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The tail flick warning signals and the molecular phylogeny and evolution of gobiid fishes associated with burrowing alpheid shrimps

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Abstract

The associations between gobiid fishes and burrowing alpheid shrimps are mutualistic partnerships. The shrimp constructs a burrow which provides the goby with a shelter, whereas, the goby provides the almost blind shrimp with a tactile alarm system. The goby warns the shrimp of danger by the emittance of tail flicks and its head or tail first burrow entrances. In this field study, gobies were stimulated to emit the tail flick warning signals by a slow approaching predator model and a live restrained predator. Three associations were tested, each consisting of a goby of a different genus, associated with a different species of alpheid shrimp: *Cryptocentrus lutheri* with *Alpheus djiboutensis*, *Amblyeleotris steinitzi* with *A. purpurilenticularis* and *Ctenogobiops maculosus* with *A. rapax*. Two patterns of high and low rate signal generation were found in the experiment with the mobile model and the live restrained predator as well. *Cryptocentrus lutheri* produced relatively few warning signals when stimulated by the model, less than a quarter of the signals produced by the other two species. This goby entered its burrows tail first, when the model was about three times further away compared with the distance from the model when *Amblyeleotris steinitzi* and *Ctenogobiops maculosus* retreated head first into their burrows. *Cryptocentrus lutheri* produced as well fewer warning signals and signal series when exposed to a live restrained predator compared with *Amblyeleotris steinitzi* and *Ctenogobiops maculosus*. Phylogenies of gobies associated with shrimps were previously found to consist of two clades nested amongst non-mutualistic gobiid fish, indicating that the goby-shrimp partnership evolved twice. The findings of this study suggest that the evolution of these two clades resulted in two behavioral types of gobies, namely low and high rate warning signal generators.

1 Introduction

The partnerships between gobiid fishes and burrowing alpheid shrimps are mutualistic, with both fish and shrimp contributing and benefitting from their association. The shrimp constructs burrows in the sandy sediments which provide the goby with a retreat from threatening predators during the day and a protected resting place during the night. Furthermore, these burrows are also used by the goby as a safe place for incubating and hatching its eggs. The goby provides the almost blind shrimp with a tactile alarm system. The shrimp while outside its burrow continuously maintains antennal contact with the goby which serves as its sentinel. The shrimp is warned from approaching predators by either tail flicks or burrow entrances of the fish. The goby remains perched at the burrow entrance while a predator is at some distance from the burrow opening, monitoring the predator while emitting tail flicks. However, as soon as the predator further approaches the burrow, the goby retreats into its shelter head first or tail first, followed by the shrimp (Karplus, 1987, 2014; Karplus and Thompson, 2011).

The first mentioning of the goby-shrimp warning system was limited to the goby withdrawal into the burrow which result in the rapid retreat of the shrimp (Luther, 1958; Smith, 1959; Herald, 1961). Magnus (1967) described for the first

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time the tail flick warning signal in C*ryptocentrus caeruleopunctatus* (Ruppel, 1830) from the Red-Sea as rapid and short tail flicks resulting in the retreat of its associated shrimp into its burrow. Subsequently, Harada (1969) described in Japan tail flicks of *Amblyeleotris japonica* (Takagi, 1957) as vigorous quivering of its tail, which result in the disappearance of its associated shrimp *Alpheus bellulus* (Miya & Miyake, 1969) into its burrow. In most studied associated gobies the tail flick signals were generated in response to the approach of the observer to the association [e.g., *Cryptocentrus caeruleopunctatus* in the Red-Sea (Magnus, 1967), *Psilogobius mainlandi* (Baldwin, 1972) in Hawaii (Moehring, 1972; Preston, 1978) and *Nes longus* (Nichols, 1914) in Southern Florida (Karplus, 1992)].

Amblyeleotris steinitzi (Klausewitz, 1974) in the northern Red-Sea produced 7.4 tail flicks per hour in the late afternoon in response to the approach of certain species of fishes. The size of the approaching fish and its feeding characteristics determine whether it will cause the emission of warning signals by the goby. All large fishes triggered the release of warning signals, while no small fishes had such an effect. The goby was selective in its response to medium sized fishes. The majority of warning signals were triggered by goatfishes which stir up the sediment and may obstruct the burrow entrances. Medium sized piscivore fishes triggered the release of warning signals, while fishes of the same size that feed on algae or corals were ignored (Karplus, 1987). *A. steinitzi* responded with a high rate of warning signals when exposed to the piscivore *Parapercis hexophthalma* (Cuvier, 1829) in a box while it ignored the empty box and *Acanthurus nigro fuscus* (Forsskal, 1775) a fish feeding on algae presented in the same box and distance (Karplus, 1979). The tail flick warning signals of *A. steinitzi* have been analyzed after being captured on films. These signals were found to be of short duration (i.e., less than one second) and small amplitude (i.e., less than 7 mm). The conspicuous nature of this signal compared with all other tail movements provides it with coding characteristics (Karplus et al. 1979).

The goby performs a head-first burrow entry when facing an extremely dangerous situation such as the close approach of a piscivore. The goby may also perform a tail first burrow entry under circumstances of lower danger such as a piscivore positioned at some distance from the burrow or perform a partial tail entry when facing an approaching conspecific. *A. steinitzi* retreated in the field head first into its burrow at a rate of 0.3 per hour. The same approaching fishes causing the release of the tail flick warning signals, also induced at closer range the goby's head first retreat. Whereas tail flicks are only produced in the presence of the shrimp outside the burrow, the head and tail first burrow entries are performed irrespective of the shrimp presence (Karplus, 1979; Karplus et al. 1979).

The evolution of mutualism between gobies and burrowing alpheid shrimps was studied with the aid of molecular phylogenies based on nuclear and mitochondrial DNA sequence data (Thacker et al. 2011). In the phylogeny 54 species of gobies were represented, including 27 Indo-Pacific shrimp gobies, which belong to seven different genera. All of the genera except *Cryptocentrus* were confirmed to be monophyletic. The phylogeny indicated that mutualistic associations with alpheid shrimp have evolved twice among the sampled gobiid genera nested amongst non-mutualistic gobiid relatives. The first clade was composed of *Amblyeleotrs*, *Ctenogobiops* and *Vanderhorstia* while the second clade consisted of *Cryptocentrus*, *Mahidolia*, *Tomyamichthys* and *Stonogobiops.* A recent phylogenetic reconstruction, based on mitochondrial DNA sequence of available shrimp associated gobies, incorporating for the first time representatives of the genera *Lotilia, Myersina* and *Psilogobius* revealed again a basal separation into two clades of shrimp gobies (Goren and Stern, 2021). Thacker and Roje (2011) stated that the identification of distinct morphological characteristics for each shrimp associated clade is difficult. They used the associated goby distribution for identification of distinct characteristics of clade one and two. Hoese and Larson (2004) noted that while *Amblyeleotris* species are associated with shrimp in sandy habitat near coral reefs, many *Cryptocentrus* species were found in more silty habitats. Thus, the clade consisiting of *Amblyeleotris*, *Cteonogbiops* and *Vanderhorstia* was named by Thacker and Roje (2011) "reef shrimp gobies", whereas the clade that consisted of *Cryptocentrus* and related shrimp associated gobies was named "silt shrimp gobies". However, these traits are not exclusive as stated by Thacker and Roje (2011) since *Cryptocentrus* may also inhabit sandy areas near coral reefs.

Despite the richness of associated gobies with more than 120 described species belonging to over twenty genera and a wide circum tropical distribution, no comparative studies on associated gobies warning signal generation were published. Studies on warning signal generation focused on a single species, and used no controlled stimulation of the goby, which may allow a comparison among species (Karplus, 2014). A comparative study of goby-shrimp communication systems was carried out in the northern Red-Sea. Three different genera of gobies, each associated with a different species of shrimp were tested. Gobies were stimulated by a slow-approaching predator model and a live restrained predator in order to reveal differences and similarities among species. The results of this study, carried out in the summer of 1974 as part of my Ph.D dissertation (Karplus, 1976), were not published so far. These findings are published now since they seem to provide a missing key to the understanding of the evolution and the recently described molecular phylogeny of the associated gobies.

2 Materials and methods

2.1 Study site and observations

The study was carried out in the sandy lagoon of the Eilat coral reef reserve at the northern tip of the Gulf of Eilat. Located between the rocky intertidal and the fringing reef, the lagoon is between 20 and 50 m wide, with a maximal depth of 2 m. A detailed description of the different microhabitats in the lagoon occupied by the associated gobies and shrimps has been described in Karplus et al. (1981). Three pairs of species were studied: *Cryptocentrus lutheri* (Klausewitz, 1960) associated with *Alpheus djiboutensis* (de Man, 1909), *Amblyeleotris steinitzi* associated with *Alpheus purpurilenticularis* and *Ctenogobiops maculosus* (Fourmanoir, 1955) associated with *Alpheus rapax* (Fabricius, 1798). Observations with SCUBA recorded on underwater slates were confined to the late afternoon hours, when the associated shrimps are most active outside their burrows (Karplus, 1987).

2.2 Signaling stimulated by a mobile predator model

The apparatus and the procedure used for stimulating the gobies to release warning signals by a mobile predator model have been described in detail by Karplus and Ben-Tuvia (1979). The results of the response of *Amblyeleotris steinitzi* to a small predator model have already been published (Karplus and Ben-Tuvia, 1979), but are presented here again as part of the three species comparison. The apparatus (Fig. 1) consisted of a two dimensional predator model that was suspended from an aluminum rod, approximately 3.5 m long, supported by two upright poles anchored to the floor by heavy bases. The aluminum rod supported a carriage composed of two wheels and a short interconnecting rod. Perpendicular to that rod was another rod which served to attach the model to the carriage in such a way that its lowest part was 5 cm above the ground. The carriage was moved slowly by means of wires at a speed not exceeding 1 cm/s. The wires were marked at 5 cm intervals in order to provide a measure of the distance of the model from the burrow entrance. The 24 cm long and 12 cm high model had a silhouette similar to a fish from the family Serranidae, a widespread piscivorous fish family (Fig. 1). The entire model was painted black, except for the white eye ring and nostril. The testing apparatus was placed so that the model was at a right angle to the goby's axis, facing its head, approximately 2.5 m away from the burrow entrance. On the opposite side of the burrow, 70 cm from the opening an observation shield was installed. 0.5 h later, the shield was slowly approached from behind by a diver. Experiments were started after at least an additional 10 min of acclimatization with no production of warning signals, to ensure that the goby habituated to the experimental set up. The model was moved towards the burrow opening only when the shrimp was outside the burrow. After a warning signal was given, the model was stopped until the goby habituated to it (i.e., the shrimp left and entered its burrow without receiving warning signals). The following events were recorded: (1) The distance of the model from the burrow entrance at the moment the goby retreated into its burrow (defined as the critical point). (2) The type of retreat of the goby, head or tail first entry. (3) The distance of the model from the critical point at the moment a signal was given by the goby. The critical point rather than the burrow entrance was determined as a reference point since for all trials and species this point has in common the highest levels of experienced escape motivation of the goby, very likely underlying its signaling behavior (Karplus, 1979; Karplus and Ben-Tuvia, 1979). All trials that were disturbed, such as by an approaching piscivore were stopped and excluded. Each of the three examined associations was tested with10 replicates and each of the replicates was only tested once.

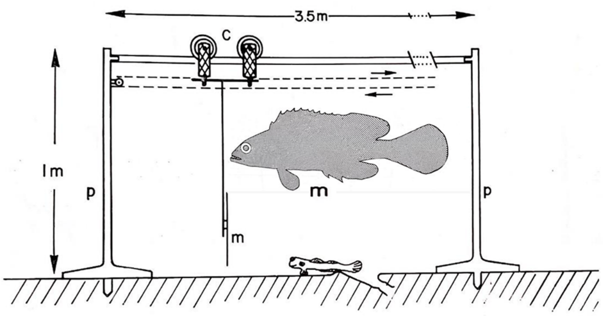

Fig. 1 Piscivore model and experimental set up for model presentation. c = carriage, m = model, p = pole, dashed lines = wires. (Karplus and Ben-Tuvia, 1979, Reproduced with permission of John Wiley & Sons)

2.3 Signaling stimulated by a restrained predator

A live restrained predator was presented to the associated gobies from the same distance in order to overcome habituation to a static model (see response to a mobile predator model). A *Parapercis hexophthalma*, a common ambush piscivore, 20.5 cm long, was introduced into a transparent perspex box (8 × 16 × 24 cm). The entire box, except for one large panel was perforated with holes to facilitate water exchange. The predator was presented in the box, covered with a white perspex sheet, at a distance of 55 cm from the burrow entrance. This was found to be the closest distance of the predator to the burrow that did not cause the retreat of the goby into its shelter. Observations were carried out from behind an observation shield, 70 cm from the burrow entrance. After at least 10 min of acclimatization, with no release of warning signals, the white cover was slowly removed from the non-perforated panel, the predator was exposed and observations for 5 min started. The following events were recorded: (a) Movement of the predator inside the box, with the switching of the position of the head with that of the tail. (b) Number of exits of the shrimp. (c) Number of warning signals and signal series given by the goby. A series of signals is composed of signals separated at most by 5 s. (d) Response of the shrimp to warning signal series (i.e., retreat or no response). Each of the three examined associations was tested with10 replicates and each of the replicates was only tested once. Warning signal generation is influenced by predator movements and dependent upon presence of the shrimp outside its burrow (Karplus, 1979; Karplus 1987). Therefore, in order to contrast inherent signal generation amongst several species of associated gobies, predator movements inside the transparent box were monitored and contrasted as well as the number of associated shrimp exits.

2.4 Statistical analysis

Results of the goby response to a mobile predator model were analyzed using a nested factorial design and orthogonal polynomes (Bennet and Franklin, 1954; Hicks, 1966). In more detail, signaling was analyzed for the effects of species and distance from the critical point (i.e., this distance was subdivided into nine sections, each 10 cm long, starting 5 cm from the critical point) and species x distance interaction effect using a nested factorial design. The linear, quadratic and cubic components of the relations between signaling and distance from the critical point were further analyzed for each species of goby using orthogonal polynomes (Bennet and Franklin, 1954), to find the best fit. Comparison of the goby response to a mobile and restrained predator amongst three species were carried out by the nonparametric Kruskal Wallis one way analysis of variance and comparison between pairs of species by the Mann-Whitney U test. All tests were two tailed. For the 3 possible pairwise post hoc comparisons, the bonferroni correction was applied and the significance level was set at $\alpha = 0.017$, to decrease the likelihood of type 1 error. Differences in the responses of the three species of associated shrimp to warning signals (i.e. retreat or no response) was carried out with the χ^2 test.

3 Results

3.1 Signaling stimulated by a mobile predator model

The three associated gobies differed in their critical distances. *Amblyeleotris steinitzi* and *Ctenogobiops maculosus* entered their burrows when the model was very close (i.e., 15 ± 4.7 cm, range 10–20 cm and 20 ± 7.4 cm, range 10–30 cm, respectively). In contrast, *Cryptocentrus lutheri*, entered the burrows when the model was about three times further away (i.e., 58 ± 19.5 cm, range 30–100 cm). *Amblyeleotris steinitzi* and *Ctenogobiops maculosus* did not differ in their critical distances (Mann-Whitney U test; $U = 31$, $n_1 = n_2 = 10$, $P > 0.1$). However, *Cryptocentrus lutheri* significantly differed in its critical distance from that of *Amblyeleotris steinitzi* (Mann-Whitney U test- $U = 0$, $n_1 = n_2 = 10$, $P < 0.01$) and *Ctenogobiops maculosus* (one tailed Mann-Whitney U test- $U = 3$, $n_1 = n_2 = 10$, $P < 0.01$). An additional important difference among the associated gobies was the way they entered their burrows when approached by a model-either head first or tail first. *Amblyeleotris steinitzi* and *Ctenogobiops maculosus* invariably entered their burrows head first when approached by the mobile model. However, *Cryptocentrus lutheri* entered its burrows in nine out of the ten trials–tail first.

The associated gobies differed in the rate of emittance of warning signals and their occurrence relative to distance from the critical point in response to an approaching predator model (Fig. 2). *Cryptocentrus lutheri* produced relatively few warning signals (i.e., 3.8 signals per trial), not related in their occurrence to distance from the critical point. *Amblyeleotris steinitzi* and *Ctenogobiops maculosus* produced about four times more signals (i.e., 21.1 and 15.0 signals per trial, respectively), negatively correlated with distance from the critical point. A significant difference in the number of emitted warning signals was found among goby species ($F_{2,18}$=9.11, $P < 0.01$), response distances from the critical point ($F_{8,216}$=5.13, $P < 0.01$) and the interaction between species and distance ($F_{8,216}$=5.97, $P < 0.05$). This significant interaction indicates that the relationship between signaling and distance differs among species. An absence of a functional relationship between signaling and distance was found for *Cryptocentrus lutheri*. The inverse relationship between the number of warning signals (Y) and distance from the critical point (r) is linear for *Ctenogobiops maculosus* being described by the polynome Y_C=4.26-0.52r and polynomic (third order) for *Amblyeleotris steinitzi* Y_A= $18.20\text{-}1.735r + 0.054r^2\text{-}0.00055r^3$ (Fig. 2).

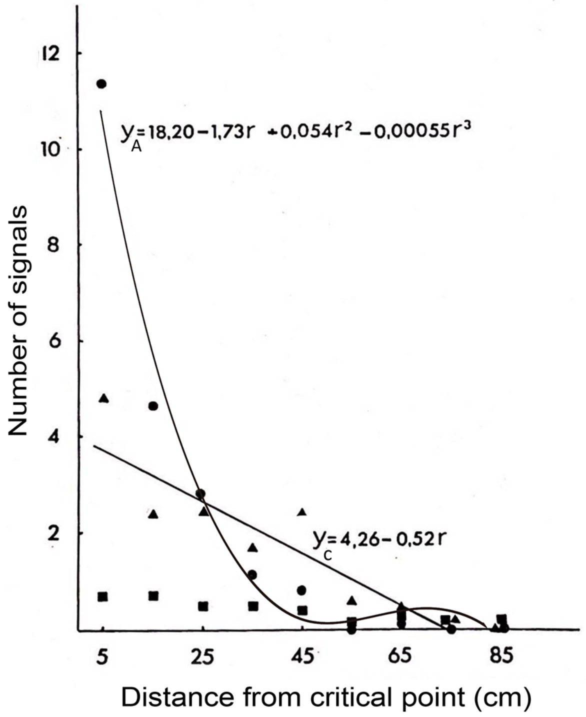

Fig. 2 Number of warning signals given by three goby species in response to a mobile model, relative to its distance from the critical point. *Cryptocentrus lutheri* (squares); *Amblyeleotris steinitzi* (circles); *Ctenogobiops maculosus* (triangles)

3.2 Signaling stimulated by a restrained predator

There was no difference in the number of predator movements inside the box when presented to the gobies (Kruskall Wallis, $H = 2.044$, d.f.=2, $P > 0.3$). Moreover, the number of associated shrimp exits did also not differ (Kruskall Wallis, $H = 2.209$, d.f.=2, $P > 0.3$), which rules out both possible effects of predator movements and shrimp activity on goby signaling frequency.

The two analyzed parameters of warning signal generation included the number of signals and signal series (Fig. 3). Overall, *Amblyeleotris steinitzi* and *Cteonogiops maculosus* were similar in warning signal generation, whereas, *Cryptocentrus lutheri* produced fewer signals, and signal series. *Amblyeleotris steinitzi* and *Cteonogobiops maculosus* did not differ in the number of generated warning signals ($U = 48$, $n_1 = 9$, $n_2 = 10$, $P > 0.1$). However, *Cryptocentrus lutheri* produced significantly fewer warning signals, approximately only a quarter of those produced by *Amblyeleotris steinitzi* ($U = 7$, $n_1 = 9$, $n_2 = 10$ $P < 0.002$) and *Cteonogobiops maculosus* ($U = 9$, $n_1 = n_2 = 10$, $P < 0.002$).

Amblyeleotris steinitzi and *Ctenogobiops maculosus* were similar in the number of warning signal series they produced ($U = 41.5$, $n_1 = 9$, $n_2 = 10$, $P > 0.1$). However, *Cryptocentrus lutheri* produced about less than half warning signal series than the other two species. This difference in number of warning signal series was near-significant for (*Amblyeleotris steinitzi* ($U = 9.5$, $n_1 = 9$, $n_2 = 10$, $P < 0.02$) but significant for *Ctenogobiops maculosus* ($U = 10$, $n_1 = n_2 = 10$, $P < 0.002$).

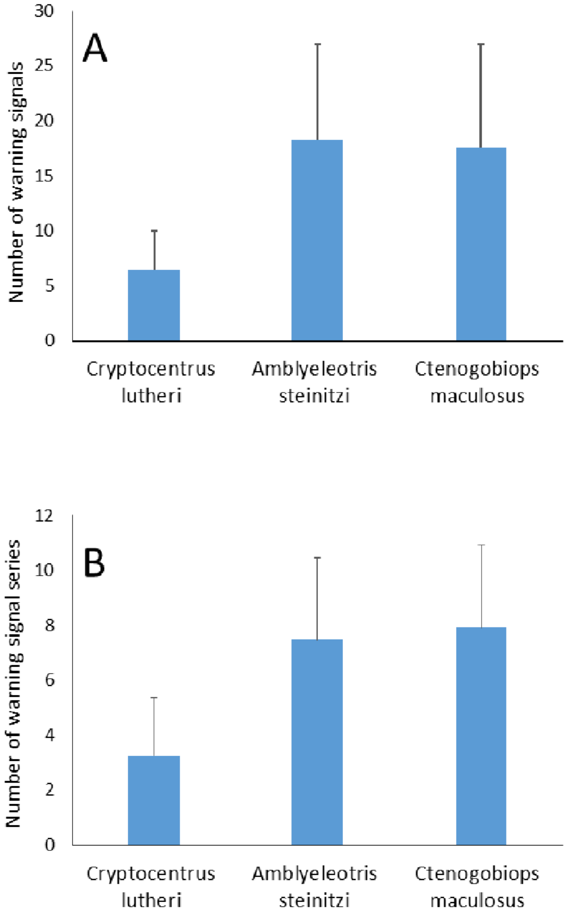

Fig. 3 Signal generation by three species of symbiotic gobies during 5 min of exposure to a restrained predator. (A) Number of warning signals. (B) Number of series of warning signals. Error bars represent standard deviation.

The responses of the associated shrimp to series of warning signals, categorized as either retreat or no response are presented in Table 1. There were no significant differences among the shrimp in their responses to warning signal series ($\chi^2 = 3.775$, d.f. = 2, $P > 0.1$).

4 Discussion

Two patterns of high and low rate signal generation were found in the associations examined by experiments with a mobile predator model and with a live restrained predator. The differences in the signaling rate are probably deeply

Table 1 Responses of symbiotic alpheid shrimps to series of warning signals of gobies. Upper number—observed number of occurrences. Numbers in parentheses—expected value given similar relationship between retreat and no response amongst the three shrimp species

Shrimp species: \ Shrimp response	*Alpheus purpurilenticularis*	*Alpheus djiboutensis*	*Alpheus rapax*	Total
Retreat	128 (131.9)	49 (49.6)	211 (204.4)	388
No Response	25 (19.0)	8 (7.1)	23 (29.5)	56
Total	153	57	234	444

rooted in the way the gobies handle a threatening piscivore. *Cryptocentrus lutheri* retreats tail first into its burrow while the threatening model is three times further away compared with the distance from the model when *Ctenogobiops maculosus* and *Ambyleotris steinitzi* retreat head first into their burrows. Furthermore, the low signaling rate of *Cryptocentrus lutheri* is independent of the distance of the model from the critical point whereas in the case of the high rate signal generators *Ctenogobiops maculosus* and *Ambyleotris steinitzi*, the closer the model to the critical point the more signals are generated. The key to understanding the differences in signal generation by these species lies in the way they enter their burrows. Rapid head first entries of fishes into their burrows or shelters seem to be induced by a stronger stimulation, i.e. the fish perception of a higher risk, than that of the slow tail first entries (Magnus, 1967; Colin, 1971; Karplus et al. 1972; Fishelson, 1975). The low frequency of signals produced by *Cryptocentrus lutheri* is probably the result of its low-risk strategy of slowly withdrawing into its burrow tail first when the danger is still distant. *Ctenogobiops maculosus* and *Ambyleotris steinitzi*, on the other hand, remain outside their burrows continuing to forage even when the danger is close, generating many warning signals prior to entering the burrow head first.

The characterization of the two shrimp-goby clades on the basis of their distribution, living in either a sandy or a silty habitat (Thacker and Roje, 2011), is ambiguous since these traits are not exclusive. Moreover, associated gobies follow their shrimp partners, occupying the microhabitat selected by the shrimp, which heavily depends for digging and feeding on sediment mean grain size, sorting, coral and stone ingredients as well as organic matter contents. [e.g., *Ctenogobiops maculosus* occupied in shallow water in the northern Red-Sea the burrows of *Alpheus rapax* found on fine silty sediments whereas in deeper waters it occurred on coarse sandy substrates in association with *A. thompsoni* (Anker, 2022) (Karplus et al. 1981)]. Based on the findings of this study, I suggest an alternative hypothesis asserting that the two clades are actually representing fundamentally different behavioral types. Communication between gobies and shrimp, a unique feature of associated gobies not found in free living gobies, probably played an important role in associated goby evolution. Thus, gobies of clade one which includes the genera *Amblyeleotris, Vanderhorstia*, and *Ctenogobiops* may be termed "high rate signal generators", whereas those of clade two which includes the genera *Cryptocentrus, Mahidolia, Tomyamichthys* and *Stonogobiops* may be termed "low rate signal generators" (Fig. 4). Testing of additional species/genera from both clades for their signaling rates and pattern is essential for validation or refutation of this 'signaling rate hypothesis'.

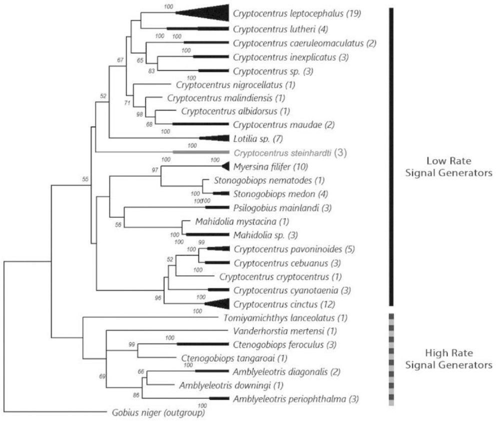

Fig. 4 Phylogenetic analysis of available COI sequences of shrimp-gobies. Numbers above nodes are > 50 bootstrap values; in parentheses—number of sequences for each species. After Goren and Stern (2021). Frequency of goby signaling replaced in present version of the figure the original designation of the clades according to goby distribution

The Atlantic *Nes longus* is not included in either of the two shrimp-goby clades but belongs to another phylogenetic group of gobies (Agorreta et al. 2013) and was not studied by either Thacker and Roje (2011) or Goren and Stern (2021). This goby shares an obligate partnership with *Alpheus floridanus* producing both head and tail first burrow entries and tail flicks (Karplus, 1992). The tail flicks seem to resemble the signals produced by the Indo-Pacific high rate signal generators. The number of signals increased the closer a barracuda model approached the critical point and all trials terminated with a head first entry of the goby (Karplus, 2014). The similarity of signaling of *Nes longus* to the Indo-Pacific high rate signal generators may be the result of convergent evolution of the effective warning of the associated shrimp.

The signaling rate hypothesis provides new insight to the evolution of the goby-shrimp partnership. The two signaling strategies probably evolved independently and differently from two ancestor gobies that sheltered in shrimp burrows. These gobies probably warned the shrimp from piscivores by both head first and tail first burrow entrances. The tail flick warning signals probably evolved in both cases from intentional movements of the goby connected with its retreat into the burrow as suggested by Magnus (1967) and Preston (1978). Support of the close relationship between the goby escape behavior and the tail flick comes from a recently published computational model. Landsittel et al. (2021) simulated by strong stimulation of the Mauthner cell command neurons, the goby escape, whereas, following some modifications of that system, simulated weak stimulation resulted in warning signal generation. The continuous antennal contact between shrimp and goby while the shrimp is outside the burrow was an important step in the evolution of the goby-shrimp warning system. Awareness of the tail flick through the antennal contact was greatly enhanced due to their conspicuous nature being different from all other tail movements. In one clade the high rate signal generation co-evolved with late withdrawl from danger whereas in the second clade the low rate signal generation co-evolved with early withdrawl from danger. Finally, the two goby-shrimp communication systems seem to be equally effective. The proportion of retreats of the shrimp upon the reception of a series of tail flicks of gobies of the two clades being similar.

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