REGULAR ARTICLE

Heterochrony and the evolution of the longjaw mudsucker (Gobiidae, Teleostei)

Jimjohn Milan[1] | Tyler Fidel[1] | Watcharapong Hongjamrassilp[1,2] | Benjamin W. Frable[3] | Zachary R. Skelton[1,4] | Philip A. Hastings[1,3]

[1]Marine Biology Research Division, Scripps Institution of Oceanography, University of California San Diego, La Jolla, California, USA

[2]Department of Marine Science, Faculty of Science, Chulalongkorn University, Bangkok, Thailand

[3]Marine Vertebrate Collection, Scripps Institution of Oceanography, University of California San Diego, La Jolla, California, USA

[4]Ocean Associates Inc. under contract to Fisheries Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, California, USA

Correspondence
Jimjohn Milan, Marine Biology Research Division, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093, USA.
Email: jimjohnmilan@gmail.com; jmilan@ucsd.edu

Funding information
Link Family Foundation

Abstract

Although longjaw mudsucker (*Gillichthys mirabilis*, Gobiidae) has been studied extensively for its ability to occupy low-oxygen environments, few studies have addressed the evolution of its exceptionally elongated jaws that extend posteriorly beyond the gill opening in large adults. In this study, the ontogeny of the maxillae of *G. mirabilis*, *Gillichthys seta*, and the out-group species *Eucyclogobius newberryi* was studied within the heterochrony framework using digitized landmarks and caliper measurements. The results show that the maxilla of both species of *Gillichthys* evolved via acceleration (increased growth rate) and that of *G. mirabilis* via hypermorphosis (continued growth to a larger body size); two forms of peramorphosis. This is in contrast to earlier studies that concluded that *G. seta* is paedomorphic. We were unable to confirm an earlier hypothesis of sexual dimorphism in the jaw length of *G. mirabilis*. The evolution of the elongated jaws and associated large buccopharyngeal membrane in *G. mirabilis* is hypothesized to increase the surface area for gas exchange during aerial respiration and may also serve to amplify the aggressive gaping display as observed in other fishes.

KEYWORDS
gobies, maxillary bone, morphometry, PCA, sexual dimorphism

1 | INTRODUCTION

Exceptionally large jaws are seen in a variety of teleost fishes. Among these is the longjaw mudsucker, *Gillichthys mirabilis* Cooper 1864, a goby found in southern California and the northern Gulf of California. Its common name derives from the prolonged maxillae that extend posteriorly past the gill openings in large adults. The genus *Gillichthys* includes two additional species restricted to the northern Gulf of California: the shortjaw mudsucker, *Gillichthys seta* (Ginsburg 1938), found in the rocky intertidal and the delta mudsucker, *Gillichthys detrusus* Gilbert & Scofield 1898, restricted to soft sediments in the Colorado River delta region (Barlow, 1961a; Swift et al., 2011). Barlow

(1961a) in a detailed systematic study on *Gillichthys* considered *G. detrusus* a synonym of *G. mirabilis* and noted that *G. seta* and *G. mirabilis* have similar growth trajectories and closely resemble each other at comparable sizes. However, *G. mirabilis* grows to a much larger size and has significantly longer jaws compared to *G. seta*. He hypothesized that *G. seta* is paedomorphic having evolved from *G. mirabilis* by a reduction in body size associated with the transition to their rocky intertidal habitat. Our study tests this hypothesis by documenting the ontogeny of the jaws of these two species in a phylogenetic context by comparison with the tidewater goby *Eucyclogobius newberryi* (Girard 1856), a closely related species (Gong et al., 2018; Zhang & Shen, 2019) within the "North Pacific Bay Goby"

lineage (Teleostei: Gobioidei: Gobionellidae; Ellingson et al., 2014; Thacker, 2015).

Two hypotheses for the selective advantage of the long jaws in *G. mirabilis* have been proposed. First, this iconic fish is well known for its ability to occupy low-oxygen environments by gulping air into the branchial cavity where gas exchange occurs across the internal lining of the cavity (Barlow, 1961a, 1961b; Todd & Ebeling, 1966). The long jaws and associated large and highly vascularized buccal chamber of *G. mirabilis* increase the surface area and may facilitate aerial respiration (Todd & Ebeling, 1966). Second, because the elongation of the upper jaw in *G. mirabilis* has been shown to be particularly pronounced in males (Crabtree, 1985; Weisel, 1947), a role for sexual selection has been suggested for the evolution of long jaws in this species. This and other species of bay gobies are known to show an agonistic gaping display in which an open mouth is presented toward another individual for territorial or nest defense during mating intervals (Crabtree, 1985; Miles, 1975; Swenson, 1997, 1999; Weisel, 1947). The prolonged jaws make this display especially pronounced in *G. mirabilis* and offer an alternative hypothesis for the evolution of this morphology. This behavior is similar to that reported for the sarcastic fringehead, *Neoclinus blanchardi* Girard 1858 (Crabtree, 1985; Hongjamrassilp et al., 2018; Hongjamrassilp et al., 2022).

To better understand the evolution of jaw length in this and related species, this study examines the role of heterochrony in the development and evolution of the prolonged jaws of *G. mirabilis*. Any genetically controlled difference in the duration or timing of an organism's developmental process can be compared to its inferred ancestor by comparison with closely related species. We examine (1) the role of heterochrony in the evolution of the maxilla in *Gillichthys* using morphometrics based on a truss network established from landmarks and additional measurements, (2) the overall shape space occupied by *Gillichthys* species, and (3) the presence of sexual dimorphism in the maxilla of *Gillichthys* species (Crabtree, 1985).

2 | MATERIALS AND METHODS

Heterochrony compares the rate, timing, and/or duration of developmental events or traits with developmental time. Although the age of preserved specimens could not be determined for our study, body size was used as a proxy for age to assess changes in morphology over developmental time (Hongjamrassilp et al., 2018; Klingenberg, 1996). Morphometric data were collected on a size series of preserved specimens of *G. mirabilis*, *G. seta*, and *E. newberryi* from the Scripps Institution of Oceanography Marine Vertebrate Collection (SIO) and the Natural History Museum of Los Angeles County (LACM). Specimens were selected based on a balanced size range and high preservation quality. The sex of specimens was identified based on genital papilla morphology. Females have a rounded papilla, whereas the papilla of males is more pointed (Barlow, 1961a; Weisel, 1947, 1949). This method of sex identification was confirmed in a subsample of specimens through dissection and examination of the gonads. Those too

small to be confidently identified by sex were considered juveniles. A total of 44 specimens of *G. mirabilis* (19 males, 21 females, 4 juveniles; 20.3–147 mm standard length [SL]), 28 specimens of *G. seta* (10 males, 13 females, 5 juveniles; 18.3–63.4 mm SL), and 30 specimens of *E. newberryi* (12 males, 12 females, 6 juveniles; 10.5–46 mm SL) were included in this study (Table S1). Each specimen was photographed in a lateral view using a camera (Nikon D3200 & iPhone 12 mini) with an included scale bar, and traditional truss distances were taken from the photographs. The following landmarks were indicated by pins in each specimen prior to photographing (Figure 1): (1) anterior tip of nasal bone, (2) insertion of first dorsal-fin spine, (3) insertion of first element of second dorsal fin, (4) upper tip of dorsal hypural plate, (5) lower tip of ventral hypural plate, (6) first anal-fin spine insertion, and (7) pelvic-fin spine base. Before digitizing the landmarks, the image editing package *magick* (Ooms, 2020) was used to sharpen the images in R Version 4.2.1 (R Core Team, 2022). The function *digitize2d* in the package *geomorph* (Adams et al., 2022) was then used to load in the images onto R and landmarks were digitized into each image, creating a TPS (or .tps) file. The *dist* function (R Core Team, 2022) was used on the TPS file to produce 13 truss distances using the digitized landmarks. Six additional measurements were taken directly from each preserved specimen using digital calipers. These included the following (Figure 1): (1) head length from snout to farthest posterior point of the operculum (HLL), (2) head length from snout to dorsal operculum insertion (HLI), (3) total upper jaw length or jaw length from snout to farthest posterior point of the maxilla (TJL), (4) free maxilla length or the posterior portion of the maxilla that is not attached to the head (FML), (5) maximum maxilla depth (MD), and (6) body depth at the origin of the anal fin (BD).
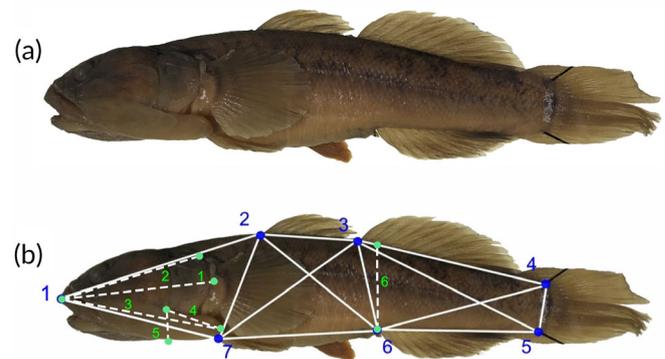

FIGURE 1 Photos of a preserved *Gillichthys mirabilis* (a) unlabeled and (b) with labeled landmarks used in geometric morphometric analysis (in blue): (1) anterior tip of nasal bone, (2) first dorsal-fin spine insertion, (3) insertion of first element of second dorsal fin, (4) upper tip of dorsal hypural plate, (5) lower tip of ventral hypural plate, (6) first anal-fin spine insertion, and (7) pelvic-fin spine base. Additional measurements used in geometric morphometric analysis (in green): (1) head length from snout to farthest posterior point of the operculum, (2) head length from snout to dorsal operculum insertion, (3) total upper jaw length, (4) free maxilla length or the posterior portion of the maxilla that is not attached to the head, (5) maximum maxilla depth, and (6) body depth at the origin of the anal fin.

The truss measurements and additional measurements were analysed using principal component analysis (PCA) under the covariance matrix using the function *princomp* (R Core Team, 2022). Because the data were not normally distributed, we log-transformed the data to satisfy assumptions using parametric statistical analyses. PC1 scores, representative of body size (Strauss & Bookstein, 1982), were plotted against log-transformed free maxilla length and total jaw length. A second PCA was performed in R after an allometric-Burnaby transformation (Klingenberg, 2016) in PAST Version 4.0 (Hammer et al., 2001) for shape space analysis. The allometric-Burnaby technique in PAST log-transforms the 19 measurements and orthogonally projects them to the first principal component. The results for the initial PCAs were analysed using a two-way ANCOVA under package *car* (Fox & Weisberg, 2018) in R to compare slope differences between the three species and between life stages (i.e., adults and juveniles) of each species. Normality of the residuals was confirmed via visual Q-Q plots and Shapiro-Wilks normality tests. A MANOVA ($\alpha = 0.05$) test (package *manova* [R Core Team, 2022]) was used to analyse the significance of the shape space data. Following findings of significance, we conducted pair-wise post hoc comparisons of means and slopes using estimated marginal means with Tukey contrasts ($\alpha = 0.05$) using *emmeans* and *emtrends* ("emmeans": Lenth et al., 2021) in R.

3 | RESULTS

From the uncorrected PCA, PC1 accounted for 97.44% of the variation in the 13 truss distances and 7 additional measurements. PC1 loadings (Table S2) were all positive, thus PC1 score was used as a representation of body size (Strauss & Bookstein, 1982). The highest loadings along PC1 were jaw measurements, more specifically free maxilla length, maximum maxilla depth, and total jaw length (Table S2). Positive correlation was seen between PC1 and both free maxilla length and jaw length in all regression lines (Figure 2). The growth rate of free maxilla length, inferred by the slopes of the regression lines in Figure 2, was shown to have significant differences in the three species (ANCOVA; $p < 0.001$). The growth rate of total jaw length significantly differed between species (ANCOVA; $p < 0.001$). However, post hoc analysis showed growth rate of total jaw length did not differ between *G. mirabilis* and *G. seta* ($p = 0.164$).

In *G. mirabilis*, there were significant differences in the free maxilla length and total jaw length slopes between adults and juveniles (ANCOVA, $p < 0.001$) but not between males and females in either measurement (ANCOVA; TJL: $p = 0.8466$, FML: $p = 0.8707$). Male, female, and juvenile *G. seta* differed significantly from each other in free maxilla length (ANCOVA, $p < 0.001$) and juveniles differed from adults in total jaw length (ANCOVA, $p < 0.001$), but male and females did not (ANCOVA; TJL: $p = 0.5562$). Only male *E. newberryi* significantly differed from juveniles in free maxilla length (ANCOVA, $p < 0.001$) whereas females did not differ from either (ANCOVA; FML: Female–Male: $p = 0.2578$, Female–Juvenile: $p = 0.1061$). In total jaw length, adult *E. newberryi* differed from juveniles (ANCOVA,

$p < 0.001$), but males and females did not differ from each other (ANCOVA; TJL: $p = 0.3953$).

There was no evidence of sexual dimorphism in the maxilla of *G. mirabilis* (Figure 3a). With PC1 representing body size, there were no sex-specific differences in either total jaw length (ANCOVA; TJL: $p = 0.6036$) or free maxilla length (ANCOVA; FML: $p = 0.6587$). Sexual dimorphism was also not seen in *G. seta* total jaw length (ANCOVA; $p = 0.3761$), and in *E. newberryi* total jaw length and free maxilla length (ANCOVA; TJL: $p = 0.2345$, FML: $p = 0.1623$). Significant sexual dimorphism in jaw-related measurements was only seen in *G. seta* free maxilla length (ANCOVA; $p = 0.0198$). In addition, standard length (instead of PC1) was compared with total jaw length and free maxilla length for *G. mirabilis*, and there were also no differences between sexes (ANCOVA; TJL: $p = 0.98615$; FML: $p = 0.5388$).

After adjusting the measurement data of mature specimens with the Burnaby transformation, PC1 accounted for 25.8% of variation, whereas PC2 accounted for 20.7% of variation (Figure 4; Table S3). The highest positive loadings along PC1 were TR10 (4–5), the vertical length of the caudal peduncle, and TR13 (6–7), the length from the insertion of the first anal-fin spine to the insertion of the pelvic fin spine. The highest negative loadings were jaw measurements: FML and MD (Table S3). *G. seta* had the lowest range of scores along PC1, whereas *E. newberryi* showed the widest range. The variables that loaded highest along PC2 were all jaw measurements: TJL and FML were positive loadings, whereas MD was a negative loading. Both species of *Gillichthys* scored more positive values along PC2 on average than *E. newberryi* with *G. seta* showing the highest range among the three. The data used in shape space analysis differed significantly between the three species (MANOVA; $p < 0.001$).

4 | DISCUSSION

The growth trajectories for total upper jaw length and free maxilla length for the two species of *Gillichthys* differed significantly between adults and juveniles. *Eucyclogobius* adults differed in the growth trajectory of total jaw length but only a partial difference was seen in free maxilla length between males and juveniles (Figure S1a,b). This indicates a faster relative growth rate in the upper jaw and especially the free posterior extension of the maxilla after reaching sexual maturity in both *Gillichthys* species but an increase in only males of *Eucyclogobius*. In addition, adults of the two species of *Gillichthys* occupy a similar shape space compared to *Eucyclogobius* (Figure 4). This is consistent with Barlow's (1961a) report that individuals of the two species of *Gillichthys* of the same size are similar and that mature individuals of *G. seta* resemble premature individuals of *G. mirabilis*. Given this similarity, it is worth noting that these two species occur in distinctly different habitats. As the name implies, the Longjaw Mudsucker is found on mud bottoms in sheltered bays (Weisel, 1947), whereas the Shortjaw Mudsucker, *G. seta*, occurs in rocky tide pools in the upper intertidal zone of the northern Gulf of California (Barlow, 1961a; Thomson et al., 2000).
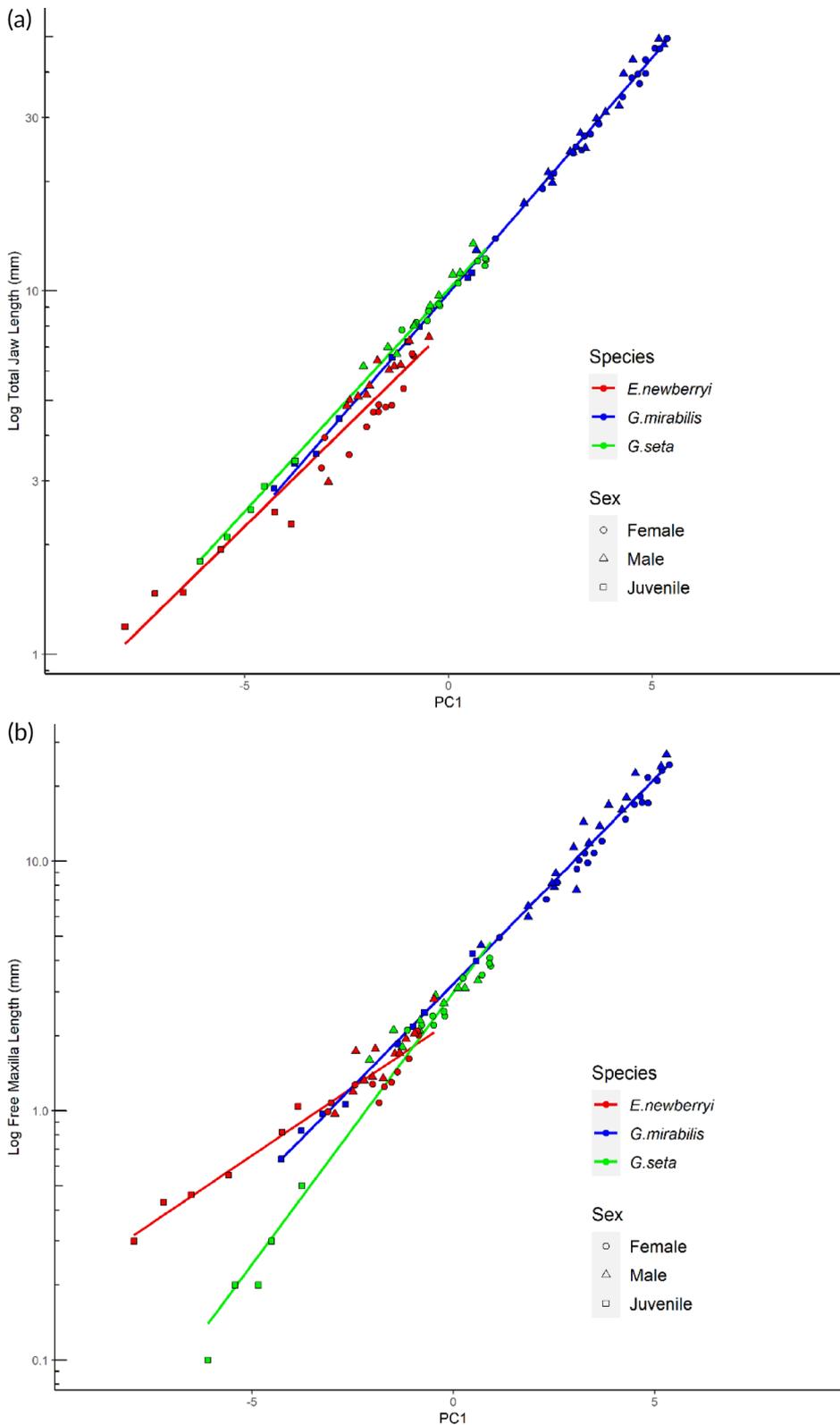
FIGURE 2 Scatter plot of principal component 1 score (representative of body size) for all three species against (a) log-transformed total jaw length and (b) log-transformed free maxilla length. Linear trendline shown as lines matching the colors for each species. Sex is shown with different shapes for each species.

Sexual dimorphism was not clearly seen in our data on *Gillichthys* (Figure 3a–d), despite a previous study that reported that males have longer jaws than females in *G. mirabilis* (Crabtree, 1985). Several possibilities may account for this discrepancy. First, and most importantly, Crabtree (1985) sampled far more males and females (*n* = *c*. 130;

c. 80 males and *c*. 50 females) than we did (*n* = 40; 19 males, 21 females) and across a larger size range. Second, our estimate of body size (PC1) is based on multiple features instead of just SL used by Crabtree. Third, whereas Crabtree sampled a single population, our samples came from multiple sites over multiple years, and patterns of
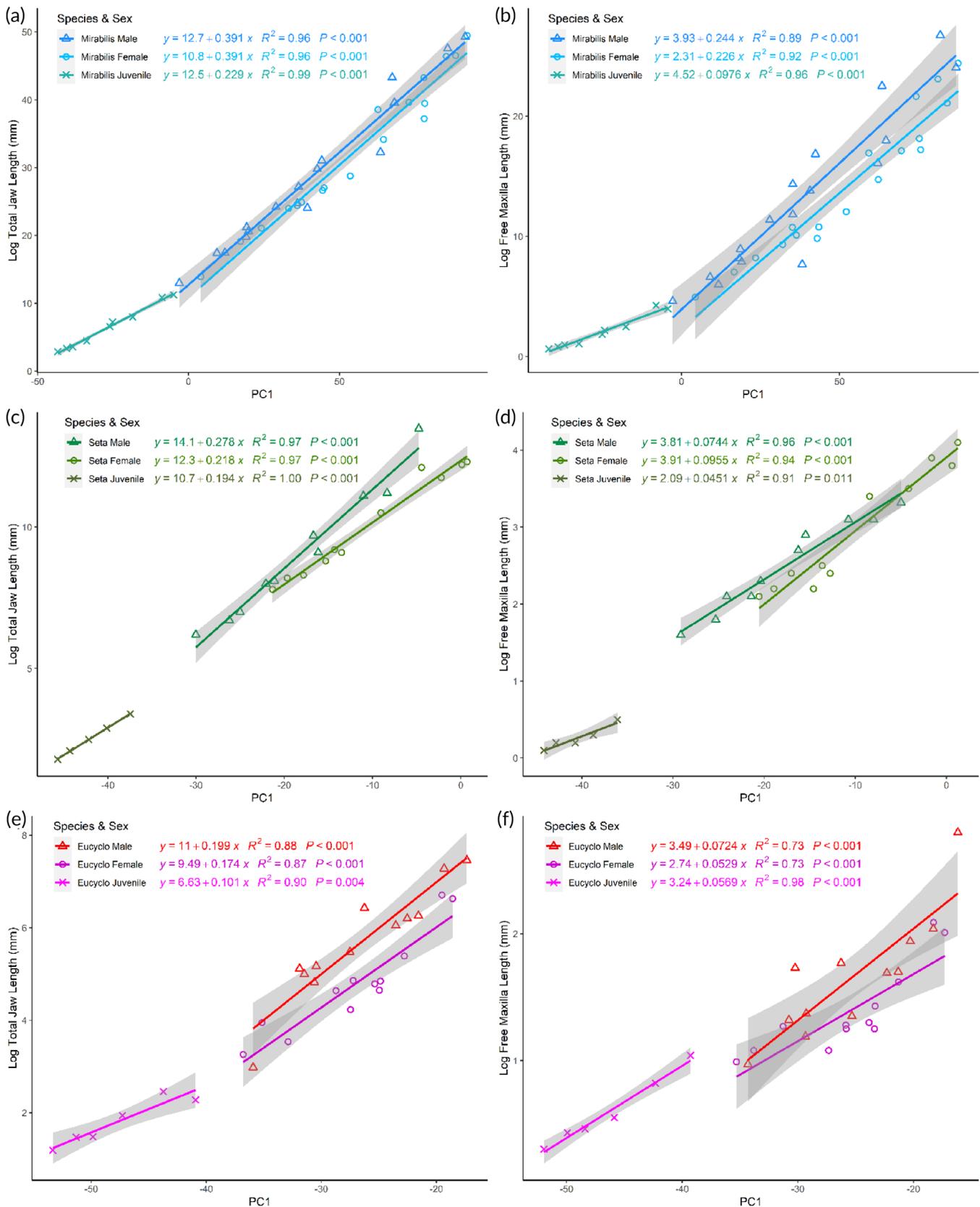
FIGURE 3 Scatter plot of principal component 1 score (representative of body size) for mature and juvenile (a) *Gillichthys mirabilis* against log-transformed total jaw length, (b) *G. mirabilis* against log-transformed free maxilla length, (c) *Gillichthys seta* against log-transformed total jaw length, (d) *G. seta* against log-transformed free maxilla length, (e) *Eucyclogobius newberryi* against log-transformed total jaw length, and (f) *E. newberryi* against log-transformed free maxilla length. Linear trendlines shown with corresponding equations matching the colors for each sex.
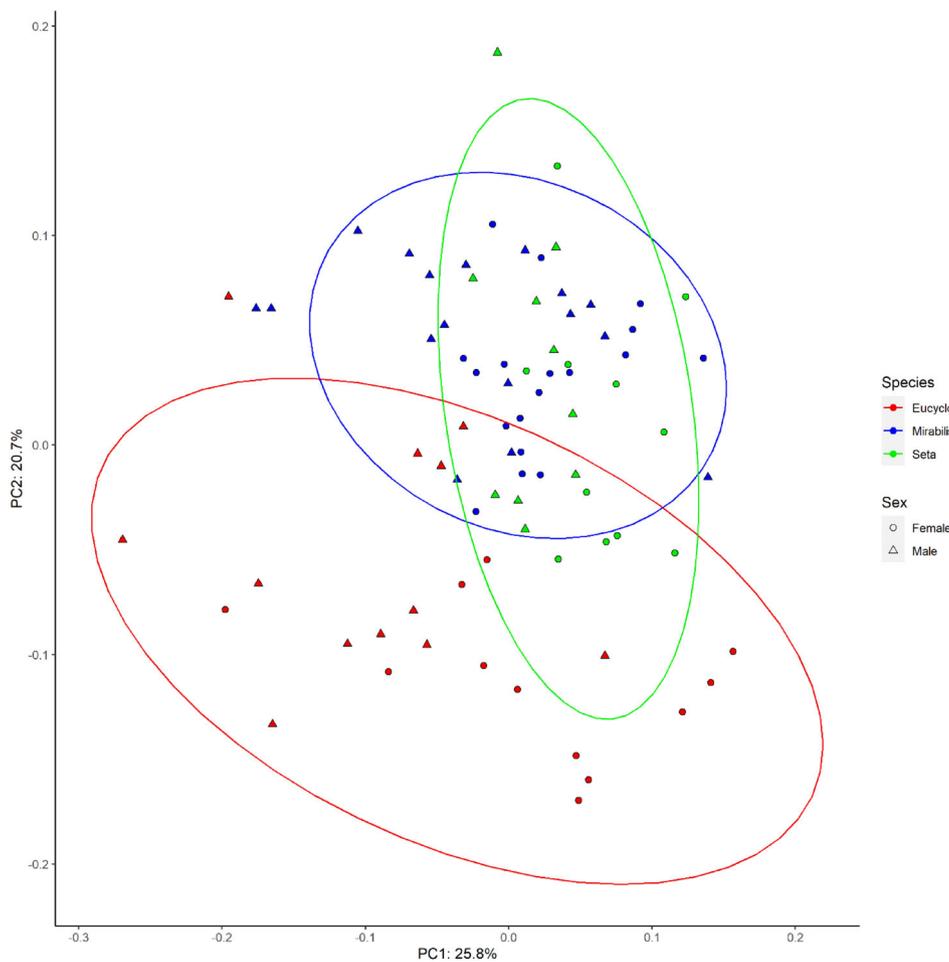
FIGURE 4 Scatterplot of principal components 1 and 2 from a principal component analysis of sexually mature *Gillichthys mirabilis*, *Gillichthys seta*, and *Eucyclogobius newberryi* (morphometric data adjusted using allometric-Burnaby transformation). Ellipses represent 95% confidence intervals.

dimorphism may differ as populations may experience different selective pressures and evolve differently (Sol et al., 2020). Although the ANCOVA found no statistical difference between the growth rates of male and female *E. newberryi*, our study found a significant difference in the overall length of the jaws between sexes (Figure 3e,f), consistent with reports that both species of *Eucyclogobius* are sexually dimorphic in jaw length (Swift et al., 2016).

This study indicates that the extraordinarily long jaws of *G. mirabilis* evolved via two separate steps of peramorphic heterochrony, acceleration and hypermorphis (Figure 5). First, compared to the out-group *Eucyclogobius*, the upper jaw and especially the free posterior jaw extension of two species of *Gillichthys* grow more rapidly in length with increasing body size (Figure 2), a pattern known as acceleration (McKinney, 2013). This interpretation of the evolutionary pattern of heterochrony in jaw length reported in this study (Figure 5) depends upon the inferred jaw allometry in the immediate ancestor of the genus *Gillichthys*. This genus is included in the so-called "bay goby" lineage (Ellingson et al., 2014; Thacker, 2015) and based on these and other recent phylogenetic studies, its closest relatives are within the monophyletic eastern Pacific clade that includes *Clevelandia*, *Eucyclogobius*, *Evermannia*, *Illypnus*, *Lepidogobius*, *Lethops*, *Quietula*, and *Typhlogobius* (Table S4). Members of the bay goby lineage tend toward relatively long jaws compared to many other lineages of

gobies. Whereas in some members, such as *Lepidogobius*, the maxilla ends at mid-orbit (Gill, 1863), in others, most notably *Quietula*, the maxilla extends well past the posterior margin of the orbit but typically not to the level of the preopercular margin (Kindermann et al., 2007). The maxilla extends beyond the preopercular margin in *G. seta*, and well past the posterior margin of the operculum in large individuals of *G. mirabilis* (and *G. detrusus*, see below). Jaw growth in *Gillichthys* species is clearly accelerated compared to that of *Eucyclogobius* (Figures 2 and 3). Inclusion of the ontogenetic trajectory of additional species of bay gobies would provide increased confidence in the ancestral condition in *Gillichthys* and may affect the inferred point on the phylogeny that acceleration of jaw growth occurred.

Second, within *Gillichthys*, *G. mirabilis* grows to a considerably larger body size than *G. seta* (maximum size 147 vs. 70 mm SL; Table S4) and, as a consequence of the positive allometry of jaw growth, has a relatively longer jaw and free posterior extension, a pattern known as hypermorphosis (McKinney, 2013). This is in contrast to the conclusion of Barlow (1961a) and Huang and Bernardi (2001) that *G. seta* evolved via paedomorphosis by a reduction in body size. From a developmental perspective, mature *G. seta* closely resembles premature, similarly sized individuals of *G. mirabilis* and thus may be considered developmentally paedomorphic. However, from an evolutionary perspective, it is clear that the uniquely elongate jaws of
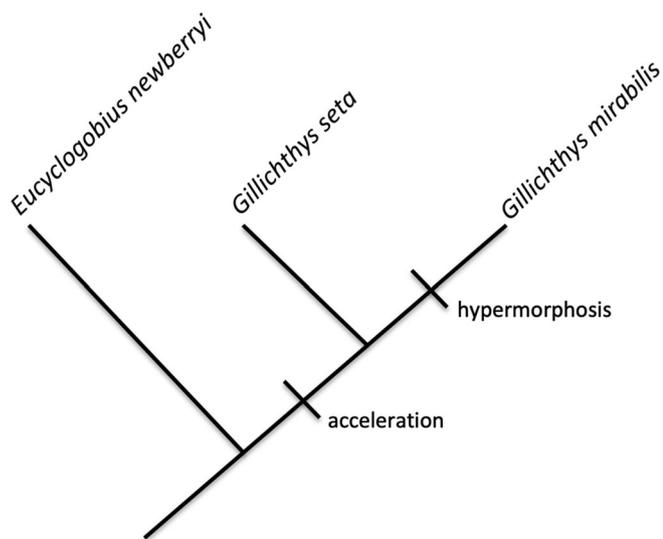
FIGURE 5 Hypothesized phylogeny and inferred patterns of heterochrony between *Eucylcogobius* and *Gillichthys*.

G. mirabilis (and *G. detrusus*, see below) evolved via hypermorphosis as a result of their increase in body size compared to *G. seta* and other members of the bay gobies. The longjaw mudsucker is the largest member of the Eastern Pacific clade of bay gobies (Table S4) and is also larger than all members of the western Pacific clade. *Chaenogobius gulosus*, with a maximum size of 117 mm SL is the largest member of that clade (Stevenson, 2002), and Ellingson et al. (2014) concluded that it is convergent with *Gillichthys* in relatively large body size. A third species of *Gillichthys* (*G. detrusus*) is morphologically similar and recently recovered as a sister taxon to *G. mirabilis* with which it was confused for decades (Swift et al., 2011). Considering *G. detrusus* grows larger than *G. seta* (maximum SL 93 vs. 70 mm; Table S4) and is more closely related to *G. mirabilis*, we predict the pattern of hypermorphosis in the jaw is similar to that of the longjaw mudsucker.

Peramorphic heterochrony is poorly documented in gobies, which are more often thought to evolve via paedomorphosis (Kon & Yoshino, 2002). A typical evolutionary trend among gobies is a reduction in body size and thus truncation of development (Miller, 1979). The increased allometry in jaw growth and increase in body size seen in *G. mirabilis* compared to other gobies appear to be relatively rare. This parallels a similar finding for the sarcastic fringehead, *Neoclinus blanchardi* (Blenniiformes), in which both acceleration and increased body size result in especially elongated jaws that function to amplify aggressive displays (Hongjamrassilp et al., 2018; Hongjamrassilp et al., 2022). The function of this extraordinary feature in the longjaw mudsucker, whether for aggression (Weisel, 1947), gas exchange (Todd & Ebeling, 1966), or other functions such as digging burrows in mud bottoms, remains to be demonstrated.

AUTHOR CONTRIBUTIONS

The study and methodology were formed by Jimjohn Milan, Tyler Fidel, Watcharapong Hongjamrassilp, Benjamin W. Frable, Zachary

R. Skelton, and Philip A. Hastings. Data collection was conducted by Jimjohn Milan and Tyler Fidel under supervision from Benjamin W. Frable and Philip A. Hastings. The data were analysed by Jimjohn Milan and validated by Watcharapong Hongjamrassilp, Benjamin W. Frable, Zachary R. Skelton, and Philip A. Hastings. The draft was written by Jimjohn Milan and edited by Tyler Fidel, Watcharapong Hongjamrassilp, Benjamin W. Frable, Zachary R. Skelton, and Philip A. Hastings.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials. Raw data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Jimjohn Milan https://orcid.org/0000-0002-0337-1689
Watcharapong Hongjamrassilp https://orcid.org/0000-0002-4498-2515
Benjamin W. Frable https://orcid.org/0000-0003-4525-0671
Zachary R. Skelton https://orcid.org/0000-0003-2422-9240
Philip A. Hastings https://orcid.org/0000-0002-9867-6601

REFERENCES

Adams, D., Collyer, M., Kaliontzopoulou, A., & Baken, E. (2022). Geomorph: Software for geometric morphometric analyses. R package version 4.0.4. https://cran.r-project.org/package=geomorph

Barlow, G. W. (1961a). Gobies of the genus *Gillichthys*, with comments on the sensory canals as a taxonomic tool. *Copeia, 1961*, 423–437.

Barlow, G. W. (1961b). Intra-and interspecific differences in rate of oxygen consumption in gobiid fishes of the genus *Gillichthys*. *The Biological Bulletin, 121*, 209–229.

Crabtree, C. B. (1985). Sexual dimorphism of the upper jaw in *Gillichthys mirabilis*. *Bulletin of the Southern California Academy of Sciences, 84*, 96–103.

Ellingson, R. A., Swift, C. C., Findley, L. T., & Jacobs, D. K. (2014). Convergent evolution of ecomorphological adaptations in geographically isolated bay gobies (Teleostei: Gobionellidae) of the temperate North Pacific. *Molecular Phylogenetic and Evolution, 70*, 464–477. https://doi.org/10.1016/j.ympev.2013.10.009

Fox, J., & Weisberg, S. (2018). *An R companion to applied regression*. Sage Publications.

Gill, T. (1863). Descriptions of the gobioid genera of the Western coast of temperate North America. *Proceedings of the Academy of Natural Sciences of Philadelphia, 15*, 262–267.

Gong, L., Lü, Z. M., Guo, B. Y., Ye, Y. Y., & Liu, L. Q. (2018). Characterization of the complete mitochondrial genome of the tidewater goby, *Eucyclogobius newberryi* (Gobiiformes; Gobiidae; Gobionellinae) and its phylogenetic implications. *Conservation Genetics Resources*, 10, 93–97.

Hammer, Ø., Harper, D. A., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4, 9.

Hongjamrassilp, W., Skelton, Z., & Hastings, P. A. (2022). Function of an extraordinary display in sarcastic Fringeheads (*Neoclinus blanchardi*) with comments on its evolution. *Ecology*, 104, e3878.

Hongjamrassilp, W., Summers, A. P., & Hastings, P. A. (2018). Heterochrony in fringeheads (*Neoclinus*) and amplification of an extraordinary aggressive display in the sarcastic Fringehead (Teleostei: Blenniiformes). *Journal of Morphology*, 279, 626–635.

Huang, D., & Bernardi, G. (2001). Disjunct Sea of Cortez–Pacific Ocean *Gillichthys mirabilis* populations and the evolutionary origin of their paedomorphic relative, *Gillichthys seta*. *Marine Biology*, 138, 421–428.

Kindermann, G., Miljkovic, N., Ahnelt, H., & Stevenson, D. E. (2007). The osteology of *Eucyclogobius newberryi* and *Quietula guaymasiae* (Teleostei: Gobiidae), two closely related Gobionellines from the East Pacific. *Annals Naturhistorisches Museum Wien*, 108B, 13–56.

Klingenberg, C. P. (1996). Multivariate allometry. In *Advances in morphometrics* (pp. 23–49). Springer.

Klingenberg, C. P. (2016). Size, shape, and form: Concepts of allometry in geometric morphometrics. *Development Genes and Evolution*, 226, 113–137.

Kon, T., & Yoshino, T. (2002). Diversity and evolution of life histories in gobioid fishes from the viewpoint of heterochrony. *Marine and Freshwater Research*, 53, 377–402.

Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2021). Emmeans: Estimated marginal means, aka least-squares means. R Package Version 1. https://cran.r-project.org/package=emmeans

McKinney, M. L. (2013). *Heterochrony in evolution: A multidisciplinary approach*. Springer.

Miles, P. S. (1975). *Agonistic behavior of some gobiid fishes from the Gulf of California*. Unpubl. PhD Dissertation (p. 158). University of Arizona.

Miller, P. J. (1979). Adaptiveness and implications of small size in teleosts. *Symposium of the Zoological Society, London*, 44, 263–306.

Ooms, J. (2020). magick: advanced graphics and image-processing in R. R package version 2.3. https://cran.r-project.org/package=magick

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing https://www.R-project.org/

Stevenson, D. E. (2002). Systematics and distribution of fishes of the Asian goby genera *Chaenogobius* and *Gymnogobius* (Osteichthyes: Perciformes: Gobiidae), with the description of a new species. *Species Diversity*, 7, 251–312.

Strauss, R. E., & Bookstein, F. L. (1982). The truss: Body form reconstructions in morphometrics. *Systematic Zoology*, 31, 113–135.

Swenson, R. O. (1997). Sex-role reversal in the tidewater goby, *Eucyclogobius newberryi*. *Environmental Biology of Fishes*, 50, 27–40.

Swenson, R. O. (1999). The ecology, behavior, and conservation of the tidewater goby, *Eucyclogobius newberryi*. *Environmental Biology of Fishes*, 55, 99–114.

Swift, C. C., Findley, L. T., Ellingson, R. A., Flessa, K. W., & Jacobs, D. K. (2011). The delta mudsucker, *Gillichthys detrusus*, a valid species (Teleostei: Gobiidae) endemic to the Colorado River delta, northernmost gulf of California, México. *Copeia*, 2011, 93–102.

Swift, C. C., Spies, B., Ellingson, R. A., & Jacobs, D. K. (2016). A new species of the bay goby genus *Eucyclogobius*, endemic to southern California: Evolution, conservation, and decline. *PLoS One*, 11, e0158543.

Thacker, C. E. (2015). Biogeography of goby lineages (Gobiiformes: Gobioidei): Origin, invasions and extinction throughout the Cenozoic. *Journal of Biogeography*, 42, 1615–1625.

Thomson, D. A., Findley, L. T., & Kerstitch, A. N. (2000). *Reef fishes of the sea of Cortez: The rocky-shore fishes of the Gulf of California*. University of Texas Press.

Todd, E. S., & Ebeling, A. W. (1966). Aerial respiration in the longjaw mudsucker *Gillichthys mirabilis* (Teleostei: Gobiidae). *The Biological Bulletin*, 130, 265–288.

Weisel, G. F. (1947). Breeding behavior and early development of the mudsucker, a gobiid fish of California. *Copeia*, 1947, 77–85.

Weisel, G. F. (1949). The seminal vesicles and testes of *Gillichthys*, a marine teleost. *Copeia*, 1949, 101–110.

Zhang, F., & Shen, Y. (2019). Characterization of the complete mitochondrial genome of *Rhinogobius leavelli* (Perciformes: Gobiidae: Gobionellinae) and its phylogenetic analysis for Gobionellinae. *Biologia*, 74, 493–499.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.