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Systematic Significance of the Burrow Form of Seven Species of Garden Eels (Congridae: Heterocongrinae)

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ABSTRACT

Garden eels are highly specialized anguilliform fishes that live in colonies worldwide in warm seas. Unlike most eels, they are sight feeders, spending their daylight hours partially extended from their burrows feeding on drifting particles. Because they live in unconsolidated sand it has been difficult to determine the form of their burrow. Using araldite epoxy plastic, we made casts of the burrows of six species representing both of the currently recognized genera. All of the casts are in the form of simple sinusoidal waves but differences in amplitude and wavelength in relation to the length of the fish and the size of the casts have potential significance in classification.

A preliminary analysis using Hennig86 indicates that the two species of *Gorgasia* in our sample are indeed each other's closest relatives and part of a lineage that includes *Heteroconger klausewitzi* and *H. hassi*. The relationships of *H. halis, H. perissodon,* and *H. polyzona,* however, cannot be resolved from our data.

INTRODUCTION

Congrid eels of the subfamily Heterocongrinae are ecologically notable because all of the species live in burrows in colonies of up to around 10,000 diurnal, planktivorous individuals (Clark, 1990). Approximately 30 species are known, most of which occur in the Indo-western Pacific, with a few species in the eastern Pacific, eastern Atlantic, and western Atlantic (personal commun. of P. Castle and J. Randall, who are revising the subfamily). Garden eel behavior has been studied extensively by Clark (1971, 1972, 1974, 1990 and contained references) and Fricke (1969) who worked on *Gorgasia* cf.

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sillneri in the Red Sea, and by Fricke (1969, 1970) who studied *Heteroconger hassi* off Madagascar.

Generic limits and relationships of heterocongrines are poorly understood, and the number of genera recognized has varied until relatively recently from five (Klausewitz and Eibl-Eibesfeldt, 1959) to four (Böhlke, 1957; Rosenblatt, 1967) to two (Böhlke and Randall, 1981; Smith, 1989). Part of the difficulty lies in interpreting reductions and simplifications of many of the external and internal morphological features associated with the eels' life in sand burrows. We follow the contemporary standard of recognizing only two broadly defined genera, *Heteroconger* and *Gorgasia,* with the latter considered to be the more primitive (Rosenblatt, 1967; Smith, 1989). Clark (1990) noted that there may be more than one species of garden eel in the Red Sea and that there is some confusion as to the name of the species she studied. For this reason we refer to that species as *Gorgasia* cf. *sillneri.*

We postulated that the form of the burrow might differ between natural groups (genera or subgenera) of garden eels and, therefore, be helpful in clarifying their systematics and interpreting their phylogeny. This would be especially true if the burrows of some species were relatively simple and those of other species more complex, with a transition series of increasing specialization.

Methods

The preferred habitat of garden eels is loose substrate varying from light-colored coral sand to muddy, pebbly, and even rocky, dark-colored volcanic sand. The fragile burrows are lined with mucus secreted by skin glands along the length of the eel (Bath, 1960; Casimer and Fricke, 1971) and collapse at the slightest disturbance. Consequently it has been difficult to determine the configuration of the burrows.

During the past four years we have been using araldite epoxy resin (Ciba-Geigy) to make casts of the burrows of as many species of garden eels as our expeditionary itinerary permitted. The araldite is supplied in three parts which have to be mixed shortly before pouring (3 parts GY 237 or 507 resin to 1 part HY 830 hardener and 1 part HY 850 hardener: for casting techniques see Shinn, 1968; Farrow, 1975; Pervesler and Dworschak, 1985). A dam (usually a metal can with the top and bottom cut out) is placed gently around the burrow opening and filled with the araldite mixture. Often the eels escape to the surface through the plastic, but frequently they are trapped in it. Once the mixture has been poured, it is allowed to harden for about 24 hours, then retrieved by digging the sand from around the hardened cast (laborious for a long cast).

In the following discussions the body length (TL) of the eel is the total length measured from the tip of the snout to the end of the tail. Body depth (D) of the eel is the greatest body depth, usually measured just behind the head. All measurements of casts were taken from tracings (except *Gorgasia* cf. *sillneri* for which measurements were taken from a photograph kindly supplied by Dr. E. Clark). The length of the cast (CL) is the overall straight-line length, corrected for any major curvature, while the length of the burrow (BL) is the curvilinear length along the course of the burrow.

The number and size range (average in parentheses) is given below for voucher specimens, collected at the same locality unless otherwise noted. Casts and voucher specimens are all at the National Museum of Natural History, Smithsonian Institution, except for paratypes of the new species of *Gorgasia* at the Bishop Museum and the National Museum of New Zealand. We cannot match a particular cast to a particular voucher specimen and in many cases our casts are incomplete at the bottom, either from failure of the epoxy to reach the deepest terminal part of the burrow or because the cast broke and the distal part could not be retrieved. Nevertheless, for five of the species (all except *Heteroconger perissodon*) we have at least one relatively complete cast, and even the incomplete casts of *H. perissodon* yield substantive data on burrow geometry.

RESULTS AND DISCUSSION

Garden Eel Burrows

The shape of the burrow has been known only for *Gorgasia* cf. *sillneri,* based on casts made with epoxy paint by Clark (1971, 1980) in the Red Sea. Her photographs and descriptions show the burrow to be a vertical sinuous curve with considerable variation in curvature and flexure toward the bottom. One of her burrow casts has two flexures so that the axes of the top and bottom sections of the burrow are vertical and that of the middle section is horizontal. Clark (1980) thought that this might be the region where a branch of the burrow could lead upward to a secondary opening. This could be one way for a male to move closer to a female during breeding, with the male taking a sighting on a female, and then burrowing horizontally through the sand before emerging alongside her (Clark, 1974).

The burrows of several other species have been figured or described but only somewhat hypothetically, i.e., not based on casts. Klausewitz and Eibl-Eibesfeldt (1959) and Klausewitz (1962) showed a straight vertical tube for *Heteroconger hassi,* a small species whose burrow was said to be about a half meter deep. A perfectly straight tube would seem unlikely for a fish with serpentine anguilliform movement, but perhaps possible if the movement of the body in the burrow were the result only of delicate undulations of the low dorsal and anal fins. Fricke (1969, 1970), based on both probing with a rod and delicately removing sand around anesthetized eels, believed that the burrow of *Gorgasia* cf. *sillneri* was vertical for the first 10 to 14 cm and then became oblique or slightly inclined downward. Fricke considered this to be reasonable since *G.* cf. *sillneri* is a large species whose burrow might reach deeper, denser levels of sand. Fricke (1970) also observed *G.* cf. *sillneri* in aquaria to dig down vertically only 5 cm before tunneling horizontally. Because the casts of the burrow of *G.* cf. *sillneri* made subsequently by Clark are all essentially vertical, Fricke's hypothesized major horizontal turning could be either a misinterpretation of the first flexure in the sinuous curve or the proper portrayal of the burrow form in an area where the upper layers are loose and easily penetrated but the deeper layers are more compacted and denser so that in fact the eel bends the lower part of the burrow horizontally. This probably accounts for at least some of Fricke's aquarium observations. Saldanha (1982), based on observing the digging behavior of a disturbed specimen of *H. longissimus* at Madeira, believed the burrow to be vertical for only the upper 8 to 9 cm before probably becoming horizontal.

With data on the araldite casts of burrows of six species from the Caribbean, eastern Pacific, and western Pacific now in hand we can report our results briefly: all six species have a burrow that is basically a sinusoidal wave in the frontal plane of the body of the eel, with the amplitude decreasing slightly and the wave length increasing slightly with increasing depth (fig. 1). This is essentially the burrow form shown by Clark (1971, 1980) for *Gorgasia* cf. *sillneri.* The sinusoidal curve in a single plane makes perfectly good functional sense since few fishes and, indeed, few vertebrates, are very flexible in the dorsal-ventral plane along much of the body. Furthermore, when driven from their burrows, garden eels swim by normal anguilliform motion of lateral flexures sending progressive waves along the body. However, among the six species for which we have burrow casts, there are interesting variations on the fundamental sinusoidal curve, as detailed below.

Some species of garden eels are able to burrow deeply vertically without a lower horizontal terminal bend even in coarse substrate. This was the case with *Heteroconger perissodon* and *H. polyzona* at Maayongtubig, Oriental Negros, Philippines, where the burrows were dug in volcanic sand in which there were large rounded pebbles and even stones up to 300 mm long. One cast of *H. polyzona* broke off at 605 mm where it curved around and below the side of a large boulder. Therefore, we believe that the usual condition is a vertical burrow (fig. 3), like most of our casts. A few of our casts of *H. halis* have a lower horizontal bend. In one of these the diameter of the horizontal section is substantially greater than that of the section above it and sand grains have not adhered to it as in more normal casts. We interpret this as an escape tube the eel had vigorously and hastily dug so that the mucus secretion did not have time to surround the sand grains.

Sexual Dimorphism and Community Structure

Like a few other species of garden eels, *Heteroconger polyzona* has long been known to have many pairs of individuals in the colony

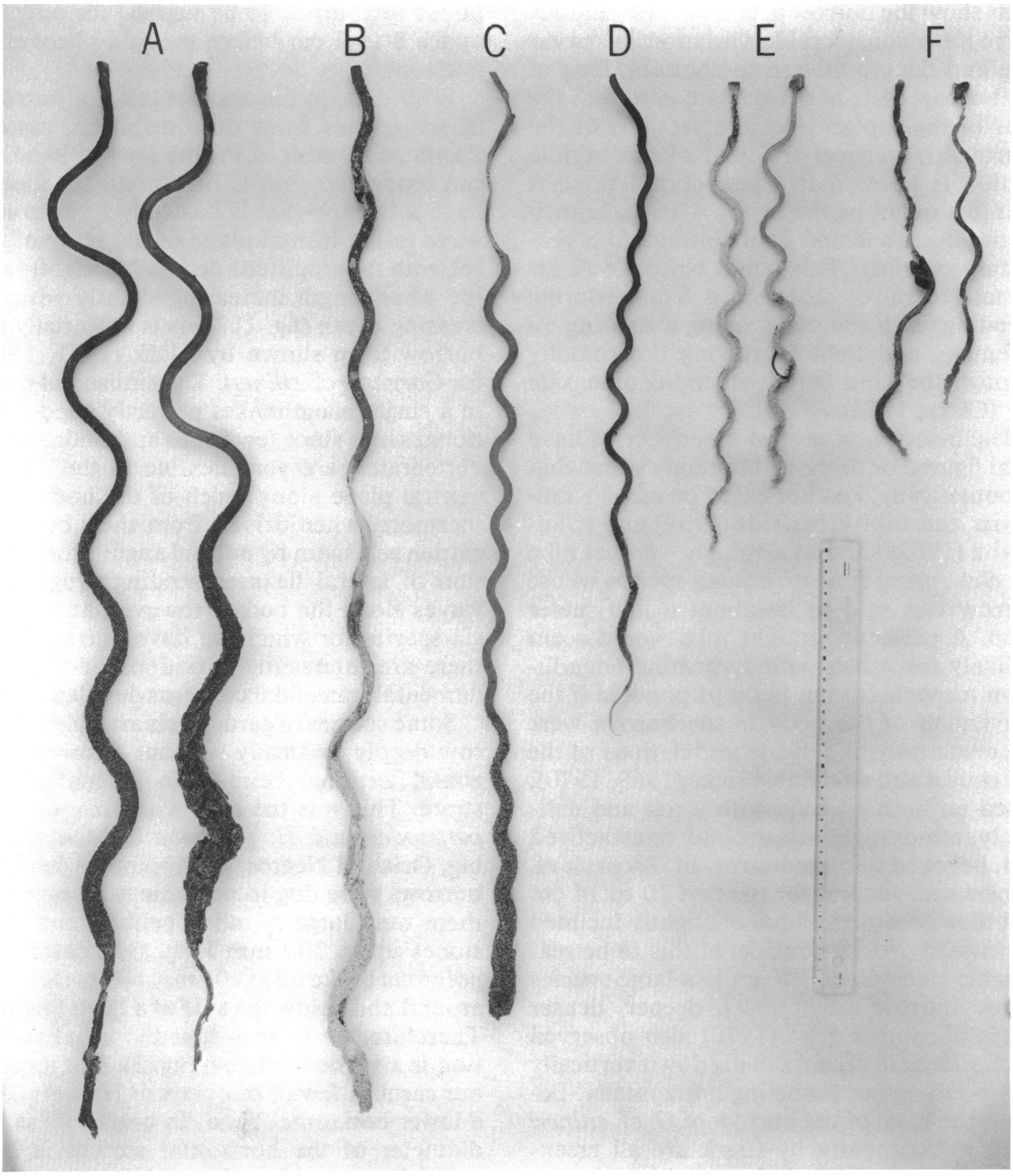

Fig. 1. Epoxy casts of the burrows of six species of garden eels. **A.** *Gorgasia* sp. nov. **B.** *Heteroconger klausewitzi.* **C.** *H. hassi.* **D.** *H. polyzona.* **E.** *H. halis.* **F.** *H. perissodon.* Ruler is 400 mm.

(Herre, 1930). To verify the presumption that these are male-female pairs, we speared both members of five such pairs with the aid of rotenone at Maayongtubig, Philippines. At this location *H. polyzona* is found in 5–10 ft of water within 100 ft of the rocky beach, while a few hundred feet farther offshore in 30–35 ft of water there is a colony of *H. perissodon,* in which pairing was not observed. Four of the five pairs from the colony of *H. polyzona* were male-female, with the ripe or ripening female the larger of the two in two instances. The remaining pair consisted of a 298 mm male of *H. polyzona* and a 345 mm

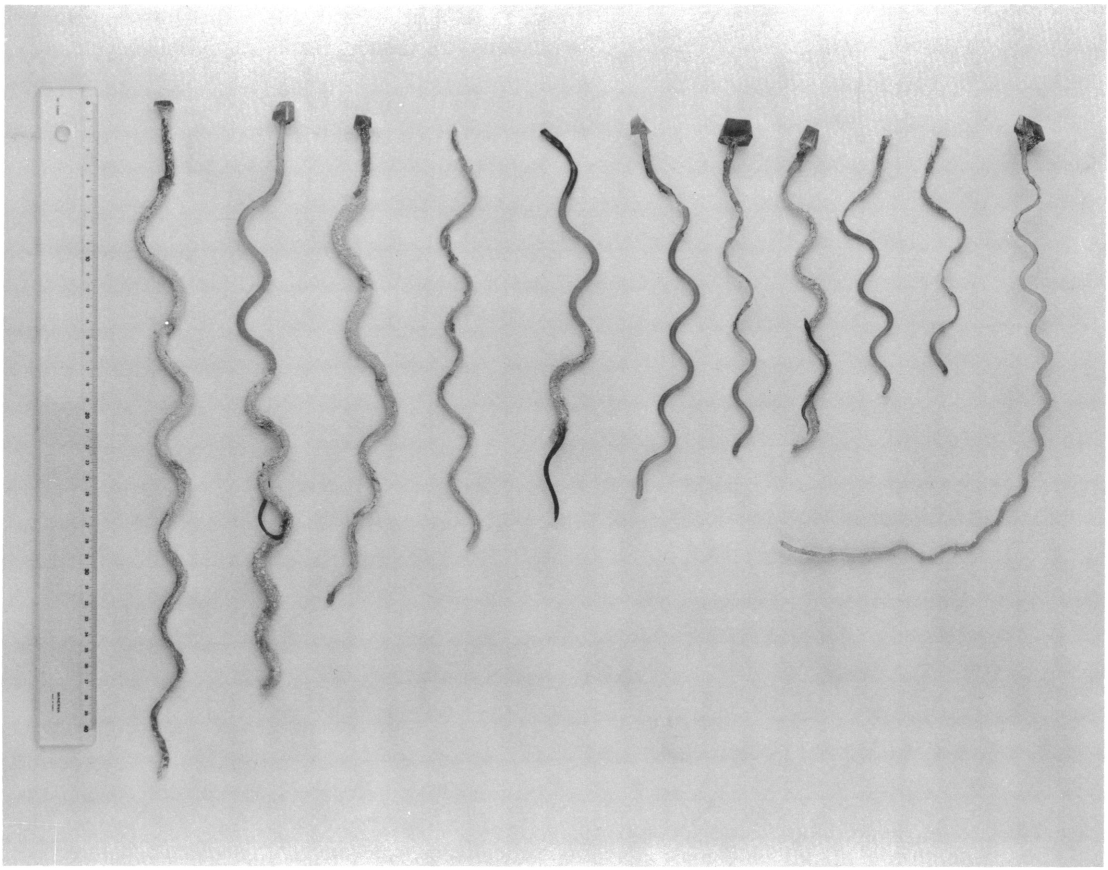

Fig. 2. Casts of the burrows of *Heteroconger halis* showing variation; cast on the far right shows horizontal tunnel, perhaps to escape from the epoxy. Ruler is 400 mm.

male of *H. perissodon,* the latter apparently misplaced from the colony of that species from farther offshore.

Species-Specific Burrow Structure

Heteroconger halis

Study Material: 11 casts, 310 to 450 mm, all slightly incomplete, from coral sand at 105 ft at Carrie Bow Cay, Belize (measurements for only the six most complete casts were utilized); 172 voucher specimens, 77–295 (221) mm from Carrie Bow Cay, Belize, and 3, 300–307 (303) mm from coral sand at 100 ft at Pine Cay, Turks and Caicos. Observations of *H. halis* on volcanic sand at 25 ft at Roseau, Dominica, on coral sand at 20 ft at Glovers Reef, Belize, on coral sand at 100 ft at Salt River Canyon, St. Croix, on coral sand in the Bahamas at 60 ft at Mayaguana, 80 ft at Cat Island, and at 80 ft in the Berry Islands, and on coral sand at 55 ft at Anguilla Island.

Heteroconger halis, the only common species of garden eel in the Caribbean, is a relatively small species (the smallest of the seven species we have studied), averaging only 221 mm at Carrie Bow Cay and 303 mm at Turks and Caicos. The ratio of cast length (straight line) to burrow length (curvilinear) ranges from 0.85 to 0.92 (mean 0.90), lower than that of all other species except *Gorgasia* sp. nov. (although overlapping *H. polyzona* and *H. perissodon*). This indicates that *H. halis* has a high degree of flexion, which is borne out by the observations that it also has the shortest wave length. There is considerable variation in the burrows (fig. 2). Most

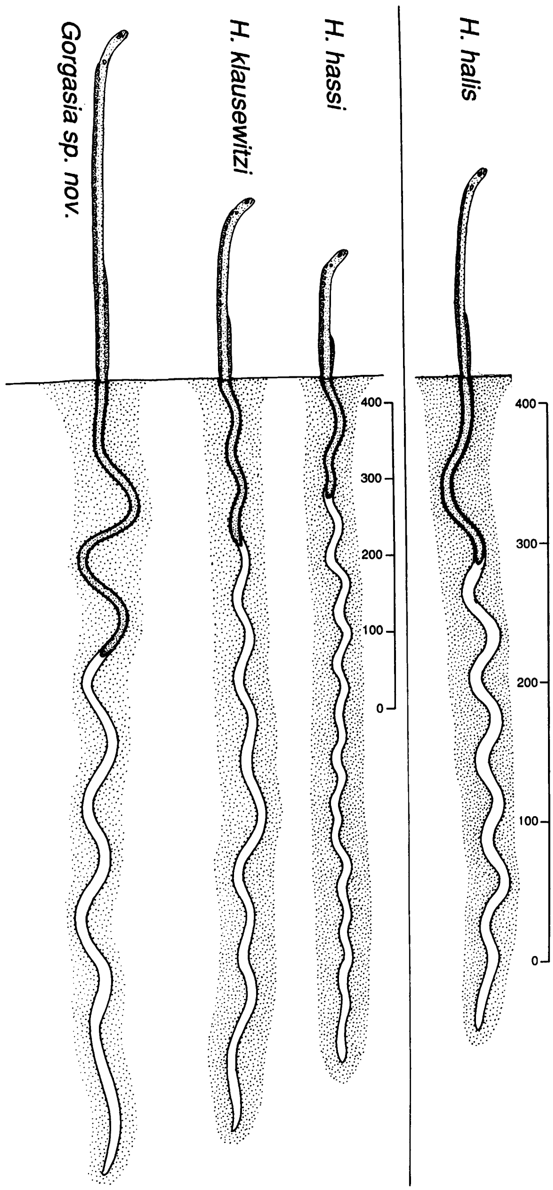

Fig. 3. **Left of vertical line**: reconstruction of garden eels in three types of burrows; left, *Gorgasia* sp. nov. (CL 980 mm, TL 928 mm), a short burrow of high amplitude and long wavelength; middle, *Heteroconger klausewitzi* (CL 960 mm, TL 466 mm), a burrow of moderate length, low amplitude and wavelength; right, *H. hassi* (CL 865 mm, TL 324 mm), a long burrow of higher amplitude than in *H. klausewitzi* and *H. perissodon* but lower than in *Gorgasia* sp. nov. **Right of vertical line**: *H. halis* (CL 450 mm, TL 292 mm), burrow form similar to that of *H. hassi,* except shorter. Cast lengths are those of the longest and most complete of the spe- ← cies for which we have at least two casts. TL is average length of the voucher specimens except for *H. halis* which is based on the longest cast (450 mm) and the largest specimen (295 mm) since our series of 172 specimens from Belize included numerous juveniles, and our casts were biased toward larger individuals.

The length of the burrows and eels are relatively accurate but the width of the eels is only approximate. The eels are shown with 50 percent of their length outside of the burrow and with the beginning of the anal fin at 33 percent of the TL.

of the 11 best casts, all from the same large colony at Carrie Bow Cay, Belize, are approximately vertical, but the lowest parts of a few of the burrows curve horizontally. It is the lower, terminal part of the burrow that bends horizontally in these casts, suggesting that the deeper sand was too firm for the eel to penetrate easily and the eel simply changed direction to make the burrow long enough to accommodate its full body length and allow it to retract safely below the surface, as proposed by Fricke (1970) for *Gorgasia* cf. *sillneri. Heteroconger halis* is a slender species with a burrow depth to total length ratio less than in any other species except *Gorgasia* sp. nov.

Heteroconger hassi

STUDY MATERIAL: One cast, 865 mm, relatively complete, from dark silty volcanic sand at 25 ft at Dauin, south of Dumaguete, Oriental Negros, Philippines; three voucher specimens, 319–335 (325) mm.

This species has the lowest ratio of average body depth to average cast diameter, indicating a less close-fitting burrow. This could be an artifact because we cannot match individual specimens with our casts or it could reflect the preference of *H. hassi* for a particular sand grain size which would bias the data on the cast diameter. In any event, our data show that *H. hassi* most closely resembles *H. halis* in this character as well as in the more reliable ratios of burrow width to total length of the eel and burrow width to wavelength.

Heteroconger klausewitzi

STUDY MATERIAL: One cast, 960 mm, relatively complete, from light-colored volcanic and shelly coarse sand at 25 ft at Isla Plaza del Norte, Isla Santa Cruz, Galapagos; six voucher specimens, 226–593 (466) mm.

Heteroconger klausewitzi is intermediate in size between the two species of *Gorgasia* and the other four sampled species of *Heteroconger*. It resembles *Gorgasia* cf. *sillneri* but not *Gorgasia* sp. nov. in the ratio of burrow width to total length of the eel.

Heteroconger perissodon

STUDY MATERIAL: Two casts, 300 and 340 mm, highly incomplete, from dark coarse pebbly and stony volcanic sand at 35 ft at Maayongtubig, south of Dumaguete, Oriental Negros, Philippines; nine voucher specimens, 251–400 (338) mm.

This is a small and relatively slender species. Its burrow width to total eel length ratio is similar to that of *Gorgasia* sp. nov. but not to that of *G.* cf. *sillneri.*

Heteroconger polyzona

STUDY MATERIAL: One cast, 605 mm, somewhat incomplete, from dark pebbly volcanic sand at 10 ft at Maayongtubig, south of Dumaguete, Oriental Negros, Philippines; 16 voucher specimens, 230–321 (284) mm.

Heteroconger polyzona is a strikingly patterned species similar in size to *H. halis.* In the relatively unreliable ratio of body depth to cast diameter it is most similar to *H. klausewitzi*; otherwise its burrow is unremarkable.

Gorgasia cf. *sillneri*

Clark (1990) has noted that there is a question as to the correct name of this species. At her suggestion we refer to the form she studied as "*Gorgasia* cf. *sillneri*" to call attention to this unresolved nomenclatural problem.

STUDY MATERIAL: Data for this species are taken from a copy of the photograph shown as figure 4 in Clark (1980). Two of the three casts shown in the photograph are suitable for measurements. This is a large species. Mature males ranged from 767 to 957 mm (mean 882) and females 556–773 mm (mean 635) (Clark, 1980); body depths of four of Clark's specimens (USNM 227695) averaged 1.3 percent of TL. The amplitude and wavelengths of these three casts are somewhat variable, with the longest cast (middle of photograph) of relatively low amplitude and short wavelength, and the one to the left, when pieced together, perhaps of higher amplitude and longer wavelength than the other two. None of the three, however, have the distinctly high amplitude and long wavelength found in our two casts of *Gorgasia* sp. nov.

Gorgasia new species (to be described by Castle and Randall)

STUDY MATERIAL: 2 casts, 920 and 980 mm, relatively complete, from dark silty volcanic sand at 20 ft at Dauin, south of Dumaguete, Oriental Negros, Philippines; five voucher specimens, 693–1015 (929) mm.

Gorgasia sp. nov. is the longest and most slender of the species we have studied; its body depth is only 1.1 percent of the total length. It also has the lowest ratio of cast length to burrow length, which reflects the high amplitude and long wavelength of the burrow. The ratio of burrow wavelength to total length of the eel is most similar to that of *G.* cf. *sillneri* but the other ratios are unremarkable.

CHARACTERISTICS OF GARDEN EELS AND THEIR BURROWS

Of the characters given below, (1) and (2) are measurements of specimens, (3) through (8) are measurements of casts, and (9) through (17) are ratios of measurements (tables 1 and 2). Our series of 11 measurable casts of *Heteroconger halis* provides an indication of intraspecific variation of these characters.

Because we cannot associate casts with individual specimens, we have used average lengths to compute certain ratios. Recognizing the pitfalls of this procedure, we have excluded such ratios from the phylogenetic analysis.

(1) Total Length (TL). Total length was taken as the average of the lengths of all voucher specimens. Two species (*Gorgasia* cf. *sillneri* and *Heteroconger polyzona*) are sexually dimorphic. On the basis of total length, garden eels in our sample fall into three groups; *H. halis, H. hassi, H. perisso-*

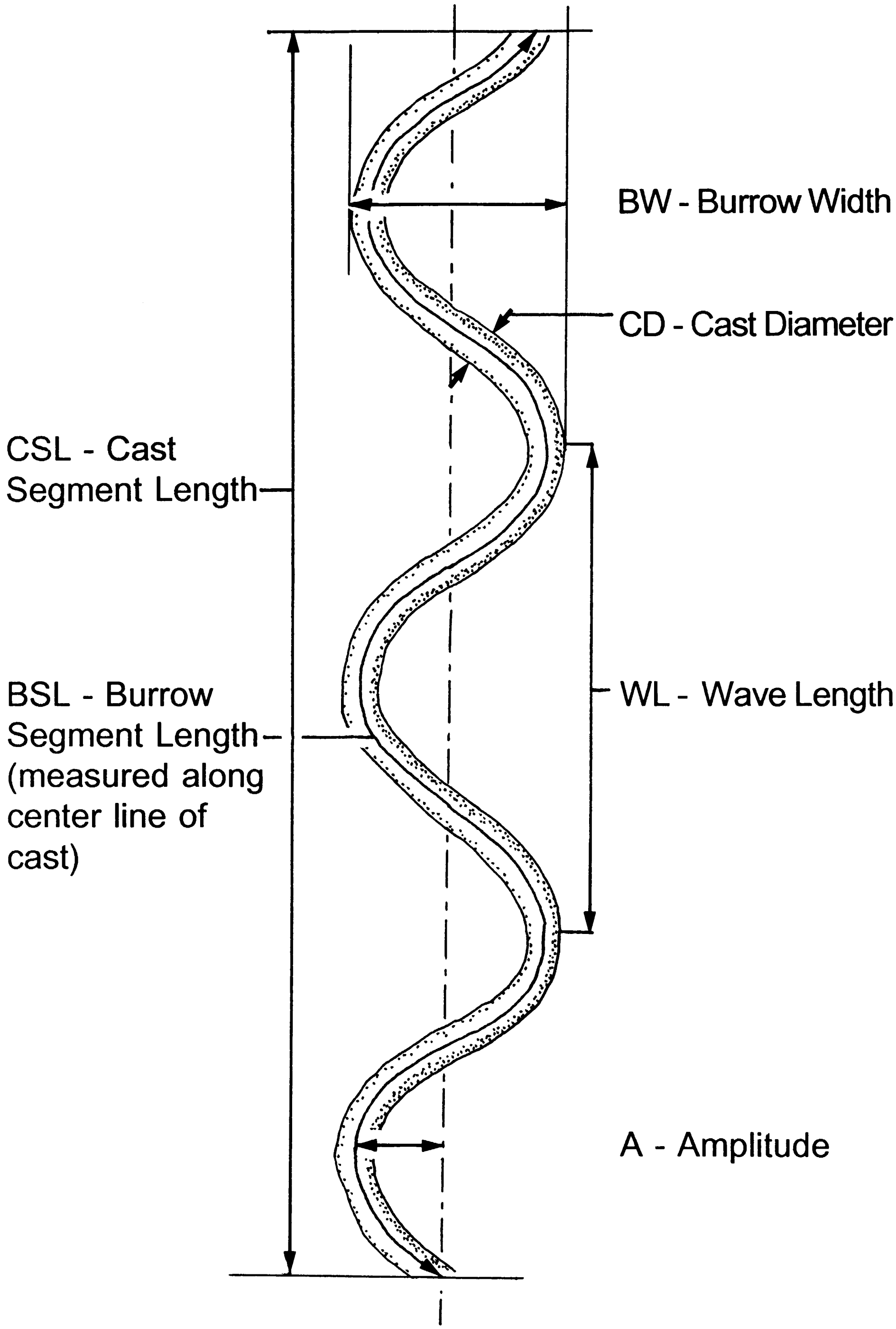

Fig. 4. Measurements taken on garden eel casts.

TABLE 1
Measurements of Garden Eels and Casts
(See text for explanation.)

Char.	Species						
	hal.	*has.*	*per.*	*pol.*	*kla.*	*G. sil.*	*G.* sp.
(1)	221	324	338	284	466	758	929
(2)	3.11	6.70	6.13	6.35	9.17	10.03	9.84
(3)	250	870	322	605	955	662	980
(4)	287	937	349	665	1016	717	1118
(5)	48.20	66.63	72.47	57.15	93.76	127.30	156.90
(6)	19.50	24.87	20.65	20.14	26.37	35.55	59.25
(7)	5.67	9.53	5.85	7.84	11.10	12.20	11.20
(8)	6.88	7.67	7.24	6.15	7.63	11.67	24.03

don, and *H. polyzona* are small species and the two species of *Gorgasia* in our sample are large, while *H. klausewitzi* is intermediate in size. Total length of three *H. halis* from Turks and Caicos Islands ranged from 300 to 307 mm (mean 303 mm, coefficient of variation [CV] = 1.2), while in 172 specimens from Carrie Bow Cay it ranged from 77 to 295 mm (mean 221). This sample apparently included several age classes, with peak frequencies at 85–90, 160–175, 200–210, 225–240, 260–265, and 280–295 mm.

(2) Body Depth (D). Body depth is an indicator of slenderness of the eels. As with total length, the body depth was averaged for all voucher specimens for comparison with cast measurements. The only exception is that for *Heteroconger halis* the body depth was measured for a small sample from the Turks and Caicos Islands, and the ratio of depth to total length was used to estimate average body depth for the large sample of *H. halis* from Carrie Bow Cay. This estimate was then used for calculations of ratios because all of the casts of this species came from Carrie Bow Cay. The body depth of three specimens from Turks and Caicos ranged from 3.9 to 4.6 (mean 4.27, CV = 8.2).

Measurements of the casts were made as shown in figure 4. As many complete waves as possible (3 to 11) were measured on each cast and the measurements were averaged for use in calculating ratios.

(3) Cast Length (CL). This is the overall length of the cast, corrected for any major curvature. Since casts are seldom if ever complete, the length of the cast by itself gives only a general indication of the length of the burrow and can be misleading. In our sample, *H. hassi* and *H. polyzona* have relatively long

TABLE 2
Ratios of Garden Eel and Burrow Measurements
(See text for explanation.)

Char.	Species						
	hal.	*has.*	*per.*	*pol.*	*kla.*	*G. sil.*	*G.* sp.
(9)	.016	.021	.018	.022	.020	.013	.011
(10)	.86	.93	.92	.91	.94	.94	.88
(11)	.14	.12	.10	.11	.08	.09	.15
(12)	.03	.02	.02	.02	.02	.02	.03
(13)	.22	.21	.21	.20	.20	.17	.17
(14)	.07	.10	.08	.11	.10	.08	.06
(15)	.45	.87	.85	1.09	1.20	.86	.41
(16)	.55	.70	.89	.81	.83	.82	.88
(17)	.72	.35	.97	.43	.46	—	.83

casts (fig. 3). This may indicate that these species withdraw farther below the surface than the others or it may simply be an artifact of our casts of those species being more complete. Our casts of the burrow of *H. halis* ranged from 125 to 445 mm (mean 250, CV = 40.0).

(4) Burrow Length (BL). This is the length of the burrow measured along the center line of the tracing. If part of the cast appeared to be abnormal only the segment with regular curves was used and the ratio of Cast Segment Length (CSL) and Burrow Segment Length (BSL), which is independent of the completeness of the cast, was used in the phylogenetic analysis. Burrow lengths of *H. halis* ranged from 163 to 494 mm (mean 287 mm, CV = 36.6).

(5) Wave Length (WL). The wavelength was measured as the average distance between successive peaks on the same side. Wavelength of *H. halis* ranged from 32 to 60 mm (mean 48.2, CV = 17.5).

(6) Burrow Width (BW). Width of the burrow is the distance between the lines tangent to the outside of the peaks on both sides. Because it is independent of the completeness of the cast it is a reliable indicator of the shape of the burrow. However, it does include the diameter of the cast which cannot be measured precisely, hence the calculated amplitude (8) is a better indication of burrow shape. Burrow width of *H. halis* ranged from 13.3 to 24.4 mm (mean 19.5, CV = 15.3).

(7) Cast Diameter (CD). Measurements of the cast diameter are imprecise reflections of the burrow diameter because the casts have sand grains embedded in their outer wall. Moreover, some error may be introduced in tracing the cast. However, this is true of all species so this measurement can be used for comparisons. In all species the burrow tends to be about 2 mm wider than the greatest body depth of the eel, excluding the fins, giving the eel a relatively close fit when the fins, even though unerected, are taken into consideration. Cast diameters of *H. halis* ranged from 4.9 to 7.7 mm (mean 5.79, CV = 14.7).

(8) Amplitude (A). The amplitude of the waves is the distance from the center line of the burrow to the midline of the burrow on one side. It was calculated by subtracting the average cast diameter from the average burrow width and dividing by two. Algebraically this calculation removes the effect of cast diameter[3] and thus amplitude is a more precise measure of the maximum deflection from the midline than is burrow width. Amplitude of *H. halis* casts ranged from 4.18 to 9.03 mm (mean 6.88, CV = 18.3).

(9) Body Depth to Total Length (D/TL). This measure of the relative slimness of the eel is obtained from measurements of specimens. For three specimens of *H. halis* from Turks and Caicos Islands it ranged from 0.014 to 0.021 (mean 0.016, CV = 18.7).

(10) Cast Segment Length to Burrow Segment Length (CSL/BSL). This indicates the amount of flexure, i.e., a higher ratio indicates less curvature. For *H. halis* this ratio ranged from 0.77 to 0.92 (mean 0.86, CV = 4.7).

(11) Amplitude to Wave Length (A/WL). This indicates the shape of the individual waves. For *H. halis* it ranged from 0.12 to 0.18 (mean 0.144, CV = 13.9).

(12) Amplitude to Total Length (A/TL). This relates flexure to body length. In *H. halis* values ranged from 0.019 to 0.041 (mean 0.031, CV = 19.4).

(13) Wave Length to Total Length (WL/TL). This also relates flexure to body length of the eel. Values for *H. halis* ranged from 0.143 to 0.257 (mean 0.218, CV = 17.4).

(14) Body Depth to Wave Length (D/WL). This relates "slenderness" of the eel to degree of flexure. In *H. halis* values ranged from 0.052 to 0.098 (mean 0.066, CV = 19.7).

(15) Body Depth to Amplitude (D/A). This is a second, but independent, measure relating slenderness to flexure. For *H. halis* values

[3] The waves in the cast can be considered as deflections on either side of a center line and the amplitude is the distance from that center line to midline of the burrow at its maximum deflection. Therefore the width of the burrow (the distance between lines tangent to the peaks on each side) is twice the amplitude plus the diameter of the cast ($W = 2A + CD$). The amplitude is calculated as $A = 0.5(W - CD)$. Substituting $(2A + CD)$ for W yields $A = 0.5[(2A + CD) - CD]$. In other words, the term for cast diameter disappears and the relationship between cast diameter and amplitude is independent of the actual cast diameter.

TABLE 3
Matrix of Coded Characters Used for Parsimony Analysis

	Characters								
Species	(1)	(2)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
halis	1	1	1	1	1	1	1	2	2
hassi	1	2	3	2	2	1	2	2	1
peri.	1	1	3	1	1	1	2	2	1
poly.	1	1	2	1	2	1	2	2	1
klaus.	2	3	4	2	3	1	2	2	1
G. sil.	3	3	5	3	3	2	1	2	1
G. sp.	3	3	5	4	3	3	1	1	2

ranged from 0.206 to 0.759 (mean 0.446, CV = 30.5).

(16) Body Depth to Cast Diameter (D/CD). This indicates the closeness of fit of the eel within the burrow. Again, since individual specimens are not matched with the casts and since cast diameter often includes sand grains embedded in the cast, this ratio is useful only for comparing species. In *H. halis* this value ranged from 0.404 to 0.648 (mean 0.546, CV = 13.6).

(17) Total Length of Eel to Burrow Length (TL/BL). This provides a measure of how far the eel can retract within the burrow, but it is subject to error due to incompleteness of the cast. Three of the *H. halis* casts were shorter than the average total length of the specimens and could not be used. For the rest the values ranged from 0.372 to 0.978 (mean 0.719, CV = 29.1).

Systematic Analysis

We included characters (1), (2), and (5) through (11) for analysis of relationships using the program Hennig86. The remaining characters (3, 4, 12–17) were rejected as being too variable (CV > 30) or dependent on average specimen measurements that are not associated with specific casts. Each character was coded by arranging the values in numeric order and coding them by gap analysis (table 3). Because the nearest relative of the garden eels is unknown and because no other eels are known to have similar burrows, the program was run using implicit enumeration, i.e., without specifying an outgroup. The result was two unrooted trees of 21 steps, with a consistency index of 85 and a retention index of 85. One tree has an unresolved trichotomy between *Heteroconger halis, H. perissodon,* and a lineage containing all the remaining species. The latter lineage is pectinate, with *Heteroconger polyzona, H. hassi,* and *H. klausewitzi* as successive branches and the two species of *Gorgasia* as terminal branches. The other tree is nearly identical but has the positions of *H. perissodon* and *H. polyzona* reversed. Both have *Heterodon hassi* as a sister group of a lineage consisting of *H. klausewitzi* and the two species of *Gorgasia,* which fall out as each other's closest relatives.

If the remaining species of garden eels turn out to have burrows like those in our sample, which represents about a quarter of the known species, then burrow form may be of some value in phylogenetic reconstruction. It would be especially intriguing to find among the species whose burrow form is still unknown a structure other than a vertical sinusoidal curve in a single plane.

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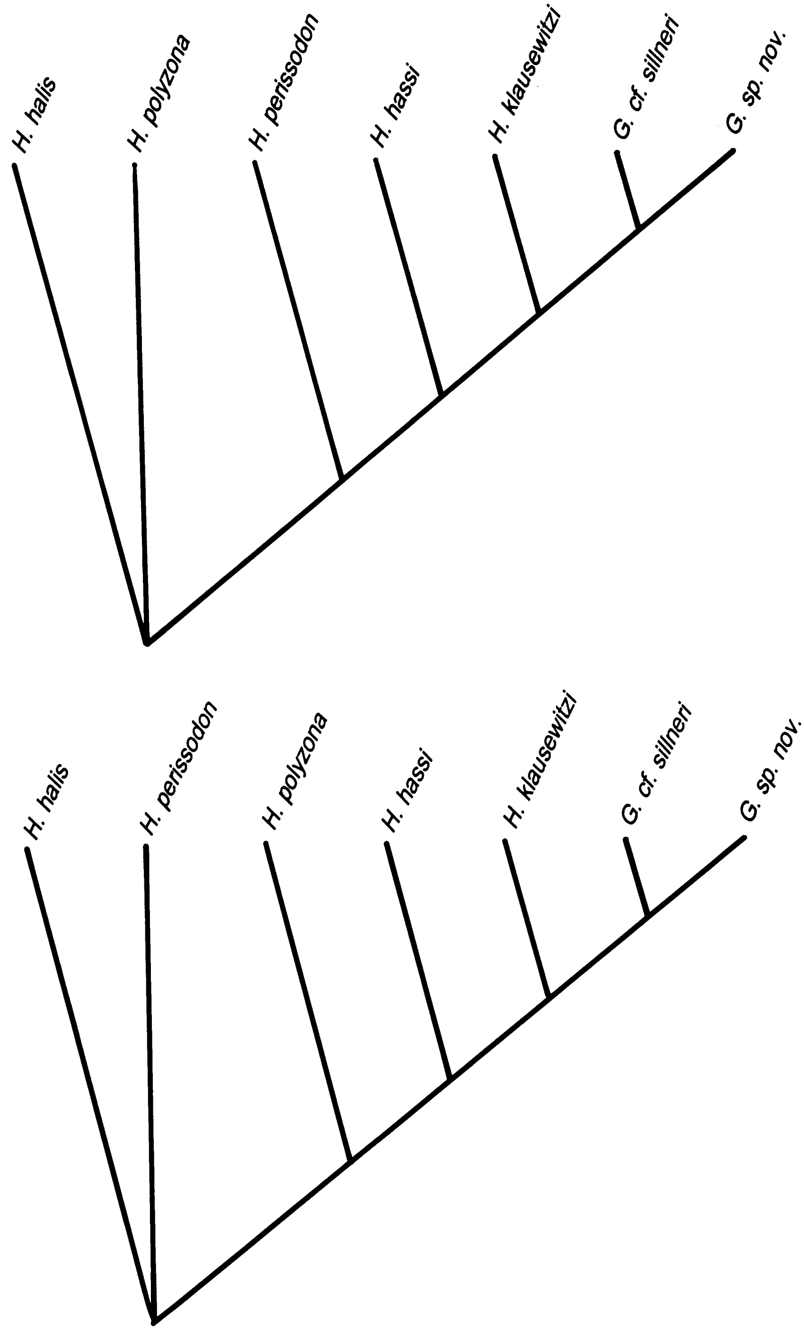

Fig. 5. Cladograms of relationships of garden eels based on measurements of burrow form. These trees are equally parsimonious.

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