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Worldwide molecular phylogenetics of the *Alpheus brevirostris* (Olivier, 1811) group (Decapoda: Caridea: Alpheidae)

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ABSTRACT

Snapping shrimps in the genus *Alpheus* Fabricius, 1798 have long been a model system in which to study symbiotic relationships, especially the mutualism between burrowing shrimps and goby fishes. There has never been a comprehensive worldwide phylogeny of goby-dwelling snapping shrimp, however, hindering evolutionary studies of these symbioses. We examine phylogenetic relationships in the *Alpheus brevirostris* (Olivier, 1811) group, which is comprised of primarily burrowing species of snapping shrimps, many of which live in mutualistic partnership with gobies, and contains many of the most well-studied taxa in goby-shrimp symbioses. We first delimited cryptic species using COI data, which indicated multiple cryptic species of *Alpheus.* We then constructed a multi-locus phylogeny of species in the *A. brevirostris* group and several closely related species of *Alpheus,* and used fossil and transisthmian calibration points to construct a chronogram and date the origins of major clades. Our phylogeny confirmed previous work indicating the *A. brevirostris* group was paraphyletic, grouping in three major clades which diverged between 11.2 to 16.9 mya. Together, these data provide a phylogenetic framework for future taxonomic and evolutionary work on the origins and extent of the shrimp-goby and shrimp-echiuran symbioses.

KEYWORDS: Crustacea; goby-shrimp symbioses; snapping shrimps; species delimitation

INTRODUCTION

Snapping shrimps in the genus *Alpheus* have long been a model system to study speciation (Knowlton, 1993; Hurt *et al.,* 2013; Alves *et al.,* 2024), morphological evolution (Anker *et al.,* 2006; Kaji *et al.,* 2018), and the ecology and evolution of symbiosis (Karplus, 1987; Karplus & Thompson, 2011; Thompson *et al.,* 2013). *Alpheus* is an exceptionally diverse group, however, and also illustrates the taxonomic challenges of studying evolution. There are currently over 330 species described in the genus (WoRMS, 2025), with numerous cryptic species complexes in need of revision (Anker, 2001a, 2012, 2024; Anker *et al.,* 2007, 2008, 2009; Bracken-Grissom & Felder, 2014). The genus was initially subdivided into seven different informal species groups (Coutière, 1905, 1899) based primarily on morphological traits of the frontal region (e.g. rostrum) and major cheliped (*A. edwardsii* Audouin, 1826, *A. sulcatus* Kingsley, 1878, *A. obesomanus* Dana, 1852, *A. crinitus* Dana, 1852, *A. macrocheles* (Hailstone, 1835), *A. brevirostris* (Olivier, 1811), and *A. diadema* Dana, 1852 species groups). Two further species groups were added more recently by Anker *et al.* 2009 (*A. levisculus* Dana, 1852 group) and Anker 2020a (*A. paracrinitus* Miers, 1881 group). Subsequent phylogenetic work indicated that most species groups were paraphyletic, except for the *A. macrocheles* group (Williams *et al.,* 2001; Hurt *et al.,* 2021). Given that many of the morphological features used to define species groups in *Alpheus* (such as modifications of the rostro-orbital region and snapping claw) may also show adaptations to host or habitat use, the paraphyly of many species groups may be linked to host- or habitat-related morphological convergence (Hurt *et al.,* 2021). The most recent phylogeny of this genus only contained about

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20% of described diversity (Hurt *et al.,* 2021), however, with many groups underrepresented, making it difficult to test these ideas on a broader scale.

The *Alpheus brevirostris* species group (Fig. 1) is a particularly noteworthy species group, and well-studied since many species dig burrows and live in symbiosis with gobies (summarized in Karplus, 1987; Karplus & Thompson, 2011) or echiuran worms (Anker *et al.,* 2005, 2007; 2015). The *A. brevirostris* group includes about 50 species, and is composed primarily of burrowing or burrow-dwelling species with a distinct set of morphological characters (Coutière, 1899; Banner & Banner, 1982). These characters include 1) absence of orbital teeth (except in one species); 2) laterally "compressed" major chela, somewhat quadrangular in cross-section, without or with a minimum of sculpture, and with typically truncate or reduced dactylar plunger; and 3) the walking legs (third to fifth pereiopods) with simple or spatulate dactyli (Banner & Banner, 1982). This group contains numerous species that dig burrows in soft sediments and live in obligate or facultative symbioses with gobies, and some of these morphological characters are likely related to burrowing behavior. Other members of the *A. brevirostris* group (e.g. *A. glaber* (Olivi, 1792); *A. richpalmeri* Anker, 2020b; *A. heterochaelis* Say, 1818 construct burrows in soft sediments in both shallow and deeper water, but do not associate with gobies (Dworschak & Ott, 1993; Hayashi and Nagata, 2000; Komai & Ohtomi, 2018; Anker, 2020b).

Previous phylogenetic and taxonomic work on species complexes within the *A. brevirostris* group, such as investigation of the *A. floridanus* Kingsley, 1878 species complex, uncovered several new species (Bracken-Grissom & Felder, 2014; Bracken-Grissom *et al.,* 2014). Despite decades of ecological work on the goby-shrimp symbioses, there has never been a phylogeny focused on goby-dwelling shrimps worldwide, nor a comprehensive attempt at species delimitation in this group. The most recent phylogenomic tree of *Alpheus*, Hurt *et al.* (2021) demonstrated that the majority of the *A. brevirostris* group (including the goby-associated species) formed a monophyletic group, while the *A. barbatus* complex containing symbionts of echiurans (*A. naos* Anker, Hurt & Knowlton, 2007 and *A. barbatus* Coutière, 1897a) formed a separate clade nested within members of the *A. edwardsii* group (Clade VII). Somewhat surprisingly, *A. glaber* (an eastern Atlantic member of the *A. brevirostris* group living on soft bottoms at moderate depths to 140 m), branched out independently from other *A. brevirostris* group members. Within Clade VIII, which contained the bulk of species assigned to the *A. brevirostris* group, obligate associations with gobies seem to have evolved at least twice independently (Hurt *et al.,* 2021); mutualisms with shrimp (*Alpheus*) have evolved at least three times independently within Gobiidae (Thacker *et al.,* 2011). It must be noted that Hurt *et al.*'s (2021) analysis included only 14 of the 50 described members of the *A. brevirostris* group, and did not include goby-associated species from the *A. edwardsii* group such as *A. randalli* Banner & Banner, 1980. Because of the paraphyly of the *A. brevirostris* group, any tree targeting this group would also have to include closely related lineages, such as members of the *A. edwardsii* group (Clades IV and VII in Hurt *et al.,* 2021) and the *A. diadema* and *A. paracrinitus* groups (Clade V).

Along with the phylogenetic challenges of reconstructing the paraphyletic relationships among species in the *A. brevirostris* group, there are also multiple cryptic species complexes and taxonomically unresolved names in this group (Anker, 2001b), including among species that live symbiotically with gobies (Thompson *et al.,* 2013). Since Anker's (2001a) preliminary and now outdated list of species complexes in *Alpheus,* several species complexes in the *A. brevirostris* group have been partly resolved. This is the case, for example, of the *A. floridanus* complex (Bracken-Grissom & Felder, 2014; Bracken-Grissom *et al.,* 2014; Anker, 2020b), and the *A. djeddensis* Coutière, 1897b – *A. djiboutensis* De Man, 1909b complex (Anker, 2024). Several presumed species complexes in the *A. brevirostris* group remain to be addressed (Anker, 2020b, 2022a, b; Purushothaman *et al.,* 2021).

We had two major goals. First, we delimited potential cryptic species in multiple species complexes (including material identified as *A. rapax* Fabricius, 1798, *A. djeddensis, A. djiboutensis, A. rapacida* Chace, 1988, and *A. longipalma* Komai & Ohtomi, 2018) by conducting a broad-scale sequencing study (using the COI barcoding gene) of specimens in the *A. brevirostris* group. We also used targeted sampling to map these species to recent species descriptions (Anker, 2020b, 2022a, b; Purushothaman *et al.,* 2021), and ecological studies of goby-shrimp symbioses (Thompson *et al.,* 2005, 2013). Second, we built a multi-gene phylogeny of the *A. brevirostris* group, using the molecular operational taxonomic units (MOTUs) from the species delimitation analysis and sequencing those taxa for multiple genes (COI-5, 16S, 12S, and 28S). We also included non-burrowing species from other groups of *Alpheus* that have been shown to be closely related to the *A. brevirostris* group (Hurt *et al.,* 2021), and a selection of burrowing or burrow-dwelling species outside of the *A. brevirostris* group.

MATERIALS AND METHODS

We used shrimp specimens from recent field expeditions (Panama, Guam, Saudi Arabia) by the authors, as well as museum specimens, primarily from the Florida Museum of Natural History (FLMNH), Oxford University Museum of Natural History (OUMNH), and Muséum national d'Histoire naturelle, Paris (MNHN). For museum specimens, we targeted those included in recent taxonomic descriptions (Anker, 2022a, b, 2024) and species checklists (Anker & De Grave, 2016). We also included several specimens with provisional names, collected during ecological studies of shrimp-goby associations (Thompson *et al.,* 2005, 2013; Thacker *et al.,* 2011). Sampling sampling (Supplementary material Table S1) included several species from the *A. brevirostris* species group, as well as species from several other species groups of *Alpheus,* that branched adjacent to burrowing species in a recent phylogeny (Hurt *et al.,* 2021), primarily from the *A. diadema* and *A. edwardsii* species groups. The related alpheid *Synalpheus belizensis* Anker & Tóth, 2008 was used as an outgroup.

We extracted DNA from all specimens using a Qiagen Blood and Tissue kit (Hilden, Germany) under standard conditions. We sequenced specimens for four different loci: the mitochondrial cytochrome oxidase I gene (COI, ~658 bp

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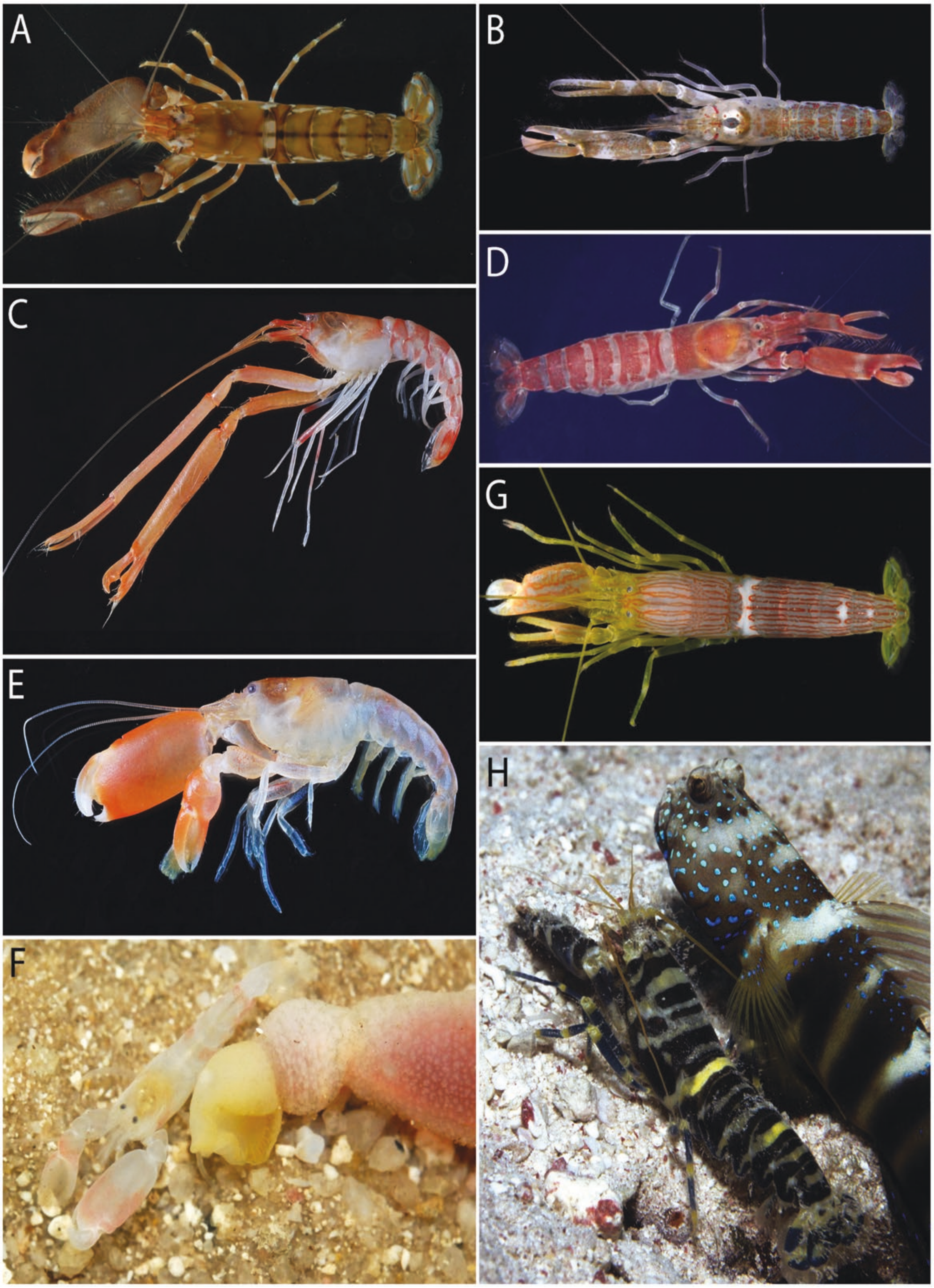

Figure 1. Representative members of the *Alpheus brevirostris* species group. *A. novaezealandiae*, New Zealand, living under rocks (**A**); *A. hephaestus*, Pacific Panama (**B**); *A. longipalma*, off Taiwan, deep-water species (**C**).; *A. glaber*, France (Mediterranean) (**D**); *A. barbatus,* Taiwan (**E**) and eastern Australia (**F**), symbiotic with echiurans (in **F**); *A. thompsoni,* Saudi Arabia (Red Sea), symbiotic with gobies (**G**); *A. tigrinus,* Egypt (Red Sea), symbiotic with gobies (**H**). Photographic credits: R.B. Taylor (A); A. Anker (B, F, G); T.Y. Chan (C, E); J. Lecomte (D); R.F. Myers (H).

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of the 5′ region used in barcoding); the mitochondrial large-subunit 16S rRNA gene (~510 bp); the mitochondrial 12S rRNA gene (12S), and the nuclear 28S rRNA gene. For COI, to avoid amplifying mitochondrial COI pseudogenes in *Alpheus* (Williams & Knowlton, 2001), we used a new forward primer to amplify the 5′ barcoding region of COI (Alp-202F: 5′ TAGCCTTCAAAGTTTCCAATAGGG- 3′) that targeted the 5′ end of the COI gene along with a ~200 bp region of the intron upstream of the COI gene (Alves *et al.*, 2024). This was typically paired with the FISH R2 primer (Zuccon *et al.*, 2012), and sequences generated with Alp-202F were trimmed to remove the 200 bp non-coding region on the 5′ end before alignment. For some specimens that did not amplify using these genes, we used different combinations of mini-barcode primers (mlCOIintF, mlCOIintR) and degenerate COI primers (jgHCO2198, jgLCO1490), and worked under the suggested annealing temperatures and PCR conditions in the reference papers (Geller *et al.*, 2013; Leray *et al.*, 2013). For 12S, we used primer sets and PCR conditions from Casaubon *et al.* (2023), and for 16S, we used the 16sar/16S-1472 primers and PCR conditions described in Hultgren *et al.* (2014). For 28S, we used the C1/D2 primers and PCR conditions described in Aznar-Cormano *et al.* (2015). PCR products were purified using a shrimp alkaline phosphate exonuclease protocol (ThermoFisher, Waltham, MA, USA) and sequenced for forward and reverse sequences using an ABI 3730XL sequencer at MCLab (South San Francisco, CA, USA).

As we used the cytochrome oxidase I (COI) gene for species delimitation analyses, we constructed a COI gene tree using sequences generated, as well as COI sequences from GenBank and BOLD, to assign species to molecular operational taxonomic units (MOTUs). Consensus (forward and reverse) COI sequences for each locus were aligned using MUSCLE (Edgar, 2004) implemented on MEGA X (Stecher *et al.*, 2020). We translated all COI sequences to amino acids to check for stop codons (none were detected) and calculated the most likely model of nucleotide substitution using jModelTest2 (Darriba *et al.*, 2012), implemented on the CIPRES server (Miller *et al.*, 2010). A Bayesian COI gene tree was then built using this dataset, coding all gap positions as missing data, and using the general model parameters from jModeltest (model, shape of rate distributions), while allowing MrBayes to estimate specific model parameters (base frequencies, nucleotide substitution rates, proportion invariable sites). We ran Markov Chain Monte Carlo (MCMC) searches with four chains for 1×10^9 generations, discarding the first 25% of the samples as burn-in, and used the program Tracer v1.72 (Rambaut *et al.*, 2018) to check for convergence.

We used three molecular species-delimitation analyses, all of which utilize data from a single locus (COI), to determine MOTUs: General Mixed Yule Coalescent (GMYC) (Pons *et al.* 2006), Assemble Species by Automatic Partitioning (ASAP) (Puillandre *et al.*, 2021), and Bayesian implementation of the Poisson Tree Processes analysis (bPTP) (Zhang *et al.*, 2013). GMYC analyses were conducted on R using the *splits* package. ASAP analyses were implemented on an online server (https://bioinfo.mnhn.fr/abi/public/asap/) using a Kimura (K80) substitution model and a TS/TV ratio (2.29) calculated on the aligned file using MEGA. bPTP analysis, which is a coalescent method, utilized our Bayesian COI tree (Fig. 2) as an input tree, and was conducted on the online bPTP server (https://species.h-its.org/). For bPTP analyses, we used 100,000 MCMC generations, the thinning parameter set to 100, and a burn-in of 0.25; *Synalpheus belizensis* was specified as the outgroup.

We constructed a consensus species tree for our samples using all of four loci (COI, 16S, 12S, and 28S). For each locus, we cleaned and aligned sequences and determined the model of evolution using methods described for COI above. For 28S data, we used GBlocks v. 0.91.1 (Castresana, 2000; Talavera & Castresana, 2007) to trim the original 833 aligned positions to 646 bp (minimum length of block = 5, allowed gap positions = all). We first ran gene trees (constructed with a single locus) for each of these loci to check for unusual taxon placements among trees. We constructed a Bayesian consensus tree using MrBayes 3.2.7a (Ronquist & Hulsenbeck, 2003; Ronquist *et al.*, 2012), implemented on the CIPRES server (Miller *et al.*, 2010). The Bayesian consensus tree was used as the input topology for the divergence time analysis. As many of the COI MOTUs were based on GenBank sequences (i.e. without access to the sequenced specimen), not all of the MOTUs were included in the four-locus consensus tree. For the consensus tree, we allowed some missing data, and included all taxa for which we had at least two out of four sequenced loci; gap positions were coded as missing data. We ran Markov Chain Monte Carlo (MCMC) searches with four chains for 2×10^8 generations, sampling the tree distribution every 1,000 generations and discarding the first 25% of the samples as burn-in. GenBank accession numbers are listed in Supplementary material Table S1; nucleotide substitution models and sequence alignments are available from the first author (KMH) upon request.

Divergence times were estimated using the Bayesian MCMC method as implemented in PhyloBayes v4.1c (Lartillot *et al.*, 2013). The Bayesian consensus tree described above (Fig. 2) was used as the input topology for the divergence time analysis. Three calibration intervals were applied to date specific nodes based on three transisthmian species pairs. Divergence times for these three sister-species pairs (*A. javieri* Anker, Hurt & Knowlton, 2009/*A. hebes* Kim & Abele, 1988, *A. colombiensis* Wicksten, 1988/*A. estuariensis* Christoffersen, 1984, and *A. millsae* Anker, Hurt & Knowlton, 2009/*A. nuttingi* (Schmitt, 1924)) were calibrated based on the final closure of the Isthmus of Panama, approximately 3 mya) (Knowlton & Weigt, 1998; Lessios, 2008). A range of 3–9 million years was used as a prior for these nodes. For the root, a log-normal prior was set with bounds fixed at 27 mya, based on estimates for the split of *Synalpheus* from *Alpheus* estimated by Hurt *et al.* (2021). We assumed a log-normal, autocorrelated, relaxed clock model for the divergence time estimation. Additional priors included a birth-death process and soft bounds for calibrations (-sb) to allow flexibility in divergence estimates. The MCMC chain was run for 200,000 generations with a 10% burn-in. Convergence of the MCMC chain was assessed by plotting the log-likelihood values over the number of iterations to ensure stationarity and robust posterior sampling.

RESULTS

Overall, our COI dataset included 177 *Alpheus* barcodes, including 115 new sequences generated for this study. The three different molecular species delimitation analyses (GMYC, ASAP, bPTP) we used generally concurred on species groupings,

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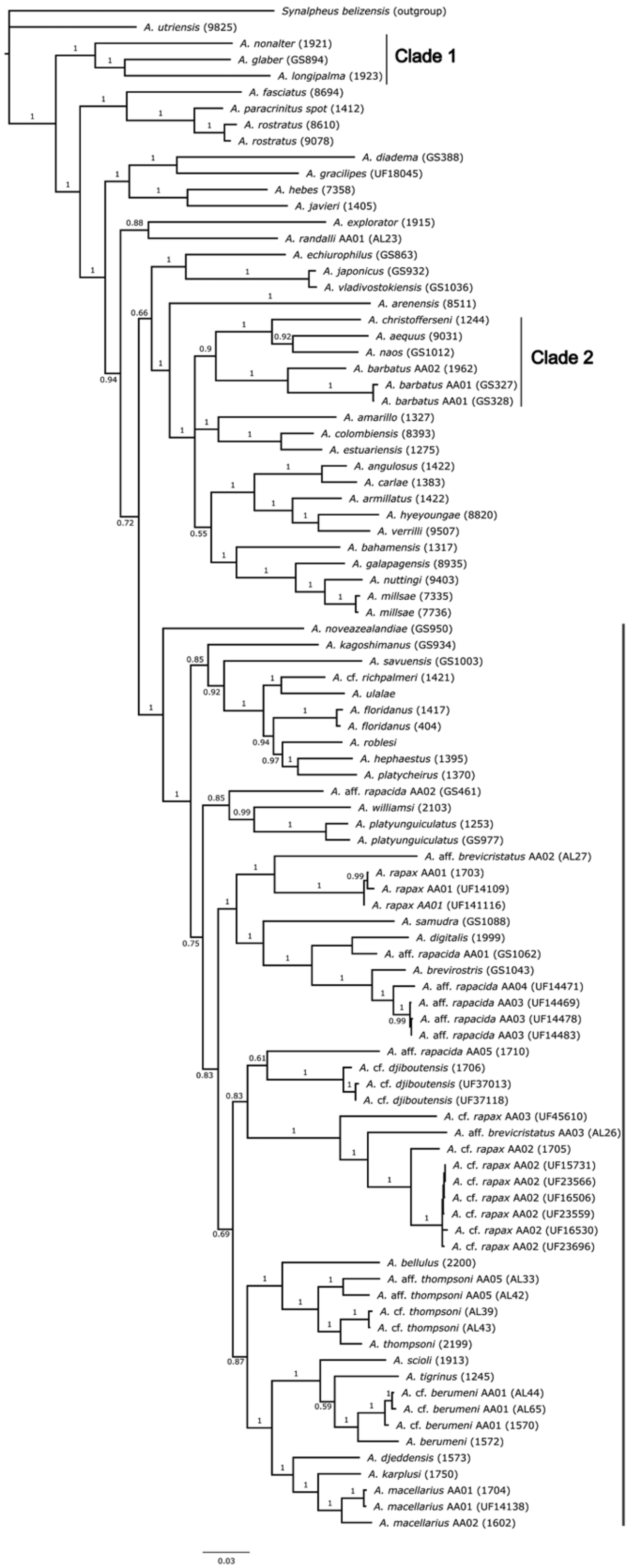

Figure 2. Bayesian consensus phylogenetic tree of the *Alpheus brevirostris* group, based on four loci (COI, 16S, 28S, 12S). Taxon names include species, followed by tree identifier (see Supplementary material Table S1) in parentheses. Numbers above or below each node indicate Bayesian posterior probability values. *Synalpheus belizensis* is the outgroup.

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though bPTP delimited more species (89) (Supplementary material Fig. S2) than ASAP analyses (83, threshold = 0.045, best score = 4.0) or GMYC analyses (82) (Supplementary material Fig. S2). Potential cryptic species complexes were found for many taxa, including *A. barbatus, A. rapax, A. rapacida, A. brevicristatus* De Haan, 1844, *A. longipalma, A. randalli,* and *A. nonalter* Kensley, 1969 (Supplementary material Fig. S2).

As expected from prior work (Hurt *et al.,* 2021), the consensus time tree indicated that the *Alpheus brevirostris* species group was paraphyletic, with members of this group recovered in four different regions of the tree. These are specified on the Bayesian tree with Bayesian posterior probabilities (bpp) (Fig. 2) and the chronogram with dated notes (Fig. 3). The first clade, Clade 1, diverged ~12.6 ± 4.2 mya, is supported by a bpp = 1. Clade 1 is composed of three species found in deeper water (38 m to > 300 m) in the eastern Atlantic (*A. glaber*) and Indo-West Pacific (*A. longipalma* and *A. nonalter*) (Anker, 2001b; Komai & Ohtomi, 2018). The little-known *A. explorator* Boone, 1935, another deep-water (> 250 m) member of the *A. brevirostris* group, was found nested within a clade containing part of the *A. edwardsii* group. The pantropical *A. barbatus* species complex (Anker *et al.,* 2007) forms Clade 2, which diverged ~11.2 ± 2.8 mya, and is supported by a bpp = 0.9. Clade 2 contains species associated with echiuran worms, as shown in previous studies (Anker *et al.,* 2015; Hurt *et al.,* 2021). Finally, the bulk of the species originally assigned to the *A. brevirostris* group, including all goby-associated snapping shrimps, group into Clade 3, with an approximate divergence date of 16.9 ± 3.4 mya. Bayesian posterior probability for Clade 3 was high (bpp = 0.99), though support for other deep nodes within this clade was < 0.95, suggesting that the exact branching patterns need further refinement. There was strong support (bpp = 1) for the *A. floridanus* species complex (Bracken-Grissom & Felder, 2014; Bracken-Grissom *et al.,* 2014).

DISCUSSION

Our phylogenetic analysis indicates that the *Alpheus brevirostris* group is paraphyletic, with members occurring in four distinct clades worldwide, corroborating previous phylogenetic work on *Alpheus* (Hurt *et al.,* 2021). Our study also delineated several potential cryptic species complexes within the *A. brevirostris* group, as noted by prior studies (Anker, 2001a, 2022a, b, 2024). Together, these provide preliminary data for future taxonomic work on the group, as well as a phylogenetic framework with which to investigate the evolution of ecological traits within the *A. brevirostris* group, such as goby-shrimp symbioses.

Species groups in *Alpheus,* including the *A. brevirostris* group, are informal taxonomic entities based on broad similarities in claw and body shape (Coutière, 1905, 1899), and are only useful as a first step in the species identification process in this challenging and speciose genus, thus it is not surprising that we found this group to be non-monophyletic. Many (but not all) of the species in the *A. brevirostris* group are burrowing species, who use their larger (major) claw to excavate and maintain burrows. Paraphyly of this group could result from convergent evolution of similar morphology in response to habitat use (e.g., burrowing), as suggested by (Hurt *et al.,* 2021). Although we used a much larger sample of species in our current tree, many of the species used here were also included in the phylogenomic analysis of Hurt *et al.* (2021: fig. 3), and we found broadly similar branching patterns. For example, *A. glaber* (Clade I in our tree), which occurs in the eastern Atlantic and Mediterranean at moderate depths (38–140 m), also grouped in a distinct clade in Hurt *et al.,* (2021). In our tree, *A. glaber* grouped with two other deep water species from the *A. brevirostris* group, *A. longipalma* and *A. nonalter* (Figs. 2, 3), that were included in our study (but missing from Hurt *et al.,* 2021). In both studies, the *A. barbatus* complex (Clade 2 in our tree) formed a sister clade to several species from the *A. edwardsii* group that also occur in the Tropical Eastern Pacific and Western Atlantic regions (e.g. *A. armillatus* H. Milne Edwards, 1837, *A. nuttingi*). By far, the vast majority of *A. brevirostris* group members were in the large Clade 3 in our study (Clade VIII in Hurt *et al.,* 2021). This clade consisted primarily of species from the Indo-West Pacific region, but also included the *A. floridanus* species complex (Bracken-Grissom & Felder, 2014; Bracken-Grissom *et al.,* 2014) from the West Atlantic and Tropical Eastern Pacific. Clade 3 included many species known to associate with gobies, such as *A. tigrinus* Anker, 2024, *A. thompsoni* Anker, 2022a, and *A. karplusi* Anker, 2022b. This clade also included many species not known to associate with gobies, such as the deep-water *A. kagoshimanus* Hayashi & Nagata, 2000 and *A. samudra* De Grave, Krishnan, Kumar K.P. & Christodoulou, 2020, the shallow-water *A. novaezealandiae* Miers, 1876, and several species (e.g. *A. rapax* AA01) for which presence or absence of goby symbionts is unknown. An extensive analysis of goby-shrimp symbioses will require additional details of the ecology of species in this clade.

Based on the chronogram, the largest clade of species from the *A. brevirostris* group (Clade 3, containing the majority of the goby species) diverged an estimated 16.9 ± 3.4 mya, during the Miocene. This time period aligns with fossil evidence of *Alpheus* claws recovered from multiple locations around the world, suggesting a major radiation of this group ~18 mya, with the earliest fossils dating to 27–28 mya (Hyžný *et al.,* 2017; Lima *et al.,* 2020). Estimates of the origin of the family Alpheidae, based on molecular clock analyses across decapods more broadly, suggest an earlier divergence (125–150 mya) (Bracken *et al.,* 2010; Wolfe *et al.* 2019).

Our molecular species delimitation analyses (Supplementary material Fig. S2) indicated the presence of many cryptic, potentially new species (MOTUs) in the *A. brevirostris* species group. Some of these MOTUs are based on sequences from GenBank, or from specimens with tentative and/or provisional names in museum databases (such as quick and unverified field identifications). For example, several specimens (initially identified as *A. rapax, A. rapacida,* and *A. brevicristatus*) did not group monophyletically in our COI or consensus trees. There were three separate clades (MOTUs) of specimens initially labeled *A. rapax,* which were not closely related to each other (Figs. 2, 3; Supplementary material Fig. S2). The *A. rapax* AA01 clade included a specimen from India, labeled in GenBank as *A. platycheirus* (GenBank OM791702; Supplementary material Table S1); *A. platycheirus* is a well-characterized species from the Western Atlantic (Bracken-Grissom & Felder, 2014; Bracken-Grissom *et al.,* 2014), and this specimen is closely related to other species (provisionally named *A. rapax* AA01) from Singapore

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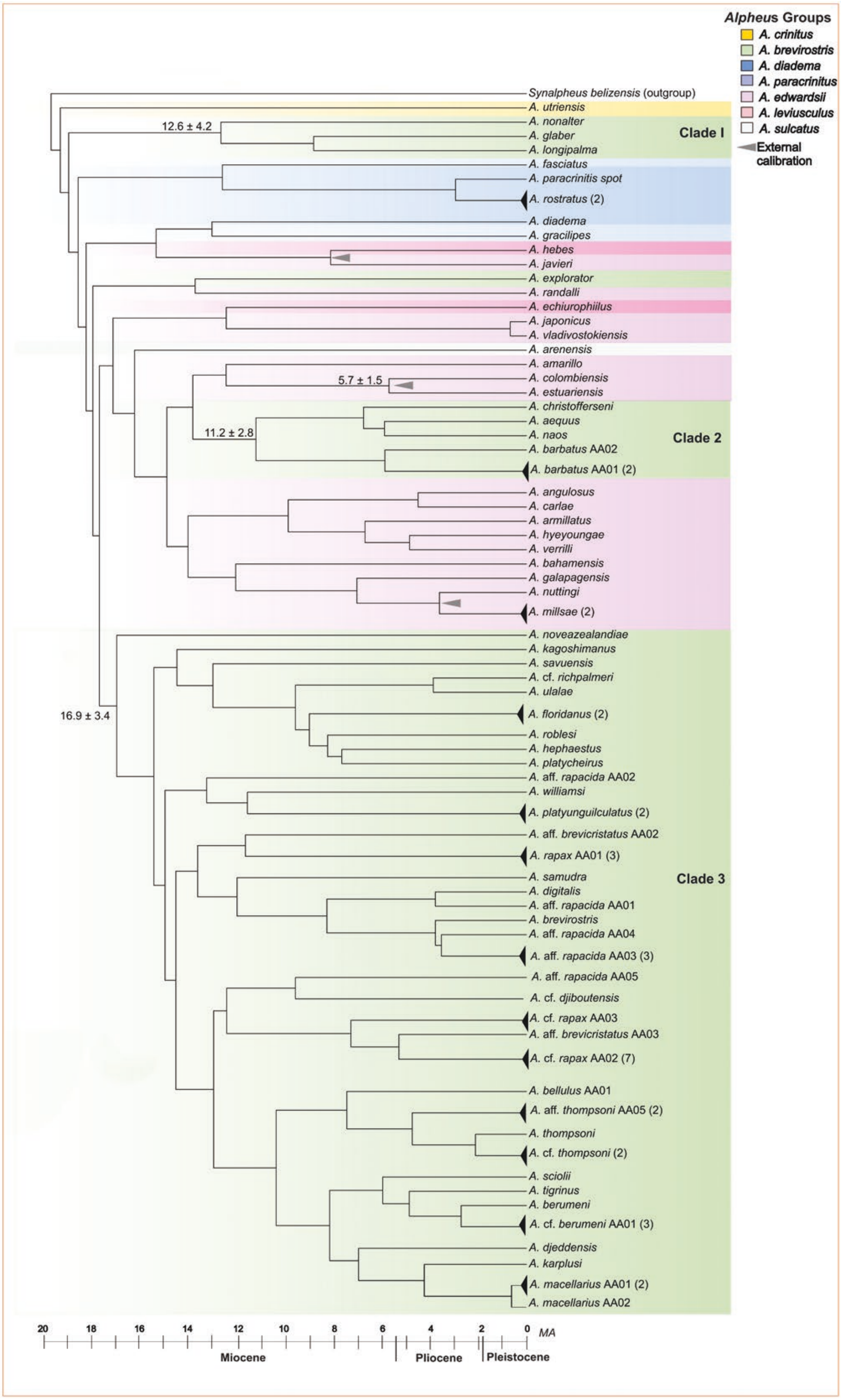

Figure 3. Chronogram of the *A. brevirostris* group with divergence time estimates, based on the Bayesian guide tree (see Fig. 2), with node ages estimated in PhyloBayes. Gray triangles indicate nodes with external calibrations; overlay colors indicate *Alpheus* groups. Parentheses after some taxa indicate multiple individuals sampled per species. Divergence time estimates for major clades are indicated at certain nodes. The three main clades of species in the *A. brevirostris* group are marked.

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and Madagascar (Supplementary material Table S1, Fig. S2). Specimens labeled *A. brevicristatus* formed four separate, unrelated MOTUs in the species delimitation tree (Supplementary material Fig. S2). Two of those clades resulted from GenBank sequences (*A. brevicristatus* AA05, Korea; *A. brevicristatus* AA04, Korea, Japan, China), and were only included in the COI species delimitation tree; the second of these (AA04) most likely represents *A. brevicristatus* s. str. Two others (*A.* aff. *brevicristatus* AA02, *A.* aff. *brevicristatus* AA03) were based on specimens used in prior work on goby-shrimp symbioses (Thompson *et al.*, 2013). Most of these provisional names (see above) will likely change upon examination of vouchered museum specimens (and color photographs, where available) associated with the sequences (Supplementary material Table S1).

Although genetic barcoding of COI has historically been a useful tool in delimiting potential cryptic species, delimitation analyses based only on a single mitochondrial gene may overestimate the number of species. For example, many marine species exhibit geographic structuring in the COI gene (e.g. allopatric lineages resulting in >1 MOTU), but still experience low levels of gene flow among lineages, and may not be reproductively isolated (Meyer *et al.*, 2005; Lasley *et al.*, 2023). In our study, species delimitation indicated several potential species complexes, which included allopatric MOTUs (strong geographic structuring) that may or may not correspond distinct species. These included several clades, such as *A. barbatus, A.* cf. *rapax* AA02, *A. bellulus* Miya & Miyake, 1969, *A. longipalma,* and *A. nonalter* (from the *A. brevirostris* group), as well as *A. randalli* from the *A. edwardsii* group (Supplementary material Fig. S2). For example, specimens identified as *A. longipalma* formed three geographic MOTUs (from Papua New Guinea, Taiwan, and the Solomon Islands), separated by 6.4%–26% divergence in COI (Supplementary material Fig. S2). Likewise, *A. berumeni* Anker, 2024, from Saudi Arabia, was 7.3% divergent in COI from a clade of specimens (*A.* cf. *berumeni* AA01) from Moorea (French Polynesia) and Fiji (Supplementary material Fig. S2). Similarly, *A. barbatus* formed a monophyletic clade with three geographically distinct MOTUs (AA01, Moorea; AA02, Taiwan, eastern Australia; AA03, Guam). Two of the three species delimitation analyses (ASAP and bPTP) split *A.* cf. *rapax* AA02 (Guam) as a separate species from other *A.* cf. *rapax* AA02 species (from Moorea and Hawai‘i; Supplementary material Fig. S2), though GMYC analyses indicated they were a single species. Finally, species delimitation analyses split *A. bellulus* (AA01, Oman; AA02, China), and *A. platyunguiculatus* (AH Banner, 1953) (cf. *platyunguiculatus*, Lombok, Indonesia; *platyunguiculatus*, Moorea) each into two separate MOTUs. In the cases above, additional morphological and ecological information (e.g., goby partners) is needed to determine whether different geographic clades are distinct allopatric species.

In a few cases, species delimitation analyses indicated two or more distinct MOTUs that were not supported by additional traits (color and/or morphological data). MOTUs delimited two sympatric species (sister clade COI divergence 4.8%) in *A. thompsoni*, but color patterns are identical between MOTUs, suggesting that *A. thompsoni* and *A.* aff. *thompsoni* AA05 may represent a single species. In *A. macellarius* Chace, 1988, species delimitation analyses delimited two (ASAP, GMYC) or three (bPTP) allopatric MOTUs, but these MOTUs are similar in color, and recent morphological examination of the specimens indicates they are a single species (Anker, 2024). Finally, in the *A. japonicus* Miers, 1879/ *A. vladivostokiensis* (Vinogradov, 1950) clade, MOTUs for ASAP and bPTP analyses delimited only a single cluster, although these two species have distinct morphological characters and very different color patterns (Anker *et al.*, 2016).

Additional taxon sampling of specimens in the *A. brevirostris* group could help resolve evolutionary relationships of this group. Recent work in the Red Sea and Oman resulted in descriptions of several new species of goby-associated species of *Alpheus* and confirmed the taxonomic identity of *A. djeddensis* (Anker, 2024). Four of the Red Sea species (*A. djeddensis*, *A. tigrinus*, *A. berumeni* and *A. cf. djiboutensis*) in Anker (2024) were included in our study (Supplementary material Table S1). There are more species of the *A. brevirostris* group that were not included in our study, however, including the largest-known goby shrimp, *A. fenneri* Bruce, 1994. There are also many noteworthy deep-water species in the *A. brevirostris* group (e.g. *A. macroskeles* Alcock & Anderson, 1899*; A. pustulosus* Banner & Banner, 1968*; A. acutocarinatus* De Man, 1909a; *A. alaincrosnieri* Anker, 2020a; *A. migrans* Lewinsohn & Holthuis, 1978, *A. talismani* Coutière, 1898) that we could not include, primarily due to the lack of fresh specimens for sequencing. Additional sampling of goby-associated shrimps, including recently collected specimens identified as *A. rapax, A. rapacida*, *A. brevicristatus*, and *A. brevirostris*, could help resolve these difficult groups. Such work could be ideally done in conjunction with examination of morphology, color patterns, and ecology, all of which is necessary to elucidate the origin, biogeography, and timing of goby-shrimp symbioses.

The relationship between gobies and shrimps is a model system to study mutualistic interactions (summarized in Thompson *et al.*, 2005, 2013; Karplus & Thompson, 2011), and the present study provides a preliminary phylogenetic framework for future taxonomic and evolutionary work on shrimp-goby symbioses. The pairing between species of gobies and shrimps is neither random (Karplus, 1981; Karplus *et al.*, 1981) nor nested (Thompson *et al.*, 2013). Some partnerships are highly specialized (e.g. the goby *Lotilia graciliosa* Klausewitz, 1960 and the shrimp *Alpheus karplusi* pair exclusively with one another) while others are quite general (e.g. *Amblyeleotris gymnocephala* (Bleeker, 1853) pairs with at least five species of alpheid shrimps; Thompson *et al.*, 2013). Furthermore, obligate goby and shrimp interactions are underpinned by tactile communication where the goby informs the shrimp of the level of danger in the environment through tail flicks and body movements (Karplus *et al.*, 1979). When a shrimp is outside of the burrow, it maintains antennal contact with the goby almost all of the time. As with partner selection, the nature of this touch-based language differs among species, and Thompson *et al.* (2013) speculated that the capacity of a given shrimp to understand a particular species of goby may constrain species pairings. Now that an alpheid phylogeny is available, it will be possible to couple it with the goby phylogeny (Thacker *et al.*, 2011) and discern patterns of coevolution that drive partner selection and communication in this iconic mutualism. Future research on this system has the potential to greatly augment our general understanding of mutualisms.

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SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Table. Table of specimens used in the study, localities, and GenBank accession numbers.

S2 Figure. COI Bayesian gene tree MOTUs delimited by GMYC, ASAP and bPTP species delimitation analyses.

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