

Research Article

Phylogeny of Gobiidae and identification of gobiid lineages

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(Received 29 June 2011; revised 1 September 2011; accepted 22 September 2011)

The teleost family Gobiidae includes at least 1120 described species of fishes, distributed worldwide in both tropical and temperate habitats. The majority of gobies inhabit marine environments, in particular Old World coral reefs. However, a radiation of gobiids inhabits the rivers and near-shore habitats of Europe and Asia, and a variety of genera are also found in the seas of the New World. This study builds on previous work in which gobiids were placed among their gobioid relatives by adding additional taxa as well as additional markers, providing a much more comprehensive portrait of gobiid intrarelationships and including all major lineages of gobies. We used DNA sequences from both mitochondrial (ND1, ND2, COI) and nuclear (RAG2, Rhodopsin, RNF213) genes to infer phylogeny among 127 representatives of 100 species of gobies, using two gobioid species as outgroups. We delineated 13 lineages within Gobiidae, including one clade of shrimp-associated gobies represented by the genera *Cryptocentrus*, *Mahidolia* and *Stonogobiops* and a second separate shrimp-associated goby clade including *Amblyeleotris*, *Ctenogobiops* and *Vanderhorstia*. The Mediterranean, Ponto-Caspian and Eastern Atlantic gobies are resolved in a clade along with two genera known from the Western Indian Ocean. Invasion of the New World is shown to have occurred multiple times among the sampled taxa, in the American seven-spined gobies, the *Coryphopterus*, *Lophogobius* and *Rhinogobiops* radiation (sister to *Fusigobius*) and separately in the wormfishes *Cerdale* and *Microdesmus*, resolved in a clade alongside the Indo-Pacific *Gunnellichthys*, *Ptereleotris* and *Nemateleotris*. The cosmopolitan genera *Bathygobius* and *Priolepis* represent further separate radiations, and *Lythrypnus* shows complex relationships with both *Priolepis* and *Trimma*.

Key words: Atlantic, biogeography, Caribbean, goby, Indo-Pacific, Mediterranean, Ponto-Caspian, systematics

Introduction

Gobiidae is one of the largest families of acanthomorph fishes, with at least 1120 species described in 170 genera and many more yet to be described (Thacker, 2011). Gobies are distributed worldwide, in marine, estuarine and freshwater habitats. They are generally benthic, and may occupy various niches in the substrate including the bodies or burrows of invertebrates. Gobies attain a small body size (often less than 50 mm), and most bear pelvic fins wholly or partially joined ventrally into a disc. Most species have separate spinous and rayed dorsal fins, and colouration ranges from drab to a variety of bright patterns. Gobies constitute a large portion of the fishes in both tropical and temperate near-shore marine, brackish and freshwater environments, including prominent representation on coral reefs, where they are estimated to constitute 35% of the total number of fishes and 20% of the species diversity (Winterbottom *et al.*, 2011). Small-bodied reef-dwellers such as *Eviota* species

mature rapidly, experience short lifespans (59–99 days), and so have rapid generation times (up to 7.4 generations per year; Depczynski & Bellwood, 2005, 2006). However, due to their small size and often cryptic ecologies, the full extent of gobiid diversity often goes unnoticed. These same characteristics have also hindered evolutionary and taxonomic studies of the group, but advances in molecular phylogenetics have provided a novel avenue for untangling gobioid relationships (Thacker, 2003, 2009; Thacker & Hardman, 2005).

Here we seek to determine the relationships among gobiid gobies, and to identify the lineage diversity in this speciose family. Gobiidae is used in the restricted monophyletic sense proposed in Thacker (2009), a clade composed of the former gobioid families and subfamilies Gobiinae, Microdesmidae, Ptereleotridae, Kraemeriidae and Schindleriidae. This group is sister to the clade Gobionellidae, which similarly includes the taxa Gobionellinae, Sicydiinae, Amblyopinae and Oxudercinae. These taxa were formally named in Thacker (2009), but were first delineated in an earlier study (Thacker, 2003) that was

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based on a smaller dataset and used different analytical methods. The previous molecular phylogenetic studies of Gobiiformes that included more than a few representatives of Gobiidae (Thacker, 2003, 2009) have provided several insights into relationships among gobiids, but discerning the evolution of lineages within Gobiidae was not their primary focus. In both those earlier studies, relationships among lineages within Gobiidae were poorly resolved, with weak support for relationships at the base of Gobiidae. Here we build on the gobiid sampling of those studies with additional taxa, representing all the common gobiid lineages and including the American seven-spined and Ponto-Caspian, Mediterranean and Eastern Atlantic radiations. We also augment a previously exclusively mitochondrial dataset with sequence from three nuclear genes. With this expanded taxon and marker dataset, we are able to provide a much more comprehensive accounting of gobiid relationships and evolution than previously, discerning a variety of lineages within Gobiidae and representing the entire geographic range of the family. Many of the lineages include taxa previously postulated to be related based on various explicitly quantified morphological characters, and also on more qualitative characteristics including overall shape, behaviour or ecology. We then review the genera not examined in our phylogeny, and based on previous systematic studies, seek to place each genus into one of the phylogenetically identified lineages. The delineation of these lineages reveals biogeographic and evolutionary patterns that span the diversity of the family, as well as providing identification of subsections of the remarkable diversity of gobies. We provide an updated (relative to Thacker, 2011), and categorized genus list that may be used to guide further studies of diversity and phylogeny, as well as facilitate communication in wider-ranging studies of ecology or evolution.

Materials and methods

This study combines DNA sequence data from an earlier, more widely focused phylogenetic analysis of Gobiiformes (Thacker, 2009) with additional data. New taxa were sequenced for three mitochondrial genes, and three nuclear gene fragments were added for the entire taxon set. All specimens are vouchered, most in the Natural History Museum of Los Angeles County Ichthyology Tissue Collection. Species examined, GenBank accession numbers for sequences, and tissue catalogue information for vouchers are listed in Appendix 1 (see supplementary material, which is available on the Supplementary Content table of the article's online page at <http://dx.doi.org/10.1080/14772000.2011.629011>).

Extraction of DNA from tissue and PCR were performed as described in Thacker *et al.* (2011) for three mitochondrial genes, cytochrome oxidase subunit 1 (CO1), NADH dehydrogenase subunits 1 (ND1) and 2 (ND2),

and two nuclear genes, recombination activating gene 2 (RAG2) and rhodopsin (Rho). An 840 bp fragment from the protein-coding region of RNF213 was initially amplified using the primer pair C17 F3150/C17 R4096 (Li *et al.*, 2009). Amplification of the target fragment was successful for approximately half of the taxa; those products were sequenced and aligned using MUSCLE (Edgar, 2004). Internal, gobiid-specific, internal primers were then designed by eye. Those primers were used to amplify and sequence a fragment approximately 675 bp in length, and have the following sequences: 5'-GGG AAA CNG AGC CNC ATC CNT AC-3' (forward) and 5'-TYA GCN CGK ACT CTG TAT CC-3' (reverse). PCR products were visualized, extracted and sequenced, and aligned as described in Thacker *et al.* (2011).

Bayesian phylogenetic analyses were performed in MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). The appropriate model for base substitution frequencies was determined by jModelTest (Posada, 2008), using the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC), for each gene partition as well as for the complete six-gene concatenated dataset. MrBayes searches were run for the concatenated dataset as well as a partitioned analysis run with each gene evaluated under its appropriate model. In both cases, the search consisted of 10,000,000 generations with two replicates, each with four simultaneous chains, and trees sampled every 10,000 generations.

Phylogenetic analyses were also performed using the maximum likelihood optimality criterion, implemented in the software package TREEFINDER (Jobb *et al.*, 2004). Searches were performed with a single model applied to the entire concatenated dataset (unpartitioned) as well as with separate models applied to each individual gene (partitioned). Support for both the partitioned and unpartitioned analyses was assessed by performance of 1000 bootstrap replications; the proportion of these replications supporting the figured hypothesis is shown on each node, except nodes supported by fewer than 50% of replicates, which are unlabelled. The alignment used in all phylogenetic analysis is available as listed in Appendix 2 (see supplementary material, which is available on the Supplementary Content table of the article's online page at <http://dx.doi.org/10.1080/14772000.2011.629011>).

Our phylogeny includes 58 genera of Gobiidae, or just over one third of the total 170. Using the lineages identified in our molecular phylogeny, we then review the 112 genera not sampled, in an attempt to postulate placement of the unsampled diversity among our phylogenetic lineages. Placements were made based on shared morphological characters, similarity of shape, distribution, habitat, ecology, behaviour, or any other characteristics identified or relationships advanced by the many workers that have treated all the various gobies. We present the hypothesized lineage groups in Table 1; throughout, vertebral counts are given in

Table 1. Generic groups within Gobiidae, inferred based on molecular and morphological data. Thirteen gobiid lineages are listed here, as identified in the phylogenetic hypothesis given in Fig. 1; the Mediterranean, Ponto-Caspian and Eastern Atlantic gobies are subdivided into their three component regions. Genera sequenced in this study are indicated in bold; genera not sequenced are placed into groups based on morphological similarity with sequenced genera. The sand gobies are listed but indicated with an asterisk because this group is likely part of Gobiionellidae, not Gobiidae. This table includes 169 of the 170 valid genera of Gobiidae: *Austrolethops* is not placed in a lineage and is *incertae sedis* within Gobiidae.

*SAND GOBIES

Economidichthys, *Gobiusculus*, *Hyrcanogobius*, *Knipowitschia*, ***Pomatoschistus***

MEDITERRANEAN, PONTO-CASPIAN AND EASTERN ATLANTIC GOBIES

PONTO-CASPIAN GOBIES

Anatirostrum, ***Babka***, ***Benthophilus***, *Benthophiloides*, *Caspiosoma*, ***Mesogobius***, ***Neogobius***, *Padogobius*, ***Ponticola***, ***Proterorhinus***

MEDITERRANEAN AND NORTHEAST ATLANTIC GOBIES

Aphia, *Buenia*, *Chromogobius*, *Corcyrogobius*, *Crystallogobius*, *Deltentosteus*, *Didogobius*, *Gammogobius*, ***Gobius***, *Gobiusculus*, *Lebetus*, *Lesuerigobius*, *Mauligobius*, *Millerigobius*, *Odondebuena*, *Pseudaphya*, *Speleogobius*, *Thorogobius*, *Vanneaugobius*, *Zebrus*, ***Zosterisessor***

AFRICAN GOBIES (SOUTHEAST ATLANTIC AND WESTERN INDIAN OCEAN)

Caffrogobius, ***Corygaleops***, *Croilia*, *Ebomegobius*, *Gorogobius*, *Heteroleotris*, *Nematogobius*, *Porogobius*, *Sufflogobius*, *Wheelerigobius*

AMERICAN SEVEN-SPINED GOBIES (EASTERN PACIFIC AND WESTERN ATLANTIC)

Akko, *Aruma*, ***Barbulifer***, *Bollmannia*, *Chriolepis*, ***Elacatinus***, *Eleotrica*, *Enypnias*, *Evermannichthys*, *Ginsburgellus*, ***Gobiosoma***, *Gobulus*, *Gymneleotris*, ***Microgobius***, ***Nes***, ***Ophiogobius***, *Palatogobius*, *Parrella*, *Pariah*, *Psilotris*, *Pycnomma*, ***Risor***, *Robinsichthys*, ***Tigrigobius***, *Varicus*, *Vomerogobius*

LAGOON GOBIES

Acentrogobius, ***Afurcagobius***, *Amoya*, *Ancistrogobius*, *Arcygobius*, ***Arenigobius***, *Aulopareia*, ***Cabillus***, *Echinogobius*, ***Exyrius***, ***Favonigobius***, *Gladiogobius*, *Hazeus*, *Heteroplopomus*, ***Istigobius***, *Macrodontogobius*, *Nesogobius*, ***Oplopomus***, *Oplopomops*, *Opuia*, ***Papillogobius***, *Parachaeturichthys*, *Silhouettea*, *Yongeichthys*

SILT SHRIMP GOBIES

Cryptocentrus, *Cryptocentroides*, *Flabelligobius*, *Lotilia*, ***Mahidolia***, *Myersina*, *Psilogobius*, ***Stonogobiops***, *Tomiyamichthys*

REEF SHRIMP GOBIES

Amblyeleotris, ***Asterropteryx***, ***Ctenogobiops***, ***Vanderhorstia***

SANDDIVERS

Kraemia, *Gobitrichonotus*, *Parkraemia*

FLAPHEADED GOBIES

Barbuligobius, ***Callogobius***, *Discordipinna*, *Drombus*, *Feia*, *Gobiopsis*, *Mangarinus*, *Palutrus*, *Phoxacromion*, *Platygobiopsis*

BURROWING PAIRED GOBIES

Amblygobius, ***Signigobius***, ***Valenciennea***

CORAL GOBIES

Bryaninops, ***Eviota***, ***Gobiodon***, *Kelloggella*, *Larsonella*, *Lobulogobius*, *Lubricogobius*, *Luposicya*, *Minisicya*, ***Paragobiodon***, *Phyllogobius*, *Pleurosicya*, *Sueviota*

TINY BANDED GOBIES

Egglestonichthys, *Ego*, ***Lythrypnus***, *Obliquogobius*, *Paratrimma*, ***Priolepis***, ***Trimma***, *Trimmatom*, *Tryssogobius*

CRESTED GOBIES

Coryphopterus, *Cristatogobius*, ***Fusigobius***, ***Lophogobius***, ***Rhinogobiops***

WORMFISHES AND DARTFISHES

Aioliops, ***Cerdale***, *Clarkichthys*, ***Gunnellichthys***, ***Microdesmus***, *Navigobius*, *Nemateleotris*, *Oxymetopon*, *Paragunnellichthys*, *Parioglossus*, ***Ptereleotris***, *Pterocerdale*, *Schindleria*

INSHORE GOBIES

Bathygobius, *Glossogobius*, *Grallenia*, ***Psammogobius***

the formula precaudal + caudal = total, and dorsal spine pterygiophore insertion patterns in the formula of Birdsong *et al.* (1988). In this formula, the first digit indicates the interneural space in which the spinous dorsal fin begins, fol-

lowed by a hyphen and then the number of pterygiophores in each successive interneural space. Thus, 3-2211 indicates a total of six dorsal spines, two in the third and fourth interneural spaces, and one each in the fifth and sixth.

Results

A total of 127 individuals representing 102 species in 60 genera (100 Gobiidae and two outgroup Gobionellidae *sensu* Thacker, 2009) were included in the analysis. The matrix consisted of 5278 aligned base pairs (bp): 978 bp of ND1, 945 bp of ND2, 1191 bp of COI, 780 bp of RAG2, 618 bp of RNF213 and 766 bp of rhodopsin.

The appropriate base substitution model for the complete dataset was determined to be GTR + I + G; the same model applied to the individual gene datasets ND1 and COI. For ND2, the GTR + G model obtained; for RAG2 and RNF213 HKY + G was selected, and for Rho, HKY + I + G. Bayesian phylogenetic analyses were run for 10 million generations (approximately 30 days) and failed to approach convergence in both the partitioned and unpartitioned analyses. Likelihood analyses for both the partitioned and unpartitioned datasets yielded hypotheses that differed only slightly, and only in the relative positions of larger subclades within Gobiidae. Bootstrap analysis of the likelihood results revealed that there was little support for relationships at the backbone of the Gobiidae tree, and confirmed that the evidence for that part of the phylogeny was scanty enough that Bayesian sampling strategies could not resolve a single optimal region of tree space. However, the lineages identified within Gobiidae are generally well-supported, and were consistently present in both partitioned and unpartitioned likelihood analyses.

The hypothesis resulting from the partitioned likelihood analysis is shown in Fig. 1. In several cases, more than one individual for a given taxon was sequenced, which validates placement of that species as well as providing evidence for species monophyly. In all but one case, multiple individuals identified as the same species grouped together, generally with very little sequence difference between them. The exception is *Valenciennesa longipinnis*, a widespread Pacific species. One of the two *V. longipinnis* individuals sampled grouped more closely to an individual of *V. strigata*, a species with an even larger range, extending throughout the Pacific and Indian Oceans. Potential causes for this result are numerous, but postulation of biological explanations is premature given the possibility of simple phylogenetic uncertainty. The node supporting the pairing has an estimated bootstrap support of 90%, and in particular the *V. strigata* branch is notably longer than those of *V. longipinnis*, potentially causing a spurious result due to uncertain resolution of a highly autapomorphic taxon.

Although recovered resolution was poor among the basal nodes of Gobiidae, our phylogeny clarifies relationships within and among smaller subgroups of gobies, and reveals lineages consisting of related genera. With this evolutionary framework, these lineages may be examined and interpreted. Thirteen separate lineages were identified among the Gobiidae sampled; 11 consisting of multiple genera, plus the single-genus lineages *Kraemeria* and *Callogobius*. Relationships among the lineages are generally poorly sup-

ported and should be considered preliminary. Many of the lineage clades identified here are supported by bootstrap percentages of 80% or above, but a few are not. In particular, the deeper splits among the lagoon gobies (including placements of *Oplopomus oplopomus*, *Arenigobius bifrenatus*, *Cabillus tongarevae* and *Acentrogobius pflaumii*), the wormfishes and dartfishes (placement of *Ptereleotris* species and *Nemateleotris magnifica*) and the American seven-spined gobies (resolution of *Microgobius microlepis*) have short internodes and low bootstrap support. In each of these cases, the poorly supported basal members are included in the described lineages, in concordance with other morphological or ecological information as discussed in the individual lineage sections. These lineages represent all the familiar groups of gobies, including Indo-Pacific shrimp gobies, coral-associated gobies, burrowing monogamous gobies, near-shore lagoon gobies, the American seven-spined gobies, the Ponto-Caspian/Mediterranean radiation, the wormfishes and dartfishes, *Coryphopterus* and its relatives, and the circumglobal *Bathygobius* and *Priolepis* lineages. Shrimp gobies were recovered in two separate clades, in accordance with another recent phylogenetic analysis (Thacker *et al.*, 2011). Invasion of New World waters has occurred multiple independent times on this hypothesis, among the American seven-spined gobies, the wormfishes (*Microdesmus* and *Cerdale*), in *Rhinogobiops*, *Lophogobius* and some *Coryphopterus*, and some species of the widespread genera *Bathygobius* and *Priolepis*. *Lythrypnus* also inhabits the western Atlantic and eastern Pacific, and is recovered as closely related to *Priolepis* and *Trimma*, species of which are all very diminutive and usually schooling or cryptobenthic in tropical reef environments.

Discussion

Our phylogenetic hypothesis (Fig. 1) resolves all but one of the gobiids sampled into a clade with shallow internodes separating the various gobiid lineages. Within Gobiidae, our hypothesis resolves three subclades, although the internodes between them are very short and poorly supported. One clade includes several Indo-Pacific genera, some of the shrimp-associated gobies, and the inshore gobies *Bathygobius* and *Psammogobius*; another small subgroup comprises the American seven-spined gobies. The third and largest subclade contains the majority of the genera, including the remainder of the New World taxa, a clade of Mediterranean, Ponto-Caspian and Eastern Atlantic taxa, and many Indo-Pacific lineages including a second clade of shrimp gobies. Overall within Gobiidae, 11 multi-genus lineages were recovered, along with isolated genera *Callogobius* and *Kraemeria*. Identification of these 13 lineages, particularly those that constitute the highly diverse Indo-Pacific reef gobies (generally, the *Priolepis* group of Birdsong *et al.*, 1988), allows interpretation of evolution and biogeography, as well as assessment of morphological patterns that could not

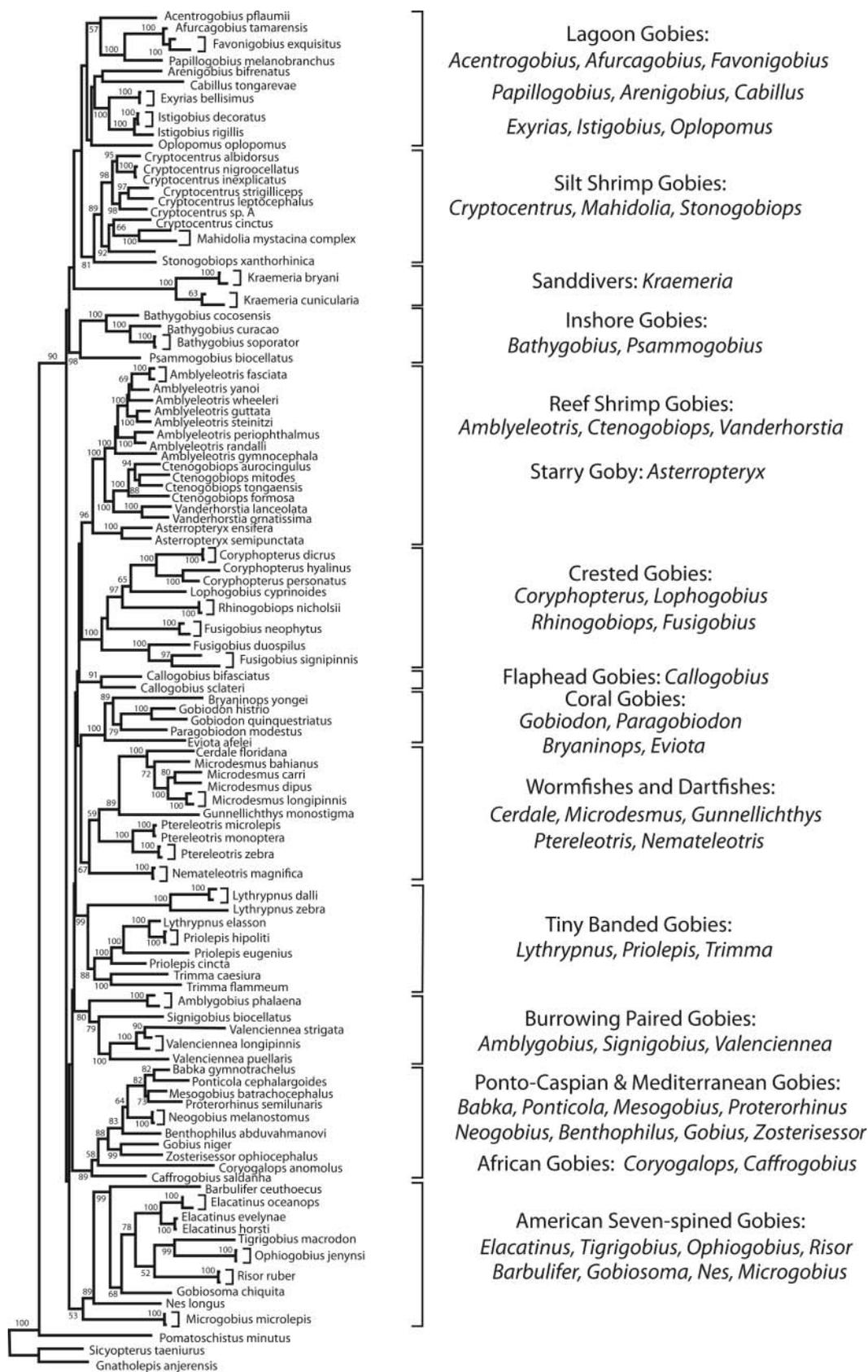


Fig. 1. Phylogenetic analysis of 100 species of Gobiidae and two outgroup Gobionellidae, based on partitioned Maximum Likelihood analysis. Numbers on nodes are bootstrap support values, shown as percentages of 1,000 replications. To the right, each larger clade is given a lineage name and the constituent genera in the hypothesis are listed.

previously be understood phylogenetically. In Fig. 1 and in the text, each clade is denoted with a lineage name that reflects common ecology, distribution or morphology for the included taxa. The names are provided for ease of communication and wherever possible, incorporate informal names already applied to lineages or their members; they are not intended to indicate that the named characteristics are unique to certain clades. Thus, the tiny banded gobies are not the only diminutive gobies with a banded colour pattern, and the burrowing paired gobies are not the only gobies who inhabit burrows. Similarly, not all lagoon gobies inhabit lagoons, not all crested gobies bear a crest, and not all coral gobies live in coral. Simply, these names enable communication and comparison better than numbers, letters or other acronyms. Given the phylogenetically identified lineages, it is also possible to postulate placement of other gobiid genera not sampled in this study, based on morphological commonalities with the sampled taxa. A list of the 13 lineages recovered in our analysis, with hypothesized placements for all gobiid genera, is given in Table 1; this table updates, expands and categorizes the list of gobiid genera given in Thacker (2011). These lineages represent reviews of character evidence and relationships hypothesized up to this point; they provide a convenient summary of knowledge, as well as facilitating meaningful communication and discussion of lineages.

Mediterranean, Ponto-Caspian and African Gobiidae

This large clade includes all the Ponto-Caspian and Mediterranean taxa sampled (except *Pomatoschistus*), with the clade of Ponto-Caspian taxa resolved as sister to the Mediterranean *Gobius* and *Zosterisessor*. Outside them, arrayed as a grade, are two genera that inhabit the inshore waters of Africa, *Caffrogobius* and *Coryogalops*. The entire large clade (Fig. 1, Table 1) is divided into its three constituent areas, in which sequenced genera along with all the additional genera postulated to be close relatives are listed. All of these Old World Gobiidae possess elevated vertebral counts compared with those of most Indo-Pacific Gobiidae (usually $10 + 16 = 26$). The African genera have 27 (rarely 28) vertebrae, the Mediterranean and North Atlantic gobies usually exhibit a vertebral count of $11 + 17 = 28$, and the Ponto-Caspian species counts are even higher, ranging from 31–35 (Hoese, 1986; Birdsong *et al.*, 1988; Simonovic *et al.*, 1996; Simonovic, 1999).

Sand gobies

The one putatively gobiid taxon placed outside all the other gobiids sampled is the Mediterranean/Eastern Atlantic *Pomatoschistus minutus*, which forms a basal grade along with outgroups *Gnatholepis anjerensis* and *Sicyopterus taeniurus* (Gobionellidae). *Pomatoschistus* and the four similar

genera *Knipowitschia*, *Gobiusculus*, *Hyracanogobius*, and *Economidichthys* are collectively known as the sand gobies. They inhabit the coastal waters of the eastern North Atlantic, the Mediterranean and the Black Sea. Salinity tolerances for species of sand goby genera range through marine (*Gobiusculus*), inshore marine/estuarine (*Pomatoschistus*), estuarine/freshwater (*Knipowitschia*) and fully freshwater (*Economidichthys*). *Hyracanogobius* is endemic to the Caspian Sea and is known from fresh, brackish, and marine water. The biology of these genera has been fairly well-studied, with visual pigment evolution (Larmuseau *et al.*, 2010), ecology and biogeography (Penzo *et al.*, 1998; Huyse *et al.*, 2004), allozyme polymorphism (Webb, 1980; Wallis & Beardmore, 1984; Miller *et al.*, 1994; McKay & Miller, 1997), karyotype and soft tissue morphology (Webb, 1980), and skeletal characters (McKay & Miller, 1997; Vasil'eva & Kuga, 2001) all having been described and analysed. *Pomatoschistus* is unusual among gobiids in that it possesses a dorsal fin pterygiophore insertion pattern more typical of gobionellids (3-122100 or 3-1221000 rather than 3-22110 or 3-22111) as well as vertebral counts that are elevated compared with most Gobiidae (Birdsong *et al.*, 1988). There is a single epural in the caudal skeleton, a condition more typical of Gobiidae, but also present among Gobionellidae (McKay & Miller, 1997; Larson, 2001; Pezold, 2004; Thacker, 2009). Allozyme-based phylogenetic hypotheses show that *Pomatoschistus* and the other sand gobies are distinct from other gobiids, including Ponto-Caspian species. Those comparisons did not include any representatives of Gobionellidae. Similarly, in phylogenies based on analysis of DNA sequence, the sand gobies are distinct from other Gobiidae, but are not compared to Gobionellidae, unsurprisingly given the scale of comparisons considered in those studies (Penzo *et al.*, 1998; Huyse *et al.*, 2004; Larmuseau *et al.*, 2010). McKay and Miller (1997) hypothesize and discuss morphological character evidence that the sand gobies are related to Gobionellidae, and provide a cladistic analysis of morphology showing the sand gobies and several other gobiid genera nested within a gobionellid clade. Neilson & Stepien's (2009) study of Ponto-Caspian goby relationships included molecular phylogenetic analyses with *Pomatoschistus* and *Knipowitschia* in addition to a variety of other gobioid outgroups. Their hypothesis places those sand gobies among other Gobiidae, not with Gobionellidae, although support values outside the Ponto-Caspian clade are low. It is possible that *Pomatoschistus* is a gobionellid, and that due to the paucity of gobionellids included here, our phylogenetic analysis may have yielded a paraphyletic reconstruction of Gobionellidae, a pattern seen in comparisons of previous analyses of gobioid phylogeny (Thacker, 2003; Thacker & Hardman, 2005). Gobionellidae lacks a diagnostic morphological character, and instead the clade is identified by combinations of characters such as dorsal fin formula (3-12210), epural number (2), interorbital pore configuration

(paired) and less easily quantifiable characteristics such as drab colouration, larger, often downturned mouths, reduced eyes and elongated caudal fins (Larson, 2001; Pezold, 2011). Gobionellidae also tend to inhabit estuarine and freshwater habitats, and if marine are usually found very near shore, in mudflats, mangroves or seagrass beds. All of these generalizations have exceptions, however, such that assignment of genera to Gobiidae or Gobionellidae (in previous classifications, Gobiinae or Gobionellinae) has frequently been uncertain, and genera have been reassigned as further evidence has been uncovered (Thacker, 2009; Pezold, 2011).

Ponto-Caspian gobies

All of the eastern Atlantic/Mediterranean species examined other than *Pomatoschistus*, as well as the amphidromous species inhabiting the Ponto-Caspian region, are part of a single clade. The Ponto-Caspian gobies (*Babka*, *Benthophilus*, *Mesogobius*, *Neogobius*, *Ponticola*, *Proterorhinus*) are a radiation of hardy freshwater species native to the Aral, Azov, Black and Caspian Seas and their drainages (Simonovic, 1999). Several of these species have invaded freshwater ecosystems in Europe, and the species *Neogobius melanostomus* and *Proterorhinus semilunaris* have been introduced into the American Great Lakes system by ballast transport. A detailed study of Ponto-Caspian goby relationships has demonstrated that the lineage is monophyletic, and comprises three subgroups or tribes (Neilson & Stepien, 2009). The same tribes were recovered in our phylogeny, but with slightly different interrelationships. Both studies are based on analysis of both mitochondrial and nuclear DNA sequences, but the markers are non-overlapping with the exception of mitochondrial COI. The largest tribe, Ponticolini, includes the majority of Ponto-Caspian gobies: *Babka*, *Mesogobius*, *Ponticola* and *Proterorhinus*. Our study includes only one exemplar for each, and the relationships recovered are the same as in Neilson & Stepien (2009). In that study, the tadpole gobies *Benthophilus* and *Caspiosoma* (tribe Benthophilini) are sister to the Ponticolini, with *Neogobius* (tribe Neogobiini) as the sister to them both. Our study included a single *Benthophilus* species, which was placed outside a Neogobiini/Ponticolini clade, but in both hypotheses these deeper relationships are not well-supported, so the relationships effectively remain unresolved.

Mediterranean and Northeast Atlantic gobies

Our hypothesis and that of Neilson & Stepien (2009) agree that the wider ranging *Gobius* and *Zosterisessor*, known from the Eastern Atlantic and Mediterranean as well as the Black Sea, are grouped together as sister to the Ponto-Caspian species. Neilson & Stepien (2009) also include an-

other Mediterranean gobiid genus in the outgroups, *Chromogobius*, that was not represented in our study. Separation of the Ponto-Caspian species as the sister clade, but distinct from Northeast Atlantic/Mediterranean gobiid lineages, is consistent with geological history. Well after the closure of the Tethys seaway and isolation of Mediterranean and Indian Oceans, the Messinian salinity crisis (approximately 5.3–6.0 million years ago) resulted in the Mediterranean experiencing cycles of desiccation, leaving relict lakes and inland seas throughout the current areas of the Mediterranean, Black, Caspian and Aral basins. Separate refugia formed in the east (Paratethys: Central Europe/Asia) and west (Mediterranean basin), isolating various euryhaline gobioid lineages. Eventually, the Mediterranean was re-filled gradually due to increased freshwater input, followed by seawater flooding, and reintroduction of marine taxa, from the Atlantic through the Strait of Gibraltar (Penzo *et al.*, 1998; Simonovic, 1999; Neilson & Stepien, 2009).

Included in this lineage are all of the gobiid genera that inhabit the Mediterranean and Northeast Atlantic; a few species distributions extend south to the Southeast Atlantic (Miller, 1973, 1988) but generally, the lineage is geographically cohesive. With the exception of *Gobius*, the other 20 genera in this lineage each contain only one to three species; some of the genera are exclusively Mediterranean (*Gammogobius*, *Millerigobius*, *Odondebuena*, *Speleogobius*), and some exclusively Atlantic (*Gobiusculus*, *Mauligobius*, *Vanneaugobius*), but the majority are widespread throughout both areas. Similarly, most species in this lineage are cryptobenthic, with a colour pattern that features few (3–7) dark lateral bands along the body (Ahnelt, 1991; Ahnelt *et al.*, 1994; Brito & Miller, 2001; Schliewen & Kovacic, 2008). Exceptions include the genera *Aphia*, *Crystallogobius*, *Gobiusculus* and *Pseudaphya*, all diminutive and wholly or partially transparent, with the habit of forming pelagic schools. *Lesuerigobius* and *Thorogobius* may attain a much larger size, inhabit muddy or silty habitats, and have spotted colour patterns (Miller, 1988; Ahnelt & Kovacic, 1997; Ahnelt & Dorda, 2004). Some *Didogobius* are commensal with shrimp, in this case the axiid *Axiopsis serratifrons* (Schliewen & Kovacic, 2008); a different group of shrimp than the alpheids that engage in most mutualistic relationships with Gobiidae (Thacker *et al.*, 2011).

African gobies (Eastern Central Atlantic; Southeast Atlantic and Western Indian Ocean)

Our Ponto-Caspian plus Northeast Atlantic/Mediterranean clade is rooted with two genera that inhabit the Western Indian Ocean and Southeast Atlantic: *Coryglops* and *Caffrogobius*. Placement of these taxa as a grade basal to the Ponto-Caspian and Atlantic/Mediterranean species is also consistent with tectonic history; the Mediterranean and Indian Ocean basins were contiguous as part of the

Tethys Sea until the Oligocene/Miocene transition, with the final closure occurring approximately 20 million years ago (Hrbek & Meyer, 2003). In Table 1, we include nine additional genera in the African Goby lineage, several of them monotypic, and all restricted to the waters of sub-Saharan Africa (Smith, 1959; Hoese, 1986) except *Heteroleotris*. That genus includes at least 17 species (*Pascua* is a synonym) and although it has its greatest species diversity in the Western Indian Ocean, there are also *Heteroleotris* species that inhabit the Western and South Pacific (Hoese & Larson, 2005).

Caffrogobius inhabits near-shore shallow habitats such as tidepools and estuaries, and was postulated by Goren (1996) to be related to *Coryogalops*, *Heteroleotris*, *Gorogobius* and *Nematogobius* due to similarity in cephalic papillae pattern and vertebral number. These genera, as well as the others grouped with the African gobies, all share with *Bathygobius*, *Glossogobius* and *Lesuerigobius* a $10 + 17 = 27$ (more rarely, $11 + 16 = 27$, and very rarely 28) vertebral count (Hoese, 1986, Miller, 1988). These elevated counts distinguish them from the majority of Indo-Pacific reef gobies, which possess $10 + 16 = 26$ vertebrae (some flapheaded gobies of the genus *Callogobius* exhibit more, as do *Bathygobius* and *Glossogobius* with 27), but not from other Atlantic and Caribbean gobies, which generally have 27 or more (Birdsong *et al.*, 1988). Individuals of *Caffrogobius* and *Coryogalops* are also generally stout-bodied, with rounded heads in profile, a mottled colour pattern, and relatively thick caudal peduncles with rounded caudal fins (Randall, 1995a; Goren, 1996). Other genera included here with *Caffrogobius* and *Coryogalops* contain just one to few species, and are not well known; they are included with the core genera in this lineage primarily based on a common distribution and often similar inshore ecology. This is the most provisional of the categories presented in Table 1. It is not monophyletic, as shown in Fig. 1, with *Coryogalops* and *Caffrogobius* forming a grade basal to the Ponto-Caspian and Mediterranean/Atlantic gobies, and none of the east central Atlantic species are represented in the analysis. Also, the diversity of the region (non-Mediterranean coasts of Africa) is simply not as well sampled as others.

New World Gobiidae: American seven-spined gobies

This large lineage is the only clade identified in our hypothesis that exclusively inhabits the waters of the New World: the Eastern Pacific, Western Atlantic and Caribbean. The American seven-spined gobies, or Gobiosomatini, includes 26 genera that represent 40% of New World gobiid genera and 50% of the species (Birdsong & Robins, 1995; Rüber *et al.*, 2003). As the name indicates, members bear seven spines (rather than the more common condition of six spines) in the first dorsal fin, have a variety of pterygiophore insertion patterns (most commonly 3-221110), and possess

27–35 vertebrae, in different proportions (this lineage comprises the *Gobiosoma* and *Microgobius* groups of Birdsong *et al.*, 1988). As with a great many of the genera within Gobiidae, 21 of the genera included in this lineage contain fewer than five species; nine are monotypic. The more diverse genera in this lineage are *Chriolepis* (10 species), *Bollmannia* (13 species), *Microgobius* (14 species), *Gobiosoma* (16 species) and *Elacatinus* (32 species; Froese & Pauly, 2011). The seven-spined gobies dominate tropical reef and near-reef environments, inhabiting live corals, sponges, sea urchins, mangroves, mudflats and seagrass beds (Böhlke & Chaplin, 1993). They include the neon gobies (*Elacatinus*), some of which engage in cleaner mutualisms with larger fishes (Colin, 1975). The monotypic *Nes longus* is commensal with the snapping shrimp *Alpheus floridanus*, and has an antennal/tail flick communication system similar to that seen in Indo-Pacific shrimp gobies and their shrimp (Karplus, 1992; Thacker *et al.*, 2011). The evolution of this diverse clade has been studied in the context of inferring patterns of marine speciation and ecological specialization (Rüber *et al.*, 2003; Taylor & Hellberg, 2005), as well as showing that local larval retention can contribute to species differentiation (Taylor & Hellberg, 2003).

Another trait that may contribute to isolation and diversification by facilitating exploitation of patchy microhabitats and tolerance of low population densities is functional hermaphroditism, the ability to change sex in response to environmental cues. One species examined, *Tigrigobius multifasciatus*, exhibits such hermaphroditism in a protogynous pattern, beginning as female and switching to male if needed. Curiously, five additional species of American seven-spined gobies that do not express a hermaphroditic pattern as adults do exhibit a transient hermaphroditic gonad as juveniles, consistent with retention of vestiges of a functional hermaphroditic gonad, inferred to be present earlier in the clade's evolutionary history (Cole, 2008).

Our hypothesis includes representatives of ten American seven-spined gobies, including the genera *Microgobius*, *Nes*, *Barbulifer*, *Gobiosoma*, *Risor*, *Ophiogobius*, *Tigrigobius* and *Elacatinus*. *Microgobius* is sister to a clade containing the remainder of the genera, a placement consistent with Birdsong *et al.*'s (1988) separation of *Bollmannia*, *Microgobius*, *Palatogobius* and *Parrella* (as the *Microgobius* group) from the remainder of the Gobiosomatini (*Gobiosoma* group); the *Microgobius* group shares vertebral and median fin meristic characters with the other American seven-spined gobies, but lacks the complete fusion of all hypural elements with the terminal vertebral element. The placement of *Microgobius* among the American seven-spined gobies is poorly supported in our molecular phylogeny, but it is retained here due to those shared meristic characters as well as concordant placement in another molecular phylogenetic analysis (Rüber *et al.*, 2003). Previous phylogenetic hypotheses of the American seven-spined gobies include two studies linking species diversification to

habitat shifts, one wide-ranging (using mitochondrial ribosomal genes) and one more *Elacatinus*-focused (based on both mitochondrial and nuclear genes; Rüber *et al.*, 2003; Taylor & Hellberg, 2005). Where the taxon sampling of those studies overlaps with ours, the relationships recovered are the same, with one small exception: both those studies recovered the part of *Tigrigobius* containing *T. macrodon* as sister to *Elacatinus*, to the exclusion of *Risor*. Our hypothesis differs slightly in that *Tigrigobius*, *Risor* and *Ophiogobius* form a clade sister to *Elacatinus*, but this result is comparatively weakly supported, and likely due to uncertainty caused by inequivalent sampling, as neither of those previous studies included *Ophiogobius*.

One additional genus is placed with this lineage, the deeper water (30–42 m) *Vomerogobius*, also known from the Western Atlantic. This genus, containing only *V. flavus*, is unusual in that it possesses $11 + 16 = 27$ vertebrae, but only six weak dorsal spines (Gilbert, 1971). In the original description, Gilbert suggested that although no close relative was clear, he considered it more likely that *Vomerogobius* was related to the six-spined Indo-Pacific Gobiidae such as *Trimma*. Radiographs of *V. flavus* (ANSP 109589 [1], ANSP 138127 [4], ANSP 150228 [1] and ANSP 150383 [4]) confirm the vertebral counts, as well as the presence of six dorsal spines arrayed as 3-2211000. It is placed here provisionally on the assumption that the loss of a dorsal spine is more likely to have occurred than the gain of a vertebra.

Pacific and Indian Ocean near-shore Gobiidae

The tropical reef environments of the Indian and Pacific oceans are home to the greatest diversity of gobiid fishes. Our hypothesis delineates several lineages of goby genera inhabiting these areas. Lineages included here encompass the majority of well-known gobiid taxa, such as the common near-reef benthic *Istigobius*, *Oplopomus* and *Asterropteryx*, the coral-dwelling *Gobiodon*, *Paragobiodon*, *Bryaninops* and *Eviota*, the larger-bodied hovering *Amblygobius* and *Valenciennesa*, the tiny, secretive *Priolepis* and *Trimma*, the circumglobal fringe-finned *Bathygobius*, and the shrimp-associated *Amblyeleotris*, *Ctenogobios*, *Cryptocentrus*, *Mahidolia* and *Vanderhorstia*. The majority of these clades include or are completely composed of species and genera that are widely distributed across the Indo-Pacific. It is among Indo-Pacific reef Gobiidae that phylogenetic relationships have traditionally been most difficult to discern. Birdsong *et al.* (1988) placed most of these genera in his single largest group, the *Priolepis* group, distinguished by possession of a dorsal fin pterygiophore formula of 3-22110, a single epural, and (with rare exceptions) a $10 + 16 = 26$ vertebral count. These Gobiidae are diverse, yet exhibit few meaningful morphological characters that can be used to delineate subgroups within the family. Previous molecular phylogenetic stud-

ies of Gobiidae have confirmed that the family contains a variety of distinct lineages, with subgroups that had been demarcated from the remainder found to be nested within the more typical, *Priolepis* group members (Thacker, 2009, 2011). This hypothesis increases sampling greatly for these gobiids, allowing clades within Gobiidae to be identified.

Lagoon gobies

The genera *Acentrogobius*, *Afurcagobius*, *Favonigobius* and *Papillogobius* are resolved together (although the placement of *Acentrogobius* is poorly supported), and all are known from the Indo-Pacific; *Acentrogobius*, *Favonigobius* and *Papillogobius* are widespread, and *Afurcagobius* is known from the temperate Australian coast and Tasmania. *Acentrogobius*, *Favonigobius* and *Papillogobius* are euryhaline and inhabit brackish as well as marine waters; *Afurcagobius* is not found in marine waters, and is known only from estuaries and rivers (Gill, 1993). *Acentrogobius* currently includes more than 20 species, and studies by both Hoese (1983) and Gill and Miller (1990) have suggested that *Acentrogobius* may contain more than one distinct lineage. Indeed, *Acentrogobius* has a generalized gobiid morphology and a complex taxonomic history, with many species having been reassigned to other genera, including *Exyrias*, *Macrodontogobius*, *Istigobius*, *Amoya*, *Yongeichthys* and *Favonigobius* (Hoese, 1983). *Favonigobius* and *Papillogobius* have been synonymized in some accounts (Hoese, 1986), but in our hypothesis, *Afurcagobius* is resolved as sister to *Favonigobius*, in accordance with the revisions of Gill and Miller (1990) and Gill (1993). *Papillogobius* and *Acentrogobius* may be distinguished from *Favonigobius* on the basis of skeletal characters, meristic counts and cephalic lateral line pore configurations (Gill & Miller, 1990; Gill, 1993). The differences among them are slight, but the species examined here are placed into distinct genera, simply because our sampling is incomplete. Even though all the species of *Afurcagobius*, *Favonigobius* and *Papillogobius* examined here form a clade, and thus could arguably be subsumed under *Favonigobius*, the names are retained here because increased sampling could yield a more complicated picture.

Our hypothesis indicates that the genera *Arenigobius*, *Cabillus*, *Oplopomus* and a clade containing both *Exyrias* and *Istigobius* are sister to the *Acentrogobius* clade, although the relationships among these genera are poorly supported. This lineage is denoted the Lagoon gobies (Fig. 1, Table 1), although as mentioned previously, not all the constituent taxa inhabit lagoons. *Arenigobius* is a genus of three species, all restricted to Australia and New Caledonia. It is also euryhaline and recorded from coastal waters and estuaries. *Oplopomus*, *Cabillus*, *Exyrias* and *Istigobius* are marine, inhabit sand or mud substrates, and are widespread throughout the Indo-Pacific. *Oplopomus* is a comparatively large goby, roughly cylindrical in shape and frequently occupying burrows; it is also distinguished

by possession of one to three small spines on the preopercle. In contrast, *Cabillus* is tiny and cryptobenthic, with a more dorsoventrally flattened aspect and dorsally placed eyes (Myers, 1999). A close relationship between *Exyrius* and *Istigobius* is well-supported in our hypothesis, and accords well with hypothesized placement based on morphology. Both genera are benthic, and feed by sifting sand through their gill rakers, filtering out the infauna (Myers, 1999). *Exyrius* is both mud and reef dwelling, estuarine and marine, and was anticipated by Murdy in his review of the genus to be related to *Istigobius*, *Acentrogobius* and *Favonigobius*, as confirmed here (Murdy, 1985). *Exyrius* is similar to *Istigobius* in pigmentation, with which it shares a ‘dash-dot’ lateral pattern of spots; the two differ in that *Istigobius* bears lighter scalation on the opercles and cheeks. *Istigobius* is also generally found over sand substrates, or areas of reef rubble, but some species may also inhabit mud, silt or mangrove habitats (Murdy & Hoese, 1985). Collectively, the lagoon gobies share a common overall squat shape and blunt head, a benthic, usually mud-dwelling ecology, and many of the lagoon gobies also bear a medio-lateral pigmentation pattern of alternating small and larger spots, denoted the “dot-dash” pattern above (Smith, 1959; Myers, 1999). Some of the genera are distinguished by the presence of opercular spines (also known from *Asterropteryx*), comparatively stout spines in the dorsal fin, and cutaneous toxin secretions (Iwata *et al.*, 1998; Myers, 1999; Shibukawa & Allen, 2007; Shibukawa *et al.*, 2010b).

Silt and reef shrimp gobies

Shrimp-associated gobies are a prominent component of the Indo-Pacific fish fauna. Our new gobiid hypothesis is consistent with the earlier study of Thacker *et al.* (2011), which demonstrated that the complex mutualistic association seen between several genera of gobiid gobies and alpheid shrimp has evolved twice. One clade, including *Cryptocentrus*, *Mahidolia* and *Stonogobiops*, was resolved separately from a second containing *Amblyeleotris*, *Ctenogobiops* and *Vanderhorstia*, as well as *Asterropteryx*, a free-living genus not associated with shrimp. In the current hypothesis, the placement of *Stonogobiops* with the silt shrimp gobies is comparatively poorly supported; it is more confidently placed there by Thacker *et al.* (2011). Within the shrimp goby clades, relationships echo those inferred in Thacker *et al.* (2011), with slightly fewer species sampled. The markers selected for that study and this one are nearly identical; our new hypothesis includes an additional nuclear gene, RNF213. Thus, the congruence of the interrelationships inferred is not surprising. This study also differs from the previous one in that far more non-mutualistic gobiid taxa are sampled, and so the more significant result is that the double evolution of the shrimp mutualism, in distantly related clades, is confirmed.

Identification of distinct diagnostic morphological characteristics for each shrimp-associated goby clade is diffi-

cult. One character hypothesized to be useful in diagnosing lineages of shrimp-associated gobies is the pattern of cheek papillae (presence or absence of transverse rows); however, the distribution of that character is not in accord with the two clades identified in this and the previous, more extensive phylogeny (Thacker *et al.*, 2011). Many shrimp-associated gobies share an overall congruence of shape and appearance, likely related to convergence given their similar, specialized ecologies. In particular, the most speciose genera, *Amblyeleotris* and *Cryptocentrus*, are quite similar, although distinguishable based on subtle meristic and shape characteristics (Chen *et al.*, 1998; Hoese & Larson, 2004). Also, species of *Cryptocentrus* exhibit pelvic fins fused into a robust, round disc, whereas *Amblyeleotris* species frequently bear unfused or weakly fused, posteriorly pointed pelvic fins. Sister taxa to *Amblyeleotris* (*Ctenogobiops* and *Vanderhorstia*) have fused pelvic fins, but the close non-mutualist relative *Asterropteryx* has separate pelvic fins. Hoese & Larson (2004) note that while *Amblyeleotris* species are associated with shrimp in sandy habitats near coral reefs (as are *Ctenogobiops* and *Vanderhorstia*), many *Cryptocentrus* are known from more silty habitats. Although not an exclusive characteristic, as *Cryptocentrus* may also inhabit sandy near-reef areas, a preference for silt and fine sandy habitats is common to many *Cryptocentrus* species as well as related genera *Mahidolia*, *Tomiyamichthys* and *Stonogobiops*, and also similar genera *Myersina* and *Flabelligobius* (Hoese & Randall, 1982; Iwata *et al.*, 2000; Winterbottom, 2002; Chen & Fang, 2003; Thacker *et al.*, 2011). Accordingly, the clade consisting of *Amblyeleotris*, *Ctenogobiops* and *Vanderhorstia* (as well as the non-mutualist starry goby *Asterropteryx*) is named the reef shrimp gobies (Table 1), and the clade of *Cryptocentrus* and related shrimp-associated genera is denoted the silt shrimp gobies.

Sanddivers

Kraemeria is an unusual, sand-dwelling gobiid, classified either in its own family (with one additional genus, *Gobitrichonotus*) or among Gobiidae (Akihito *et al.*, 1988), and as a distinct morphological group in Birdsong *et al.* (1988). Those genera are identified as the Sanddivers (Fig. 1, Table 1). Species of *Kraemeria* inhabit near shore sandy habitats throughout the Indo-Pacific, and are characterized by several reductions in elements of the pectoral and caudal skeletons (Matsubara & Iwai, 1959). *Parkraemeria* shares with both *Kraemeria* and *Gobitrichonotus* a similar body shape, sensory pore pattern, and fin configuration, although the head is much less pointed and the eyes are not as reduced (Akihito *et al.*, 1998). A previous study (Thacker, 2003) placed the species *K. cunicularia* among Gobionellidae, but it was resolved in Gobiidae by both Thacker (2009) and this study. This changed placement represented the major discrepancy between those earlier analyses; however,

some differences are to be expected considering the use of different samples and analytical methods among the various studies. The hypothesis of Thacker (2003) was inferred using parsimony analysis, while model-based inferences and much larger datasets characterize Thacker (2009; Bayesian inference) and this study (maximum likelihood inference and a matrix including nuclear as well as mitochondrial markers). In this study, the addition of two individuals of *K. bryani* in addition to the two *K. cunicularia* examined in Thacker (2009) has confirmed the monophyly of *Kraemeria* and that it is placed within Gobiidae. However, the uncertainty in both these hypotheses still precludes definitive identification of the sister taxon. The *Kraemeria* lineage is distinct from other clades in Gobiidae, either because no closer sister taxon exists, or because its sister taxon has simply not been sampled yet.

Flapheaded gobies

Similarly, the genus *Callogobius* is recovered in our hypothesis without a strongly supported placement within the family. Two species, *C. bifasciatus* and *C. sclateri*, are included, and their pairing is well-supported. *Callogobius* is a complex genus of tiny, cryptic gobies with flattened heads bearing prominent ridges of dermal papillae and large pectoral fins. They inhabit reef and near-reef habitats throughout the western Pacific. At least 30 valid species are described, but the genus is in need of revision (Myers, 1999; Chen *et al.*, 2006). Several additional genera are proposed to be relatives of *Callogobius*, and are included in the flapheaded goby lineage (Table 1). The majority of these genera share the presence of a network of raised ridges on the head which bear sensory papillae. Many also exhibit a dorsolaterally compressed body and head shape, and a pigmentation pattern featuring a few large and irregular dark splotches on the head and body, often also with relatively large pectoral fins (Smith, 1959; Hoese, 1986). *Feia*, *Callogobius*, *Gobiopsis*, *Platygobiopsis* and *Mangarinus* have been postulated as relatives due to shared similar arrangements of the cranial papillose ridges (Winterbottom, 2003), and the flattened, elongate *Platygobiopsis* is postulated to be either the sister to *Gobiopsis* or possibly nested within it (Springer & Randall, 1992). *Gobiopsis* is the second largest genus in this lineage, with 14 included species currently considered valid. These fishes also exhibit ridges of papillae on the head, as well as longer barbels around the mouth in some species, and the same overall shape and colour patterns of *Callogobius* (Lachner & McKinney, 1978, 1979.) *Drombus* differs from *Callogobius* in having fused pelvic fins, as well as a less dorsoventrally flattened shape, however, they share the presence of papillose ridges as well as similar colour patterns in some species (Smith, 1959; Hoese, 1986). *Palutrus* and *Phoxacromion* share cranial sensory papillae configurations with some *Drombus*, although neither *Palutrus* nor *Phoxacromion* exhibits those papillae on

raised dermal flaps (Shibukawa *et al.*, 2010a). *Discordipinna* also lacks the cranial flaps of the flapheaded gobies, but is placed therein due to its similar overall head and body shape (Hoese & Fourmanoir, 1978). *Barbuligobius* bears some papillar flaps and barbels around the mouth, and additionally shares with *Callogobius* a similar head and body shape, blotchy colour pattern, and common fin spine and ray counts as well as dorsal fin formula (Lachner & McKinney, 1974). *Callogobius* is unusual in that individuals may have vertebral counts ranging from 26 to 30; others in this lineage exhibit the typical count of 26 (Hoese, 1986; Birdsong *et al.*, 1988).

Burrowing paired gobies

Two additional clades of Indo-Pacific reef gobies were identified, and in both cases the phylogeny indicates close relationships among genera that are behaviourally and ecologically similar. The three genera *Amblygobius*, *Signigobius* and *Valenciennea* are recovered together (with moderate bootstrap support of 79% and 80%), as predicted by Hoese & Allen (1977), with *Amblygobius* outside the pairing of *Signigobius* plus *Valenciennea*. These genera are collectively called the burrowing paired gobies (Fig. 1, Table 1), due to their shared ecological and reproductive characteristics. All of these gobies are relatively large, laterally compressed, and feed by sifting sand through their gill rakers. All are benthic but are frequently seen hovering above the substrate; at night and when alarmed, they will shelter in burrows they construct. These burrows are also where egg-laying and guarding take place (Hoese & Allen, 1977; Myers, 1999). Species of all three genera participate in a mating system in which adults live as monogamous pairs and occupy and guard a territory, but are not hermaphroditic (Reavis & Barlow, 1998; Takegaki & Nakazono, 1999; Takegaki, 2000; Mazzoldi, 2001; Hernaman & Munday, 2007). They are prominent and colourful members of the reef-associated gobiid fauna, notable due to their conspicuous behaviours including a defensive posture adopted by *Signigobius biocellatus* in which the fish orients itself side-on to the viewer, flares its fins to display prominent large ocelli, and imitates the movements of a crab (Hoese & Allen, 1977; Myers, 1999).

Coral gobies

The final lineage of exclusively Indo-Pacific reef gobiids is comprised of the genera *Bryaninops*, *Eviota*, *Gobiodon*, *Kelloggella*, *Larsonella*, *Lobulogobius*, *Lubricogobius*, *Luposicya*, *Minisicya*, *Paragobiodon*, *Phyllogobius*, *Pleurosicya* and *Sueviota*. Individuals in these genera are associated with corals and attain a minute adult body size. The coral association is obligate in *Bryaninops*, *Gobiodon*, *Paragobiodon* and *Pleurosicya*, and facultative in *Eviota* (Herler *et al.*, 2009). Species of *Bryaninops* and *Pleurosicya* hover

near or perch in the branches of gorgonians, including deposition and guarding of egg clutches on cleared areas of the coral. *Gobiodon* and *Paragobiodon* are found in the branches of stony corals; *Acropora* (Acroporidae) in the case of *Gobiodon*, and *Pocillopora*, *Seriatopora* or *Stylophora* (Pocilloporidae) for *Paragobiodon* (Munday *et al.*, 1998, 2002; Herler *et al.*, 2009). The diverse genus *Eviota* includes species that are found perching or hovering among coral branches, as well as others that inhabit reef or rock rubble, not coral. Ongoing studies of cryptobenthic reef gobies have documented that *Eviota* species experience very short lifespans (maximum 59 days, with 40% of that time spent as larvae), rapid reproduction (estimated at 7.4 generations per year), and great abundance on Western Pacific coral reefs (Depeczynski & Bellwood, 2003, 2005, 2006). Both *Bryaninops* and *Eviota* are tiny, even among gobies, with most species reaching lengths of only 15–20 mm. *Gobiodon* and *Paragobiodon* differ in that they are slightly larger (25–50 mm), and with a distinctive shape: laterally compressed, with a large head, rounded in profile, and a squat body shape (Myers, 1999; Herler *et al.*, 2009). They exhibit a monogamous mating system, as also recorded for *Amblygobius*, *Signigobius* and *Valenciennesa* (Mazzoldi, 2001). *Gobiodon* species have a high fidelity to their host corals, so much so that some species have diversified by sympatric speciation associated with a host shift (Munday *et al.*, 2004), and overall phylogenetic patterns within the genus parallel those of host *Acropora* corals (Herler *et al.*, 2009).

Several genera in this lineage are fairly speciose, including *Bryaninops* (10 species), *Gobiodon* (20 species) and *Pleurosicya* (18 species); *Eviota* is by far the most diverse, with 62 species currently described and likely many additional undescribed (Herler *et al.*, 2009; Froese & Pauly, 2011). Other genera in this lineage contain just one to five species, and are often quite similar to one of the more speciose genera. Our molecular phylogeny includes two *Gobiodon* species and single exemplars of *Paragobiodon*, *Bryaninops* and *Eviota*. The hypothesis indicates that *Gobiodon* and *Paragobiodon* are sister taxa, with *Bryaninops* and then *Eviota* resolved outside that clade. This result is in accordance with the molecular phylogenetic results of Herler *et al.* (2009), showing distinct *Gobiodon*/*Paragobiodon* and *Bryaninops*/*Pleurosicya* clades, with *Eviota* resolved as sister to both. The diversity of coral gobies may be divided into three types: laterally compressed, round-headed species that generally inhabit stony corals (*Gobiodon*, *Paragobiodon*, *Larsonella*, *Lubricogobius*); elongate, delicate, pointy-snouted inhabitants of gorgonians, staghorn corals or sponges (*Bryaninops*, *Lobulogobius*, *Luposicya*, *Minisicya*, *Phyllogobius*, *Pleurosicya*); and elongate but blunt-snouted species not obligately associated with coral (*Eviota*, *Kelloggella*, *Sueviota*). *Larsonella* and *Lubricogobius* differ from *Gobiodon* and *Paragobiodon* primarily in that they are partially (*Larsonella*) or com-

pletely (*Lubricogobius*) scaleless; *Lubricogobius* individuals have been captured from non-coraline shelters such as worm tubes, urchin tests, mollusc shells and tunicates (Randall & Senou, 2001). *Lobulogobius*, *Luposicya*, *Minisicya* and *Phyllogobius* all differ from *Pleurosicya* or *Bryaninops* in slight variations of soft tissue characters, but all share a common overall morphology and commensal ecology (primarily with gorgonians, but also with other soft corals or sponges; Larson, 1983, 1986, 1987, 2002; Goren, 1984). *Sueviota* is very similar to *Eviota*, differing only in the condition of the medial (5th) pelvic ray (Winterbottom & Hoese, 1998). *Kelloggella* is included in this lineage due to its small size and general similarity to *Eviota*, although *Kelloggella* species are more elongate. *Kelloggella* is known from tide pools throughout the Indian and Pacific Oceans, including Hawaii and Easter Island, and is distinctive in that it has tricuspid teeth and an 11 + 15 = 26 vertebral count, a condition only very rarely observed among Gobiidae (Hoese, 1975; Birdsong *et al.*, 1988).

Circumglobal Gobiidae clades

Several clades identified in this study include members that inhabit both Old and New World oceans. In two cases, *Bathygobius* and *Priolepis*, a single genus contains species distributed around the world. Other lineages contain taxa classified into distinct genera in the Eastern Pacific/Western Atlantic and the Indo-Pacific. The lineages of gobies detailed below, along with the American seven-spined gobies (exclusively New World distribution), comprise all the gobiid gobies known from the Eastern Pacific, Western Atlantic and Caribbean.

Tiny banded gobies

Nine genera are assigned here to a lineage that is characterized by very small size (most less than 50 mm in length, and many less than 30 mm), a stocky ovoid body with a narrow caudal peduncle, and in many species, a colour pattern of several (commonly 7–12) brightly coloured bands on a pale ground. *Lythrypnus*, *Priolepis* and *Trimma* were sequenced for this analysis, with results indicating that *Lythrypnus* and *Priolepis* are not monophyletic. Our hypothesis resolves the Eastern Pacific species of *Lythrypnus* examined, *L. dalli* and *L. zebra*, outside the other species sampled, apart from the Caribbean/Western Atlantic *L. elasson*, itself nested within *Priolepis*. The two species of *Trimma* form a clade sister to *Priolepis* and *L. elasson*. These are the most speciose genera; *Lythrypnus* contains 20 species, *Priolepis* 34 and *Trimma* 63, with many still to be described (Winterbottom & Southcott, 2008; Froese & Pauly, 2011) and precise relationships still to be investigated. *Lythrypnus* is known from the Eastern Pacific and Western Atlantic, *Trimma* from throughout the Indo-Pacific, and *Priolepis* from around the world. All inhabit tropical marine near-shore environments,

many are cryptobenthic, and others occur swimming in schools. As with the coral gobies, the other genera in this lineage are much less diverse, and often very similar to the more speciose genera. *Egglestonichthys* (Indo-Pacific) encompasses three species, and *Ego* (Red Sea) is monotypic; species of both resemble *Priolepis* (Miller & Wongrat, 1979; Randall, 1995a; Larson & Hoese, 1996; Froese & Pauly, 2011). *Trimmatom* (seven species in the Indo-Pacific) and *Paratrimma* (two Southeastern Pacific species) are both close relatives of *Lythrypnus*, *Priolepis* and *Trimma* (Hoese & Brothers, 1976; Winterbottom, 1989; Winterbottom & Burrige, 1992). *Obliquogobius* and *Tryssogobius* are two genera known from deepwater (27–82 m for *Tryssogobius*; 99–165 for one *Obliquogobius* species, 394–404 m for another) in the Western Pacific. They are placed here provisionally; although they share broad similarities of shape, colouration and meristics with the other genera in this lineage, they also differ in some respects, such as possessing fully scaled heads, an unusual condition (Larson & Hoese, 2001; Larson & Chen, 2007; Shibukawa & Aonuma, 2007).

The tiny banded gobies have been the subject of a number of phylogenetic and evolutionary analyses based on osteology and external morphology, including cladistic analyses of heterochrony (Winterbottom, 1990), biogeography (Santini & Winterbottom, 2002), and evolution of cutaneous papillae patterns (Winterbottom & Burrige, 1992). The age and growth patterns of several *Trimma* species have also been examined, and have yielded the notable result that these cryptobenthic reef fishes, similar to *Eviota*, experience quite short lifespans (87–140 days in the *Trimma* examined, with 24–39% of that time spent as pelagic larvae; Winterbottom & Southcott, 2008; Winterbottom *et al.*, 2011) and high mortality (2.9–6.3% per day). This level of turnover in the fish community is remarkable and indicates that these gobies are major contributors to reef biomass production and energy flow.

Crested gobies

This lineage includes five genera (*Coryphopterus*, *Cristatogobius*, *Fusigobius*, *Lophogobius* and *Rhinogobiops*), of which all but *Cristatogobius* are represented in our phylogeny. This lineage spans the Indo-Pacific (*Fusigobius* and *Cristatogobius*) as well as the Eastern Pacific and Western Atlantic (*Coryphopterus*, *Lophogobius* and *Rhinogobiops*). The name crested gobies is applied to this lineage because *Lophogobius*, *Rhinogobiops* and *Coryphopterus* species bear a fleshy nuchal crest on the dorsal midline of the head, behind the eyes and extending to or nearly to the origin of the first dorsal fin (Thacker & Cole, 2002). A similar crest is present in the Western Pacific *Cristatogobius*, and that genus is grouped here for that reason along with its overall similarity in shape to *Lophogobius*, although Akihito and Meguro (2000) list differences in tooth, scapula

and papillae morphology between the two genera. A few other gobioids, such as *Cryptocentroides gobioides*, also display nuchal crests but lack other shared morphological similarities with the crested gobies and are not hypothesized to be related to that lineage.

Crested goby genera have been the subject of active taxonomic study, particularly *Coryphopterus* and *Fusigobius* (Smith & Tyler, 1977; Randall, 1995b, 2001); a phylogeny of crested gobies based on both morphological characters and molecular data indicated that *Lophogobius* was the sister taxon to most *Coryphopterus*, and reassigned the Eastern Pacific blackeye goby to *Rhinogobiops nicholsii* (Thacker & Cole, 2002). Two *Fusigobius* species were placed separately outside the remainder of the crested gobies. These conclusions were supported in phylogenetic studies with much more extensive sampling (Thacker, 2003, 2009). Both of those analyses indicated that *Coryphopterus* and *Lophogobius* were sister taxa, with some *Fusigobius* also closely related, but with others placed as distantly related in the hypothesis, a strange result also highlighted by Cole (2008). None of those earlier studies included *Rhinogobiops*, and the sampling of *Fusigobius* was also sparse. In our analysis, we include not only *Coryphopterus* and *Lophogobius*, but also *Rhinogobiops* and three *Fusigobius* species, adding second individuals of *F. neophytus* and *F. signipinnis*, as well as an exemplar of *F. duospilus*. This expanded sampling yields a hypothesis that is consistent with earlier efforts; where the sampling overlaps, the relationships within *Coryphopterus* are concordant with those depicted in Thacker and Cole (2002; note that one individual identified in that work as *C. punctiptectophorus* was misidentified and is here corrected to *C. dicrus* [Carole Baldwin, pers. comm.]). The new hypothesis also confirms that *Coryphopterus* and *Lophogobius* are sister taxa, and *Rhinogobiops* is placed outside them, as sister to that pairing. In contrast to the earlier analyses, here *Fusigobius* species are placed together, forming a grade outside the other three genera. However, support for the placement of *F. neophytus* apart from the remainder of *Fusigobius* is very weak, and thus, evidence for the paraphyly of this genus should not be considered conclusive.

A reproductive pattern shared by a variety of gobiid genera is the ability to change sex, most commonly in a protogynous pattern. Hermaphroditic gonads have been recorded in four of the lineages outlined here: the coral gobies (*Bryaninops*, *Eviota*, *Gobiodon* and *Paragobiodon*), the tiny banded gobies (*Priolepis*, *Trimma*, *Lythrypnus*), the crested gobies (*Coryphopterus*, *Rhinogobiops*) and the American seven-spined gobies (*Tigrigobius*; Cole, 1990, 2008, 2010; Cole & Hoese, 2001). Various behavioural and gonadal characteristics are associated with the hermaphroditism, including whether or not sex change can be bidirectional, and whether both ovarian and testicular tissue are simultaneously present in the gonad. Cole (2010) examined the phylogenetic distribution of hermaphroditism among

gobies using the phylogeny of Thacker (2009). Multiple independent origins of hermaphroditism were postulated based on the phylogeny, which differed from the current hypothesis in the placement of *Fusigobius neophytus* separate from the remainder of the crested gobies, which were in turn resolved in a basal polytomy with *Kraemeria*. Similarly, our current hypothesis features weak resolution along the backbone of the phylogeny, however, additional species and sequence data have confirmed monophyly of the crested gobies, including all *Fusigobius* sampled, a result that is in better concordance with the distribution of reproductive characteristics enumerated by Cole (2010).

Wormfishes and dartfishes

This clade includes two groups that in older classifications were united as subfamilies in a single family, Microdesmidae (Hoese, 1984). The New World *Cerdale*, *Clarkichthys* and *Microdesmus* were grouped with the Indo-Pacific *Gunnellichthys* and *Paragunnellichthys* as the Microdesminae (wormfishes), with *Aioliops*, *Nemateleotris*, *Oxymetopon*, *Parioglossus* and *Ptereleotris* comprising the Ptereleotriinae (dartfishes; two new genera, *Navigobius* and *Pterocerdale*, have since been described [Hoese & Motomura, 2009]). Wormfishes in the New World are elongate, benthic and burrowing, with thick skin and blunt heads. They inhabit near-shore sandy and muddy habitats, including the intertidal. The Indo-Pacific *Gunnellichthys* and *Paragunnellichthys* are known from flat sandy habitats, in which they may hover or burrow. All five wormfish genera exhibit single, long dorsal fins rather than the separate spinous and rayed dorsals of most gobioids. Dartfishes are exclusively Indo-Pacific and known from reef and near-reef habitats, where they hover above the substrate, forming monogamous pairs and feeding on zooplankton. They do not construct burrows, but will shelter in burrows or crevices when threatened (Myers, 1999; Thacker, 2000).

These lineages have also been the focus of phylogenetic investigations based both on morphological and on molecular data. A morphological phylogeny focusing just on the five wormfish genera confirmed the monophyly of each genus, and of the wormfishes as a group, but proposed that dartfishes were not closely related and assigned them to a distinct family (Thacker, 2000). Subsequent molecular phylogenies yielded divergent results; an initial study based on three mitochondrial genes and analysed with parsimony methods postulated a separation of wormfishes into distinct Old and New World lineages, with the Old World taxa placed in a clade along with the dartfishes, *Schindleria*, and one *Fusigobius* species (Thacker, 2003). A later analysis with more extensive taxon sampling and an additional mitochondrial gene, using Bayesian phylogenetic methods, yielded another rearrangement, in which the dartfishes sampled formed a clade sister to the wormfishes (Old and New World), as well as *Schindleria* and three members of the

American seven-spined goby lineage: *Risor*, *Barbulifer* and *Tigrigobius* (depicted there as *Gobiosoma*; Thacker, 2009). The hypotheses were consistent in that both wormfishes and dartfishes were found to be nested within Gobiidae, obviating the need for distinct family names. In each analysis, the discussion of the molecular phylogenies included the implications of the new hypothesis for morphological character interpretation. This re-evaluation of interpretations based on additional data and new hypotheses was found to be quite disturbing by some (Gill & Mooi, 2010; Mooi & Gill, 2010), who additionally scorned the possibility that another phylogenetic hypothesis would yield further reinterpretations. Amusingly, our study provides just such an opportunity; our current hypothesis represents a further increase in sampling of markers (three mitochondrial and three nuclear) and of wormfish species (*Microdesmus carri* and *M. dipus*), and we infer a third set of relationships among wormfishes and dartfishes. The groups are united into a single lineage here, without other gobiid taxa, but within this clade, dartfishes are recovered as paraphyletic with respect to wormfishes. This possibility, that the wormfishes may be nested within the dartfishes, was also put forth by Hoese & Motomura (2009), based on similarities between their newly described *Pterocerdale* and both dartfishes and wormfishes. However, in this as well as previous phylogenies, caution is warranted in interpreting parts of the phylogeny characterized by short internodes and low support values. Clearly, the relationships among these taxa are difficult to discern, and discrepancies among hypotheses may also be influenced by differences in both taxon and marker sampling, and of analytical methods. In any case, the homology of any character, morphological or molecular, must be inferred from a broader phylogenetic hypothesis and cannot be asserted in isolation, so reinterpretation based on new, augmented datasets is not just desirable but necessary. Characters proposed by Gill and Mooi (2010) as supporting a close relationship between dartfishes and wormfishes include some discussed previously by Thacker (2000, 2003), as well as newly identified characteristics of the cleithrum and dorsal gill arches. No phylogenetic analysis is attempted, and thus the characters identified are not homologies or synapomorphies; Gill and Mooi (2010) also discuss the occurrence of their characters in other gobioid taxa. Even so, the character evidence is in accordance with the placement here of wormfishes and dartfishes in a single lineage, as well as the inclusion of *Schindleria*. The paedomorphic genus *Schindleria* is included in this lineage due to its resemblance to larval and juvenile *Gunnellichthys*, as well its placement with the group in earlier phylogenetic analyses (Thacker, 2003, 2009).

Inshore gobies

Bathygobius species are known from tropical regions worldwide, where they inhabit shallow sand or rocky habitats,

including tidepools. The upper pectoral fin rays are free from the fin membrane, and thus they are commonly called frillfin gobies or frillgobies (Myers, 1999; Tornabene *et al.*, 2010). *Bathygobius* may be very common where they are found; the genus currently includes 29 species, with new species recently revealed through analysis of sequence diversity and phylogeny (Tornabene *et al.*, 2010; Tornabene & Pezold, 2011). Our hypothesis includes three *Bathygobius* species, and they are resolved as a clade sister to *Psammogobius biocellatus*, the mangrove goby. The speciose genus *Glossogobius*, although not sequenced here, is placed in this lineage due to its close similarities with *Psammogobius*; *Glossogobius* species are distributed throughout the Indo-Pacific, inhabit brackish and freshwater, and individuals are distinguished by their flattened heads (Akihito *et al.*, 1998; Allen *et al.*, 2002). Species of *Bathygobius*, *Glossogobius* and *Psammogobius* exhibit drab overall spotted or spotted pigmentation patterns, as well as the unusual condition of 27–30 vertebrae, also documented from Atlantic lineages including the African gobies and the American seven-spined gobies (Hoese, 1986; Birdsong *et al.*, 1988). *Glossogobius* species also possess bilobed tongues (Hoese & Allen, 2009), as do some *Bathygobius*. One additional genus is included in this lineage, *Grallenia*, a western Pacific genus of two species described from sandy near-reef environments of the Western Pacific (Shibukawa & Iwata, 2007). *Grallenia* species have 27–28 vertebrae, and thus are tentatively postulated to be in the same lineage as *Bathygobius* and *Glossogobius*, the only western Pacific Gobiidae with that vertebral count (except some *Callogobius*, but *Grallenia* lacks the distinguishing characteristics of that lineage). The African gobies also are characterized by the presence of 27 vertebrae, and some species of *Caffrogobius*, *Corygobius* and *Heteroleotris* have the upper pectoral fin rays free, similar to the condition seen in *Bathygobius* (Hoese, 1986). This pectoral fin condition is also seen in some Atlantic *Gobius* and *Mauligobius* (Brito & Miller, 2001), but not in *Glossogobius* or *Grallenia* (Allen *et al.*, 2002; Shibukawa & Iwata, 2007).

Only one of the 170 genera of Gobiidae was so distinctive that we were not able to postulate placement for it among the 13 lineages (Table 1). *Austrolethops*, a monotypic genus containing only *A. wardi*, is a small-eyed, laterally compressed, scaleless, pinkish fish that is widespread in the Indo-Pacific. There are no cephalic sensory canals, but sensory papillae are present on the head, and unusually for gobies, on the body along the lateral midline (Kneer *et al.*, 2008). It was described from muddy habitats (Whitley, 1935), has been reported to inhabit coral rubble, hiding in daylight and emerging at night (Myers, 1999), and also has been recorded from seagrass beds, living commensally with the thalassinid shrimp *Neaxius acanthus* (Kneer *et al.*, 2008; a third group of gobiid-associated shrimp, distinct from alpheids and axiids). *Austrolethops wardi* does not have fused pelvic fins, but examination of radiographs

of the holotype (IA.6175, from the collection of the Australian Museum, Sydney) confirms that it has six dorsal spines arrayed in a 3-22110 pattern and $10 + 16 = 26$ vertebrae, similar to the majority of Indo-Pacific Gobiidae. *Austrolethops wardi* also exhibits the distinctive suspensorium configuration, with the symplectic/metapterygoid strut well-separated from the preopercle that is characteristic of Gobioidae. However, other than those characters consistent with relationships somewhere among the Indo-Pacific lineages of Gobiidae, no more distinctive characters are evident that could be used to postulate a specific placement for *Austrolethops*.

Conclusions

Overall, the progression of phylogenetic analyses for Gobiidae has yielded a relatively consistent portrayal of lineage evolution; some lineages have been consistently identified throughout previous studies, even though marker and taxon sampling and analysis methods have varied (Thacker, 2003, 2009). Others have varied in their composition and interpretations, and in each case of broader gobioid sampling, a notable result has been the uncertainty among backbone relationships in Gobiidae, a condition which persists in our current analysis. Gobiidae is by far the most diverse clade of Gobioidae, and this significantly greater diversity may have been due to elevated speciation rates as gobies invaded marine reef habitats (Thacker, 2009). A burst of speciation over a short time is one of the ways that backbone phylogenetic signal could be obscured. Given the uncertainty regarding the interrelationships of lineages in this analysis, we have focused instead on discussion of each lineage and postulation of other gobiid genera, unsampled here, that are likely also included in each lineage. The initial identification of lineages is phylogenetic, and the assignment of remaining gobiid genera to lineages is phenetic, based on similarity of morphology, ecology or biogeography. These lineages are identified, and additional members beyond those sampled are proposed, as a guide for ongoing phylogenetic and evolutionary studies, both of gobioids and of acanthomorphs more broadly.

Acknowledgements

We are grateful to all the individuals who have provided gobioid tissue samples, for this and other studies. In particular, we are indebted to Carol Stepien and Matt Neilson for providing the Ponto-Caspian goby samples and to Ed Wiley and Andy Bentley for their efforts in establishing and maintaining the fish tissue collection at the University of Kansas Natural History Museum. Carole Baldwin pointed out that a previously sequenced specimen had been misidentified, allowing correction of GenBank records for *Coryphopterus dicrus*. Helen Larson provided helpful suggestions regarding the appropriate placements of

Austrolethops, *Heteroleotris*, *Mangarinus*, *Pascua* and *Tryssogobius*. Rick Winterbottom shared his extensive expertise on *Trimma* and *Trimmatom*, and Koichi Shibukawa kindly provided a wealth of information on gobies inhabiting the waters of Japan. Mark McGrouther, Amanda Hay and Sandra Raredon provided radiographs of *Austrolethops wardi*, and Kyle Luckenbill and Mark Sabaj provided radiographs of *Vomerogobius flavus*. Finally, CT would like to express her ongoing gratitude for the work of R. S. Birdsong (deceased), E. O. Murdy and F. L. Pezold. Their classic 1988 paper provided the first comprehensive assessment of gobioid morphology, and the groups delineated there have guided this and many other studies. This work was supported by grants from the W. M. Keck and R. M. Parsons foundations in support of the programme in Molecular Systematics and Evolution at the Natural History Museum of Los Angeles County.

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Associate Editor: Kevin W. Conway