N/A	DSFAL702-11	*Careproctus reinhardti*
Careproctus lerikimae	UAM 6317-02	N/A	DSFIB093-11	*Careproctus reinhardti*
Careproctus lerikimae	UW 117918	N/A	DSFIB063-11	*Careproctus reinhardti*
Careproctus longifilis	RBCM TagR5826	FJ164427	TZFPA102-06	*Careproctus attenuatus*
Careproctus longipectoralis	MNHN 2008-2593	HQ712899	EATF268-10	
Careproctus marginatus	FAKU 144616	LC337285	N/A	
Careproctus melanurus	RBCM 006-026-022	FJ164453	TZFPB264-05	
Careproctus melanurus	RBCM 006-026-026	FJ164454	TZFPB268-05	
Careproctus melanurus	RBCM 006-030-003	FJ164452	TZFPB321-05	
Careproctus melanurus	RBCM TagG5015	FJ164450	TZFPA143-06	
Careproctus melanurus	RBCM TagG5018	FJ164451	TZFPA144-06	
Careproctus melanurus	SIO 95-2	EU403073	GBGC4113-08	
Careproctus melanurus	SIO 95-2	GU440262	MFC043-08	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Careproctus melanurus	UW 153307-02*	MH715572	N/A	
Careproctus sp. cf. *melanurus*	UW 151029	KU053662	N/A	
Careproctus sp. cf. *melanurus*	UW 151215	KU053663	GBMIN119742-17	
Careproctus sp. cf. *melanurus*	UW 152101*	MH715571	N/A	
Careproctus sp. cf. *melanurus*	UW 153536	KU053665	GBMIN95092-17	
Careproctus sp. cf. *melanurus*	UW 154478*	MH715570	N/A	
Careproctus micropus	TMU AL-9228	N/A	DSFNG031-11	
Careproctus micropus	TMU AL-9230	N/A	DSFNG029-11	
Careproctus micropus	TMU AL-9295	N/A	DSFNG030-11	
Careproctus micropus	TMU AL-9298	N/A	DSFNG032-11	
Careproctus micropus	ZMUB JYP1659	N/A	GLF307-16	
Careproctus ostentum	UW 49435*	MH715573	N/A	
Careproctus ovigerus	RBCM TagR5832	FJ164448	TZFPA096-06	*Careproctus georgianus*
Careproctus phasma	UW 117919	N/A	DSFIB064-11	*Careproctus reinhardti*
Careproctus phasma	UW 117936	KU053661	GBMIN95091-17	
Careproctus rastrinus	FAKU 131542*	LC416714	N/A	
Careproctus rastrinus	FAKU 200416*	LC416715	N/A	
Careproctus reinhardti	ARC 26430	KC015258	SCAFB624-07	
Careproctus reinhardti	ARC 26709	KC015260	SCAFB219-07	
Careproctus reinhardti	ARC 26836	KC015257	SCAFB626-07	
Careproctus reinhardti	UAM PSR 2386	N/A	DSFIB357-13	
Careproctus reinhardti	UAM PSR 2387	N/A	DSFIB358-13	
Careproctus reinhardti	UAM PSR 2388-01	N/A	DSFIB359-13	
Careproctus reinhardti	UAM PSR 2388-02	N/A	DSFIB360-13	
Careproctus reinhardti	TMU AL-9056	N/A	DSFNG027-11	
Careproctus reinhardti	TMU AL-9223	N/A	DSFNG028-11	
Careproctus reinhardti	TMU AL-9231	N/A	DSFNG024-11	
Careproctus reinhardti	TMU AL-9252	N/A	DSFNG022-11	
Careproctus reinhardti	TMU AL-9254	N/A	DSFNG023-11	
Careproctus reinhardti	TMU AL-9276	N/A	DSFNG025-11	
Careproctus reinhardti	TMU AL-9277	N/A	DSFNG026-11	

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APPENDIX TABLE 2. (Continued)

Species	**Catalog number**	**Genbank accession**	**BOLD sequence**	**Original identification**
Careproctus reinhardti	TMU AL-9281	N/A	DSFNG021-11	
Careproctus reinhardti	ZIN 54800	HQ712338	DSFAL600-09	
Careproctus reinhardti	ZMUB 22795	N/A	NBMF092-15	
Careproctus reinhardti	ZMUB GLF077	N/A	GLF077-14	
Careproctus reinhardti	ZMUB GLF160	N/A	GLF160-14	
Careproctus reinhardti	ZMUB GLF162	N/A	GLF162-14	
Careproctus reinhardti	ZMUB Vp2013-42	N/A	DSFIB525-14	
Careproctus reinhardti	ZMUB Vp2013-75	N/A	DSFIB533-14	
Careproctus reinhardti	ZMUB Vp2013-82	N/A	DSFIB537-14	
Careproctus scottae	UW 113526	KU053646	GBMIN119736-17	
Careproctus scottae	UW 113906-02	KU053648	N/A	
Careproctus scottae	UW 113906-03	KU053647	N/A	
Careproctus scottae	UW 113906-06	KU053649	N/A	
Careproctus scottae	UW 113906-08	KU053650	N/A	
Careproctus scottae	UW 117912-01	KU053651	N/A	
Careproctus scottae	UW 117912-02	KU053652	GBMIN119738-17	
Careproctus scottae	UW 117935-04*	MH715574	N/A	
Careproctus simus	UW 116031*	MH715575	N/A	
Careproctus simus	UW 119437*	MH715576	N/A	
Careproctus simus	UW 119438*	MH715577	N/A	
Careproctus simus	UW 119778*	MH715578	N/A	
Careproctus simus	UW 119791*	MH715579	N/A	
Careproctus simus	UW 153140	KU053704	GMMIN129881-17	
Careproctus simus	UW 154482-01*	MH715580	N/A	
Careproctus simus	UW 154482-02*	MH715581	N/A	
Careproctus simus	UW 154482-03*	MH715582	N/A	
Careproctus n. sp.	RBCM 15908	FJ164429	TZFPB867-08	*Careproctus canus*
Careproctus n. sp.	RBCM INV792	FJ164430	TZFPA034-06	*Careproctus canus*
Careproctus n. sp.	RBCM 15946	FJ164431	TZFPA070-06	*Careproctus canus*
Crystallichthys cyclospilus	UW 48076*	MH715583	N/A	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Crystallichthys cyclospilus	UW 111992*	MH715586	N/A	
Crystallichthys cyclospilus	UW 111993*	MH715587	N/A	
Crystallichthys cyclospilus	UW 111994*	MH715588	N/A	
Crystallichthys cyclospilus	UW 112060	KU053758	GBMIN124636-17	
Crystallichthys cyclospilus	UW 119217*	MH715584	N/A	
Crystallichthys cyclospilus	UW 119224*	MH715585	N/A	
Elassodiscus caudatus	UW 49350-05*	MH715600	N/A	
Elassodiscus caudatus	UW 49350-06*	MH715599	N/A	
Elassodiscus sp. cf. *caudatus*	UW 116040	KU053761	GBMIN119760-17	
Elassodiscus sp. cf. *caudatus*	UW 117985*	MH715589	N/A	
Elassodiscus sp. cf. *caudatus*	UW 117999*	MH715590	N/A	
Elassodiscus sp. cf. *caudatus*	UW 119621*	MH715598	N/A	
Elassodiscus sp. cf. *caudatus*	UW 119307*	MH715592	N/A	
Elassodiscus sp. cf. *caudatus*	UW 119290*	MH715591	N/A	
Elassodiscus sp. cf. *caudatus*	UW 151506	KF918870	FMV702-13	
Elassodiscus sp. cf. *caudatus*	UW 119364-01*	MH715593	N/A	
Elassodiscus sp. cf. *caudatus*	UW 119364-02*	MH715594	N/A	
Elassodiscus sp. cf. *caudatus*	UW 119364-03*	MH715595	N/A	
Elassodiscus sp. cf. *caudatus*	UW 119593-01*	MH715597	N/A	
Elassodiscus sp. cf. *caudatus*	UW 119593-02*	MH715596	N/A	
Elassodiscus tremebundus	UW 117991*	MH715589	N/A	
Elassodiscus tremebundus	UW 117998*	MH715602	N/A	
Elassodiscus tremebundus	UW 118001*	MH715603	N/A	
Elassodiscus tremebundus	UW 118703*	MH715604	N/A	
Elassodiscus tremebundus	UW 119301*	MH715605	N/A	
Elassodiscus tremebundus	UW 119302*	MH715606	N/A	
Elassodiscus tremebundus	UW 119356*	MH715607	N/A	
Elassodiscus tremebundus	UW 119439*	MH715608	N/A	
Elassodiscus tremebundus	UW 150845-01*	MH715611	N/A	
Elassodiscus tremebundus	UW 150845-02*	MH715609	N/A	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Elassodiscus tremebundus	UW 150845-03*	MH715610	N/A	
Liparis agassizii	NSMK PI-000088	HM180656	ANGBF892-12	
Liparis bathyarcticus	CAS PSR 2276-02	N/A	DSFIB271-13	
Liparis bathyarcticus	ARC 25596	KC015566	SCFAC723-06	
Liparis bathyarcticus	ARC 25711	KC015563	SCAFB482-07	*Liparis gibbus*
Liparis bathyarcticus	ARC 25731	KC015560	SCAFB345-07	
Liparis bathyarcticus	ARC 26506	KC015564	SCAFB243-07	
Liparis bathyarcticus	ARC 26517	KC015561	SCAFB597-07	
Liparis bathyarcticus	ARC 26750	KC015562	SCAFB603-07	
Liparis bathyarcticus	CAS 228468	HQ712568	DSFAL487-09	
Liparis bathyarcticus	CAS 228481	GU804862	DSFAL497-09	
Liparis bathyarcticus	CAS 228525	GU804883	DSFAL576-09	
Liparis bathyarcticus	CAS 228555	HM421802	DSFAL664-09	
Liparis bathyarcticus	CAS 230348-03	HQ712563	DSFAL340-07	
Liparis bathyarcticus	CAS PSR 2276-01	N/A	DSFIB269-13	
Liparis bathyarcticus	CAS PSR 2276-03	N/A	DSFIB275-13	
Liparis bathyarcticus	CMN 2002-00372	N/A	CMNAF034-06	
Liparis bathyarcticus	DFO ML-37	N/A	DSFIB784-16	
Liparis bathyarcticus	DFO ML-38	N/A	DSFIB785-16	
Liparis bathyarcticus	DFO ML-66	N/A	DSFIB786-16	
Liparis bathyarcticus	DFO ML-83	N/A	DSFIB787-16	
Liparis bathyarcticus	DFO MLE-50	N/A	DSFIB789-16	
Liparis bathyarcticus	TMU AL-9232	N/A	DSFNG069-11	
Liparis bathyarcticus	TMU AL-9233	N/A	DSFNG068-11	
Liparis bathyarcticus	TMU AL-9245	N/A	DSFNG066-11	
Liparis bathyarcticus	TMU AL-9253	N/A	DSFNG067-11	
Liparis bathyarcticus	UAM 3760	N/A	DSFIB614-14	
Liparis bathyarcticus	UAM 5509	HQ712566	DSFAL555-09	
Liparis bathyarcticus	UAM 5522	HQ712567	DSFAL570-09	
Liparis bathyarcticus	UAM 5554	HM421752	DSFAL613-09	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Liparis bathyarcticus	UAM 6278	N/A	DSFAL752-11	
Liparis bathyarcticus	UAM 6440	N/A	DSFAL761-11	
Liparis bathyarcticus	UAM PSR 2272-01	N/A	DSFIB264-13	
Liparis bathyarcticus	UAM PSR 2272-02	N/A	DSFIB265-13	
Liparis bathyarcticus	UAM PSR 2441-01	N/A	DSFIB409-13	
Liparis bathyarcticus	UAM PSR 2446-01	N/A	DSFIB412-13	*Liparis* sp.
Liparis bathyarcticus	UAM PSR 2454-02	N/A	DSFIB421-13	*Liparis* sp.
Liparis bathyarcticus	UAM PSR 2454-03	N/A	DSFIB422-13	*Liparis* sp.
Liparis bathyarcticus	ZIN 54761	HM400299	DSFAL554-09	
Liparis bathyarcticus	ZMUB 11541	N/A	NBMF121-16	
Liparis bathyarcticus	ZMUB 16137	N/A	DSFIB609-14	
Liparis bathyarcticus	ZMUB 16139	N/A	DSFIB445-13	
Liparis bathyarcticus	ZMUB 16736	AM498312	GBGC5053-08	
Liparis bathyarcticus	ZMUB 19716	N/A	DSFIB446-13	
Liparis bathyarcticus	ZMUB 20092	N/A	DSFIB447-13	
Liparis bathyarcticus	ZMUB 20923	N/A	DSFIB448-13	
Liparis bathyarcticus	ZMUB JYP1541	N/A	GLF217-14	
Liparis bathyarcticus	ZMUB JYP1594	N/A	GLF224-14	*Liparis tunicatus*
Liparis bathyarcticus	ZMUB JYP1595	N/A	GLF227-14	
Liparis curilensis	UW 44503-02*	MH715612	N/A	
Liparis curilensis	UW 44503-03*	MH715615	N/A	
Liparis curilensis	UW 44503-04*	MH715613	N/A	
Liparis curilensis	UW 44503-05*	MH715614	N/A	
Liparis dennyi	RBCM 0736-B07	FJ164720	TZFPB889-08	
Liparis dennyi	UW 112148	KY570339	FMV234-08	
Liparis dennyi	UW 112757	JQ354182	FMV246-08	*Liparis mucosus*
Liparis dennyi	UW 112759	JQ354183	FMV248-08	*Liparis mucosus*
Liparis dennyi	UW 119996	JQ354190	FMV531-11	*Liparis* sp.
Liparis dennyi	UW 155676*	MH715616	N/A	
Liparis fabricii	ARC 26710	KC015559	SCAFB242-07	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Liparis fabricii	ARC 26712	KC015558	SCAFB241-07	
Liparis fabricii	CAS 228488	HQ712554	DSFAL502-09	
Liparis fabricii	CAS 228490	GU804866	DSFAL506-09	
Liparis fabricii	CAS 228496	HQ712555	DSFAL515-09	
Liparis fabricii	CAS 228509	HM400291	DSFAL532-09	
Liparis fabricii	CAS 228517	HM400295	DSFAL540-09	
Liparis fabricii	CAS 228521	HM400297	DSFAL548-09	
Liparis fabricii	CAS 228531	HQ712551	DSFAL593-09	
Liparis fabricii	CMN 2002-00211	N/A	CMNAF008-06	
Liparis fabricii	TMU AL-9288	N/A	DSFNG065-11	
Liparis fabricii	UAM 6305	N/A	DSFAL767-11	
Liparis fabricii	UAM 6320	N/A	DSFIB097-11	
Liparis fabricii	UAM 6451	N/A	DSFAL737-11	
Liparis fabricii	UAM 5518-01	HQ712549	DSFAL564-09	
Liparis fabricii	UAM 5518-02	HQ712550	DSFAL565-09	
Liparis fabricii	UAM PSR 2449	N/A	DSFIB415-13	
Liparis fabricii	UAM PSR 2450-01	N/A	DSFIB416-13	
Liparis fabricii	UAM PSR 2450-02	N/A	DSFIB417-13	
Liparis fabricii	UAM PSR 2453	N/A	DSFIB419-13	
Liparis fabricii	ZMUB 9188	N/A	DSFIB753-16	
Liparis fabricii	ZMUB 9863	N/A	GLF072-14	
Liparis fabricii	ZMUB 10355	N/A	DSFIB752-16	
Liparis fabricii	ZMUB 16114	N/A	DSFIB449-13	
Liparis fabricii	ZMUB 16119	N/A	DSFIB450-13	
Liparis fabricii	ZMUB 16994	AM498311	GBGC5054-08	
Liparis fabricii	ZMUB 19749	N/A	NBMF093-15	
Liparis fabricii	ZMUB 20496	N/A	DSFIB451-13	
Liparis fabricii	ZMUB 20980	N/A	DSFNG061-11	
Liparis fabricii	ZMUB 20981	N/A	DSFNG062-11	
Liparis fabricii	ZMUB 20982	N/A	DSFNG063-11	

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APPENDIX TABLE 2. (Continued)

Liparis fabricii	ZMUB 21707	N/A	NBMF123-16	
Liparis fabricii	ZMUB 23200	N/A	NBMF124-16	
Liparis fabricii	ZMUB JYP1539	N/A	GLF215-14	
Liparis fabricii	ZMUB JYP1545	N/A	GLF220-14	
Liparis fabricii	ZMUB JYP1582	N/A	GLF166-14	
Liparis fabricii	ZMUB Vp2013-38	N/A	DSFIB523-14	
Liparis fabricii	ZMUB Vp2013-63	N/A	DSFIB527-14	
Liparis florae	UW 151666*	MH715617	N/A	
Liparis gibbus	UAM PSR 2437	N/A	DSFIB407-13	
Liparis gibbus	UAM PSR 2439-01	N/A	DSFIB408-13	
Liparis gibbus	UAM PSR 2455	N/A	DSFIB423-13	
Liparis gibbus	CAS 230156	HQ712560	DSFAL237-07	
Liparis gibbus	CAS 230339	HQ712562	DSFAL320-07	
Liparis gibbus	CAS 230151-01	HQ712557	DSFAL228-07	
Liparis gibbus	CAS 230151-02	HQ712558	DSFAL229-07	
Liparis gibbus	CAS 230151-03	HQ712559	DSFAL230-07	
Liparis gibbus	CAS PSR 2275-01	N/A	DSFIB268-13	
Liparis gibbus	CAS PSR 2275-02	N/A	DSFIB273-13	
Liparis gibbus	CAS PSR 2291	N/A	DSFIB279-13	
Liparis gibbus	UAM 5541	HQ712564	DSFAL607-09	
Liparis gibbus	UAM 5555	HM421753	DSFAL614-09	
Liparis gibbus	UAM 6263	N/A	DSFAL697-11	
Liparis gibbus	UAM 6264	N/A	DSFAL696-11	
Liparis gibbus	UAM PSR 2263	N/A	DSFIB262-13	
Liparis gibbus	UAM PSR 2448	N/A	DSFIB414-13	
Liparis gibbus	UAM PSR 2452	N/A	DSFIB418-13	
Liparis gibbus	UW 119133	N/A	DSFIB067-11	
Liparis gibbus	UW 119134	N/A	DSFIB068-11	
Liparis gibbus	ZIN 54878	HM421748	DSFAL608-09	
Liparis liparis	MT 1807	KJ204968	BNSF316-11	
Species	**Catalog number**	**Genbank accession**	**BOLD sequence**	**Original identification**

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Liparis liparis	MT 1808	KJ204972	BNSF317-11	
Liparis liparis	MT 1809	KJ204973	BNSF318-11	
Liparis liparis	MT 2134	KJ204966	BNSF205-11	
Liparis liparis	MT 2135	KJ204964	BNSF206-11	
Liparis liparis	MT 2626	KJ204970	BNSF572-12	
Liparis liparis	MT 4200	KJ204977	BNSFI009-12	
Liparis mucosus	SIO 00-166	EU403074	GBGC4112-08	
Liparis pulchellus	RBCM NEOCAL07-0037	FJ164723	TZFPA184-07	
Liparis pulchellus	RBCM NEOCAL07-0038	FJ164722	TZFPA185-07	
Liparis pulchellus	UW 115845*	MH715618	N/A	
Liparis tunicatus	CAS 228501	HM400286	DSFAL519-09	
Liparis tunicatus	CAS 228508	GU804871	DSFAL531-09	
Liparis tunicatus	CAS 228522	HQ712583	DSFAL549-09	
Liparis tunicatus	CAS 230096	HQ712570	DSFAL156-07	
Liparis tunicatus	CAS 230167	HQ712577	DSFAL243-07	
Liparis tunicatus	CAS 230301	HQ712578	DSFAL285-07	
Liparis tunicatus	CAS 228495-01	HM400282	DSFAL512-09	
Liparis tunicatus	CAS 228495-01	HM400285	DSFAL518-09	
Liparis tunicatus	CAS 230101-01	HQ712571	DSFAL168-07	
Liparis tunicatus	CAS 230101-02	HQ712573	DSFAL198-07	
Liparis tunicatus	CAS 230136-01	HQ712574	DSFAL210-07	
Liparis tunicatus	CAS 230136-02	HQ712575	DSFAL211-07	
Liparis tunicatus	CAS 230348-02	HQ712579	DSFAL338-07	
Liparis tunicatus	CAS PSR 2277-01	N/A	DSFIB270-13	
Liparis tunicatus	CAS PSR 2277-02	N/A	DSFIB272-13	
Liparis tunicatus	CAS PSR 2277-03	N/A	DSFIB274-13	
Liparis tunicatus	UAM 5519	HQ712552	DSFAL567-09	
Liparis tunicatus	UAM 5547	HM421750	DSFAL610-09	
Liparis tunicatus	UAM 5563	HM421758	DSFAL620-09	
Liparis tunicatus	UAM 5564	HM421759	DSFAL621-09	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Liparis tunicatus	UAM 5565	HM421760	DSFAL622-09	
Liparis tunicatus	UAM 5572	HM421771	DSFAL633-09	
Liparis tunicatus	UAM 5575	HM421772	DSFAL634-09	
Liparis tunicatus	UAM 6277	N/A	DSFAL774-11	
Liparis tunicatus	UAM 6291	N/A	DSFAL748-11	
Liparis tunicatus	UAM 6292	N/A	DSFAL751-11	
Liparis tunicatus	UAM 6309	N/A	DSFAL776-11	
Liparis tunicatus	UAM 6310	N/A	DSFAL775-11	
Liparis tunicatus	UAM 6311	N/A	DSFAL777-11	
Liparis tunicatus	UAM 6315	N/A	DSFAL773-11	
Liparis tunicatus	UAM 6474	N/A	DSFIB138-11	
Liparis tunicatus	UAM 6490	N/A	DSFIB140-11	
Liparis tunicatus	UAM 6503	N/A	DSFIB139-11	
Liparis tunicatus	UAM 5995-01	HQ712581	DSFAL440-08	
Liparis tunicatus	UAM 5995-02	HQ712582	DSFAL442-08	
Liparis tunicatus	UAM 6391-01	N/A	DSFAL706-11	
Liparis tunicatus	UAM 6484-01	N/A	DSFIB132-11	
Liparis tunicatus	UAM 6484-02	N/A	DSFIB133-11	
Liparis tunicatus	UAM PSR 2124	N/A	DSFIB164-12	
Liparis tunicatus	UAM PSR 2444-01	N/A	DSFIB410-13	
Liparis tunicatus	UAM PSR 2445-01	N/A	DSFIB612-14	
Liparis tunicatus	UW 150718	N/A	DSFIB589-14	
Liparis tunicatus	UW 153041	N/A	DSFIB662-15	
Liparis tunicatus	UW 153088	N/A	DSFIB663-15	
Liparis tunicatus	UW 150654D	N/A	DSFIB658-15	
Lipariscus nanus	UW 117239-02*	MH715619	N/A	
Nectoliparis pelagicus	RBCM NEOCAL07-0026	FJ164909	TZFPA173-07	
Nectoliparis pelagicus	RBCM NEOCAL07-0045	FJ164908	TZFPA192-07	
Nectoliparis pelagicus	UAM PSR 2143-01	N/A	DSFIB188-12	
Nectoliparis pelagicus	UAM PSR 2143-02	N/A	DSFIB189-12	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Nectoliparis pelagicus	UW 117244-02*	MH715621	N/A	
Nectoliparis pelagicus	UW 117244-01*	MH715620	N/A	
Nectoliparis pelagicus	UW 151316	KU053771	GBMIN95104-17	
Osteodiscus cascadiae	RBCM TagG5003	FJ164434	TZFPA131-06	*Careproctus cypselurus*
Osteodiscus cascadiae	RBCM TagG5004	FJ164435	TZFPA132-06	*Careproctus cypselurus*
Osteodiscus cascadiae	RBCM TagG5007	FJ164438	TZFPA135-06	*Careproctus cypselurus*
Osteodiscus cascadiae	RBCM TagG5008	FJ164439	TZFPA136-06	*Careproctus cypselurus*
Paraliparis antarcticus	MNHN 2008-2596	HQ713129	EATF397-10	
Paraliparis antarcticus	MNHN 2008-2598	HQ713131	EATF399-10	
Paraliparis antarcticus	MNHN 2008-2599	HQ713132	EATF443-10	
Paraliparis antarcticus	MNHN 2008-2600	HQ713134	EATF550-10	
Paraliparis antarcticus	MNHN 2008-2601	HQ713127	EATF075-10	
Paraliparis antarcticus	MNHN 2008-2603	HQ713128	EATF388-10	
Paraliparis antarcticus	NMNZ P.043389	JN641076	FNZB136-08	
Paraliparis antarcticus	NMNZ P.043422	JN641074	FNZB055-08	
Paraliparis antarcticus	NMNZ P.04347	JN641072	FNZB040-08	
Paraliparis antarcticus	NMNZ P.043480	JN641073	FNZB041-08	
Paraliparis antarcticus	NMNZ P.043481	JN641071	FNZB042-08	
Paraliparis antarcticus	NMNZ P.043559	JN641089	FNZB274-08	
Paraliparis bathybius	TMU AL-EX20	N/A	DSFNG108-11	
Paraliparis bathybius	TMU AL-EX8	N/A	DSFNG106-11	
Paraliparis bathybius	ZMUB 2317	N/A	NBMF127-16	
Paraliparis bathybius	ZMUB 20993	N/A	DSFNG109-11	
Paraliparis bathybius	ZMUB 20994	N/A	DSFNG107-11	
Paraliparis bathybius	ZMUB 23169	N/A	NBMF125-16	
Paraliparis bathybius	ZMUB 23170	N/A	NBMF126-16	
Paraliparis bathybius	ZMUB 23227	N/A	NBMF128-16	
Paraliparis bathybius	ZMUB Vp2013-99	N/A	DSFIB548-14	
Paraliparis cephalus	UW 119880	JQ354257	FMV474-11	
Paraliparis cephalus	UW 49443-01*	MH715622	N/A	

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APPENDIX TABLE 2. (Continued)

Paraliparis cephalus	UW 49443-02*	MH715623	N/A	
Paraliparis charcoti	MNHN 2008-2611	HQ713135	EATF582-10	
Paraliparis charcoti	MNHN 2008-2612	HQ713137	EATF392-10	
Paraliparis copei	ZMUC 9878	N/A	GLF075-14	
Paraliparis dactylosus	RBCM 0738-A08	FJ164562	TZFPB862-08	*Elassodiscus caudatus*
Paraliparis dactylosus	UW 119178	KU053765	GBMIN124637-17	
Paraliparis dactylosus	UW 119293*	MH715629	N/A	
Paraliparis dactylosus	UW 119296	KU053766	N/A	
Paraliparis dactylosus	UW 119893	JQ354258	FMV487-11	
Paraliparis dactylosus	UW 119894	JQ354259	FMV488-11	
Paraliparis dactylosus	UW 151503	KF918890	FMV701-13	
Paraliparis dactylosus	UW 151504*	MH715630	N/A	
Paraliparis dactylosus	UW 152422*	MH715631	N/A	
Paraliparis dactylosus	UW 152682*	MH715632	N/A	
Paraliparis dactylosus	UW 154897*	MH715639	N/A	
Paraliparis dactylosus	UW 117764-01*	MH715625	N/A	
Paraliparis dactylosus	UW 117764-02*	MH715624	N/A	
Paraliparis dactylosus	UW 117982-01*	MH715626	N/A	
Paraliparis dactylosus	UW 117983-01*	MH715627	N/A	
Paraliparis dactylosus	UW 117983-02*	MH715628	N/A	
Paraliparis dactylosus	UW 152473-01*	MH715633	N/A	
Paraliparis dactylosus	UW 152473-02*	MH715634	N/A	
Paraliparis dactylosus	UW 152683-02*	MH715635	N/A	
Paraliparis dactylosus	UW 152683-03*	MH715636	N/A	
Paraliparis dactylosus	UW 152683-04*	MH715637	N/A	
Paraliparis dactylosus	UW 154451-01*	MH715638	N/A	
Paraliparis garmani	ZMUB 9995	N/A	GLF122-14	
Paraliparis garmani	ZMUB JYP1664	N/A	GLF312-16	
Paraliparis grandis	UW 119394	KU053767	GBMIN95102-17	*Paraliparis dactylosus*
Paraliparis grandis	UW 155715*	MH715640	N/A	
Paraliparis leobergi	MNHN 2008-2615	HQ713142	EATF363-10	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Paraliparis leobergi	MNHN 2008-2616	HQ713141	EATF356-10	
Paraliparis leobergi	MNHN 2008-2621	HQ713144	EATF546-10	
Paraliparis leobergi	MNHN 2008-2622	HQ713145	EATF547-10	
Paraliparis mawsoni	MNHN 2008-2605	HQ713146	EATF089-10	
Paraliparis mawsoni	MNHN 2008-2607	HQ713149	EATF305-10	
Paraliparis mawsoni	MNHN 2008-2608	HQ713148	EATF302-10	
Paraliparis mawsoni	MNHN 2008-2609	HQ713150	EATF545-10	
Paraliparis neelovi	MNHN 2008-2630	N/A	FKCI001-10	
Paraliparis operculosus	MNHN 2008-2633	N/A	FKCI004-10	
Paraliparis operculosus	MNHN 2008-2635	N/A	FKCI006-10	
Paraliparis operculosus	MNHN 2008-2637	N/A	FKCI008-10	
Paraliparis operculosus	MNHN 2008-2638	N/A	FKCI009-10	
Paraliparis operculosus	MNHN 2008-2640	N/A	FKCI011-10	
Paraliparis operculosus	MNHN 2008-2641	N/A	FKCI012-10	
Paraliparis operculosus	MNHN 2008-2645	N/A	FKCI016-10	
Paraliparis operculosus	MNHN 2008-2646	N/A	FKCI017-10	
Paraliparis operculosus	MNHN 2008-2647	N/A	FKCI018-10	
Paraliparis paucidens	RBCM 006-037-001	FJ164960	TZFPB380-05	
Paraliparis paucidens	RBCM Tag0984	FJ164961	TZFPA031-06	
Paraliparis paucidens	RBCM Tag0986	FJ164962	TZFPA035-06	
Paraliparis paucidens	UW 49433*	Pending (#4870)	N/A	
Paraliparis pectoralis	RBCM Tag0991	FJ164970	TZFPA040-06	
Paraliparis pectoralis	RBCM Tag0992	FJ164971	TZFPA041-06	
Paraliparis pectoralis	RBCM Tag0993	FJ164972	TZFPA042-06	
Paraliparis pectoralis	RBCM TagG5038	FJ164977	TZFPA115-06	
Paraliparis pectoralis	RBCM 006-041-003	FJ164966	TZFPB416-05	
Paraliparis pectoralis	RBCM 006-041-004	FJ164967	TZFPB417-05	
Paraliparis pectoralis	RBCM 006-041-002	FJ164968	TZFPB415-05	
Paraliparis pectoralis	RBCM Tag0996	FJ164974	TZFPA045-06	
Paraliparis pectoralis	RBCM TagG5037	FJ164976	TZFPA114-06	

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APPENDIX TABLE 2. (Continued)

Species	Catalog number	Genbank accession	BOLD sequence	Original identification
Paraliparis pectoralis	RBCM TagR5070	FJ164975	TZFPA071-06	
Paraliparis pectoralis	UW 116815*	MH715642	N/A	
Paraliparis pectoralis	UW 118633	KU053768	N/A	
Paraliparis pectoralis	UW 153526-02*	MH715643	N/A	
Paraliparis rosaceus	RBCM INV0698	FJ164979	TZFPA008-06	
Paraliparis rosaceus	RBCM INV0702	FJ164980	TZFPA012-06	
Paraliparis rosaceus	UW 119873	JQ354260	FMV472-11	
Paraliparis rosaceus	UW 153323	KY570350	FMV863-16	
Paraliparis sp. cf. *rosaceus*	RBCM INV0713	FJ164982	TZFPA023-06	*Paraliparis* sp.
Paraliparis sp. cf. *rosaceus*	RBCM TagG5044	FJ164983	TZFPA120-06	*Paraliparis* sp.
Paraliparis thalassobathyalis	BU JRAS06-349	EU326328	ANTFI349-06	
Paraliparis ulochir	RBCM TagG5031	FJ164954	TZFPA108-06	*Paraliparis dactylosus*
Paraliparis ulochir	RBCM TagG5032	FJ164955	TZFPA109-06	*Paraliparis dactylosus*
Paraliparis ulochir	RBCM TagG5033	FJ164956	TZFPA110-06	*Paraliparis dactylosus*
Paraliparis ulochir	RBCM TagG5035	FJ164957	TZFPA112-06	*Paraliparis dactylosus*
Paraliparis ulochir	UW 119776*	MH715644	N/A	
Rhinoliparis attenuatus	KU 2294/SIO 06-15	GU440505	MFC416-08	*Rhinoliparis barbulifer*
Rhodichthys regina	TMU AL-EX4	N/A	DSFNG120-11	
Rhodichthys regina	ZMUB 20999	N/A	DSFNG118-11	
Rhodichthys regina	ZMUB 21000	N/A	DSFNG121-11	
Rhodichthys regina	ZMUB 21246	N/A	NBMF129-16	
Rhodichthys regina	ZMUB 21247	N/A	NBMF130-16	
Rhodichthys regina	ZMUB 21765	N/A	NBMF131-16	
Rhodichthys regina	ZMUB 22390	N/A	NBMF132-16	
Rhodichthys regina	ZMUB Vp2013-97	N/A	DSFIB547-14	
Squaloliparis dentata	FAKU 144609	LC337283	N/A	

APPENDIX TABLE 3. Material examined in 31 groups of species designated for RADseq analysis. SRA = National Center for Biotechnology Information sequence read archive.

Group	Catalog number	Species	SRA sample number
1	UW 119822	*Eumicrotremus orbis*	Eorbis822
2	UW 119829	*Lopholiparis flerxi*	Lflerx9829
3	UW 119776	*Paraliparis ulochir*	Pulochir76
4	UW 156086-1	*Allocareproctus jordani*	Ajordani86
4	UW 156089	*Allocareproctus jordani*	Ajordani89
4	UW 155938	*Allocareproctus ungak*	Ajordan938
5	UW 112756	*Liparis rutteri*	Lrutteri56
6	UW 49350-2	*Elassodiscus caudatus*	Ecaudatus2
6	UW 119593-1	*Elassodiscus* sp. cf. *caudatus*	Ecaudatus3
6	UW 155734	*Elassodiscus* sp. cf. *caudatus*	Ecaudatus4
6	UW 49350-1	*Elassodiscus caudatus*	Ecaudatus1
7	UW 152008	*Paraliparis dactylosus*	Pdactyl08
7	UW 154451	*Paraliparis dactylosus*	Pdactyl51
8	UW156091-1	*Careproctus candidus*	Ccandidus
8	UW 156091	*Careproctus candidus*	Ccandidu2
9	UW 116030	*Careproctus cypselurus*	Ccypselur
10	UW 156087-2	*Careproctus* sp. cf. *melanurus*	Ccfmelanu2
11	UW 152476	*Lipariscus nanus*	Lnanus2476
12	UW 119187	*Crystallichthys cyclospilus*	Crystall87
12	UW 48076-2	*Crystallichthys cyclospilus*	Crystalli2
12	UW 48076-1	*Crystallichthys cyclospilus*	Crystalli1
13	UW 119291	*Careproctus bowersianus*	Cbowersian
14	UW 151304	*Careproctus scottae*	Cscottae04
14	UW 151302	*Careproctus scottae*	Cscottae02
15	UW 155711	*Careproctus staufferi*	Cstauffe11
15	UW 119196	*Careproctus staufferi*	Cstauffe96
16	UW 119197	*Careproctus comus*	Ccomus970
16	UW 119197-1	*Careproctus comus*	Ccomus971
17	UW 119821	*Eumicrotremus orbis*	Eorbis821
17	UW 151223	*Eumicrotremus orbis*	Eorbis223
17	UW 152461	*Eumicrotremus orbis*	Eorbis461
18	UW 151666	*Liparis florae*	Lflorae666
19	UW 116036	*Prognatholiparis ptychomandibularis*	Pptychoman
20	UW 154481-1	*Careproctus gilberti*	Cgilberti81
21	UW 117244	*Nectoliparis pelagicus*	Npelagicus
22	UW 119176	*Liparis gibbus*	Lgibbus176
22	UW 119043	*Liparis gibbus*	Lgibbus043
23	UW 156084	*Careproctus faunus*	Cfaunus841
24	UW 113696	*Allocareproctus ungak*	Aungak696
25	UW 119298	*Careproctus furcellus*	Cfurcellu98
26	UW 151307	*Careproctus phasma*	Cphasma07
26	UW 151261	*Careproctus phasma*	Cphasma61
27	UW 119192	*Paraliparis penicillus*	Ppenicillu
28	UW 115871	*Rhinoliparis attenuatus*	Rattenuatu
29	UW 150589	*Careproctus melanurus*	Cmelanu89
30	UW 150588	*Careproctus melanurus*	Cmelanu88
31	UW 118920	*Careproctus* sp. cf. *melanurus*	Ccfmelanu1