

The Osteology of the Congrid Eel *Gorgasia punctata* and the Relationships of the Heterocongrinae¹

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ABSTRACT: The osteology of *Gorgasia punctata* is described, figured, and compared with that of other congrids. *Gorgasia* is clearly referable to the subfamily Heterocongrinae. The heterocongrines agree with the Congridae in several important features, and do not differ in fundamental respects. Therefore, the group is recognized as a subfamily of the Congridae. *Gorgasia* is the most primitive heterocongrine, and agrees with the anagoine congrids in having a lateral ethmoid process. Because of this and other similarities it is suggested that the Anagoine and Heterocongrinae arose from a common stem. The genus *Xarifania* was erected on the erroneous basis of lack of caudal rays. It is synonymized with *Taenioconger*.

THE CONGRID EEL *Gorgasia punctata* was placed by its describers in the little known apodal family Derichthyidae (Meek and Hildebrand, 1923). Böhlke (1951) was the first to point out that the affinities of *Gorgasia* were with *Heteroconger*. Gosline (1952) provisionally placed *Heteroconger* and *Gorgasia* in the Congridae. Böhlke (1957) described the osteology of the related *Nystactichthys halis* and placed the eels allied to *Heteroconger* in the Congridae, but considered them to constitute the distinct subfamily Heterocongrinae.

Böhlke considered *Gorgasia* to be the most primitive genus of the Heterocongrinae on the basis of its more complete complement of head pores, its uncoalesced upper labial flanges (called by him the "free edge of lip"), a well-developed pectoral fin, and its unspecialized maxillary dentition. He considered *Gorgasia* to be specialized, however, in that the caudal rays are much reduced and covered by thick skin. Internal characters were not considered, since the only complete specimen then available was the holotype.

Recent collections made by personnel of the Scripps Institution of Oceanography have amassed rich material of several species of

eastern Pacific heterocongrines, including *Gorgasia punctata*. Because of previous uncertainties regarding the exact position of *Gorgasia* in eel classification, a study of the osteology of this species seemed worthwhile.

ACKNOWLEDGMENTS

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MATERIALS AND METHODS

The two adults of *Gorgasia punctata* were taken from a series of 69 (SIO62-720-26A, Bahía Magdalena, Baja California, Mexico). These were bone-stained with alizarin and cleared in glycerine. The neurocranium was dissected out of one specimen, and the drawings were made from the dried preparation. In addition I have utilized single-stained and cleared specimens of *Taenioconger digueti* Chabanaud (SIO65-278, Gulf of California), *T. herrei* Wade (SIO61-261, Gulf of California), *T. bassi*³ (Klauswitz and Eibl-Eibesfeldt)

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³ *Taenioconger bassi* was originally described in the genus *Xarifania*, of which it is the type species

(unnumbered, D'Arros Island, Amirantes Islands), *T. n.sp.* (SIO62-42, Bahía Banderas, Mexico), and *Ariosoma gilberti* (Ogilby) (SIO62-77, Sinaloa, Mexico).

OSTEOLOGY

NEUROCRANIUM (Fig. 1): The skull is truncated posteriorly, except where the exoccipital flanges break the outline. The premaxillaries, ethmoid, and vomer are fused, with no suggestion of articulations, such as were reported by Böhlke (1957) for *Nystactichthys halis*. The anterior, triangular tooth-patch may represent the premaxillary dentition. The dorsal or ethmoid portion of the complex is very thin, and is reduced medially to a septum, so that it is shaped much like an I-beam in cross section. Laterally the ethmoid portion is expanded, and gives rise to two heavy, forward-curving processes. These are very similar to the "lateral ethmoid processes" reported by Asano (1962) for *Anago* and *Alloconger*. Below this are two small projections from the lateral face of the vomer. These vomerine processes are difficult to distinguish from the base of the lateral ethmoid process. They are more evident in *Taenioconger* and, judging from Böhlke's figures 3B and 3C, are developed in *Nystactichthys* as well. Posteriorly on the under side of the cranium, parts of the prootic and basioccipital are expanded to form a prominent auditory bulla, which contains a large otolith (presumably the sagitta). The foramen magnum is surrounded by exoccipital flanges, which grasp the first vertebra. The supraoccipital is well developed, but does not completely separate the epiotics, which are in contact posteriorly. The parietals are sutured in the specimen figured,

(Klausowitz and Eibl-Eibesfeldt, 1959). The sole distinction of the genus *Xarifania* was the supposed lack of caudal rays. The tail-tip of *X. bassi* is fleshy but flexible and clearly contains well-developed caudal rays. These are visible under direct light and are obvious when transmitted light is used. In addition to the Amirantes specimen, I have examined a paratype of *X. bassi* (ANSP 94706) through the courtesy of J. Böhlke. I can find no other important differences, either in external morphology or osteology, between *X. bassi* and the species of *Taenioconger* examined. The nominal genus *Xarifania* is considered, therefore, to be a synonym of *Taenioconger*.

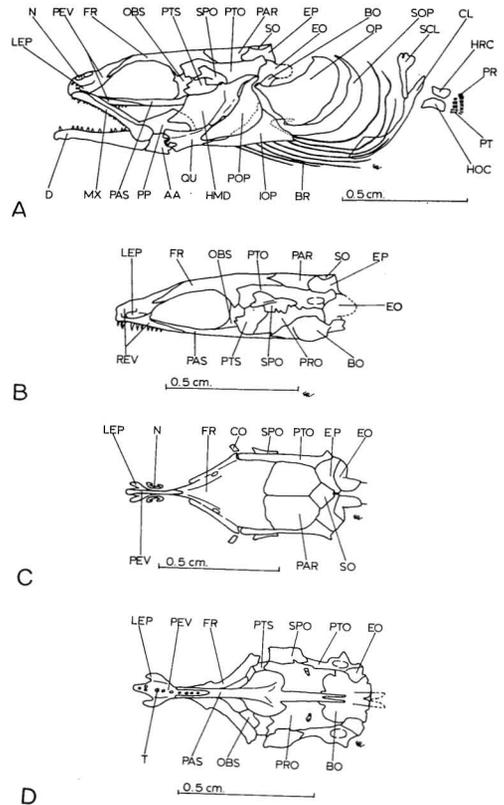


FIG. 1. Head skeleton of *Gorgasia punctata*. A, Lateral view, including pectoral girdle; B, neurocranium, lateral view; C, neurocranium, top view; D, neurocranium, bottom view. AA, Articular angular; BO, basioccipital; BR, branchiostegal ray; CL, cleithrum; CO, circumorbital; D, dentary; EO, exoccipital; EP, epiotic; FR, frontal; HMD, hyomandibular; HOC, hypocoracoid; HRC, hypercoracoid; IOP, interopercle; LEP, lateral ethmoid process; MX, maxillary; N, nasal; OBS, orbitosphenoid; OP, opercle; PAR, parietal; PAS, parasphenoid; PEV, premaxillary ethmiovomerine block; POP, preopercle; PP, palatopterygoid; PR, pectoral ray; PRO, prootic; PT, pterygiophore; PTO, pterotic; PTS, pterosphenoic; QU, quadrate; SCL, supraclathrum; SO, supraoccipital; SOP, subopercle; SPO, sphenoic.

but in another they are fused for the anterior one-quarter of their lengths. The frontals are completely fused, with no sign of a suture or median ridge. There are well-developed canals along the lateral margins of the pterotics and frontals, with two large foramina anteriorly, but there is no transverse canal across the frontals.

SUSPENSORIUM AND JAWS (Fig. 1): As

might be expected from the short oblique mouth, the suspensorium is strongly inclined forward. The hyomandibular and quadrate are massive. The palatopterygoid is developed as a broad lamina, which is attached by a ligament to the vomer. The maxillary contacts the neurocranium at the tip of the snout. The posterior end of the maxillary is expanded, but the remainder is a narrow lamina. There is no pedicel anteriorly.

OPERCULAR SERIES (Fig. 1): The well-developed opercular bones are strongly ossified. The preopercle is triangular, like that of *Taenioconger*, but unlike that of *Nystactichthys* as illustrated by Böhlke (1957). The blocky and subtriangular interopercle has a pronounced anterior extension. The crescentic subopercle curves upward under the lower angle of the opercle. The dorsal margin of the broadly crescentic opercle is deeply concave; its upper-rear corner is far above the upper end of the hyomandibular.

HYOID ARCH (Fig. 2): This arch consists of the unpaired glossohyal and urohyal, and paired upper hypohyal, ceratohyal, and epihyal. The interhyal is absent. All the branchiostegal rays are inserted on the lateral surfaces of the arch, one on the ceratohyal and seven on the epihyal. In *Nystactichthys* and *Taenioconger*, in contrast, two branchiostegals are inserted on the ceratohyal. The urohyal is needle-like, with an expanded and flattened anterior end. The dorsal surface of the glossohyal is grooved.

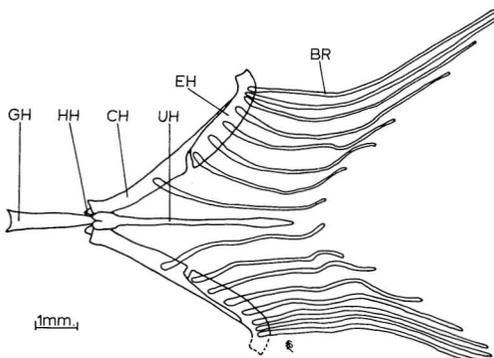


FIG. 2. Hyoid apparatus of *Gorgasia punctata* from below. BR, Branchiostegal ray; CH, ceratohyal; EH, epihyal; GH, glossohyal; HH, hypohyal; UH, urohyal.

SHOULDER GIRDLE (Fig. 1): The cleithrum and supracleithrum are well developed. The expanded head of the supracleithrum is bifurcate in the specimen illustrated, but not in another. The well-ossified hypercoracoid and hypocoracoid are connected by cartilage. The four hour-glass-shaped actinosts are small, but well ossified. According to Böhlke *Nystactichthys* has no actinosts, but the species of *Taenioconger* that I have examined are like *Gorgasia* in this respect.

VERTEBRAE AND ASSOCIATED BONES (Fig. 3): In one specimen the vertebrae number 144, of which 45 precede the anus. Figure 3A represents a cross section at the level of the 17th vertebra; Figure 3B illustrates the 17th to 19th vertebrae in lateral view. The vertebrae anterior to the dorsal origin bear well-developed, crest-like neural spines. The remainder of the abdominal vertebrae have large neural arches, but

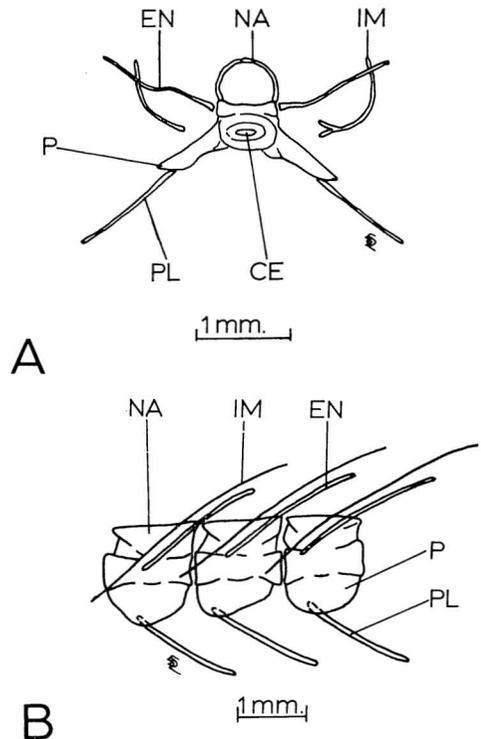


FIG. 3. Vertebrae and associated bones of *Gorgasia punctata*: A, Front view of 17th vertebra; B, side view of 17th to 19th vertebrae. CE, Centrum; EN, epicentral; IM, intermuscular; NA, neural arch; P, parapophysis; PL, pleural rib.

no neural spines. The first 4 vertebrae bear strongly-developed, winglike transverse processes. These curve out and back, and each has on its posterior margin a long, thin, backward-directed process that seems to represent a fused epicentral (these structures lie on the same plane as the epicentrals associated with the more posterior vertebrae; furthermore, epicentrals are otherwise lacking on the first 4 vertebrae). The 5th through 9th vertebrae bear epicentrals, and weak transverse processes without backward prolongations. Böhlke mentioned no such peculiar condition in *Nystactichthys halis*, nor can I find transverse processes on the anterior vertebrae in *Taenioconger digueti* or *T. herri*. In *T. bassi*, however, weak transverse processes are developed on the first few vertebrae. In *Gorgasia* the transverse processes are more weakly developed posterior to the 4th vertebra, and are not noticeable posterior to the 10th vertebra.

The abdominal vertebrae bear strong parapophyses to which, posterior to the 6th vertebra, are articulated strong pleural ribs. There is a strong median vertical ridge on each parapophysis. The first haemal spine appears 15 vertebrae behind the anal origin, and the pleural ribs are present to this point.

The caudal vertebrae bear transverse processes, commencing 6 vertebrae behind the anal origin. The transverse processes regress toward the tail-tip and are no longer apparent on the 10th vertebra before the caudal. The neural arches of the caudal vertebrae are smooth until about the 60th postanal vertebra, which bears the first neural spine, in the form of a small projection. The neural spines persist as low conical projections until 17 vertebrae from the tail-tip, behind which they become increasingly higher and more bladelike until they assume the shape shown in Figure 3. The haemal spines are also small and inconspicuous anterior to the 17th vertebra from the tail-tip. Thereafter, like the neural spines, they become increasingly higher and more bladelike. Shortly before the tail-tip the haemal spines become divided, so that the haemal arches are again open, as on the precaudal vertebrae (Fig. 4).

Epicentrals are associated with all vertebrae except the last 10. Epipleurals appear 6 vertebrae behind the anus and persist until 15 vertebrae before the tail-tip.

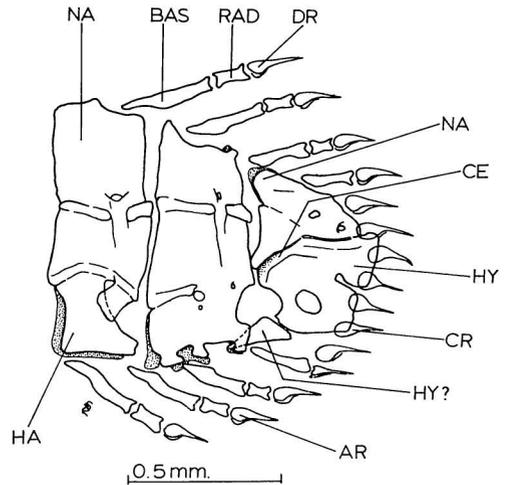


FIG. 4. Last 3 vertebrae of *Gorgasia punctata*, lateral view. AR, Anal ray; CE, centrum; BAS, basal element of pterygiophore; CR, caudal ray; DR, dorsal ray; HY, hypural; NA, neural arch; RAD, radial element of pterygiophore.

Dorsal and ventral intramuscular bones are well developed, and associated with all but the first 12 and last 4 vertebrae. Most of the intramusculars are simple; one of those illustrated in Figure 3 happens to be bifurcate.

CAUDAL AND ASSOCIATED STRUCTURES (Fig. 4): The tail-tip of *Gorgasia* is hard and pointed, with the fin rays concealed. However, the caudal skeleton is well developed and complex. As mentioned above, the neural and haemal arches and associated spines become expanded posteriorly, and the haemal and, to a lesser extent, the neural arches become open. According to the terminology of Nybelin (1963), there is but one ural centrum. Fused to it is a large hypural plate, probably consisting of several fused hypurals. The structure labeled HY? in Figure 4 is somewhat problematical. It has a basal-less fin ray associated with it and thus might be termed a hypural, but from its position it is difficult to determine whether it is itself associated with the last preural centrum or the ural centrum. Likewise, the nature of the dorsal element labeled NA is somewhat ambiguous. It might be termed an epural, but since it is fused to the centrum, and divided anteriorly like the preceding neural arch, I term it a neural arch, despite the circumstance that it bears two "prin-

cipal" caudal rays. A strong process curves forward and downward from the neural arch element. It probably serves as a muscle attachment and may be associated with tail-first digging in sand. An essentially similar caudal skeleton has been figured by Böhlke for *Nystacichthys balis*, and I have found the caudal skeleton of *Taenioconger digueti*, *T. herrei*, *T. bassi*, and *T. n.sp.* to be basically the same.

CIRCUMORBITALS AND LATERAL LINE CANALS: The circumorbital ring is complete, consisting of at least five weakly-ossified and roofless bones. Apparently the small "supraorbital" illustrated by Asano (1962) for several Japanese congrid is absent. The temporal canal is encased in bone in *G. punctata* only, among the species examined. The lateral-line canal along the body is contained in a series of ossicles (lateral-line scales?). Anteriorly these are developed as unconnected but closely opposed tubes, which posteriorly gradually become less strongly ossified, so that along the midbody there is an open trough consisting of a series of ossified half-rings. In the species of *Taenioconger* examined, the lateral-line ossicles are developed as short, widely-spaced, troughlike ossifications.

RELATIONSHIPS OF THE HETEROCONGRINAE

The heterocongrines resemble the Ophichthidae in several respects. In both groups the ribs are laminar, and the neural spines reduced (vestigial in the ophichthids), as are the circumorbitals. In *Gorgasia* and in some species of *Taenioconger* the caudal fin is short and the tail-tip fleshy. In all, the body is elongate and circular in cross section. The pectoral fin, as in many ophichthids, is reduced (varying from small in *Gorgasia* to minute in *Nystacichthys* and *Taenioconger* to absent in *Heteroconger*). In addition to these structural characters, both groups share the sand-dwelling habit. However, the characters given by Gosline (1951) to separate the Congridae and the Ophichthidae (except that it is now known that many congrid have an auditory bulla) serve to distinguish *Gorgasia* and its allies from the ophichthids as well. In addition, it may be noted that the Congridae have the parapophyses divided by a vertical ridge and have a vomerine process,

to which the palatopterygoid is ligamentously attached—features that appear to be lacking in the Ophichthidae.

The superficial similarities between *Gorgasia* and the ophichthids are certainly parallel adaptations to a similar mode of life, and the minor osteological similarities may be adaptations as well.

Although recognizing the close relationship between the two groups, Klausewitz and Eibl-Eibesfeldt (1959) maintained the family Heterocongridae as distinct from the Congridae. Their action was based on behavioral differences and on bone reduction and "Fensterbildung" (fenestration?) in the skeleton. However, their illustration of the head skeleton of *Xarifania b. bassi* shows a well-developed skull and well-integrated jaws, suspensorium, and opercular series. On the basis of the present investigation there are no grounds (except that the circumorbital series is less well developed) for the contention that the skeleton has undergone important reduction in comparison with that of the Congridae.

There is, in fact, nothing in the osteology of the heterocongrines I have examined that would preclude the inclusion of the group in the Congridae. The heterocongrines possess the basic congrid characters of ankylosed frontals, forward-inclined suspensorium, few and nonoverlapping branchiostegals, maxillary-ethmoid articulation near tip of snout, caudal vertebrae with transverse processes, skull truncate posteriorly, parapophyses divided by a vertical ridge, and a lateral process on the vomer.

The chief osteological differences are: neural spines absent on most abdominal vertebrae (and on most caudal vertebrae as well in *Gorgasia*); neural and haemal arches becoming high and bladelike near the tail-tip; urostylar vertebra better developed, and supporting structure of caudal more complex; epineurals and epipleurals lost 10–15 vertebrae before tail-tip; circumorbital series reduced and less ossified. Stronger divergences from the basic congrid type are found in nonosteological characters. In most of the Congridae the muzzle is elongate, and the olfactory organ is well developed, with numerous lamellae. In the heterocongrines the muzzle is short, the eye is relatively large, and the olfactory rosette is much smaller, with

few lamellae (ca. 20). This distinction is no doubt correlated with a change in food habits (Klausewitz and Eibl-Eibesfeldt, 1959). Also the habit of living colonially in sand tubes is unknown in other congrid.

These differences and similarities seem to bear out Böhlke's (1957) contention that the Heterocongrinae should be regarded as a well-defined subfamily within the Congridae. That there are profound differences in behavior and ecology is undoubted, but these have not involved any fundamental changes in the basic congrid body plan.

Until recently, little information has been available on the osteology of the family Congridae. However, Asano (1962) has presented detailed information on the anatomy of 10 genera and 14 species of Japanese congrid. On the basis of his study, Asano recognized two subfamilies, the Anagoinae and the Congrinae (the Heterocongrinae were not considered). The Anagoinae were said to differ from the Congrinae in that there is a forward and laterally directed process on the ethmoid, the supraoccipital is absent, there are only four suborbitals, the abdominal and caudal vertebrae are about equal in number, the gas bladder is attached to the parapophyses, the tail-tip is hard, the caudal rays are short, the fin rays are unsegmented, and the lateral-line scales are well developed.

Asano assigned two genera, *Anago* and *Alloconger*, to the Anagoinae. I can confirm that *Ariosoma* belongs here, as does the recently described *Paraconger* Kanazawa 1961.

The heterocongrines share characters with both the Anagoinae and the Congrinae. They agree with the congrines in that the supraoccipital is present, there are many more caudal than abdominal vertebrae, and the gas bladder is free from the parapophyses. They agree with the anagoines in that the fin rays are unsegmented, the caudal is reduced, and the lateral-line scales are well ossified (corresponding to Asano's "*Anago* type"). I have been unable to determine with certainty the number of suborbitals in the heterocongrines.

Gorgasia alone agrees with the Anagoinae in having a lateral ethmoid process. In this connection it is important to establish the evolutionary position of *Gorgasia*. Böhlke (1957)

gave reasons for considering *Gorgasia* to be in most respects the most primitive of the Heterocongrinae. His conclusions are borne out in this study, except for the discovery in *Gorgasia* of peculiar, expanded transverse processes on the anterior vertebrae, and the loss of an anterior maxillary pedicel. These specializations probably preclude *Gorgasia* as an ancestor, but they do not militate against the hypothesis that *Gorgasia* is more generalized over-all, and probably was an earlier offshoot of the heterocongrine line.

The retention in *Gorgasia* of a lateral ethmoid process indicates relationship with the anagoine line. It seems unlikely that the agreement represents convergence. Eels have evolved a number of structures bracing the maxillary, correlated with elongation of the gape and with the use of the jaws in biting and crushing (Gosline, 1951; Asano, 1962). However, the trend in heterocongrine evolution has been in the other direction, toward shortening of the gape and development of a jaw structure and dentition suitable for snapping at planktonic prey. It may be that the retention of the lateral ethmoid process in *Gorgasia* has allowed the loss of the maxillary pedicel.

It seems plausible to hypothesize that the Heterocongrinae and Anagoinae arose from a common ancestor which had a lateral ethmoid process, a supraoccipital, unsegmented fin rays, and well-developed lateral-line scales. It seems likely that the sand-burrowing habit (known for *Anago*) had already been developed. The two groups have diverged sharply, however. The development of the plankton-feeding habit in the heterocongrines has been accompanied by important changes in the head. The mouth has become short and oblique, and the dentition specialized. The development of a short oblique mouth as an adaptation to snapping at plankton or small prey has taken place in a number of fishes. Compare, for example, the serranid genus *Epinephelus*, which feeds on relatively large prey, with the plankton-feeding *Paranthias*. A similar phenomenon can be seen if the bottom-feeding embiotocid genus *Micrometrus* is compared with the closely related genus *Brachyistius*, which feeds in midwater (Hubbs and Hubbs, 1954). Walter A. Starck II has pointed out to me that the shortening of the

muzzle in these fishes results in the placement of the eye close to the tip of the snout, and thus allows for close-up binocular vision. Thus, vision has become more important in prey finding in heterocongrines, and the eye is much enlarged and the olfactory organ much reduced. The lateral-line system on the head has likewise become reduced, again probably correlated with the increased dependence on vision. The great elongation of the slender body would seem to be an adaptation to getting the head well off the bottom, and yet maintaining contact with the sand tube which is used for cover. (The normal posture of a heterocongrine is vertical, with the anterior one-half to two-thirds of the body out of the sand tube.)

On the other hand, the anagoines, except in the loss of the supraoccipital, have diverged much less from the basic congrid type, either in structure or in behavior.

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