Review of *Stathmonotus*, with Redefinition and Phylogenetic Analysis of the Chaenopsidae (Teleostei: Blennioidei)

PHILIP A. HASTINGS
and
VICTOR G. SPRINGER

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY · NUMBER 558

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Review of *Stathmonotus*, with Redefinition and Phylogenetic Analysis of the Chaenopsidae (Teleostei: Blennioidei)

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ABSTRACT

Hastings, Philip A., and Victor G. Springer. Review of *Stathmonotus*, with Redefinition and Phylogenetic Analysis of the Chaenopsidae (Teleostei: Blennioidei). *Smithsonian Contributions to Zoology*, number 558, 48 pages, 29 figures, 5 tables, 1994.—The study of new material and the use of additional characters, including the sensory pores, of *Stathmonotus* corroborates the taxonomic assignments of Springer (1955). The osteology of *S.* (*Parastathmonotus*) *sinuscalifornici* is described, illustrated, and compared to that of the other five species of *Stathmonotus*. A key, distribution maps, color descriptions, and illustrations for all species are given.

The Chaenopsidae of Stephens (1963) is expanded, based primarily on osteological characters, to include *Neoclinus*, *Mccoskerichthys*, and *Stathmonotus*. This expanded family is characterized by at least eight apomorphies, but its outgroup relationships are uncertain. Character evidence supporting the monophyly of the included taxa (*Neoclinus*, *Mccoskerichthys*, *Stathmonotus*, and the Chaenopsinae) is presented. Parsimony analysis of 61 morphological characters resulted in two most-parsimonious trees of relationships within the Chaenopsidae (differing only in the relationships of *S. sinuscalifornici*). *Neoclinus* is hypothesized to be the sister group of the remainder of the Chaenopsidae. *Mccoskerichthys* is hypothesized to be the sister group of a clade comprising *Stathmonotus* and the Chaenopsinae (= Chaenopsidae of Stephens, 1963). Within *Stathmonotus*, *S. stahli* and *S. gymnodermis* are hypothesized to form a monophyletic group (subgenus *Auchenistius*) that is the sister group of the remaining four species. *Stathmonotus hemphilli* is hypothesized to be the sister group of the remaining three species (subgenus *Parastathmonotus*). Within *Parastathmonotus*, *S. lugubris* and *S. culebrai* are hypothesized to be sister species. An equally parsimonious topology places *S. sinuscalifornici* as the sister species of *S. hemphilli*. Character support for these relationships is discussed, a classification of the Chaenopsidae is presented, and the biogeography of *Stathmonotus* is discussed.

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Review of *Stathmonotus*, with Redefinition and Phylogenetic Analysis of the Chaenopsidae (Teleostei: Blennioidei)

Philip A. Hastings
and Victor G. Springer

Introduction

Stathmonotus includes six species of small (< 55 mm SL), rarely observed, eel-like blennioid fishes that are found within reefs, rock and shell rubble, or grassbeds in tropical coastal regions of the Caribbean and eastern Pacific. The relationships of *Stathmonotus* have been uncertain since the genus was described by Bean in 1885. At one time, *Stathmonotus* was considered to have affinities with chaenopsids (Jordan, 1923), based primarily on its lacking scales. However, because Springer (1955) included the scaled species *Auchenistius stahli* together with five unscaled species in *Stathmonotus*, he and more recent workers excluded *Stathmonotus* from the Chaenopsidae. *Stathmonotus* has been placed most recently in the Labrisomidae (Nelson, 1984; Eschmeyer, 1990), a "waste-basket" for scaled blennioids not clearly falling into other families (Springer, 1993). Our studies on the morphology of the species of *Stathmonotus* have led us to revive the hypothesis of Jordan (1923) and include *Stathmonotus* within the Chaenopsidae.

The Chaenopsidae is recognized by most recent workers as a distinctive, apparently monophyletic group of blennioids that is restricted to the New World (Stephens, 1963; Nelson, 1984). However, questions of familial limits and relationships within the perciform suborder Blennioidei, including those of chaenopsids, are unresolved (Springer, 1993). Hubbs (1953a) considered chaenopsids, together with *Neoclinus* and part of *Stathmonotus*, to be related to the Blenniidae, but this hypothesis has received little additional support. Stephens (1963) diagnosed chaenopsids, elevated them to family level, and agreed with Böhlke (1957) that their affinities were with the "clinid" blennies (at that time including what are now considered the Clinidae and Labrisomidae), especially the genus *Neoclinus*. Other workers have questioned the appropriate taxonomic level to be accorded chaenopsids (e.g., Böhlke and Robins, 1974), but no one has questioned their monophyly or ventured further hypotheses of their outgroup relationships.

Stephens (1963) diagnosed the Chaenopsidae as having no scales, no lateral line, and two, rather than four, infraorbitals. The unusual blennioid, *Mccoskerichthys sandae*, discovered subsequently, did not fully agree with this diagnosis, because, although quite chaenopsid-like in having no scales and no lateral line, it has four, rather than two, infraorbitals (Rosenblatt and Stephens, 1978). Rosenblatt and Stephens (1978) also noted that *Mccoskerichthys* has another unique feature common to it and the Chaenopsidae not mentioned by Stephens (1963): its maxillary is not exposed laterally but is sheathed by a fold of skin. Because *Mccoskerichthys* also has several other traits considered to be derived characters of certain lineages within the Chaenopsidae, Rosenblatt and Stephens (1978) tentatively considered it to be a highly derived chaenopsid (perhaps related to *Acanthemblemaria*) that had reverted to the plesiomorphic condition of four infraorbitals.

Herein, we review *Stathmonotus*, describe the osteology of *Stathmonotus sinuscalifornici*, and compare it to other species of *Stathmonotus* and to other blennioids. We then redefine the

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Chaenopsidae based on our study of the morphology and phylogenetic relationships of these fishes and our desire to recognize monophyletic groups in classification. We present evidence that the Chaenopsidae (sensu Stephens, 1963), *Stathmonotus, Mccoskerichthys,* and *Neoclinus* form a monophyletic group, and we include these in an expanded Chaenopsidae. We present morphological evidence of the monophyly of each of these included clades, their phylogenetic interrelationships, and the possible outgroup relationships of chaenopsids.

METHODS

Osteological specimens were prepared according to Taylor (1967) or Dingerkus and Uhler (1977). The osteological drawings of *Stathmonotus,* with the exception of Figure 4, are based on a specimen, 47 mm SL, of *S. sinuscalifornici* (now lost) from the W side of Punta de las Cuevas, Gulf of California, Sonora, Mexico, that was stained only with alizarin. The description of cartilage is based on other specimens (see "Material Examined"). Names of bones are those in common usage with the exception of our substitution of epineurals for epipleural ribs, in accordance with the findings of Johnson and Patterson (1993). Counts of epineurals and pleural ribs for the species of *Stathmonotus* were made from radiographs. The posteriormost epineurals often are difficult to discern, possibly accounting for the wide range in counts reported herein. Standard lengths (SL), used throughout, are approximate because *Stathmonotus* specimens frequently exhibit the eel-like feature of curling in preservative.

Several characters used in the phylogenetic analysis involve details of the distribution of pores of the cephalic sensory system. This system was studied in detail for all chaenopsid genera and for representatives of all tribes of the Labrisomidae (see below). However, the cephalic sensory system was not fully studied in the remaining blennioid clades (Tripterygiidae, Dactyloscopidae, Blenniidae, and Clinidae) used as outgroups, consequently, all cephalic sensory pore characters were scored as unknown for these taxa.

Sensory canal and pore terminology follows Coombs et al. (1988) and Smith-Vaniz and Palacio (1974) with the following modifications. (1) The "nasal series" (N) always includes a pore (N1) at the anterior terminus of each nasal bone and sometimes a second pore (N2) opening dorsally near the middle of each bone (see Figure 29*a*). (2) The "mandibular series" (M) includes a line of pores beginning near the dentary symphysis and continuing posteriorly to, but not including, a "common pore" (C) located between the anguloarticular and preopercle. The symphyseal region of the dentary has a pore at the anterior terminus of the canal (M1A), and sometimes it has a second, slightly more posterior pore (M1B) opening on the medial side of the canal (see Figure 25). (3) In blennioids, the region where the "preopercular canal" and the "supratemporal commissure" connect with the "trunk canal" is compressed relative to many fishes (Coombs et al., 1988). Because details of the innervation of these canals are unknown for blennioids, the homology of canals and pores in this region with those of other fishes remains uncertain. We follow Smith-Vaniz and Palacio (1974) in calling the canal extending from the dorsal end of the preopercle, arching dorsally and posteriorly above the opercle, and passing through the posttemporal bone, the "posttemporal canal"; it may include portions of the "postotic" and "temporal" canals of Coombs et al. (1988). The last posttemporal pore opens at the posterior end of the posttemporal bone (in chaenopsins and *Mccoskerichthys*) or at the posterior end of a tubular bone posterior to the posttemporal (in *Stathmonotus;* see Figure 5*c*). (4) The "otic canal" (Coombs et al., 1988; = temporal canal of Fukao, 1987) connects the posttemporal and supratemporal commissure with the supraorbital canal and may have one or more "otic pores" along its length.

PHYLOGENETIC ANALYSIS.—Characters and their alternate states are presented in the text. Taxa expressing more than one character state were scored as polymorphic. Parsimony analyses were conducted using the branch and bound option of PAUP (Swofford, 1990). Character states were polarized by outgroup analysis (Maddison et al., 1984). Because outgroup relationships of chaenopsids are uncertain, the outgroup substitution method (Donoghue and Cantino, 1984) was used to determine the effect of alternative outgroups on the composition and intrarelationships of the Chaenopsidae. Alternative topologies were explored and character evolution was studied using MacClade (Maddison and Maddison, 1992).

Taxa used in the parsimony analyses (see Table 1) included both individual species as well as higher taxonomic categories. Because this study focuses on the Chaenopsidae, we examined representatives of all chaenopsid genera (sensu Stephens, 1963); however, we combined the genera in three terminal taxa, based on recent hypotheses of their phylogenetic relationships. These three taxa are (1) the "*Acanthemblemaria* clade," including *Acanthemblemaria* and *Ekemblemaria* (Hastings, 1990, 1992a), (2) the "*Chaenopsis* clade," including *Chaenopsis, Lucayablennius, Hemiemblemaria, Emblemaria,* and *Tanyemblemaria* (Hastings, 1992b), and (3) the "*Coralliozetus* clade," including *Coralliozetus, Protemblemaria,* and *Emblemariopsis* (Hastings, in prep.). Hypotheses of relationships within these groups are beyond the scope of the present study (but see Stephens, 1963, 1970; Acero, 1984; Hastings, 1990, 1992a, 1992b, in prep.).

We focused on genera previously hypothesized to be related to chaenopsids including *Stathmonotus, Neoclinus,* and the monotypic *Mccoskerichthys.* We scored *Mccoskerichthys sandae* and the six species of *Stathmonotus* as separate taxa, but included the nine species of *Neoclinus* together under one taxon (Table 1).

We also scored a wide variety of the Blennioidei (sensu Springer, 1993) including the Tripterygiidae, Dactyloscopidae, Blenniidae, Clinidae, all tribes of the Labrisomidae (Hubbs, 1952), as well as the enigmatic labrisomid genera *Nemaclinus*

Table 1.—Character scores for parsimony analysis of relationships of the Chaenopsidae. Character numbers refer to those given in text. ? = state unknown; p = polymorphic, states 0 and 1.

Character number	1—10	11—20	21—30	31—41	41—50	51—61
Chaenopsidae						
Stathmonotus hemphilli	1120011111	1111111110	1100000010	11?1111121	1111001111	11111000101
Stathmonotus stahli	1121011111	1111111110	1100000010	1111111112	1111110000	00000000000
Stathmonotus gymnodermis	1121011111	1111111110	1100000010	1111111112	1111110000	00000000001
Stathmonotus sinuscalifornici	1121011111	1111111110	1100000010	1111111122	1111001111	11111110101
Stathmonotus culebrai	1121011111	1111111110	1100000010	1111111122	1111001111	11111111001
Stathmonotus lugubris	1121011111	1111111110	1100000010	1111111122	1111001111	11111111001
Acanthemblemaria clade	11311111p1	1111111110	1p11111100	0000000000	0p00000000	000?101?011
Chaenopsis clade	1131p1p1p0	1111111110	1111111p01	0000000000	00pp000000	000?1p1?011
Coralliozetus clade	1131p1p11p	11111p1110	1p11111101	0000000000	000p000000	00p?101?011
Mccoskerichthys	1231111011	1111110001	0000200010	0000000000	0000000000	000?001?111
Neoclinus	111111pp00	0000000001	0000000010	0000000000	0000000000	000?000?00p
Labrisomidae						
Cryptotremini	0000000000	p000000001	0000000010	0000000000	0000000000	000?000?000
Labrisomini	0000000000	00000p0001	0000000010	0000000000	0000000000	000?000?0p0
Mnierpiini	0000000000	0000000001	0000000010	0000000000	0000000000	000?000?000
Paraclinini	000p000000	00010p0001	0000000010	0000010p00	0000000000	000?000?000
Starksiini	000000p000	0011110001	0000?00010	0000010000	0000000000	000?000?000
Haptoclinus	01?1?0??00	1?01100?00	1000?00010	0??0?00000	0?00000000	001?100?000
Nemaclinus	0010000000	0001110001	0000000010	0000000000	0000000000	000?000?000
Clinidae	0p00000000	1001p00000?	?000?00010	00000000p0	000000000??	??????00??0p
Blenniidae	00p00110p0	ppppp0p00?	?p00?pp000	000000p00p	pp00p000??	?????01??01
Dactyloscopidae	0100010000	0001000000?	?000?01100	0000000000	0100000???	?????10??00
Tripterygiidae	0000000000	1000000000?	?000000000	0000000000	1000000???	?????00??00

(Böhlke and Springer, 1975) and *Haptoclinus* (Böhlke and Robins, 1974). An exhaustive list of material examined is not given here, but it may be found in our earlier publications (see "Literature Cited"). Material examined of *Stathmonotus* species is given in each species account. Institutional abbreviations follow Leviton et al. (1985).

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Review of *Stathmonotus* Bean

HISTORY OF CLASSIFICATION OF *Stathmonotus*

The relationships of the blennioid genus *Stathmonotus* have long been enigmatic. This is illustrated by following the varied and complex history of its classification. Bean (1885) described *Stathmonotus* (*S. hemphilli* Bean, 1885, type species by monotypy) from Florida, believing that it was closely related to *Muraenoides* Lacepede, 1800 (= *Pholis* Scopoli, 1777, Stichaeoidei, Pholidae), although he did not actually assign *Stathmonotus* to any family.

Jordan and Evermann (1896) first assigned *Stathmonotus* to a family, the Xiphidiidae (presumably based on *Xiphidion* Girard, 1858), in which they otherwise included representatives only of cold-temperate stichaeoid genera. Jordan and Evermann (1898) included *Stathmonotus* as the only genus in their subfamily Stathmonotinae (first use of a family group name based on *Stathmonotus*) of the Blenniidae. They also recognized the subfamilies Clininae and Xiphidiinae within the Blenniidae. Evermann and Kendall (1899) included *Stathmonotus* in the Xiphidiidae, but Evermann and Marsh (1899), in

describing a new genus, *Auchenistius* (= *Stathmonotus*, see Springer, 1955), included it in the Blenniidae. Evermann and Marsh (1900) and Jordan and Evermann (1900), a continuation of Jordan and Evermann (1898), included *Auchenistius* in the subfamily Clininae of the Blenniidae.

The next major change in the classification of *Stathmonotus* was Regan's (1912) assignment of the genus to the family Stichaeidae. Regan failed to note that *Stathmonotus* did not conform to his definition of the family, and he mentioned nothing about the relationships of *Auchenistius*.

Metzelaar (1919) described a new genus and species, *Histioclinus veliger* (= *Stathmonotus stahli*), which he placed in the Blenniidae, commenting that the characters that had been used to separate the Blenniidae and Clinidae were unsatisfactory and that the two families should be combined. Jordan (1923) placed *Auchenistius* and *Histioclinus* in the Clinidae and *Stathmonotus* in the Chaenopsidae (the first association of *Stathmonotus* with the family name Chaenopsidae). Beebe and Tee-Van (1928), following Jordan, also placed *Auchenistius* in the Clinidae and their new species, *Stathmonotus corallicola* (= *S. hemphilli*), in the Chaenopsidae.

Up to 1928, the placement by any author of two species of what is currently considered to constitute the genus *Stathmonotus* in different families is understandable, because in all such cases the authors were separating the scaled from the nonscaled species. Jordan, Evermann, and Clark (1930) compounded the confusion by placing the nominal scaled species *Histioclinus veliger* and *Auchenistius stahli* in the Clinidae, and *Stathmonotus tekla* Nichols, 1910 (erroneously described as scaleless) and the unscaled *Stathmonotus hemphilli* in the Chaenopsidae.

Fraser-Brunner (1932) described a new genus and species, *Parviclinus spinosus* (= *Stathmonotus stahli*) from Great Britain, which he placed in the Clinidae. Wheeler (1958) noted several inaccuracies and errors of omission in the description (e.g., no cirri mentioned or illustrated), synonymized Fraser-Brunner's species with *Stathmonotus stahli*, and noted that the supposed type locality of *P. spinosus* was in error. Seale (1940) described *Stathmonotus culebrai*, which he placed in the Chaenopsidae. Berg (1940), in his classification of fishes, recognized the Clinidae as distinct from the Blenniidae, with which he synonymized the Chaenopsidae, as well as some other families. Chabanaud (1942) described a new genus *Parastathmonotus* (= *Stathmonotus*) and species, *P. sinuscalifornici*, which he placed in the family Stathmonotidae. Chabanaud excluded *Stathmonotus* from the Chaenopsidae and Stichaeidae, but he gave no reasons for this action.

Hubbs (1952) revised the higher classification of the Clinidae. He included *Auchenistius* and a junior synonym, *Histioclinus*, in the tribe Paraclinini Hubbs (spelling emended here), which he included in the Clinidae. He also recognized the Blenniidae as a distinct, but closely related family. Hubbs (1953a) revised the higher classification of the subfamily Chaenopsinae, which he included in the Blenniidae. He recognized the Stathmonotini (spelling emended here) as one of the four tribes of the Chaenopsinae but did not list the genera he recognized in the tribe (*Stathmonotus* is implicit). In doing so, Hubbs continued the confusion of placing the scaled forms of *Stathmonotus* in the Clinidae and the naked forms in the Blenniidae.

Böhlke (1953) reviewed *Stathmonotus* (including the description of a new species, *S. lugubris*), but he did not consider the scaled species. Springer (1955) again reviewed *Stathmonotus* (including the description of a new species, *S. gymnodermis*). He brought together all the scaled and unscaled species (except the nominal species *Parviclinus spinosus* Fraser-Brunner, 1932, of which he was unaware) into *Stathmonotus* and recognized three subgenera, *Stathmonotus* (including only *hemphilli*), *Auchenistius* (including *stahli* and *gymnodermis*), and *Parastathmonotus* (including *lugubris*, *culebrai*, and *sinuscalifornici*). Springer also discussed the existing confusion surrounding the familial relationships of the genus. He followed Hubbs (1952) in separating the Blenniidae and Clinidae primarily on characteristics of the infraorbital bones and assigned *Stathmonotus* to the Clinidae, tribe Paraclinini Hubbs. Unknown to Springer (1955), Norman had anticipated him and included *Auchenistius*, *Parviclinus*, and *Stathmonotus* in the Clinidae in his unpublished Draft Synopsis of Fishes (not published or generally available until 1966). Most, if not all, subsequent authors (e.g., Böhlke and Chaplin, 1968) have followed Springer and included *Stathmonotus* in the expanded Clinidae, but assignment has shifted between lineages within this group from the Chaenopsinae (Nelson, 1978) to the recently elevated Labrisomidae (Nelson, 1984; Eschmeyer, 1990).

Osteology of *Stathmonotus*

The following description is based on the largest species, *S. sinuscalifornici*. Morphological features differing between this and the other species of *Stathmonotus* are indicated by an asterisk (*), and the differences are described at the end of each morphological section. For the most part, the description is unilateral for bilaterally paired elements.

Neurocranium

FIGURES 1, 2

The neurocranium is relatively elongate compared to that of most chaenopsins and labrisomids, especially the region posterior to the orbits and anterior to the occipital region. Elongate elements include the parasphenoid, pterosphenoid, sphenotic, and posterior region of the frontals. The median ethmoid and the toothless vomer* form the anterior tip of the cranium. There is no septal bone (confined to some tripterygiids among the blennioids; Springer, 1993). The wing-shape lateral ethmoids form the anterior margin of the orbits; dorsally, they extend relatively far posteriorly, to the level of the middle

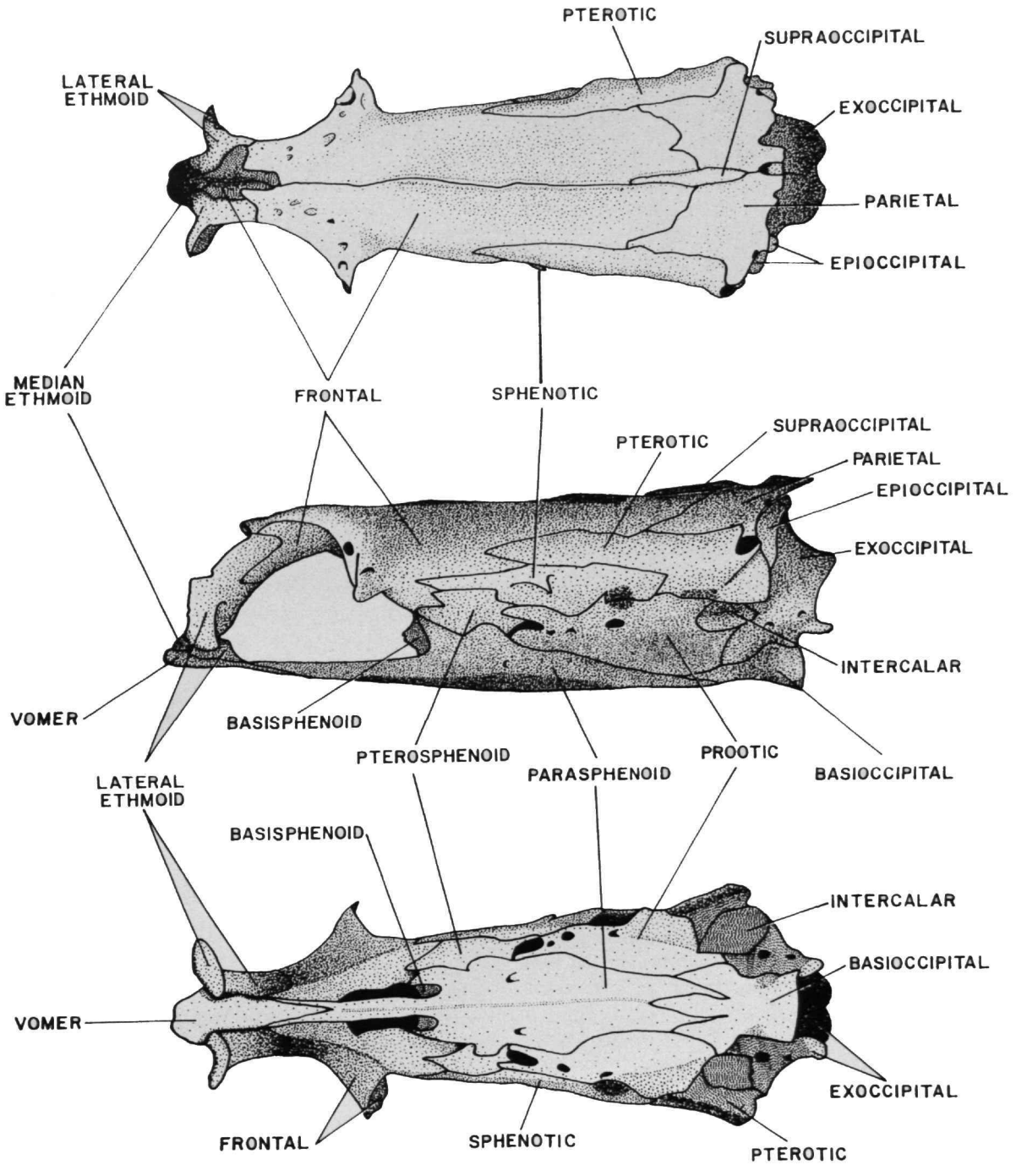


FIGURE 1.—*Stathmonotus sinuscalifornici*, dorsal, lateral, and ventral views of neurocranium.

of the orbit; ventromedially, each is tightly connected to a process just dorsoposterior to the anterior end of its respective palatine bone. There is a small area of cartilage between the ventromedial ends of the two lateral ethmoids.

The frontals, the largest bones of the neurocranium, extend from the midorbital region posteriorly to border the sphenotics,

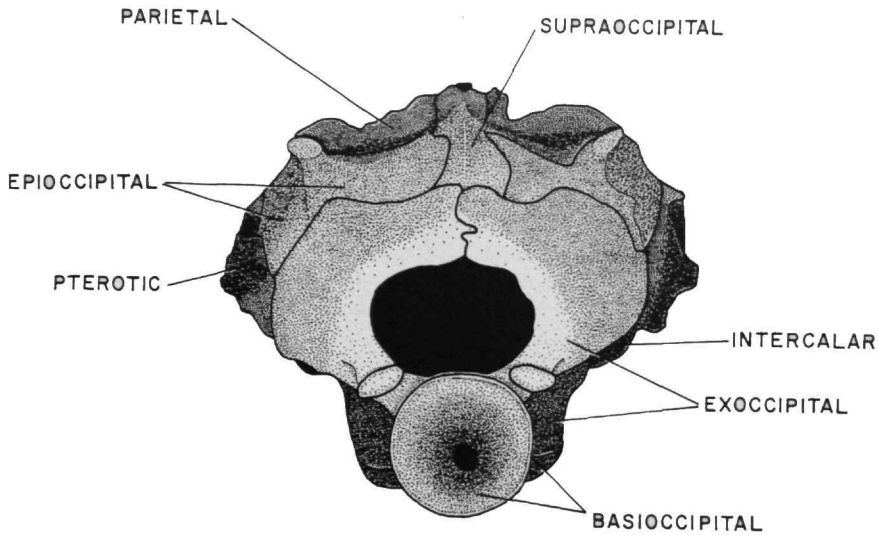


FIGURE 2.—*Stathmonotus sinuscalifornici*, posterior view of neurocranium.

pterotics, parietals, and supraoccipital. In large individuals, there is a raised medial flange* where the left and right frontals meet, which extends posteriorly onto the supraoccipital. At the posterior margin of the orbits, the frontals are expanded sharply laterally* (~90 degrees) to form the supraorbital margin. The interorbit is broad and flat.

The parietals are relatively small, forming the dorsoposterior margin of the neurocranium. A raised shelf of bone is present along the supratemporal commissure at the posterior margin of the neurocranium*; its size increases with body size. Although present in large females, this ridge appears to be relatively larger in males than in females of comparable SL. Muscles of the adductor mandibularis A2 complex (Winterbottom, 1974) extend dorsally across the neurocranium and insert on the anterior face of this ridge; epaxial musculature inserts on its posterior face. The supraoccipital separates the left and right parietals. Lateral and median extrascapulars are not evident (i.e., not autogenous).

The base of the neurocranium comprises the vomer anteriorly, the parasphenoid medially, and the basioccipital posteriorly. The parasphenoid has a prominent median keel on its ventral surface. The basioccipital bears a large condyle posteriorly, and each exoccipital bears a smaller condyle posteriorly; all three condyles articulate with the first vertebra. Anteriorly, the exoccipitals abut the pterotics, epioccipitals, small intercalars, and supraoccipitals. The pterotic is long, extending anteriorly above the prootic and pterosphenoids. The sphenotics bear a small spur (sphenotic spine of Springer, 1968) that projects posterolaterally toward the anterior insertion of the hyomandibula. The basisphenoid is represented only by the meningost portion, the belophragm being absent.

OTHER SPECIES.—The vomer has a few small, pointed teeth in *S. stahli*, *S. gymnodermis*, and *S. hemphilli*, but it is edentulous in the other species. All species, except *S. sinuscalifornici*, lack a raised medial crest on the frontals; this crest is weak or absent on small specimens (< 25 mm SL) of *S. sinuscalifornici*. The posterior lateral crest along the supratemporal commissure is present, but small, in all other species. The frontal is not expanded at the dorsoposterior orbital margin in *S. stahli*, *S. gymnodermis*, and *S. hemphilli*. It is slightly expanded in *S. culebrai* and, like *S. sinuscalifornici*, greatly expanded in *S. lugubris*.

Jaws, Suspensorium, and Superficial Bones of the Head

FIGURES 3, 4

There are four infraorbital bones; a dermosphenotic is not evident.* The infraorbital series is autogenous, but it is tightly joined to the neurocranium both anteriorly, at the lateral ethmoid,* and dorsoposteriorly, at the frontal.* The first infraorbital (lacrimal) forms the entire ventral margin of the orbit and has a notch in its dorsal margin for articulation with the lateral ethmoid. The remaining three infraorbitals form a more-or-less linear series along the posterior margin of the orbit; the second is short, the third long and slender, and the fourth slender. The fourth extends posterior to, and articulates with, the raised supraorbital region of the frontal.*

The infraorbitals of males are larger than those of females of similar SL.* This is especially true of the first infraorbital: in males it extends posteriorly well beyond the orbit, paralleling the upper jaw; in females it is thin and does not extend posterior to the orbital region. The posterior three infraorbitals, which are

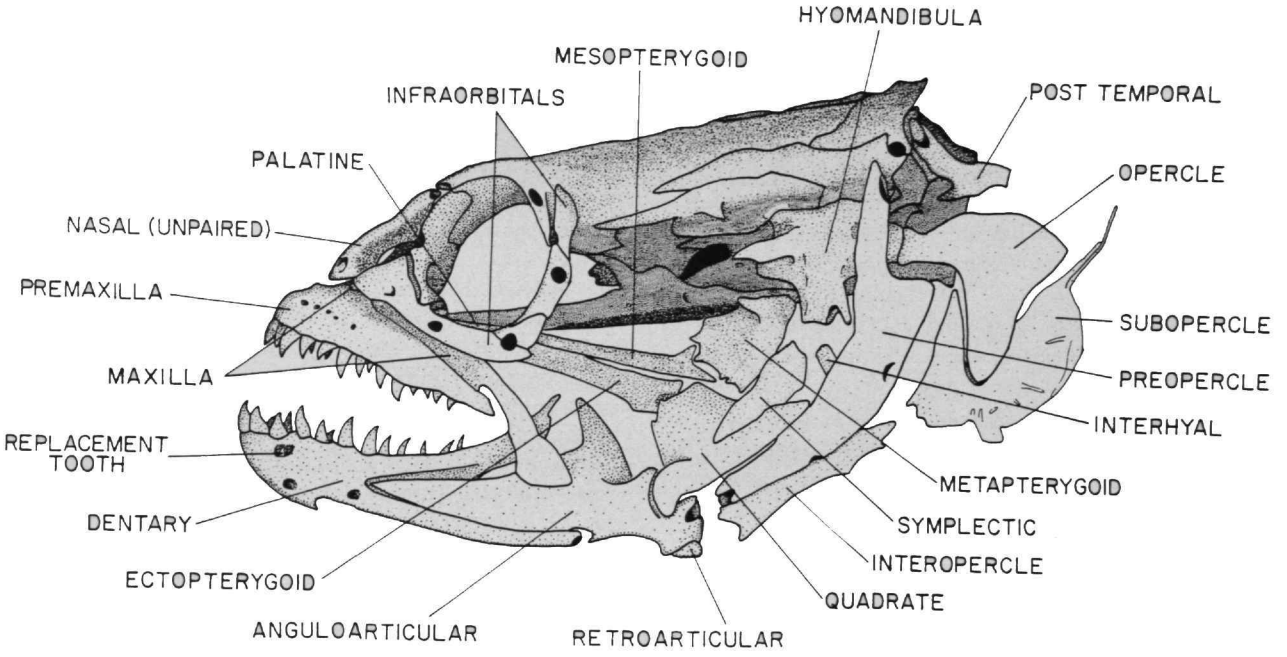


FIGURE 3.—*Stathmonotus sinuscalifornici*, lateral view of neurocranium with superficial bones, jaws, and suspensorium.

thin in females, are also more robust in males; in some large males, the joint between the second and third is difficult to discern.*

The nasals are broadly fused along their medial margins into a single, hourglass-shape bone (i.e, they are expanded anteriorly and posteriorly and constricted medially; see also Figure 29*b*). The nasals form the anterior margin of the snout, overlie the ascending processes of the premaxillae, and extend posteriorly to the middle of the interorbital region, where they abut (but are not fused to) a raised ridge on each frontal. These ridges surround the left and right segments of the cephalic sensory canals that continue anteriorly through the nasals.

The premaxilla bears an outer row of large canine teeth; anteriorly, there is a row of a few small canines* medial to the outer row. The premaxilla is slightly protrusible, and the ascending process extends posteriorly to the interorbital region when the jaws are closed. The maxilla rests on the dorsomedial portion of the premaxilla and bears a groove anteroventrally that saddles the premaxilla. The small anterolateral tip of the palatine overlaps the dorsal edge of the maxilla (this relationship is hidden from view in Figure 3 by the anterior end of the lacrimal). The posterior tip of the maxilla is visible externally. The length of the upper jaw is sexually dimorphic*; in males, the maxilla may extend posteriorly well past the posterior margin of the orbit to near the level of the articulation of the anguloarticular and quadrate; in females, the maxilla is shorter, extending only to the posterior margin of the orbit.

The dentary bears an outer row of large canines and, anteriorly, about three small canines medial to the outer row.* The dentary symphysis is broad. Posteriorly, the dentary has a deep medial notch into which the anguloarticular inserts. The anguloarticular is large, extending anteriorly for over half the length of the lower jaw. Meckel's cartilage extends more than half the length of the anguloarticular. A tiny coronomeckelian bone (not illustrated) is attached to the medial side of the anguloarticular just dorsal to the posterior end of the Meckel's cartilage. Dorsally, the anguloarticular has a large, blade-like ascending process, which is opposite the dorsoposterior ascending process of the dentary. The outer margin of the anguloarticular bears a posterolateral spur* just anterior to its

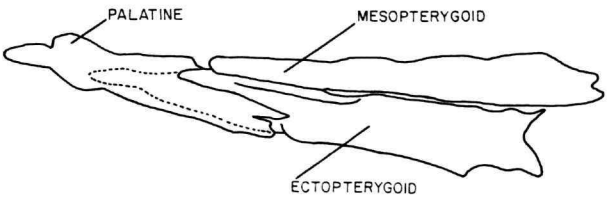


FIGURE 4.—*Stathmonotus sinuscalifornici*, lateral view of palatine, mesopterygoid, and ectopterygoid; dotted line indicates extent of ectopterygoid on medial surface of palatine.

articulation with the quadrate. A small retroarticular is attached to the posteroventral end of the anguloarticular.

The quadrate is a fan-shape bone bordered dorsoanteriorly with cartilage and has a deep medial notch into which the symplectic inserts. The ectopterygoid is long, slender, and extends from the quadrate to the palatine; it is weakly joined at its posterolateral end to the dorsoanteriormost medial surface of the quadrate. The ectopterygoid joins and lies ventromedial of the palatine for most of the length of the palatine. The edentate palatine closely abuts the vomer. The palatine is relatively short, its total length being about 60% the length of the ectopterygoid. The elongate, slender mesopterygoid is weakly attached to the metapterygoid posteriorly and ectopterygoid ventrally. It parallels the dorsal edge of the ectopterygoid (see also Figure 28*d*) but does not contact the palatine. The metapterygoid is approximately rectangular; dorsolaterally, it bears a strong anteriorly projecting process or flange of bone*; it is capped with cartilage posteroventrally.

The prominent preopercle extends dorsally above the articulation of the opercle with the posterior condyle of the hyomandibula. The roughly triangular (inverted) opercle, which lacks a spine, has a relatively long, prominent socket for attachment to the hyomandibula. The ventral half of the opercle inserts into a broad, deep notch in the subopercle, which bears a thin, dorsal, filamentous extension on its posterior margin. The slender interopercle lies just medial to the ventral portion of the preopercle and is separated by a wide membranous attachment to the anguloarticular-retroarticular anteriorly and by another to the subopercle posteriorly.

OTHER SPECIES.—A fifth infraorbital, presumably the dermosphenotic, is present in *S. hemphilli*, *S. stahli*, and *S. gymnodermis* (Figure 5*a*). It may be separate from the frontal or, more often, rests within a fossa in the frontal. Infraorbital four does not extend posterior to the frontal in *S. hemphilli*, *S. stahli*, and *S. gymnodermis*. In *S. culebrai* and *S. lugubris*, a small process of infraorbital four extends posterior to the frontal, but in *S. sinuscalifornici*, this process is larger and more firmly attached to the frontal. Similarly, the first infraorbital of all species except *S. sinuscalifornici* is only weakly joined to the lateral ethmoid. The infraorbitals are relatively thin in both males and females of *S. stahli*, *S. hemphilli*, and *S. lugubris*; the pattern of sexual dimorphism in the infraorbitals is unknown for the other two species. Males of all species except *S. hemphilli* have longer jaws than females. In *S. hemphilli*, the maxillary extends only to the posterior orbital margin in both sexes. The inner row of teeth on both the dentary and premaxilla is longer in *S. gymnodermis* than in the other species. The lateral surface of the anguloarticular lacks a lateral spur just anterior to the ventral articulating condyle of the quadrate in *S. stahli* and *S. gymnodermis*. A small spur is present in *S. hemphilli*, and a large spur, similar in size to that of *S. sinuscalifornici*, is present in *S. culebrai* and *S. lugubris* (Figure 5*b*). The metapterygoid of *S. hemphilli* is relatively the smallest of all the species, and it has no, or only a very small, anteriorly projecting process on its lateral surface.

Hyoid Arch

FIGURES 3, 6, 7

The medial surface of the dorsal hypohyal forms a condyle for articulation with the first basibranchial. Anteriorly, the ventral hypohyal extends ventrally as a rounded projection, the medial surface of which is tightly joined to its counterpart on the opposite hypohyal. Short, strong ligaments bind the ventroposterior surface of the ventral hypohyal to the anterior end of the urohyal. One or two small ossifications (osseous inclusions) may be present ventromedially in the connective tissue binding the ventral hypohyals. The anterior and posterior ceratohyals are joined by two horizontal V-shape sutures on both their lateral and medial surfaces; cartilage fills the narrow gaps dorsal and ventral to the sutures and between the anterior and posterior ceratohyals. There are six slender branchiostegals; two are attached to the lateral surface of the posterior ceratohyal, two to the lateral surface of the expanded ventroposterior portion of the anterior ceratohyal, and two to the ventromedial margin of the slender portion of the anterior ceratohyal, which is notched for their reception. The long, cartilage-tipped basihyal is broadest anteriorly and tapers gently to its posterior end,* which is slightly enlarged and convex and attaches to the comparably concave anterior end of the first basibranchial. The urohyal is roughly triangular in lateral view and dorsally bears a large condyle that articulates with a counterpart at the posterior end of the first basibranchial. The urohyal bears an enlarged process ventroanteriorly on each side; short ligaments extend anteriorly from these processes to the ventral hypohyals.

The dorsoanterior condyle of the hyomandibula articulates in a socket formed by the sphenotic dorsally and the prootic ventrally. This socket is well posterior to the point where the infraorbital series contacts the frontal. The dorsoposterior condyle of the hyomandibula inserts in a fossa near the posterolateral end of the pterotic. The lateral surface of the hyomandibula bears a strong, anteriorly directed spur and a posterior shelf against which rests much of the dorsal arm of the preopercle (see also Figure 28*d*). A sheet of ligamentous tissue stretches from just posterior to the orbital region of the skull to the area above the axil of the hyomandibular spur and the anteriorly projecting process of the metapterygoid. Posteroventrally, there is a notched foramen in the hyomandibula that leads into a canal from which the truncus hyomandibularis nerve exits. The dorsal opening to the canal is on the dorsomedial surface of the hyomandibula. The symplectic is capped with cartilage both ventrally and dorsally, where it and the cartilaginously capped dorsal end of the interhyal join the cartilaginous ventral end of the hyomandibula.

OTHER SPECIES.—The hyoid arch is similar in all species, except that the basihyal of *S. stahli* and *S. hemphilli* is slender anteriorly and does not taper posteriorly; that of *S. culebrai* tapers only slightly.

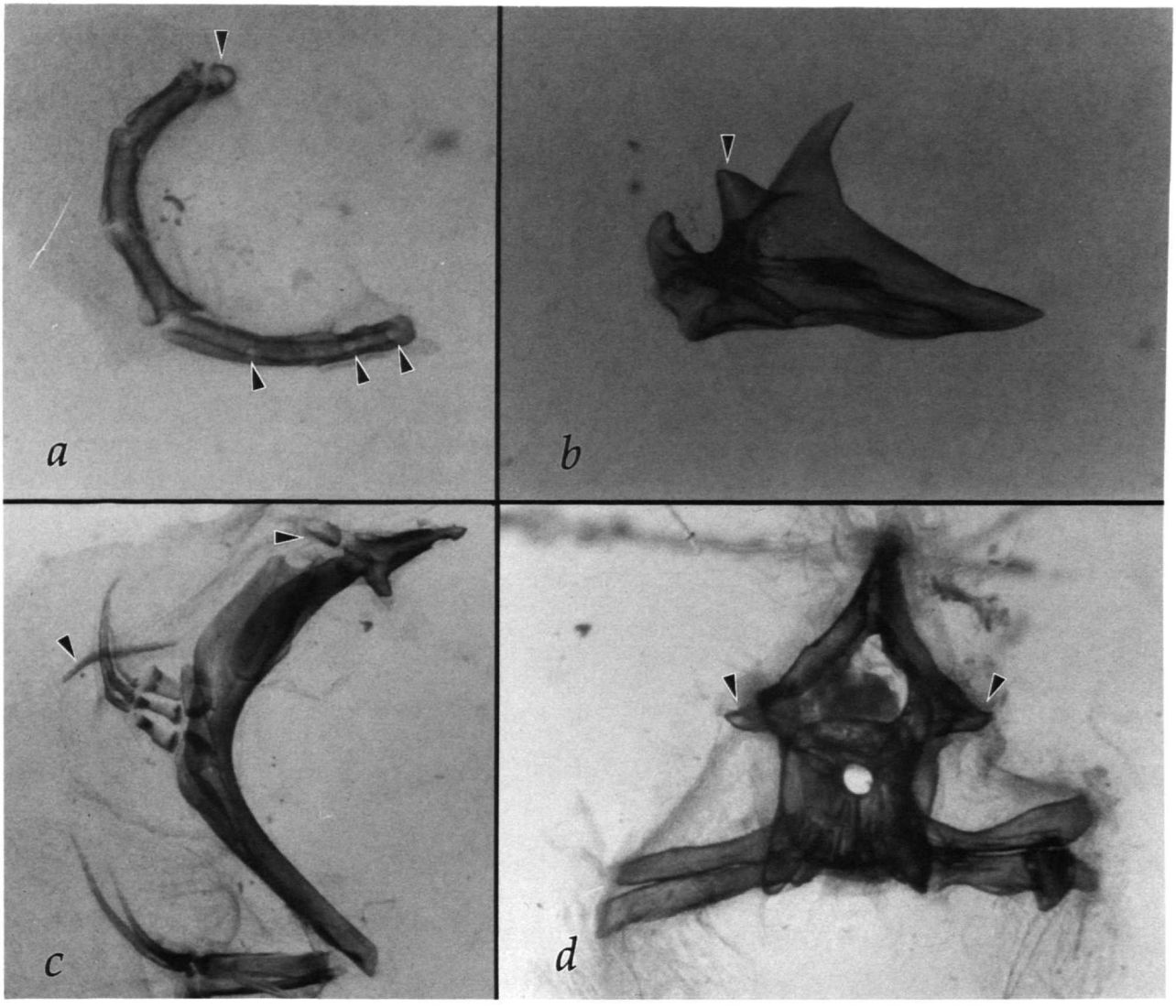


FIGURE 5.—*a*, Lateral view of right infraorbitals of *S. gymnodermis* (UAZ 69-91-1); lower arrows indicate the 3 pores in the lacrimal, upper arrow indicates dermosphenotic. *b*, Lateral view of right anguloarticular of *S. lugubris* (UAZ 71-70-24); arrow indicates articular spur. *c*, Lateral view of right pectoral girdle and pelvic girdle of *S. hemphilli* (ANSP 75231); arrow to the right indicates first (and only) tubular bone of lateral line; arrow to left indicates postcleithrum (single). *d*, Anterior view of fourth precaudal vertebra of *S. sinuscalifornici* (UAZ 75-37-23); arrows indicate neural spurs.

Branchial Arches

FIGURES 7, 8

The branchial arches are relatively slender. Basibranchial 1 is present and ossified; it may be thinly capped with cartilage. Basibranchials 2, 3, and 4 are completely absent (i.e., neither ossified nor cartilaginous). Similarly, only hypobranchials 1 and 2 are ossified, and 3 and 4 are absent. Ceratobranchials 1–5 are present; there are up to five small, widely spaced gill rakers (not illustrated) in each inner and outer row on ceratobranchials 1–4. The anterior end of epibranchial 1 lies ventral to the anterior end of infrapharyngobranchial 3, which is the only infrapharyngobranchial present; epibranchial 2 abuts the anterolateral extension of infrapharyngobranchial 3, and

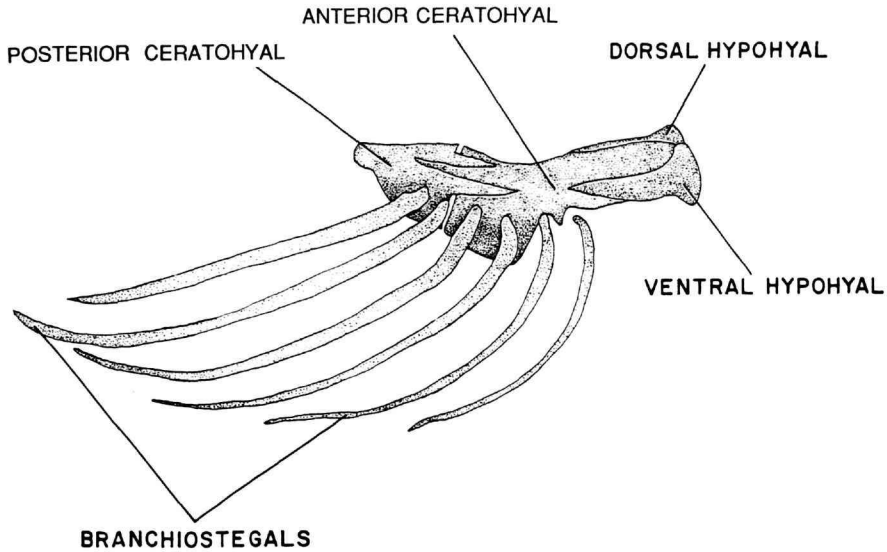


FIGURE 6.—*Stathmonotus sinuscalifornici*, lateral view of right hyoid arch.

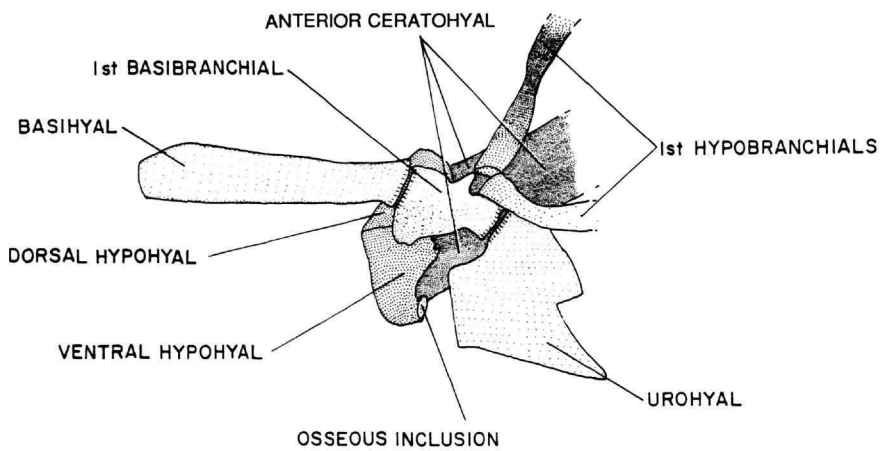


FIGURE 7.—*Stathmonotus sinuscalifornici*, lateral view of left side of basihyal, basibranchial 1, and urohyal, showing relationship of these bones to anterior bones of right hyoid arch and hypobranchials 1 of both sides.

epibranchials 3 and 4 abut its posterior margin. The posterior region of infrapharyngobranchial 3 is rectangular and bears a rounded patch of teeth on its ventral surface; the anterior portion bears a rod-shape ossification, which is tipped with cartilage, and, medially, a thin sheet of bone. The upper and lower pharyngeal tooth patches are differently shaped; the upper (infrapharyngobranchial 3) is a more-or-less rounded patch of about 15 teeth in large adults, whereas the ventral is elongate with two rows of about 10 teeth in each row. Both ends of hypobranchials 1 and 2, ceratobranchials 1–4, and epibranchials 1–4 are capped with cartilage. Ceratobranchial 5 bears a minute bit of cartilage on its anteromedialmost surface. The anterolateral process of infrapharyngobranchial 3 ends in a rod-like cartilage, and the posterior end of the infrapharyngobranchial, where it articulates with epibranchials 3 and 4, appears to have a small bit of cartilage.

OTHER SPECIES.—The branchial arches are similar in all species; however, the extent of cartilage present in the arches is highly variable. In two of four cleared and stained specimens of *S. stahli* examined, basibranchial 1 has a short, slender

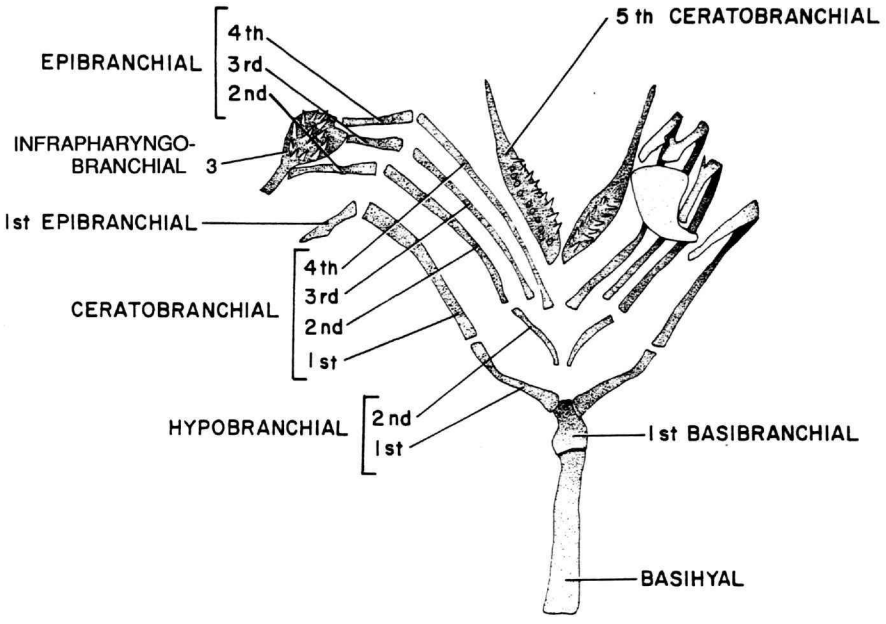


FIGURE 8.—*Stathmonotus sinuscalifornici*, dorsal view of gill arches (gill rakers omitted), basihyal, and basibranchial 1; dorsal gill-arch elements of right side have been rotated 180° to show ventral surfaces of these elements; dorsal ends of epibranchials 2 have been displaced slightly anteriorly from their normal position of just ventral to the anterior arm of infrapharyngobranchial 3.

cartilaginous core posteriorly that exits from the bone and extends posteriorly halfway to the level of the anterior end of hypobranchial 2; one specimen has the equivalent posterior extension of the core ossified (it was not possible to determine if the ossified portion is autogenous or if it had been broken at its connection with basibranchial 1); the fourth specimen appears to have only a small bit of cartilage at the posterior end of basibranchial 1. Additionally, one of the four specimens completely lacks hypobranchial 2 on one side, whereas the other side is normal.

Pectoral and Pelvic Girdles

FIGURE 9

The cleithrum is by far the largest bone in the pectoral girdle, with the coracoid and scapula being reduced in size compared to those of most other blennioids (comparable or greater reduction has been reported only for blenniids and some species of the clinid tribe Ophiclinini; George and Springer, 1980). The dorsal margin of the cleithrum has a central notch separating an anterior, spine-like process, and a posterior, blade-like process. On the medial surface of the cleithrum ventral to the notch, a well-developed posteroventral process, bearing broad ligamentous attachments to the scapula, may be present or absent (different sides of the same specimen). The supracleithrum is broad distally and attaches for most of its length to the outer surface of the cleithrum; dorsally, it attaches to the medial surface of the posttemporal. There are no postcleithra.* The dorsal arm of the posttemporal articulates with the epiotic (see Figure 3). The ventral arm of the posttemporal is short and separate from the neurocranium, being connected to the intercalar by a ligament. A sensory canal passes through the posttemporal and then through a single tubular bone just posterior to the posttemporal (see Figure 5*c*). This tubular bone is presumably the only remnant of a tubed lateral line.

The small, cleaver-like scapula touches the cleithrum but is well separated by cartilage from the coracoid. The thin, cartilage-capped dorsal arm of the scapula extends to the pectoral-fin base, but it is well separated from the cleithrum. A well-developed horizontal scapular stay (Hastings, 1992b) extends to the cleithrum, dorsally enclosing a prominent scapular foramen.* The small coracoid is autogenous, displaced ventrally relative to that of most other blennioids, has a single, small foramen (not shown in Figure 9) at its midlength, and is tipped with cartilage anteroventrally. The four proximal pectoral-fin radials* increase in size from dorsal to ventral and are capped with cartilage at both ends. The upper two radials contact the scapula, the next contacts the scapula and the space

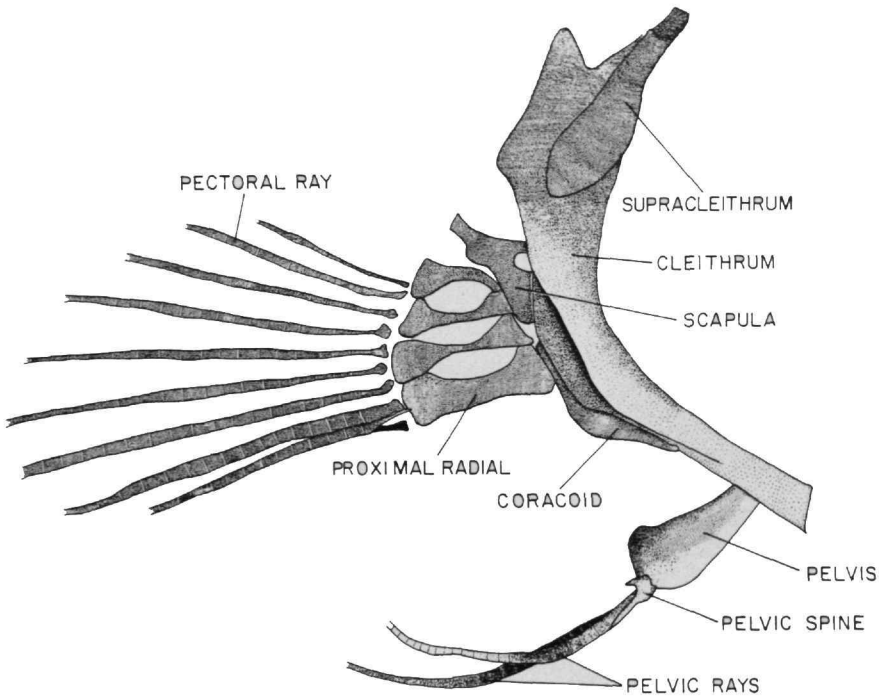


FIGURE 9.—*Stathmonotus sinuscalifornici*, lateral view of right-side pectoral and pelvic fins and girdles.

between the scapula and the coracoid, and the lowermost contacts the coracoid. There are no pectoral-fin rays articulating with the scapula, and the dorsalmost radial supports only two fin rays that articulate along the ventral half of the posterior end of the radial. The remaining proximal radials support fin rays. Like the supporting radials, the pectoral-fin rays increase in size from dorsal to ventral. A tiny, cartilaginous distal radial is present between the split basal halves of some rays (minute in size, the degree of staining makes it difficult to determine if a distal radial is present; in some instances, it appears that only the three or four dorsalmost rays have distal radials).

The bean-shape pelvis is tipped anteriorly with cartilage and inserts slightly dorsal to the juncture of the left and right cleithra. The symmetrical halves of the pelvis touch anteriorly and posteriorly but are separate along their dorsal and ventral margins. The pelvis is short; its length is less than twice its greatest depth in lateral view.* The single pelvic spine is short, closely appressed to the first ray, and not evident in intact specimens. Two well-developed, unbranched, pelvic-fin rays are present.

OTHER SPECIES.—The pectoral girdle of *S. hemphilli* (Figure 5*c*) is greatly reduced. Its scapula is especially small; the upper scapular arm does not extend to the level of the fin base. The upper two proximal radials are fused, and only four or five vestigial fin rays are present. A splint-like dorsal postcleithrum is present in *S. hemphilli;* all other species have neither dorsal nor ventral postcleithra. This is surprising, given the otherwise greatly reduced pectoral girdle of *S. hemphilli* relative to the pectoral girdles of the other species of *Stathmonotus*. A horizontal scapular stay enclosing the scapular foramen is absent in *S. culebrai* and some specimens of *S. lugubris*. The pelvis of *S. hemphilli* (Figure 5*c*) is long and thin, its length being about four times its greatest depth; that of all other species is short as in *S. sinuscalifornici*.

Vertebral Column, Ribs, and Caudal Fin

FIGURE 10

The neural arches of the precaudal vertebrae are relatively broad, and the neural spines are short and slender. The first vertebra lacks a neural spine, and it is debatable whether there is one on the second vertebra. Neural spurs (Hastings, 1990), or lateral projections on the neural arch (see Figure 5*d*), are present on at least the third and fourth vertebrae*; other vertebrae appear to lack these spurs. All hemal spines, including those of preural vertebrae two (pu_2) and three (pu_3), are fused with their respective centra. The ventral end of the hemal spine of pu_2 is tipped with cartilage; otherwise all the hemal spines are fully ossified.

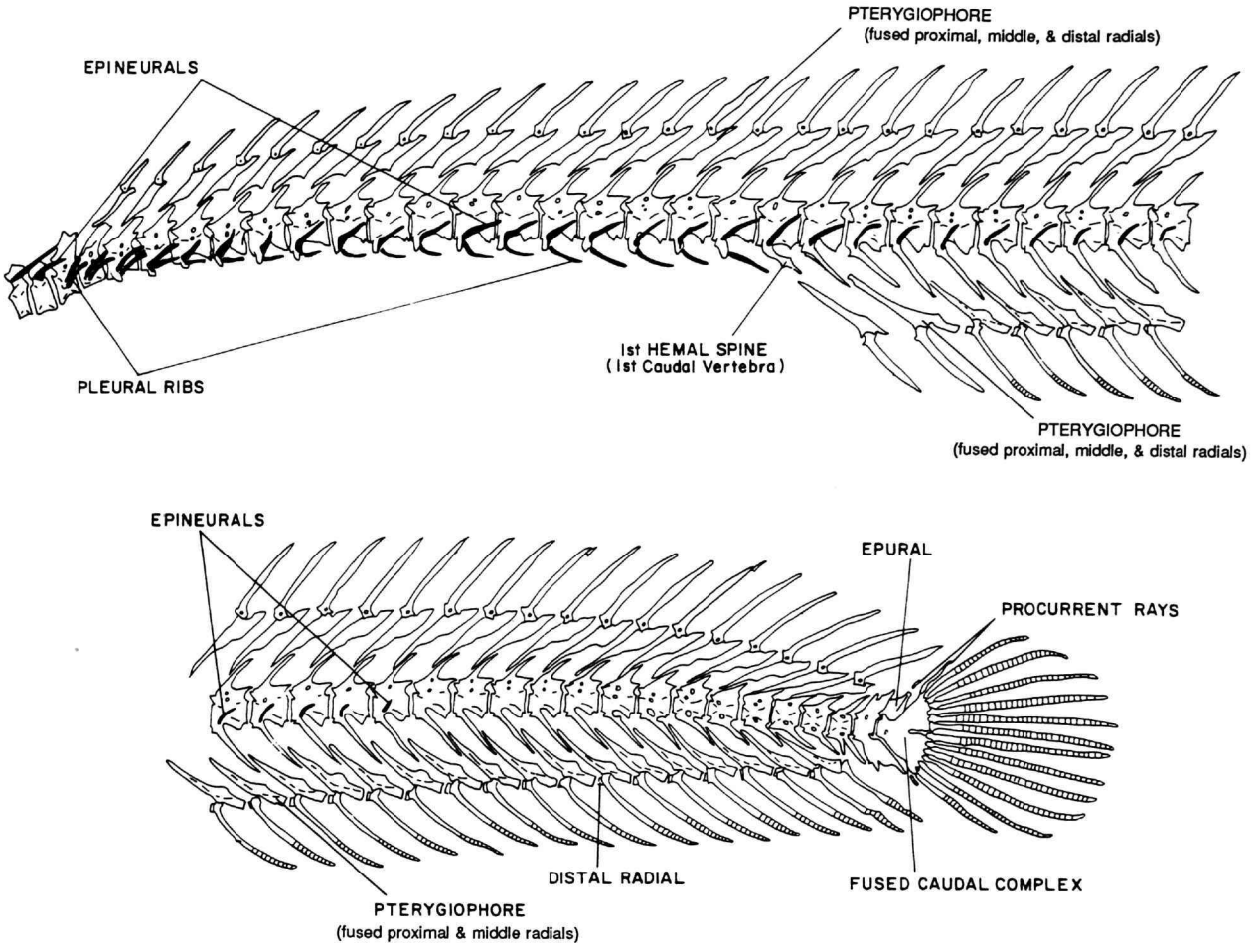


FIGURE 10.—*Stathmonotus sinuscalifornici*, lateral view of left side of vertebral column and of dorsal, anal, and caudal fins.

Pleural ribs are present on all precaudal vertebrae except the anteriormost two.* Epineurals are present on all precaudal vertebrae and 10–20 caudal vertebrae. On the first two vertebrae, the epineurals insert on the lateral surface of the neural arch. On more posterior vertebrae, epineurals, when present, insert more ventrally, on the lateral surface of the ventral prezygopophyses. The pleural ribs and epineurals are similar in size on the anteriormost vertebrae, but the epineurals are larger on more posterior precaudal vertebrae. The proximal ends of the precaudal epineurals are expanded,* increasing the surface area for insertion on the vertebrae. The epineurals on the caudal vertebrae gradually decrease in size posteriorly.

The caudal-fin complex is characterized by its relative simplicity. The urostylar vertebra is a single fused element; the lower hypural plate (probably comprising the parhypural and hypurals 1 and 2) is not autogenous. The single epural, tipped with cartilage dorsally, is broad proximally and inserts in a slot of bone on the urostylar vertebra. Hypural 5 is not evident. The posterior edges of the dorsal and ventral hypural plates are narrowly margined with cartilage. There are five to six upper, and five to seven lower, segmented caudal-fin rays. There are one or two dorsal, and one or two ventral, procurrent rays. A small ventral procurrent cartilage may be present just dorsal to the ventral procurrent rays (not always possible to tell if cartilage is present because of ineffectiveness of staining); there is no dorsal procurrent cartilage.

OTHER SPECIES.—Neural spurs apparently are present on the anterior vertebrae of all species, but they are most prominent in *S. lugubris* and *S. sinuscalifornici*. The first vertebra bearing a pleural rib is the fourth or fifth in *S. stahli* and the seventh in *S. gymnodermis*. The epineurals of *S. stahli* (Figure 11*a*) and *S. gymnodermis* are thin, but they are expanded proximally in *S.*

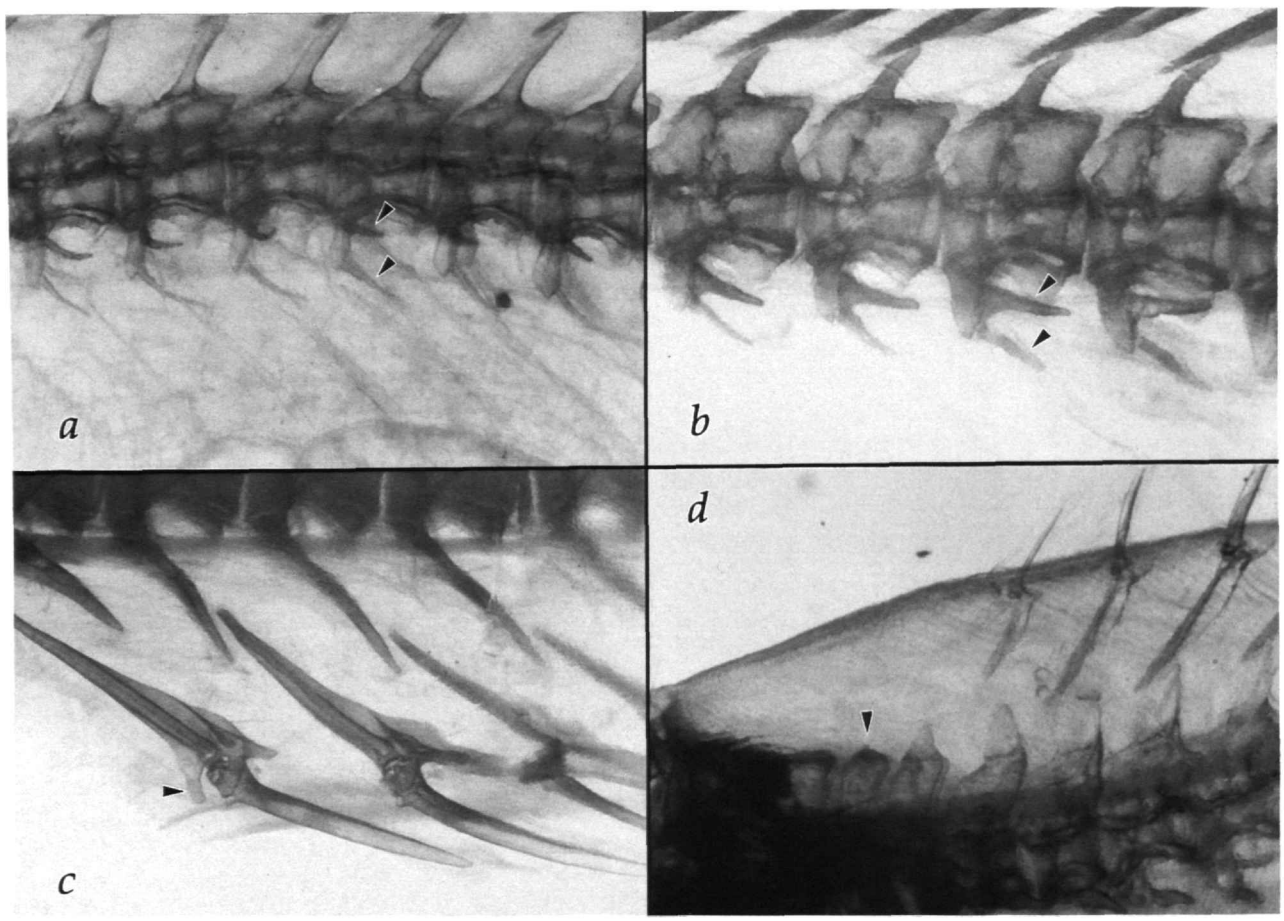


FIGURE 11.—*a*, Lateral view of left side of several precaudal vertebrae of *S. stahli* (UF 18902); upper and lower arrows indicate, respectively, an epineural and a pleural rib. *b*, Lateral view of left side of several precaudal vertebrae of *S. hemphilli* (ANSP 75231); arrows as in *a*. *c*, Lateral view of left side of anterior anal fin of *S. sinuscalifornici* (UAZ 71-36); arrow indicates open strut on first pterygiophore; note widely spaced pterygiophores. *d*, Lateral view of anterior dorsal fin and vertebral column of *S. stahli* (UF 18902); arrow indicates first vertebra; note insertion of first full dorsal-fin pterygiophore is posterior to second vertebra.

hemphilli (Figure 11*b*) and in the remaining three species. In *S. hemphilli*, the pleural ribs are smaller than the epineurals, but they are similar in size in all other species.

Dorsal and Anal Fins

FIGURE 10

The dorsal fin contains only spines, all of which are stout, pointed, and fully ossified. The pterygiophores supporting the spines probably consist of fused proximal, middle, and distal radials; ventrally each pterygiophore is tipped with cartilage. The pterygiophore supporting the first spine inserts anterior to the neural spine of the fourth vertebra*; the pterygiophore supporting the last spine inserts three to five vertebrae anterior to the urostylar vertebra. The dorsal-fin pterygiophores are stout, with lateral supporting ridges along both their anterior and posterior margins. All dorsal-fin pterygiophores have a blade-like dorsal extension posterior to the insertion of the spines.

The anal fin comprises two widely separated, stout, pointed, fully ossified spines and a series of segmented rays. All of the anal-fin pterygiophores, except the first, have cartilaginous tips at their proximal ends. The first anal-fin pterygiophore probably consists of fused proximal, middle, and distal radials. The composition of the second pterygiophore, which supports the second (supernumerary) anal-fin spine and first segmented ray, is more problematic. The second pterygiophore is serially

associated with the first segmented ray, which saddles an autogenous distal radial, and one might expect, therefore, that the second pterygiophore consists only of fused proximal and middle radials. All the segmented rays subsequent to the first also saddle autogenous distal radials, and the composite portion of the pterygiophores associated with them probably consists only of fused proximal and middle radials. The anterior anal-fin pterygiophores are widely spaced relative to those of other blennioids. Usually one pterygiophore inserts anterior to the first hemal arch and single pterygiophores are associated with subsequent hemal arches, except that one hemal arch (usually the second to fourth) lacks an associated pterygiophore (see Figure 11*c*). Occasional specimens exhibit a one-to-one relationship of pterygiophores with hemal arches. The pterygiophore supporting the first anal-fin spine has a bony flange extending distally anterior to the insertion of the spine (see Figure 11*c*). This flange appears to be the anterior portion of an incomplete ring joint. The fused proximal + middle segments of the pterygiophores supporting the segmented anal-fin rays have only an anterior lateral supporting flange. The anal fin extends approximately the same distance posteriorly as does the dorsal fin, i.e., the last pterygiophore inserts three to five vertebrae anterior to the urostylar vertebra.

OTHER SPECIES.—In *S. gymnodermis* and *S. stahli* (Figure 11*d*), the first dorsal-fin pterygiophore inserts anterior to the second vertebra; in *S. stahli*, the first pterygiophore is reduced in size and supports a small, thin spine. In the other 4 species, the first dorsal-fin pterygiophore inserts anterior to the fourth vertebra. The first one to four dorsal-fin spines and their associated pterygiophores in *S. gymnodermis*, *S. hemphilli*, and *S. stahli* (Figure 11*d*) are less robust than the other spines and pterygiophores. The first spine may even be reduced to a nubbin or be completely absent, leaving only the pterygiophore.

CEPHALIC SENSORY SYSTEM OF *Stathmonotus* SPECIES

FIGURE 12, TABLE 2

The cephalic sensory system of *Stathmonotus* conforms to the generalized system described by Coombs et al. (1988). In all species of *Stathmonotus*, as well as in *Mccoskerichthys* and chaenopsins, pore openings in the bones exit through the skin as simple pores, whereas in *Neoclinus* (Fukao, 1980, 1987) and most labrisomids (Hubbs, 1952), certain of the openings in the bones usually exit through the skin as multiple, closely spaced pores.

The cephalic sensory system exhibits considerable variation within *Stathmonotus* (Table 2), and its evolution appears to have been characterized by a reduction in the number of pores. Within *Stathmonotus*, the most generalized condition (i.e., the most similar to outgroups such as *Neoclinus*, chaenopsins, and labrisomids) occurs in *S. stahli* and *S. gymnodermis*, and the most derived condition (i.e., with the greatest number of reductions) occurs in *S. hemphilli*.

The mandibular (M) series includes four pores in most specimens of *S. stahli* and *S. gymnodermis*, the first near the symphysis and the fourth in a space between the dentary and articular. In all other species, there are only three mandibular pores, the third being absent. Mandibular pore 1B (see Figure 25) is absent in all species. Four preopercular (POP) pores usually are present in *S. gymnodermis* (mean = 3.9, Table 2), three or four pores are present in *S. stahli* (3.3), and two usually are present in the other species. The ventralmost pore of *S. gymnodermis* often is absent in *S. stahli;* this is evident, because the ventralmost pore in *S. stahli* and the second ventralmost in *S. gymnodermis* each bear a small, fleshy flap (the preopercular cirrus), and specimens of *S. stahli* with four pores have one pore below the flap-bearing pore. Four posttemporal (PT) pores are present in *S. stahli*, four usually are present in *S. gymnodermis* (3.9), *S. culebrai* (4.0), and *S. lugubris* (3.9), but only three are present in *S. hemphilli* and *S. sinuscalifornici*. All species have a single median supratemporal (MST) pore. Five of the six species have a single lateral supratemporal pore (LST), but this pore usually is absent in *S. hemphilli* (0.1). The first infraorbital bone (anterior infraorbital series or AIO) has three pores in *S. stahli* and *S. gymnodermis* and two pores in the remaining four species, which appear to have lost the anteriormost pore. In *S. stahli* and *S. gymnodermis*, the anteriormost AIO pore opens near the anterodorsal margin of the lacrimal, and the second and third AIO pores open along the length of the lacrimal. In the other four species, only the more posterior two pores are present; no pore is present at the anterodorsal margin of the lacrimal. The posterior infraorbital (PIO) series includes four pores in *S. stahli* and *S. gymnodermis*, with pores being present at the juncture of infraorbitals 1 and 2, 2 and 3, 3 and 4, and 4 and the dermosphenotic. The other species have reduced numbers of PIO pores. Three species always have two PIO pores; these are present between infraorbitals 1 and 2, and 3 and 4 (the dermosphenotic is not autogenous in these species). Specimens of *S. lugubris* usually have two, but also may have one or three PIO pores (mean = 1.9). One supraorbital (SO) pore is present in all species, although rare specimens of *S. lugubris* have two or lack any SO pores. A median commissural (CM) pore is present in *S. stahli* and *S. gymnodermis*, but usually absent in all other species (present in only one specimen of *S. sinuscalifornici*). A single anterofrontal (AFO) pore, at the juncture of the frontal and nasal, is present in all species. No other frontal pores are present in any species. All species have a single pore (N1) at the anterior tip of each nasal canal, but only *S. stahli* and *S. gymnodermis* have a second pore (N2), located in the middle of each nasal canal.

Stathmonotus Bean

Stathmonotus Bean, 1885:191 [type species by monotypy *S. hemphilli* Bean]. *Auchenistius* Evermann and Marsh, 1899:359 [type species by monotypy *A. stahli* Evermann and Marsh; here retained as a subgenus].

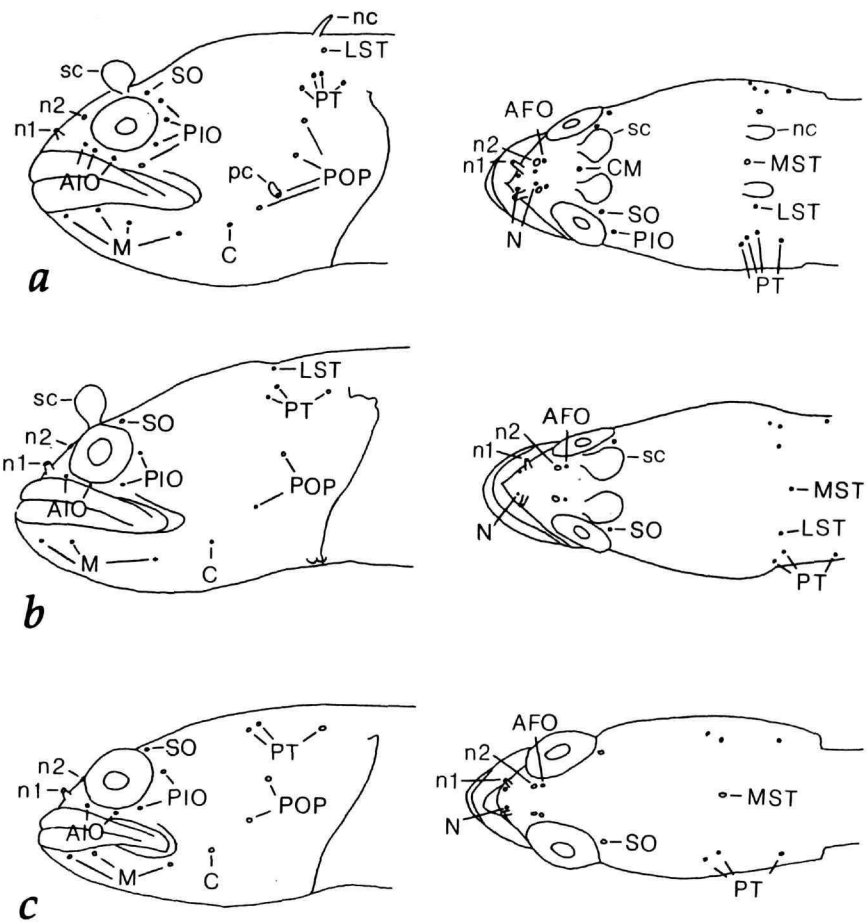


FIGURE 12.—Lateral (left) and dorsal (right) views of the heads of three species of *Stathmonotus* illustrating their cephalic sensory pores. *a*, *S. gymnodermis* (ANSP 113209, 28.1 mm SL). *b*, *S. sinuscalifornici* (UAZ 73-54-5, 37.7 mm SL). *c*, *S. hemphilli* (ANSP 75231, 28.3 mm SL). Abbreviations for cephalic sensory pores (upper case letters) are as follows: AFO = anterofrontals; AIO = anterior infraorbitals; C = common; CM = commissural; LST = lateral supratemporals; M = mandibulars; MST = median supratemporal; N = nasals; POP = preopercular; PT = posttemporals; SO = supraorbitals. Abbreviations for other morphological features (lower case letters) are as follows: n1 = anterior nostril; n2 = posterior nostril; nc = nuchal cirrus; pc = preopercular cirrus; sc = supraorbital cirrus.

Histioclinus Metzelaar, 1919:157 [type species by monotypy *H. veliger* Metzelaar (= *S. stahli*)].

Parviclinus Fraser-Brunner, 1932:827 [type species by original designation *P. spinosus* Fraser-Brunner (= *S. stahli*)].

Parastathmonotus Chabanaud, 1942:115 [type species by original designation *P. sinuscalifornici* Chabanaud; here retained as a subgenus].

DIAGNOSIS.—A tropical Western Hemisphere genus of small, elongate fishes (maximum 55 mm SL) inhabiting reefs, rock and shell rubble, and grassbeds in shallow marine habitats (known to occur in depths as shallow as a few centimeters to depths of about 6 m, Nichols, 1910:161 and authors' personal observations). Unique among the Blennioidei in having widely spaced anterior anal-fin pterygiophores, the first anal-fin pterygiophore open (i.e., not forming a ring joint with the first spine), and the lateral line represented by a single tubular bone and a series of mid-lateral placodes. Distinctive in having the posterior margin of the preopercle completely covered by a fleshy membrane, a reduced number of procurrent caudal-fin rays, the dorsal fin with spines only, the first dorsal-fin spine inserted well posterior to the neurocranium, a reduced pectoral fin (4–11 rays), pelvic fin I,2, nasal bones fused into a single element, and a medial notch in the upper lip.

COMMENTS.—Restricted to the tropical western Atlantic and eastern Pacific. Three subgenera and six species are included.

Table 2.—Frequency distributions for numbers of head pores in species of Stathmonotus. Abbreviations: M = mandibular; POP = preopercular; PT = posttemporal; LST = lateral supratemporal; AIO = anterior infraorbital; PIO = posterior infraorbital; CM = commissural; N = nasal.

	M			POP					PT			LST		
Species	3	4	$\bar{x}$	1	2	3	4	$\bar{x}$	3	4	$\bar{x}$	0	1	$\bar{x}$
hemphilli	22	-	3.0	-	26	-	-	2.0	23	-	3.0	23	2	0.1
stahli	1	39	4.0	-	-	32	12	3.3	-	44	4.0	-	44	1.0
gymnodermis	7	25	3.8	-	1	3	30	3.9	2	30	3.9	-	30	1.0
sinuscalifornici	22	-	3.0	1	21	-	-	2.0	22	-	3.0	-	22	1.0
culebrai	22	-	3.0	-	21	1	-	2.0	1	19	4.0	-	22	1.0
lugubris	35	-	3.0	1	37	-	-	2.0	2	36	3.9	-	36	1.0

	AIO			PIO					CM				N		
	2	3	$\bar{x}$	1	2	3	4	$\bar{x}$	0	1	2	$\bar{x}$	1	2	$\bar{x}$
hemphilli	22	-	2.0	-	24	-	-	2.0	13	-	-	0.0	25	-	1.0
stahli	-	43	3.0	-	-	-	43	4.0	-	21	1	1.0	-	44	2.0
gymnodermis	-	30	3.0	-	-	1	29	4.0	-	16	-	1.0	-	32	2.0
sinuscalfiornici	21	1	2.0	-	22	-	-	2.0	10	1	-	0.1	22	-	1.0
culebrai	22	-	2.0	-	22	-	-	2.0	11	-	-	0.0	22	-	1.0
lugubris	36	-	2.0	5	33	2	-	1.9	19	-	-	0.0	38	-	1.0

Key to the Subgenera and Species of *Stathmonotus*†

A. Preopercular cirrus present (on ventralmost or second ventralmost preopercular sensory pore) [Figure 12*a*]; nuchal cirrus present; vomerine teeth present; three anterior infraorbital (AIO) pores . . . . . subgenus ***Auchenistius***

B. Scales present; dorsal and anal fins broadly confluent with caudal fin . . . . . ***S. stahli***

BB. Scales absent; dorsal and anal fins not or slightly confluent with caudal fin . . . . . ***S. gymnodermis***

AA. Preopercular cirrus absent; nuchal cirrus absent; vomerine teeth present or absent; two AIO pores.

C. Pectoral fin reduced to four or five weak rays; dorsal fin with 45–53 spines; vomerine teeth present; lateral supratemporal (LST) pore usually absent; supraorbital cirrus absent . . . . . subgenus ***Stathmonotus*** . . . . . ***S. hemphilli***

CC. Pectoral fin with 6–11 rays; dorsal fin with 36–46 spines; vomerine teeth absent; one LST pore; supraorbital cirrus present or absent . . . . . subgenus ***Parastathmonotus***

D. Dorsal-fin spines 40–46; total vertebrae 47–52; supraorbital cirrus present; three posttemporal (PT) pores . . . . . ***S. sinuscalifornici***

DD. Dorsal-fin spines 36–40; total vertebrae 43–47; supraorbital cirrus present or absent; usually four PT pores.

E. Supraorbital cirrus present . . . . . ***S. lugubris***

EE. Supraorbital cirrus absent . . . . . ***S. culebrai***

† The key presented by Springer (1955) remains valid, except that *S. culebrai* has a small nasal cirrus.

Subgenus *Stathmonotus* Bean

Stathmonotus Bean, 1885:191 [type species by monotypy *S. hemphilli* Bean].

DIAGNOSIS.—See account of only included species, *S. hemphilli*.

Stathmonotus hemphilli Bean

FIGURE 13

Stathmonotus hemphilli Bean, 1885:191 [Key West, Florida; lectotype USNM 37193].

Stathmonotus corallicola Beebe and Tee-Van, 1928:249 [Lamentin Reef, Port au Prince Bay, Haiti; holotype, originally New York Zoological Society 7463, now USNM 170571].

DIAGNOSIS.—Unique among the species of *Stathmonotus* in having an extremely reduced pectoral fin with four or five weak rays, an elongate pelvis, an ossified dorsal postcleithrum (Figure 5*c*), high numbers of vertebrae and dorsal-fin spines (Table 3), the maxillary of males short, similar to that of females, and usually no lateral supratemporal (LST) sensory pore (present on one side of only one specimen). Dorsal-fin spines 45–53; segmented anal-fin rays 23–29; segmented caudal-fin rays 10–12; total vertebrae 50–58; precaudal vertebrae 20–25; caudal vertebrae 30–34 (Tables 3, 4); pleural ribs 19–24; epineurals 33–46. Body naked; supraorbital, nasal, nuchal, and preopercular cirri absent.

COLORATION.—Sexually dimorphic and variable in males, with both light and dark morphs present. Some males lack any evident melanophores. Others have the head and abdomen covered with fine, evenly distributed melanophores (e.g., ANSP 147163), or the head covered with fine melanophores except for a network of pale spots and lines on the cheek and interorbit (e.g., ANSP 75231). In the dark morph, the head, body, and fins are completely dark, being covered with uniform, fully expanded melanophores, except for the distal margin of the caudal fin, the distal tips of the dorsal-fin and anal-fin elements posteriorly, the distal half of the pelvic fin, and the nostril tubes, all of which are pale (e.g., ANSP 111920). Some dark morphs have a darker blotch on the cheek, a pale distal margin on the pectoral fin, V-shape pale areas along the distal margin of the dorsal fin posteriorly, and inverted Vs along the anal fin posteriorly (e.g., ANSP 75231). These V-shape markings are especially large in two males from the Bahamas (ANSP 115005, see "Comments," below). In one male, the dorsal Vs extend ventrally about one-fourth of the body depth but are not continuous with one another along the dorsal-fin base, and the ventral Vs are restricted to the anal fin. In the other male, the dorsal Vs are continuous with one another

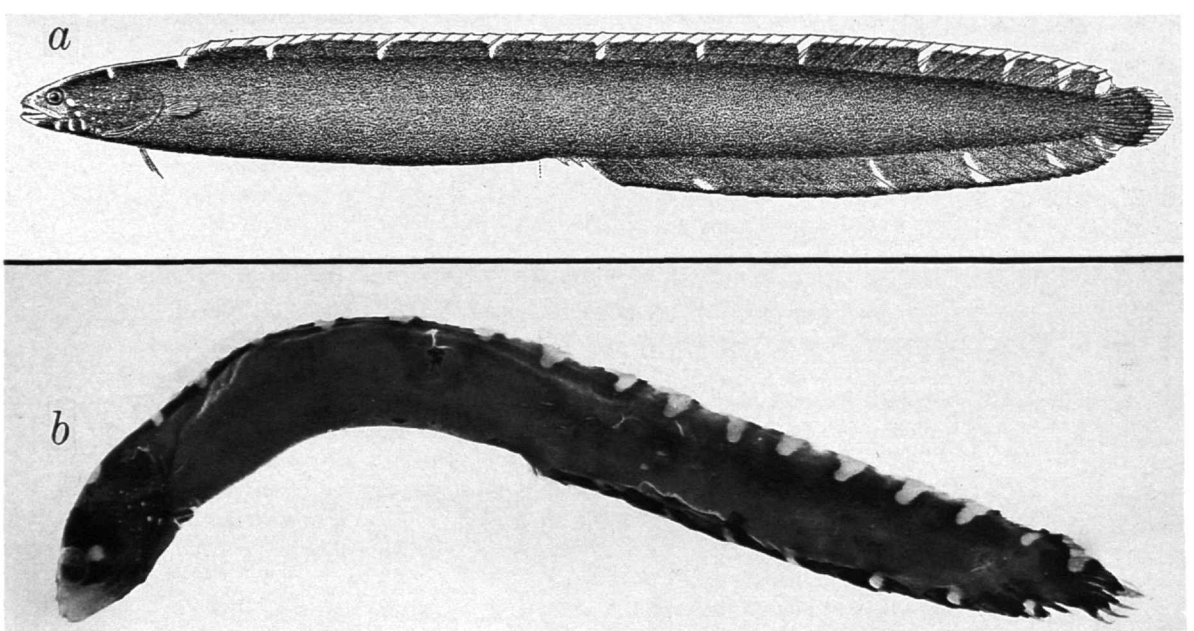


FIGURE 13.—*Stathmonotus hemphilli: a*, Key West, Florida, probably based on the paralectotype (USNM 324027, ~45 mm SL), which originally was cataloged with the lectotype as USNM 37193 (now restricted to the lectotype). Reproduced here from the original drawing by H.L. Todd, first published in Bean, 1885, pl. 13. *b*, Looe Key, Florida, USNM 261339, ~25 mm SL (note: dark spot on dorsoposterior portion of abdomen is an area where mucus that was covering the body had been removed and body color appears darker; irregular pale mark extending from dark spot is reflection of light; photograph by T.B. Griswold).

Table 3.—Occurrence of states of meristic characters in species of Stathmonotus. X in column indicates character occurs commonly; M indicates strong mode (one for each subspecies in S. stahli); U indicates uncommon state; - indicates not present; caudal-fin rays are segmented rays. Geographic variation for certain characters is given in Tables 4 and 5).

	Dorsal-fin spines																		Segmented anal-fin rays									Caudal-fin rays				
Species	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	20	21	22	23	24	25	26	27	28	29	10	11	12	13	14
hemphilli	-	-	-	-	-	-	-	-	-	X	X	X	X	X	X	X	U	U	-	-	-	U	X	X	X	X	X	U	U	X	M	-	-
stahli	-	-	-	U	X	X	X	X	X	U	-	-	-	-	-	-	-	-	-	U	X	X	X	X	U	-	-	-	U	M	M	U	-
gymnodermis	-	-	-	-	-	X	X	X	X	X	U	-	-	-	-	-	-	-	-	U	X	X	X	X	X	-	-	-	U	M	X	U	-
sinuscalifornici	-	-	-	-	U	X	X	X	X	U	U	-	-	-	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	U	M	X	U
culebrai	-	X	X	X	X	U	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	X	U	U	-	-	-	-	-	-	M	-	-
lugubris	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-	-	-	X	M	U	-

	Total vertebrae																Precaudal vertebrae										Caudal vertebrae								
Species	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
hemphilli	-	-	-	-	-	-	-	U	-	X	X	X	X	X	X	X	-	-	-	-	U	X	X	X	X	U	-	-	-	-	U	X	X	X	X
stahli	-	U	X	X	X	X	X	-	-	-	-	-	-	-	-	-	U	X	X	X	-	-	-	-	-	-	-	U	X	X	X	X	-	-	-
gymnodermis	-	-	-	X	X	X	X	X	U	-	-	-	-	-	-	-	-	U	X	X	X	-	-	-	-	-	-	U	X	X	X	X	-	-	-
sinuscalifornici	-	-	-	-	U	X	X	X	X	X	-	-	-	-	-	-	-	-	U	X	X	U	-	-	-	-	-	-	-	X	X	X	-	-	-
culebrai	-	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-	X	X	X	U	-	-	-	-
lugubris	X	X	X	U	-	-	-	-	-	-	-	-	-	-	-	-	X	X	U	-	-	-	-	-	-	-	X	X	X	X	-	-	-	-	-

(such that the entire dorsal fin and the upper body are pale), the ventral Vs extend onto the body but are not continuous, the nape, interorbit, and snout are pale, there is a pale spot on the cheek, and the lateral-line placodes lack pigment.

Females lack pigment on the body, but they have a network of four to six dark lines extending from the orbit across the jaws, cheek, branchiostegals, and sometimes the nape and interorbit. These bands may be variously interrupted, appearing as spots in some specimens.

COMMENTS.—*Stathmonotus hemphilli* was described from two specimens, syntypes, from Key West, Florida, and originally cataloged as USNM 37193. Both syntypes are strongly arched and impossible to straighten without causing severe damage; however, both are of about the same size, ~45 mm SL, and both have (or had) 51 dorsal-fin spines and II,27 anal-fin elements. One of the syntypes is now damaged and lacks four of the dorsal-fin spines. We designate the specimen with the total complement of dorsal-fin spines to be the lectotype. The lectotype retains the original catalog number and the paralectotype is now cataloged as USNM 324027. On a radiograph, a cluster of large eggs is evident in the abdominal cavity of the lectotype, but none are evident in the paralectotype.

One collection from the Bahamas (ANSP 115005) exhibits unusually low meristics compared to other collections. The eight specimens from this lot have 45–47 dorsal-fin spines (range for other specimens = 47–53), 24–26 segmented anal-fin rays (23–29), 50–54 total vertebrae (52–58), 20–22 precaudal vertebrae (22–25), and 30–33 caudal vertebrae (31–34). They also exhibit an extreme color variation (see above). They have cephalic sensory pore counts similar to those of specimens from other localities, except that they have only a single posterior infraorbital pore; other specimens usually have two, but only one is present in some other specimens from the Bahamas (e.g., ANSP 147163). Given the amount of localized variation observed in this and other species of *Stathmonotus* (Table 4), we believe that recognition of a separate taxon for the specimens in ANSP 115005 is unwarranted.

DISTRIBUTION.—*Western Atlantic*: Primarily northern Caribbean, including the Bahamas and Florida, but also collected at Haiti, St. Croix, Yucatán, Belize, Corn Island off Nicaragua, and as far east as Antigua, according to Böhlke and Chaplin (1968:512), but we have seen no specimens from this locality (Figure 14). James C. Tyler informed us that the specimen he collected at Carrie Bow Cay, Belize, came from a hole in a coral, *Monastrea annularis*, at a depth of about six meters.

MATERIAL EXAMINED.—*Bahamas:* Sandy Cay, ANSP 75231 (9, 2 cleared and stained), 115005 (8); High Cay, UF 14371 (2); Green Cay, ANSP 147163 (1); Treasure Island, Salt Cay, ANSP 98929 (1); Grand Bahama Island, ANSP 98930 (2); North Bimini, ANSP 98931 (1); Eleuthera, ANSP 111920 (1); Hog Island, USNM 53225 (1). *Florida:* Long Reef, UMML 899 (1); Ragged Key, UMML 2960 (1), 3522 (1); Margot Fish Shoal, UMML 3394 (1); Soldier Key, UMML 7377 (1); Lower Matecumbe Key, UMML 15402 (1); Content Key, UMML 17118 (3); Looe Key, UF 16195 (1), USNM 261339 (1); Alligator Reef, UMML 18092 (1); Key West, USNM 37193 (lectotype of *Stathmonotus hemphilli*), 324027 (paralectotype); Crawfish Bay, USNM 62800 (1); Tortugas, USNM 116808 (1), 116809 (1), 116810 (1), 192381 (2). *Mexico, Yucatán, Quintana Roo:* Ascension Bay, USNM 192381 (2). *Belize:* Carrie Bow Cay, USNM 325132 (1). *Nicaragua:* Corn Island, USNM 320775 (2). *Virgin Islands:* St. Croix, USNM 38775 (6). *Haiti:* Port au Prince Bay, Lamentin, USNM 170571 (holotype of *Stathmonotus corallicola*).

Table 4.—Frequency distributions for certain characters in W Atlantic species and subspecies of Stathmonotus from various localities (Venezuela and Belize data in part from Cervigon, 1966, and Greenfield and Johnson, 1981). SCFR = segmented caudal-fin rays.

Species or subspecies	Dorsal-fin spines																	$\bar{x}$	Segmented anal-fin rays									$\bar{x}$	Caudal vertebrae								$\bar{x}$
	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53				21	22	23	24	25	26	27	28	29		27	28	29	30	31	32	33	34	
hemphilli																																					
Corn I, Nicar.	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	50.0	-	-	-	-	-	-	1	-	1	-	27.0	-	-	-	-	-	-	1	-	
Belize	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	49.0	-	-	-	-	-	1	-	-	1	-	26.5	-	-	-	-	1	-	-	-	
Yucatan	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	49.5	-	-	-	-	-	-	-	1	-	1	28.0	-	-	-	-	1	-	-	1	32.5
Florida	-	-	-	-	-	-	-	-	-	1	2	4	7	1	1	50.5	-	-	-	-	-	-	5	7	4	1	27.0	-	-	-	-	1	1	3	3	33.0
Bahama Is	-	-	-	-	-	-	3	1	2	1	5	8	-	-	-	48.4	-	-	-	3	2	5	7	3	-	26.2	-	-	-	1	2	4	9	2	32.5
Virgin Is	-	-	-	-	-	-	-	-	3	1	1	-	-	-	-	47.6	-	-	1	-	1	2	2	-	-	25.7	-	-	-	-	1	2	2	-	32.2
Haiti	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-		-	-	-	-	1	-	-	-	-		-	-	-	-	1	-	-	-	
stahli tekla																																					
Panama	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	41.8	-	-	2	1	1	-	-	-	-	-	23.8	-	-	-	-	-	-	-	-	
Belize	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	42.0	-	-	2	3	-	-	-	-	-	-	23.6	-	3	-	-	-	-	-	-	28.0
Providencia I	-	3	7	13	3	2	-	-	-	-	-	-	-	-	-	41.8	-	-	6	13	8	-	-	-	-	-	24.1	-	7	11	6	-	-	-	-	29.0
Yucatan	-	3	5	2	1	-	-	-	-	-	-	-	-	-	-	41.1	-	3	5	3	-	-	-	-	-	-	23.0	1	3	6	-	-	-	-	-	28.5
Florida	-	-	1	1	2	1	-	-	-	-	-	-	-	-	-	42.6	-	-	1	2	2	-	-	-	-	-	24.2	-	-	3	2	-	-	-	-	29.4
Bahama Is	-	3	8	14	5	-	-	-	-	-	-	-	-	-	-	41.7	-	2	8	17	4	-	-	-	-	-	23.7	-	6	16	7	-	-	-	-	29.0
Cay Sal Bank	-	-	3	9	2	-	-	-	-	-	-	-	-	-	-	41.9	-	1	4	7	3	-	-	-	-	-	23.8	-	3	3	3	1	-	-	-	29.2
Cuba	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	42.0	-	-	-	1	2	-	-	-	-	-	24.7	-	-	1	2	-	-	-	-	29.7
Cayman Is	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-		-	-	2	-	-	-	-	-	-	-	23.0	-	1	-	-	-	-	-	-	
Haiti	2	4	11	5	1	-	-	-	-	-	-	-	-	-	-	41.0	1	3	11	8	-	-	-	-	-	-	23.1	2	6	9	2	-	-	-	-	28.6
Mona I	-	-	1	4	2	-	-	-	-	-	-	-	-	-	-	42.1	-	1	6	2	-	-	-	-	-	-	23.1	-	2	5	-	-	-	-	-	28.7
stahli stahli																																					
Puerto Rico	-	-	2	5	5	2	1	-	-	-	-	-	-	-	-	42.7	-	-	2	10	1	1	-	-	-	-	24.1	-	-	7	4	1	-	-	-	29.5
Virgin Is	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	43.0	-	-	-	1	1	-	-	-	-	-	24.5	-	-	-	1	-	-	-	-	
Leeward Is	-	-	-	10	20	8	-	-	-	-	-	-	-	-	-	42.9	-	-	9	19	9	-	-	-	-	-	24.0	-	2	16	17	1	-	-	-	29.5
Windward Is	-	-	1	7	16	5	-	-	-	-	-	-	-	-	-	42.9	-	-	4	13	11	-	-	-	-	-	24.2	-	1	8	11	2	-	-	-	29.6
Venezuela	-	-	-	-	4	2	-	-	-	-	-	-	-	-	-	43.3	-	-	-	4	2	-	-	-	-	-	24.3	-	-	-	-	-	-	-	-	
gymnodermis																																					
Panama	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	41.5	-	2	-	-	-	-	-	-	-	-	22.0	-	-	-	-	-	-	-	-	
Belize	-	-	1	5	-	-	-	-	-	-	-	-	-	-	-	41.8	-	1	4	1	-	-	-	-	-	-	23.0	-	-	-	-	-	-	-	-	
Yucatan	-	-	-	10	4	1	-	-	-	-	-	-	-	-	-	42.5	-	2	10	1	-	-	-	-	-	-	22.9	2	4	5	-	-	-	-	-	28.3
Bahama Is	-	-	6	28	25	5	-	-	-	-	-	-	-	-	-	42.4	1	8	25	24	4	2	-	-	-	-	23.4	1	16	24	15	1	-	-	-	29.0
Cay Sal Bank	-	-	-	1	3	2	-	-	-	-	-	-	-	-	-	43.2	-	-	2	3	-	-	-	-	-	-	23.6	-	1	3	-	-	-	-	-	28.8
Cayman Is	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	42.2	-	1	1	2	-	-	-	-	-	-	23.2	-	2	1	-	-	-	-	-	28.3
Puerto Rico	-	-	-	-	-	2	1	1	-	-	-	-	-	-	-	44.8	-	-	1	2	-	1	-	-	-	-	24.2	-	-	-	1	-	-	-	-	
Virgin Is	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	43.3	-	-	-	2	1	-	-	-	-	-	24.3	-	-	-	3	-	-	-	-	30.0
Leeward Is	-	-	-	4	7	28	9	1	-	-	-	-	-	-	-	43.9	-	2	6	25	14	1	-	-	-	-	24.1	-	-	13	16	6	-	-	-	
Windward Is	-	-	-	-	6	5	3	-	-	-	-	-	-	-	-	43.8	-	3	3	7	1	-	-	-	-	-	23.4	-	1	3	8	2	-	-	-	29.8
Venezuela	-	-	-	-	1	2	3	-	-	-	-	-	-	-	-	44.3	-	1	2	3	-	-	-	-	-	-	23.3	-	-	-	-	-	-	-	-	

Species or subspecies	Precaudal vertebrae											$\bar{x}$	Total vertebrae														$\bar{x}$	SCFR				$\bar{x}$
	16	17	18	19	20	21	22	23	24	25			44	45	46	47	48	49	50	51	52	53	54	55	56	57	58		10	11	12	13	
hemphilli																																	
Corn I, Nicar.	-	-	-	-	-	-	-	-	1	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	1	-	
Belize	-	-	-	-	-	-	-	1	-	-			-	-	-	-	-	-	-	-	-	-	1	-	-	-	-		-	1	-	-	
Yucatan	-	-	-	-	-	-	-	-	2	-	24.0		-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	56.5	1	1	-	-	10.5
Florida	-	-	-	-	-	-	-	3	12	1	23.9		-	-	-	-	-	-	-	-	-	-	1	2	2	5	5	56.7	1	2	9	-	11.7
Bahama Is	-	-	-	-	2	3	5	8	-	-	22.0		-	-	-	-	-	-	2	-	2	2	4	1	8	1	-	54.3	-	3	10	-	11.8
Virgin Is	-	-	-	-	-	-	3	-	-	-	22.0		-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	54.0	-	-	1	-	
Haiti	-	-	-	-	-	-	1	-	-	-			-	-	-	-	-	-	-	-	-	1	-	-	-	-	-		-	-	1	-	
stahli tekla																																	
Panama	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	3	-	-	11.0
Belize	-	-	3	-	-	-	-	-	-	-	18.0		-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	46.0	-	15	-	-	11.0
Providencia I	-	14	8	-	-	-	-	-	-	-	17.4		-	3	10	7	2	-	-	-	-	-	-	-	-	-	-	46.4	1	25	5	-	11.1
Yucatan	-	6	1	-	-	-	-	-	-	-	17.1		-	3	4	2	-	-	-	-	-	-	-	-	-	-	-	45.9	1	5	1	-	11.0
Florida	-	1	4	-	-	-	-	-	-	-	17.8		-	-	-	4	1	-	-	-	-	-	-	-	-	-	-	47.2	-	4	1	-	11.2
Bahama Is	1	28	7	-	-	-	-	-	-	-	17.2		-	2	20	6	1	-	-	-	-	-	-	-	-	-	-	46.2	-	40	2	-	11.0
Cay Sal Bank	1	8	2	-	-	-	-	-	-	-	17.1		-	2	2	4	1	-	-	-	-	-	-	-	-	-	-	46.4	-	13	-	-	11.0
Cuba	-	4	-	-	-	-	-	-	-	-	17.0		-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	46.7	-	2	-	-	11.0
Cayman Is	-	1	-	-	-	-	-	-	-	-			-	1	-	-	-	-	-	-	-	-	-	-	-	-	-		-	2	-	-	11.0
Haiti	-	11	7	-	-	-	-	-	-	-	17.4		1	7	7	6	-	-	-	-	-	-	-	-	-	-	-	45.9	2	14	2	-	11.0
Mona I	-	3	2	2	-	-	-	-	-	-	17.8		-	2	2	1	3	-	-	-	-	-	-	-	-	-	-	46.6	-	7	3	-	11.3
stahli stahli																																	
Puerto Rico	-	-	11	-	-	-	-	-	-	-	18.0		-	-	-	8	4	1	-	-	-	-	-	-	-	-	-	47.5	-	1	14	-	12.0
Virgin Is	-	-	1	-	-	-	-	-	-	-			-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	47.0	-	-	2	-	12.0
Leeward Is	-	4	29	-	-	-	-	-	-	-	17.9		-	-	3	18	12	1	-	-	-	-	-	-	-	-	-	47.3	-	1	32	-	12.0
Windward Is	-	2	17	2	-	-	-	-	-	-	18.0		-	-	1	11	10	1	-	-	-	-	-	-	-	-	-	47.5	-	-	23	1	12.0
Venezuela	-	-	-	-	-	-	-	-	-	-			-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	48.5	-	-	6	-	12.0
gymnodermis																																	
Panama	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	2	-	-	11.0
Belize	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	6	-	-	11.0
Yucatan	-	-	4	9	2	-	-	-	-	-	18.9		-	-	1	6	4	-	-	-	-	-	-	-	-	-	-	47.3	1	11	-	-	10.9
Bahama Is	-	1	38	19	1	-	-	-	-	-	18.3		-	-	9	27	21	3	-	-	-	-	-	-	-	-	-	47.3	-	57	3	2	11.1
Cay Sal Bank	-	-	-	3	1	-	-	-	-	-	19.2		-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	48.5	-	5	-	-	11.0
Cayman Is	-	-	2	-	-	-	-	-	-	-	18.0		-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	46.5	1	3	-	-	10.8
Puerto Rico	-	-	-	1	-	-	-	-	-	-			-	-	-	-	-	1	-	-	-	-	-	-	-	-	-		-	1	-	-	
Virgin Is	-	-	3	-	-	-	-	-	-	-	18.0		-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	48.3	-	3	-	-	11.0
Leeward Is	-	-	2	29	6	-	-	-	-	-	19.1		-	-	-	2	9	18	9	1	-	-	-	-	-	-	-	48.9	1	22	2	1	11.1
Windward Is	-	-	2	7	6	-	-	-	-	-	19.3		-	-	-	-	2	11	2	-	-	-	-	-	-	-	-	49.0	-	10	-	-	11.0
Venezuela	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	6	-	-	11.0

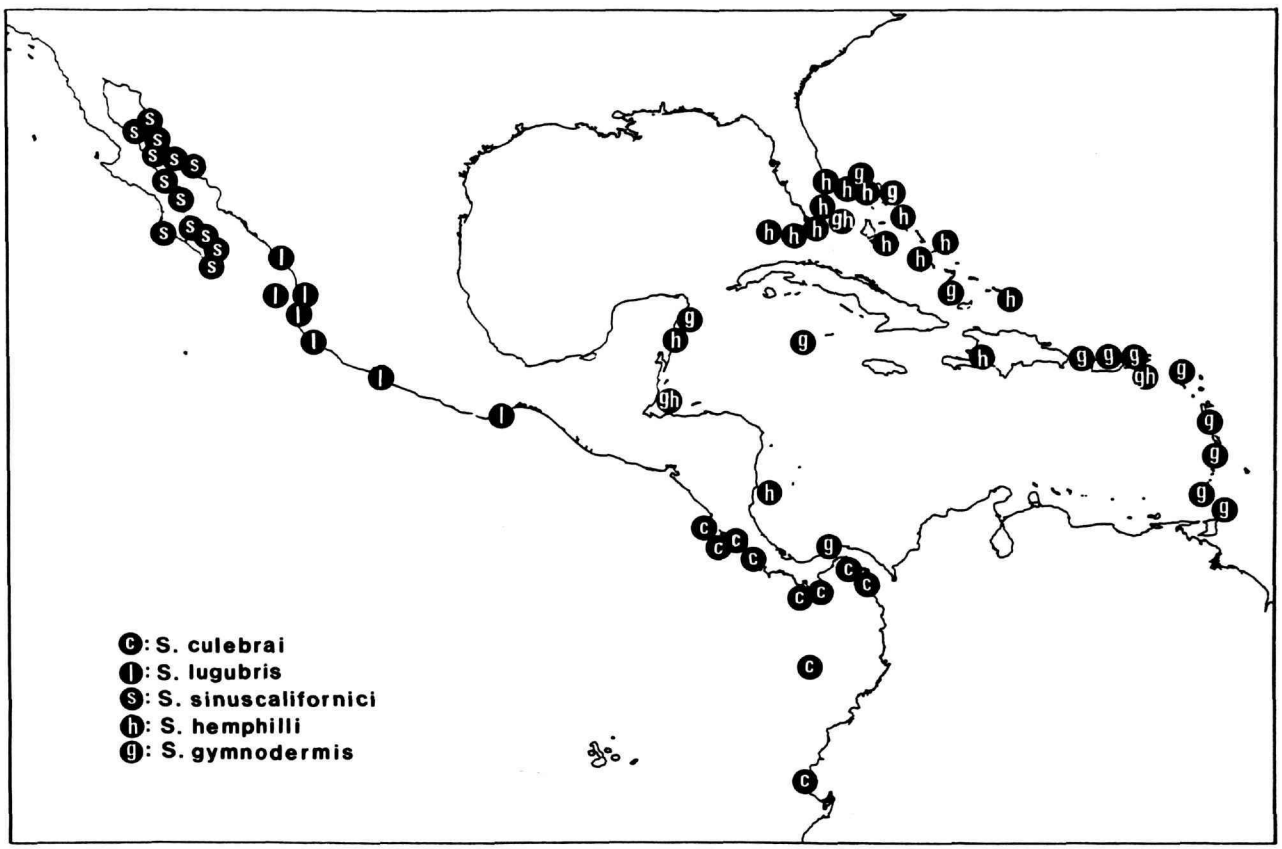


FIGURE 14.—Distributions of five of the six species of *Stathmonotus*. The northernmost locality in Florida for *S. hemphilli* is based on Gilmore et al. (1983).

Subgenus *Auchenistius* Evermann and Marsh

Auchenistius Evermann and Marsh, 1899:359 [type species by monotypy *A. stahli* Evermann and Marsh].

Histioclinus Metzelaar, 1919:157 [type species by monotypy *H. veliger* Metzelaar (= *S. stahli*)].

Parviclinus Fraser-Brunner, 1932:827 [type species by original designation *P. spinosus* Fraser-Bruner, 1932:828 (= *S. stahli*)].

DIAGNOSIS.—Preopercular and nuchal cirri present. Anterior pleural ribs absent such that the anteriormost vertebra with both epineurals and pleural ribs is the fourth to the seventh.

Stathmonotus stahli (Evermann and Marsh)

FIGURE 15

Auchenistius stahli Evermann and Marsh, 1899:359 [Ponce, Puerto Rico; holotype USNM 49372].

Stathmonotus tekla Nichols, 1910:161 [Sand Key, off Key West harbor, Florida; holotype AMNH 2536].

Histioclinus veliger Metzelaar, 1919:157 [Bonaire; "several specimens" (syntypes), depository not indicated; Wheeler, 1958:255, stated that "co-types" were at BMNH].

Parviclinus spinosus Fraser-Brunner, 1932:828 [mouth of the Conway River, near Tal-y-cafn bridge, North Wales; holotype BMNH 1932.10.22.1].

DIAGNOSIS.—Unique among the species of *Stathmonotus* in having a fully scaled body. Dorsal-fin spines 39–45; segmented anal-fin rays 21–26; pectoral-fin rays 8 or 9; segmented caudal-fin rays 10–13; total vertebrae 44–49; precaudal vertebrae 16–19; caudal vertebrae 27–31 (Tables 3, 4); pleural ribs 16–19; epineurals 25–33. Supraorbital cirrus rounded and flap-like; nasal, nuchal, and preopercular cirri present. Large males with a swollen, fleshy head, maxillary extending well posterior to the orbit (not extending beyond orbit in females), and pronounced lateral fleshy folds along the jaws.

COLORATION.—Most specimens in preservative have few, if any, melanophores. In some males, there are one or two small, irregular concentrations of melanophores just posterior to the orbit. Others may have the supraorbital cirri and/or the pelvic fins uniformly covered with fine melanophores. Some males

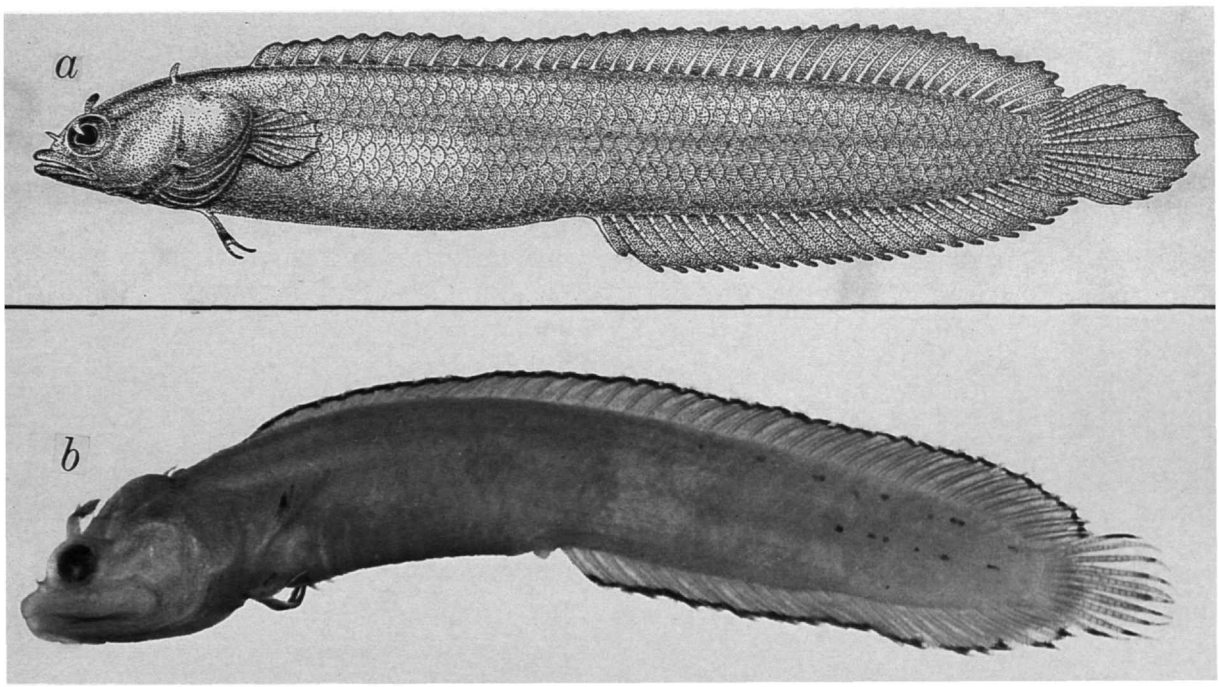


FIGURE 15.—*Stathmonotus stahli*: *a*, *Stathmonotus stahli stahli* USNM 49372, holotype, Ponce, Puerto Rico (from Evermann and Marsh, 1900, fig. 102). Reproduced here from the original drawing by C.B. Hudson. The drawing is in error in showing 42 dorsal-fin spines and 25 segmented anal-fin rays as the holotype has 41 spines and 24 segmented rays. As described and illustrated, the holotype, in poor condition, has only one anal-fin spine, and it is not possible to determine if a spine was lost through damage or if the condition is anomalous. *b*, *Stathmonotus stahli tekla*, MPM 19708, ~22.5 mm SL, Akumal, Mexico.

(e.g., ANSP 98948) are pale overall, with a border of melanophores along the distal margin of the dorsal fin. One male from Panama (CAS 31638) has a distinct dark border on the distal margins of the median fins, the pectoral fin, and the supraorbital cirrus, and diffuse melanophores on the distal half of the pectoral fin (proximal to the dark border) and nuchal cirrus, but otherwise lacks melanophores. One specimen from Mexico (MPM 19708; Figure 15*b*) also has the distal margin of the dorsal and anal fins dark, an irregular row of dark spots subdistally on the caudal-fin rays, two rows of dark spots on the posterior one-third of the body, a dark spot on the pectoral fin, and a dark spot on the supraorbital cirrus. Dark morphs, with the entire body covered with dense melanophores, are unknown.

Females may completely lack melanophores or have only faint concentrations of melanophores along the body, faint melanophores and a series of pale spots on the head, especially on the ventral surface (giving the chin a banded appearance), and weakly banded pelvic and pectoral fins (e.g., ANSP 98948). Four color morphs of living specimens are mentioned in Böhlke and Chaplin (1968:513) but how these relate to the patterns described above is unknown.

COMMENTS.—*Stathmonotus stahli* is represented by two subspecies, *S. s. stahli* from Puerto Rico (type locality), the Virgin Islands, Leeward and Windward Islands, and Venezuela, and *S. s. tekla* from the Bahamas, Florida (type locality), Cuba, Haiti, Mona Island (Puerto Rico), Cayman Islands, Yucatán, Providencia Island, Belize, Panama, and Colombia (Figure 16). Springer (1955) distinguished them primarily by the number of segmented caudal-fin rays (12 in *stahli* versus 11 in *tekla*). This difference largely holds, although variants occur within the geographic ranges of both forms (Table 4). The forms also tend to differ in modal number of dorsal-fin spines (43 vs. 42) and precaudal vertebrae (17 vs. 18; Table 4). The frequencies of these meristic elements appear to change abruptly between Hispanola to the west and the main island of Puerto Rico to the east. Specimens from Mona Island (ANSP 145875), located between these areas, exhibit counts of both forms (Table 4) and were assigned to *S. s. tekla*, based on the higher frequency of counts typical of that form.

The synonym *Histioclinus veliger* Metzelaar (1919) apparently refers to *S. s. stahli;* the types have 12 segmented caudal-fin rays, and the type locality, Bonaire, is within the range of this subspecies (Springer, 1955). We are unable to

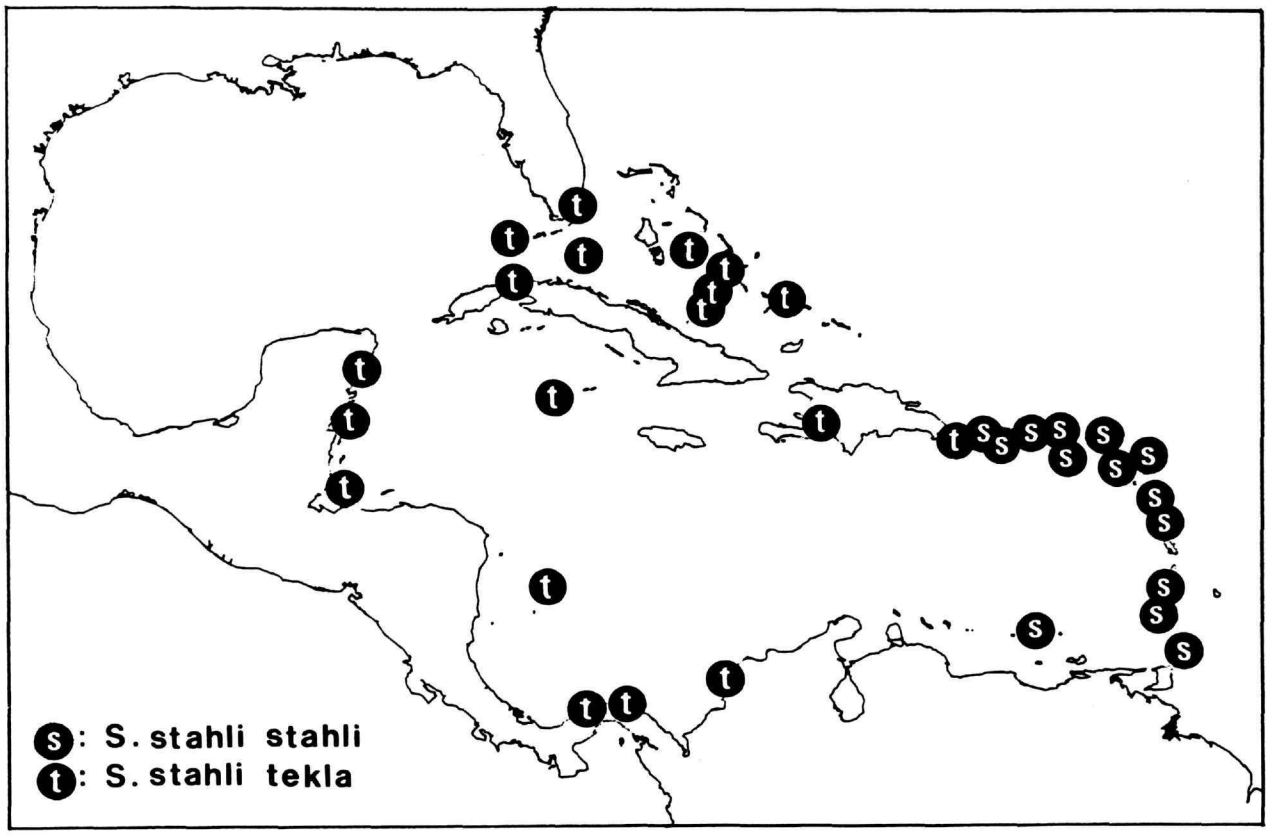


FIGURE 16.—Distributions of *S. stahli stahli* and *S. stahli tekla*. The locality in Colombia is based on Acero (1979).

assign the synonym *Parviclinus spinosus* Fraser-Brunner (1932) to a subspecies. The reported type locality, North Wales, is clearly in error, and the caudal fin is abnormal (Wheeler, 1958).

There is an apparent error in the original illustration of the holotype of *S. stahli stahli* in Evermann and Marsh (1900, fig. 102; our Figure 15*a*), which also is alluded to by the uncertainty of the fin-ray counts given in their description. They illustrate 42 dorsal-fin spines, whereas we count 41 on a radiograph of the holotype. Also, they illustrate the anal fin with one spine and 25 segmented rays, whereas we count 24 segmented rays on the radiograph; one of the anal-fin spines appears to be broken in the holotype.

DISTRIBUTION.—*Western Atlantic:* Widespread in the Caribbean; collected from the Bahamas, Florida, Greater and Lesser Antilles, off Venezuela, Colombia, Panama, Belize, and Yucatán (Figure 16).

MATERIAL EXAMINED.—*Stathmonotus stahli stahli: Puerto Rico:* Ponce, USNM 49372 (holotype); Puerto Real, USNM 50163 (3); Culebra Island, USNM 126078 (7); Cabo Rojo, UF 13358 (1), USNM 128815 (1); La Parguera, USNM 205219 (1); Mayagüez, USNM 205220 (1). *Virgin Islands:* St. Thomas, USNM 117440 (2); St. Croix, Buck Island, USNM 120485 (1). *Leeward Islands:* Anguilla, USNM 191419 (3); St. Christopher, USNM 170315 (8); Barbuda, USNM 291696 (6); Guadeloupe, USNM 170261 (4); Dominica, UMML 29289 (31). *Windward Islands:* Little St. Vincent Island, ANSP 127032 (17); Grenadines, Carriacou, USNM 170200 (1); Grenadines, Tobago, USNM 170203 (1). *Venezuela:* Los Roques, USNM 195749 (2).

Stathmonotus stahli tekla: Bahamas: Hog Island, ANSP 72499 (6); Exuma Cays, ANSP 98944 (3); Double Headed Shot Cays (Cay Sal Bank), ANSP 98948 (16); Plana Cays (French Cays), ANSP 147641 (25); Ragged Islands, Nurse Cay, ANSP 148989 (4); Flamingo Cay, UMML 6333 (5); Stocking Island, UMML 6387 (2); Oyster Cay, Exuma chain, UMML 12610 (1). *Florida:* Key Biscayne, UMML 2624 (1); Elliot Key, UMML 5186 (1); Sand Cay, AMNH 2536 (holotype); Tortugas, UF 3411 (2), USNM 116825 (3), 116827 (1). *Cuba:* Havana, USNM 192114 (4). *Haiti:* Port au

Prince, USNM 178291 (25). *Puerto Rico:* Mona Island, ANSP 145875 (10). *Cayman Islands:* Grand Cayman, ANSP 102238 (1), UF 12386 (1). *Mexico, Yucatán, Quintana Roo:* Akumal, MPM 19708 (1), 22473 (5), 30219 (1); Chinchorro, UMML 9339 (2); Ascension Bay, USNM 192382 (2). *Belize:* Carrie Bow Cay, USNM 218258 (2), 274945 (1), 276218 (2); Southwater Cay, USNM 274939 (2). Colombia: Providencia Island, UF 18902 (10, 2 cleared and stained), 19045 (3), 24366 (1), 24545 (1), 25112 (6), 25347 (6), 25403 (6), 25672 (1), 25803 (3), 25824 (1), USNM 107115 (4). *Panama:* Bahia Limón, Coco Solo, SIO 72-6 (2); Toro Point, SIO 67-45 (1); San Blas, CAS 31638 (1).

Stathmonotus gymnodermis Springer

FIGURE 17

Stathmonotus gymnodermis Springer, 1955:77 [Fort San Geronimo, San Juan, Puerto Rico; holotype USNM 117436].

DIAGNOSIS.—Unique among the species of *Stathmonotus* in not having the dorsal and anal fins broadly confluent with the caudal fin. Dorsal-fin spines 41–46; segmented anal-fin rays 21–26; pectoral-fin rays 8 or 9; segmented caudal-fin rays 10–13 (usually 11); total vertebrae 45–51; precaudal vertebrae 17–20; caudal vertebrae 27–31 (Tables 3, 4); pleural ribs 17–20; epineurals 29–36. Body naked; supraorbital cirrus rounded and flap-like; nasal, nuchal, and preopercular cirri present. Large males with a swollen, fleshy head; maxillary of males extending well posterior to the orbit (not extending beyond orbit in females).

COLORATION.—Most specimens in preservative have few if any melanophores. Some males are pale except for an irregular dark border along the supraorbital cirrus (e.g., ANSP 113209). Others have one or two small concentrations of melanophores posterior to the orbit, or one or two irregular rows of small spots along the body (e.g., ANSP 113209) or along the body and dorsal fin (e.g., ANSP 127034). One specimen from Mexico (MPM 24881; Figure 17*b*) has the distal margin of the dorsal fin narrowly and variably dusky (especially anteriorly), a row of three to five dark spots on the body above the abdomen, a midlateral row of 13–14 irregularly appearing dark spots on the body, and dark spots on the supraorbital cirri, posterior to the orbit, above the opercle, and at the pectoral-fin base. Dark morphs are unknown.

Females usually lack melanophores, but they may have fine melanophores on the head and pale spots or bands, especially

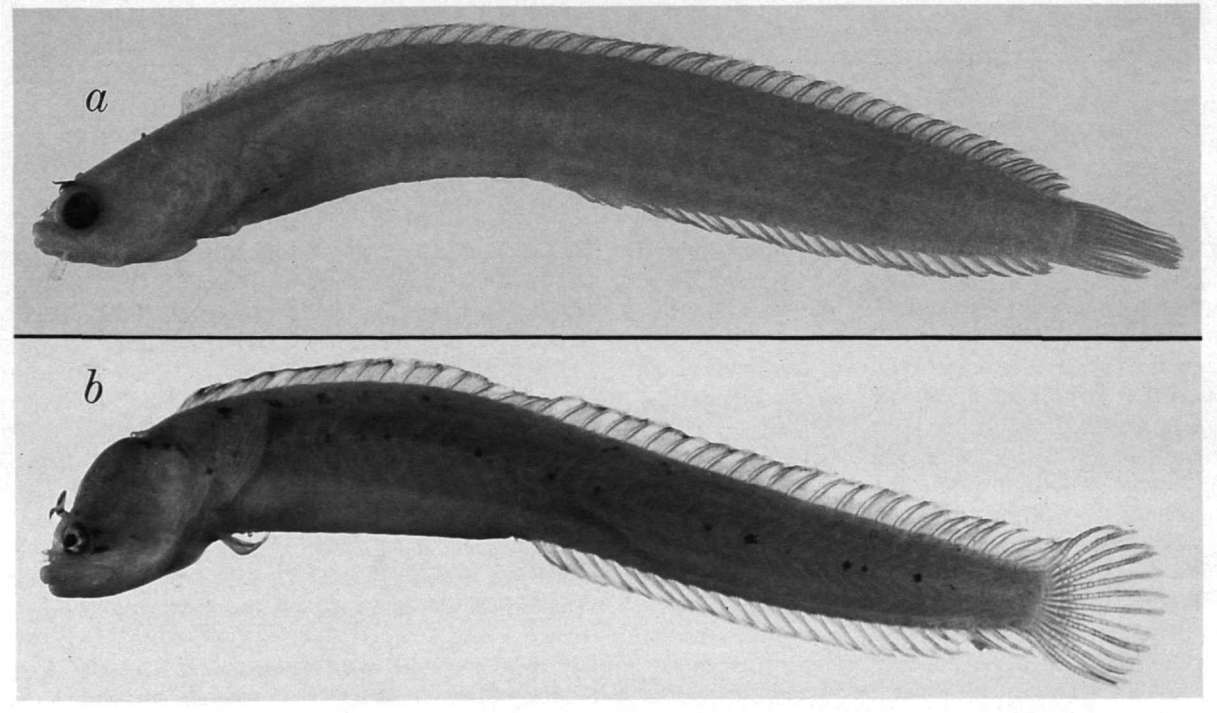


FIGURE 17.—*Stathmonotus gymnodermis*: *a*, USNM 320842, ~20 mm SL, Tobago; preopercular cirrus not evident in photograph (photograph by T.B. Griswold). *b*, MPM 24881, ~24 mm SL, Cozumel, Mexico. In this specimen, the caudal fin is structurally aberrant, as is the attachment of the last fin-spine.

on the chin, banded pelvic and pectoral fins, a few spots posteriorly on the body, or a completely mottled body with spots on the dorsal fin (e.g., ANSP 127034).

COMMENTS.—This species exhibits noticeable geographic variation, similar to that of *S. stahli* (Table 4). The number of dorsal-fin spines and total, precaudal, and caudal vertebrae are modally higher in specimens from Puerto Rico westward and southward through the Antilles than they are in specimens from northward and eastward of Puerto Rico.

DISTRIBUTION.—*Western Atlantic:* Widespread in the Caribbean; collected from the Bahamas, Greater and Lesser Antilles, Yucatán, and Belize, but not recorded from Florida (Figure 14).

MATERIAL EXAMINED.—*Bahamas:* Hogsty Reef, ANSP 98932 (8); Treasure Island, Salt Cay, ANSP 98934 (3), 98935 (4); Sandy Cay, ANSP 115014 (54, 4 cleared and stained); North Bimini, UMML 10039 (3); Cay Sal Bank, Elbow Cay, ANSP 98938 (5), UF 93291 (2). *Cayman Islands:* Grand Cayman, ANSP 102243 (1), UF 10750 (2), 12385 (1). *Puerto Rico:* San Juan, USNM 117436 (holotype), 163419 (1); Desecheo Island, ANSP 147680 (2). *Virgin Islands:* St. Thomas, USNM 163324 (2); St. Croix, Christiansted, USNM 163325 (1). *Leeward Islands:* St. Barthélemy, Isle Snydare, ANSP 127034 (47); Dominica, USNM 198268 (2), 198273 (10, 2 cleared and stained), 198286 (1). *Windward Islands:* St. Lucia, Castries, ANSP 113209 (5); Grenada, Martins Bay, ANSP 127030 (9); Tobago, USNM 320842 (2). *Mexico, Yucatán, Quintana Roo:* Akumal, MPM 27398 (4); Cozumel, MPM 24881 (14), UAZ 69-91-1 (3, 1 cleared and stained). *Panama:* Toro Point, SIO 67-45 (2).

Subgenus *Parastathmonotus* Chabanaud

Parastathmonotus Chabanaud, 1942:115 [type species by original designation *Parastathmonotus sinuscalifornici* Chabanaud].

DIAGNOSIS.—Vomerine teeth absent; dermosphenotic not autogenous; two (rather than three) anterior infraorbital sensory pores (Table 2).

COMMENTS.—The subgenus is restricted to the eastern Pacific, where the three included species are apparently allopatric.

Stathmonotus sinuscalifornici (Chabanaud)

FIGURE 18

Parastathmonotus sinuscalifornici Chabanaud, 1942:115 [Bahia San Gabriel, Isla Espiritu Santo, Golfo de California; holotype MNHN 1942-28].

DIAGNOSIS.—The largest of the species of *Stathmonotus*, with both sexes reaching at least 55 mm SL (SIO 62-124). Dorsal-fin spines 40–46; segmented anal-fin rays 22–26 (lower value from Böhlke, 1953); pectoral-fin rays 6–10; segmented caudal-fin rays 11–14; total vertebrae 47–52; precaudal vertebrae 18–21; caudal vertebrae 29–32 (Tables 3, 5); pleural ribs 18–20; epineurals 33–38. Body naked; supraorbital cirrus rounded and flap-like; other cirri absent. Head more swollen and maxillary longer in males than in females.

COLORATION.—Sexually dimorphic and variable. Some males (in preservative) lack evident melanophores. Others have only a small, dark spot posterior to the orbit at the dorsalmost posterior infraorbital (PIO) sensory pore and a dark line above

Table 5.—Frequency distributions for certain characters in Stathmonotus sinuscalifornici from the coasts of three Mexican states bordering the Gulf of California and the Bahia Magadalena area on the Pacific coast of Baja California (SAFR =segmented anal-fin rays; SCFR = segmented caudal-fin rays).

	Dorsal-fin spines								SAFR					SCFR				
Areas	40	41	42	43	44	45	46	$\bar{x}$	23	24	25	26	$\bar{x}$	11	12	13	14	$\bar{x}$
Gulf of California																		
Sonora	-	-	6	22	8	-	1	43.1	2	14	22	2	24.6	1	23	7	2	12.3
Baja California N	-	-	-	7	8	1	-	43.6	1	6	6	-	24.4	-	11	1	-	12.1
Baja California S	2	11	11	8	1	-	-	41.8	8	17	9	1	24.1	-	24	2	-	12.1
Bahia Magdalena area	-	-	2	4	3	-	-	43.1	1	4	4	-	24.3	1	6	1	1	12.2

	Total vertebrae							Precaudal vertebrae					Caudal vertebrae				
Areas	47	48	49	50	51	52	$\bar{x}$	18	19	20	21	$\bar{x}$	29	30	31	32	$\bar{x}$
Gulf of California																	
Sonora	-	1	7	14	13	2	50.2	-	17	15	1	19.5	1	9	16	6	30.8
Baja California N	-	-	-	6	6	2	50.7	-	4	10	-	19.7	-	3	8	3	31.0
Baja California S	1	5	5	8	-	-	49.0	3	15	1	-	18.9	4	8	3	-	29.9
Bahia Magdalena area	(no data)							(no data)					(no data)				

FIGURE 18.—*Stathmonotus sinuscalifornici*: *a,b*, USNM 201162, 30.2 and 36.5 mm SL, Isla Ildefonso, Gulf of California, Mexico. *c*, UAZ 77-50, 32.7 mm SL, Puerto Lobos, Gulf of California, Sonora, Mexico, right side reversed (photographs by T.B. Griswold).

the jaw, or they have these markings plus a dark spot on the cheek (at the dorsalmost preopercular sensory pore), a series of dark spots, one at each lateral-line placode, a dark margin on the supraorbital cirrus, and a dark spot on the middle of the pelvic fin. Still others have larger and more numerous spots on the head and body, a row of spots on the distal margin of the anal fin, and spots along the ventral margin of the pectoral fin (e.g., USNM 201162, Figure 18*a,b*). In the dark morph, the head, body, and fins may be completely dark, being covered with uniform, fully expanded melanophores, except for the distal margin of the caudal fin, the distal tips of the dorsal fin and anal fin posteriorly, the distal half of the pelvic fin, the supraorbital cirri, the interorbit, and the nostril tubes, all of which are pale (e.g., UAZ 82-2). Some dark morphs have pale Vs or pale spots along the dorsal fin and inverted pale Vs or pale spots on the anal fin (e.g., UAZ 77-50; Figure 18*c*). Dark morphs, like the pale morphs, often have the lateral-line placodes recognizably darker than the background. Some specimens (e.g., UAZ 75-33-11) are intermediate between the pale and dark morphs. The head and body may be mottled with both dark and pale spots; V-shape pale areas, which may be continuous with one another, may be present along the distal margin of the dorsal fin posteriorly, and inverted Vs may be present along the anal fin posteriorly.

Females often lack pigment on the body but have a network of about six dark lines extending from the eye ventrally across the jaws, cheek, and branchiostegals, and dark spots on the middle of the pelvic fin. Some females also have rows of small spots along the body, usually at the lateral-line placodes (e.g., UAZ 75-33-11). Females also may have dark morphs (e.g., SIO 65-352), in which the body and fins are dark except for V-shape pale areas along the dorsal fin, small inverted V-shape pale areas along the anal fin, a narrow pale margin on the anal fin, and, unlike dark males, pale bands on the lower jaw.

COMMENTS.—This species exhibits considerable geographic variation in meristics (Table 5). Specimens from the southern Gulf of California (Baja California Sur) generally exhibit the lowest mean numbers of dorsal-fin spines, anal-fin rays, and total, precaudal, and caudal vertebrae.

DISTRIBUTION.—*Eastern Pacific:* Gulf of California, from Puerto Lobos southward to Cabo San Lucas, and the adjacent outer coast of Baja to Bahia Magdelena (Figure 14). Reports of this species from Mazatlán, Sinaloa, Mexico (van der Heiden and Findley, 1988), are doubtful. All specimens that we have examined from Mazatlán and southward along the coast of Mexico are *S. lugubris*.

MATERIAL EXAMINED.—*Mexico, Sonora:* Puerto Lobos, UAZ 69-8-6 (2), 69-16-9 (1), 77-50 (4); Isla Tiburón, UAZ 70-8-13 (2); Isla San Pedro Nolasco, UAZ 75-37-23 (19, 2 cleared and stained), 75-38-23 (4), 76-37-23 (15), USNM 323272 (1); Caleta Venecia, UAZ 82-2 (1); Bahia San Carlos, UAZ 69-65-8 (7), 73-54-5 (2), USNM 181252 (6); Isla Venado, UAZ 75-33-11 (15); Bahia Bacochibampo, SIO 68-176 (1, from the oscule of a sponge), UAZ 71-36 (23, 2 cleared and stained); Guaymas, UAZ 73-53 (2). *Mexico, Baja California Norte:* Isla Ángel de la Guarda, USNM 167589 (3), 167593 (1); Isla San Pedro Mártir, USNM 323273 (2), 323274 (8). *Mexico, Baja California Sur:* Isla San Marcos, SIO 76-273 (2); Punta Concepción, SIO 65-314 (2); Isla Coronado, UAZ 74-34 (1); Isla Carmen, SIO 65-328 (1), UAZ 74-35-6 (2); Isla Ildefonso, USNM 201162 (6, 2 cleared and stained), 323275 (1); Puerto Chileno, USMN 323271 (2); Bahia Agua Verde, USNM 200390 (3); Isla San Jose, SIO 65-265 (1), UAZ 77-42 (6); Isla Espíritu Santo, UAZ 74-37-15 (3); Pichilingue, USNM 323269 (2), 323270 (1); La Paz, SIO 65-352 (5); Cabo Pulmo, SIO 76-284 (2); Bahia Los Frailes, SIO 61-243 (1), UAZ 74-46-8 (1); Cabo San Lucas, UAZ uncataloged (1 cleared and stained); Bahia Almejas, SIO 62-121 (1), 62-124 (2 cleared and stained), 65-180 (6); Bahia Magdalena, SIO 62-713 (2), 64-54 (1).

Stathmonotus culebrai Seale

FIGURE 19

Stathmonotus culebrai Seale, 1940:42 [Port Culebra, Costa Rica; holotype CAS 5745].

DIAGNOSIS.—Unique among the subgenus *Parastathmonotus* in lacking a supraorbital cirrus. Dorsal-fin spines 37–41; segmented anal-fin rays 20–25; pectoral-fin rays 9–11; segmented caudal-fin rays 12; total vertebrae 44–47; precaudal vertebrae 17–18; caudal vertebrae 27–30 (Table 3); pleural ribs 17–18; epineurals 32–34. Body naked; a small nasal cirrus present; nuchal cirrus absent. Maxillary of males longer than that of females.

COLORATION.—Variable (pale, dark, and spotted morphs known) and similar to that described for *S. sinuscalifornici* (above). Dark morphs have pale distal margins on the median fins (e.g., GCRL 15068). A spotted morph (Figure 19) has dark spots and mottling over the head and body, a largely unpigmented dorsal fin, a series of diagonal blotches on the anal fin, rows of spots on the caudal and pectoral fins, and a single spot on the middle of the pelvic fin.

COMMENTS.—The original description and illustration of *S. culebrai* are in error in reporting and depicting 42 dorsal-fin spines and 24 segmented anal-fin rays. We count 39 dorsal-fin spines and 22 segmented anal-fin rays from a radiograph of the holotype.

DISTRIBUTION.—*Eastern Pacific:* Central America from Costa Rica southward to Ecuador, including Isla Malpelo (Figure 14).

MATERIAL EXAMINED.—*Costa Rica:* Port Culebra, CAS 5745 (radiograph of holotype); Uvita Bay, CAS 46338 (1); Guanacaste, GCRL 15068 (1), UAZ 68-74-45 (1 cleared and stained); Golfo de Nicoya, UAZ 68-73-19 (1); Punta Arenas, USNM 212254 (1 cleared and stained). *Panama:* Isla Ladrones, SIO 70-359 (1); Isla Jicarón, SIO 70-356 (1), 71-51 (1); Azuero peninsula, USNM 312975 (1), 323268 (2); Isla del Rey, Perlas Islands, USNM 312976 (1); Bahia Piñas, ANSP

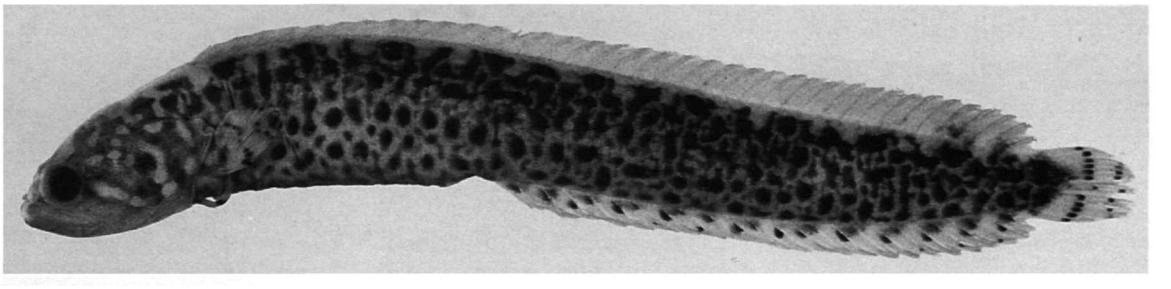


FIGURE 19.—*Stathmonotus culebrai*, USNM 312975, 25.6 mm SL, Azuero Peninsula, Panama, Pacific coast (photograph by T.B. Griswold).

102617 (3, 1 cleared and stained). *Columbia:* Isla Malpelo, CAS 31544 (1), SIO 72-96 (3), 72-97 (1), USNM 210660 (1). *Ecuador:* Isla La Plata, ANSP 102492 (1), 102621 (1), 102639 (1).

Stathmonotus lugubris Böhlke

FIGURE 20

Stathmonotus lugubris Böhlke, 1953:145 [Port Guatulco, Golfo de Tehuantepec, Mexico; holotype SU 17748].

DIAGNOSIS.—No unique features are known. Distinguishable by a combination of having no vomerine teeth, a low number of dorsal-fin spines, and a supraorbital cirrus. Dorsal-fin spines 36–39; segmented anal-fin rays 20–23; pectoral-fin rays 10 or 11; segmented caudal-fin rays 11–13; total vertebrae 43–46; precaudal vertebrae 16–18; caudal vertebrae 26–29 (Table 3); pleural ribs 16–17; epineurals 32–35. Body naked; supraorbital cirrus rounded and flap-like; nasal cirrus present; nuchal and preopercular cirri absent. Head more swollen and maxillary longer in males than in females.

COLORATION.—Variable and similar to that described for *S. sinuscalifornici* (above). Light, spotted, and dark morphs are known. Dark morphs have the distal margin of the median fins pale (e.g., UAZ 71-70-24).

DISTRIBUTION.—*Eastern Pacific:* Mexico, from Mazatlán, Sinaloa, southward to Puerto Huatulco, Oaxaca (Figure 14). This species should replace *S. sinuscalifornici* in the list of fishes from Sinaloa, Mexico (van der Heiden and Findley, 1988).

MATERIAL EXAMINED.—*Mexico, Sinaloa:* Mazatlán, CAS 30924 (1), UAZ 69-46-17 (1). *Mexico, Nayarit:* Isla Jaltemba, UAZ 71-66-17 (3); Islas Tres Marías, Isla Maria Madre, SIO 62-19 (1); Islas Tres Marías, Isla Cleopha, SIO 62-55 (36), USNM 210659 (3). *Mexico, Jalisco:* Bahia Banderas, Puerto Vallarta, SIO 62-26 (18), UAZ 71-61-23 (2 cleared and stained), 71-63-21 (1), 71-69-20 (1), 71-70-24 (11, 2 cleared and stained); Bahia Chamela, SIO 70-165 (1). *Mexico, Guerrero:* Zihuatanejo, UAZ 70-18-16 (1). *Mexico, Oaxaca:* Puerto Huatulco, SU 17748 (holotype).

Phylogenetic Relationships of the CHAENOPSIDAE

Our phylogenetic analysis indicates that the Chaenopsidae should be expanded to include *Stathmonotus, Mccoskerichthys,* and *Neoclinus,* as well as the Chaenopsinae (= Chaenopsidae of Stephens, 1963). Regardless of the single outgroup or combination of outgroups used, these taxa constituted a monophyletic group in all most-parsimonious topologies. In all analyses, two equally parsimonious topologies of the relationships within this expanded Chaenopsidae were obtained (Figure 21). When single outgroups were used, the two trees varied in length from 96 to 110 steps and in consistency index from 0.85 to 0.91, depending upon the outgroup used. The same two shortest ingroup trees (Figure 21) were obtained using various combinations of two or more outgroups. These trees differ only in the placement of *S. sinuscalifornici.* In one, it is the sister group of *S. lugubris* and *S. culebrai* (node I; = subgenus *Parastathmonotus*), and in the other, it is the sister group of *S. hemphilli* (node K; see below).

The following discussion is organized by nodes labelled in Figure 21. Synapomorphies supporting each internal node and selected terminal taxa are discussed. Character numbers used in the text are the same as those scored in Table 1.

NODE A: CHAENOPSIDAE.—The expanded Chaenopsidae can be characterized by as many as eight apomorphies (characters 1–8), but these vary in their degree of homoplasy. Some of these apomorphies appear to be unique to chaenopsids, whereas others may hold evidence of their outgroup relationships (see below).

Character 1: Chaenopsids are unique among the Blennioidei in having a relatively long palatine (state 1), which is 70 percent or more of the palatovomerine length (distance from anteriormost tip of vomer to posteriormost reach of palatine; Figure 22*a,b*). In other blennioids, the

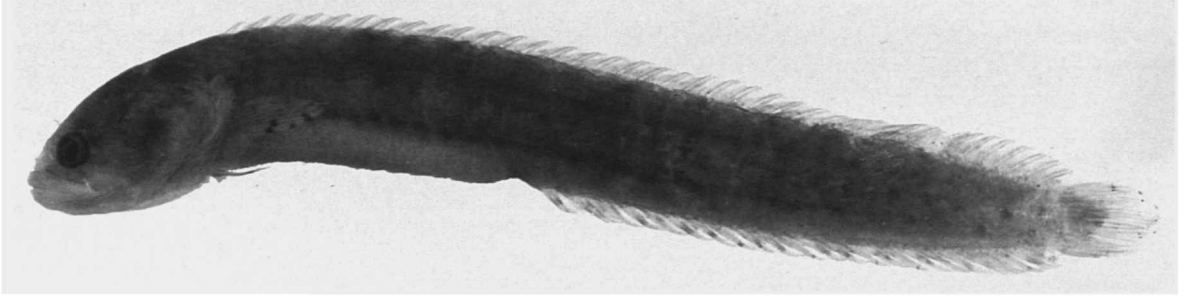
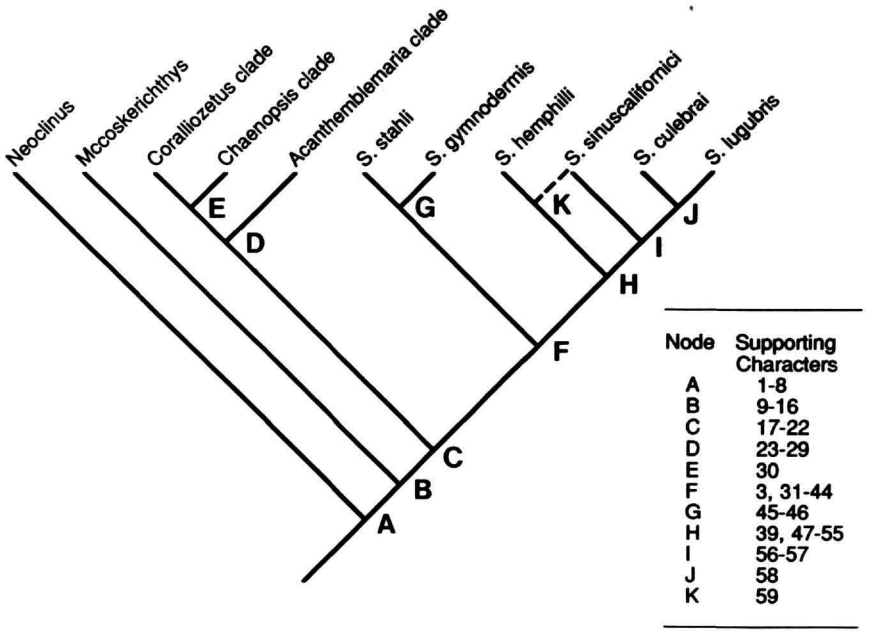


FIGURE 20.—*Stathmonotus lugubris,* UAZ 71-70-24, Puerto Vallarta, Jalisco, Mexico, right side reversed (photograph by T.B. Griswold).



Node	Supporting Characters
A	1-8
B	9-16
C	17-22
D	23-29
E	30
F	3, 31-44
G	45-46
H	39, 47-55
I	56-57
J	58
K	59

FIGURE 21.—Hypothesized phylogenetic relationships of the Chaenopsidae. Each node (designated by letters), and its supporting apomorphies, are discussed in text. Two equally parsimonious topologies differ only in the relationships of *S. sinuscalifornici*. In one, indicated by the solid line to node I, it is the sister group of *S. culebrai* and *S. lugubris;* in the second, indicated by the dashed line to node K, it is the sister group of *S. hemphilli*.

palatine is relatively shorter (Figure 22*d*), attaining only 60 percent or (usually) less of the palatovomerine length (state 0). One consequence of the elongated palatine of chaenopsids is that palatine teeth, when present, oppose those of the dentary (Figure 22*c*). This condition has been elaborated in some chaenopsins such as *Acanthemblemaria,* in which a double row of palatine teeth oppose those of the dentary (Smith-Vaniz and Palacio, 1974; Rosenblatt and Stephens, 1978; Hastings, 1990).

Character 2: In chaenopsids, the finger-like ventral arm of the posttemporal does not contact the neurocranium, but it is connected to the intercalar by a relatively long ligament (state 1; Figure 23*a*). The ventral arm of the posttemporal of *Mccoskerichthys* is unique in that it is short and rounded rather than finger-like, but it is not particularly close to the skull (state 2; Figure 23*b*). In most other blennioids, the ventral posttemporal arm is slender and lies close to the neurocranium, and the ligament is relatively short (state 0). Exceptions include the Dactyloscopidae and some clinids, such as *Cancelloxus, Ophioclinops, Springeratus,* and *Xenopoclinus,* in which the ventral arm is well separate from the neurocranium, as it is in chaenopsids.

Character 3: The posterior portion of the lateral line is absent in all members of the Chaenopsidae. The lateral line of many blennioids consists of tubed scales (or tube-shape ossicles in blenniids) that extend posteriorly to, or near to, the caudal-fin base (state 0). In *Neoclinus, Nemaclinus,* and some blenniids, ossifications associated with the lateral line extend only about midway along the body, the posterior portion being absent (state 1). In *Stathmonotus* (as well as the blenniids *Andamia* and some species of *Alticus*), a single tube-shape bone, presumably homologous with the first lateral-line ossification of other blennioids, is present just posterior to the posttemporal (state 2; Figure 5*c*); the remainder of the lateral line is absent except for a mid-lateral row of placodes. In *Mccoskerichthys* and all chaenopsins, lateral-line ossifications are completely absent (state 3). Although chaenopsins have been said to have a few pores posteriorly along the body (e.g., Böhlke, 1957), no pores were observed in our study. However, pits with neural placodes may be evident in some chaenopsins (e.g., *Acanthemblemaria* species), but these are not associated with any observable ossification. *Haptoclinus* also lacks an anterior and posterior lateral line, but we could not confirm the presence or absence of the first tube typical of *Stathmonotus*.

Character 4: In chaenopsids, the upper jaw of males is long, with the maxillary extending to or beyond the

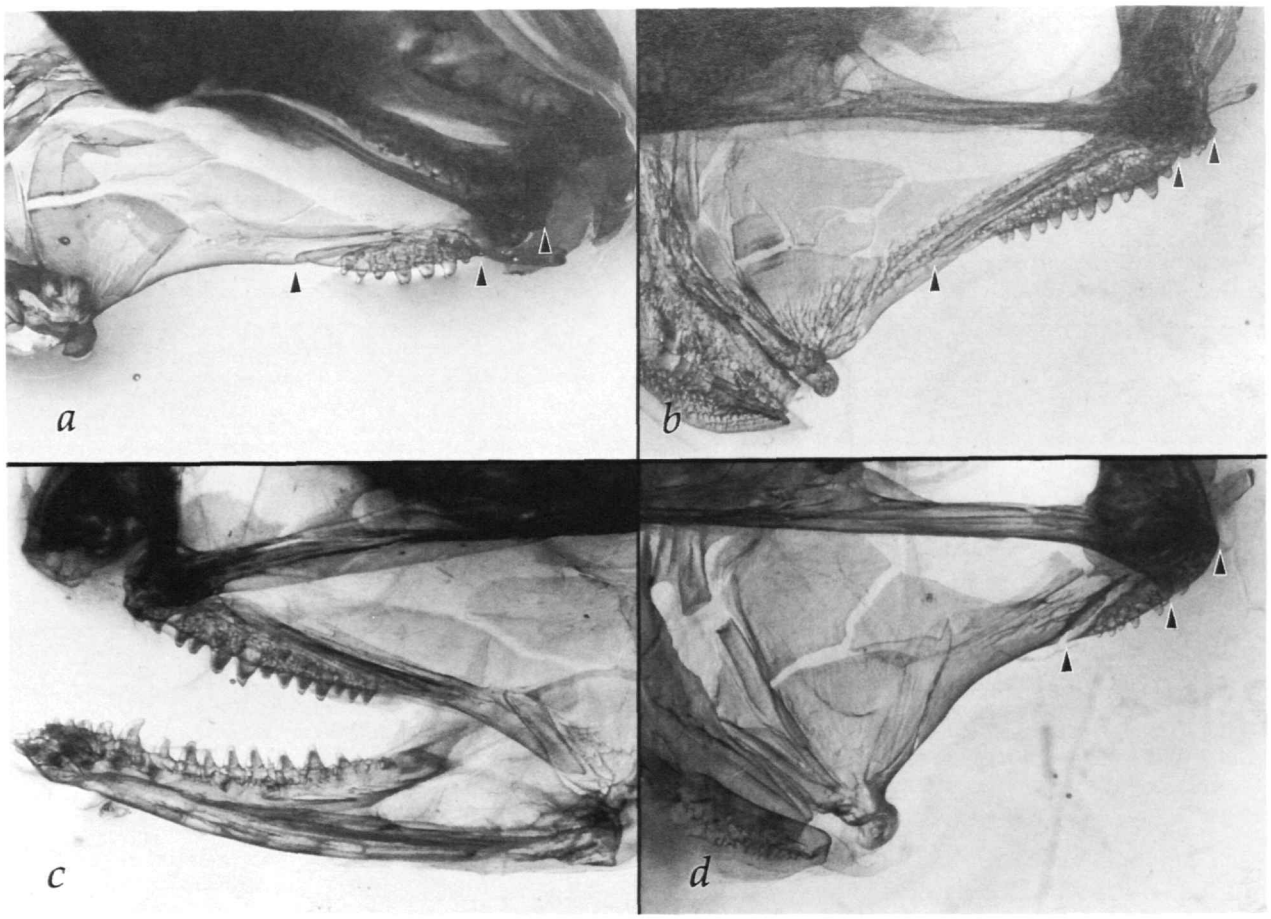


FIGURE 22.—*a*, Medial view of left suspensorium of *Neoclinus stephensae* (LACM 38626). *b*, Medial view of left suspensorium of *Ekemblemaria myersi* (UAZ 69-48). *c*, Medial view of right suspensorium of *Ekemblemaria myersi* (UAZ uncat., PAH 8222) with lower jaw intact; note that palatine teeth oppose those on ramus of lower jaw. *d*, Medial view of left suspensorium of *Starksia spinipenis* (UAZ 74-48). In *a*, *b*, and *d*, right, central, and left arrows indicate, respectively, anterior tip of vomer, anterior end of palatine, and posterior end of palatine.

posterior margin of the orbit (state 1; see Figure 24*a*,*b*). Exceptions within chaenopsids include *S. hemphilli* and the paedomorphic *Lucayablennius zingaro* (see Hastings, 1992b), in which males have a short jaw. The jaw of males of most other blennioids does not extend posteriorly past the level of the posterior margin of the orbit (state 0; see Figure 24*c*). Exceptions include a few species of labrisomids, in which the maxillary extends to near the posterior orbital margin (e.g., *Labrisomus bucciferus*, *Starksia galapagensis*) or well beyond the orbit (e.g., *Paraclinus cingulatus*, *P. grandicornis*, and *P. nigripinnis*).

Character 5: The jaw of females of *Neoclinus*, *Mccoskerichthys*, and most chaenopsins, like that of males, is long and extends posteriorly beyond the level of the posterior margin of the orbit (state 1). The jaw of females of most other blennioids does not extend posteriorly past the level of the posterior margin of the orbit (state 0). Exceptions within chaenopsids include females of *Stathmonotus*, *Coralliozetus*, *Emblemaria*, and *Chaenopsis* (Stephens, 1963; Hastings, 1991), which have a short jaw.

Character 6: All members of the Chaenopsidae exhibit a posterior shift in the relative position of the hyomandibula (state 1). The anterior condyle on the dorsal margin of the hyomandibula inserts on the neurocranium well posterior to the junction of the infraorbital series with the frontal (Figure 24*a*,*b*); the

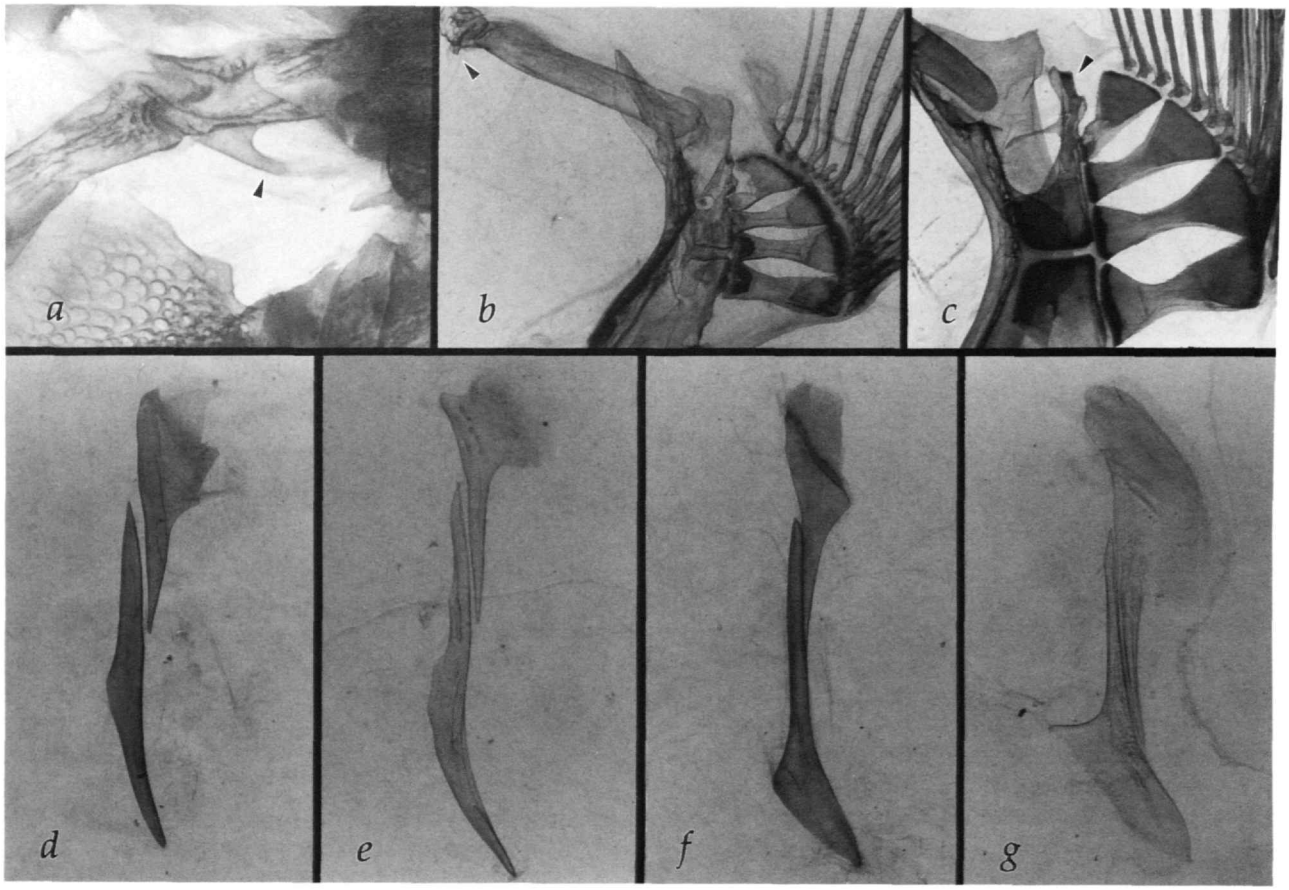


FIGURE 23.—*a*, Lateral view of right posttemporal of *Ekemblemaria myersi* (UAZ uncat., PAH 8222); note that lower arm (indicated by the arrow) is well separated from neurocranium, but it is connected to it by a ligament. *b*, Lateral view of left pectoral girdle of *Mccoskerichthys sandae* (USNM 214706); arrow indicates reduced lower process of posttemporal. *c*, Lateral view of left pectoral girdle of *Neoclinus stephensae* (LACM 38626); arrow indicates upper scapular arm. *d–g*, Lateral views of left, upper and lower postcleithra; anterior is to left. (*d* = *Neoclinus stephensae*, LACM 38626; *e* = *Emblemaria atlantica*, UWF 2937; *f* = *Gibbonsia montereyensis*, SIO 50-279; *g* = *Malacoctenus margaritae*, UAZ uncat., PAH 8125.)

distance from the point on the frontal where the dorsalmost infraorbital inserts to the anterior condyle of the hyomandibula is one-third or more of the distance from the frontal/infraorbital juncture to the anteriormost point of the posttemporal on the dorsal part of the neurocranium (i.e., near the posterior end of the neurocranium). In clinids, tripterygiids, and most labrisomids (Figure 24*c*), the anterior condyle on the dorsal margin of the hyomandibula inserts on the neurocranium just posterior to the junction of the infraorbital series with the frontal (state 0); the distance from the point on the frontal where the dorsalmost infraorbital inserts to the anterior condyle of the hyomandibula is less than one-fourth of the distance from the frontal/infraorbital juncture to the anteriormost point of the posttemporal on the dorsal part of the neurocranium. However, the apparently derived condition of this character is not restricted to chaenopsids; the labrisomid tribe Starksiini, some blenniids (Springer, 1968), and the Dactyloscopidae also have the hyomandibular insertion shifted posteriorly (see below).

Character 7: In most chaenopsids, the sphenotic bears a lateral process, the sphenotic spine (Springer, 1968), which projects posteroventrally toward the anterior insertion of the hyomandibula (state 1; Figures 1, 3). Within the Chaenopsidae, exceptions include the chaenopsin genera *Protemblemaria* and *Coralliozetus*, which lack a sphenotic spine (Hastings, in prep.), and

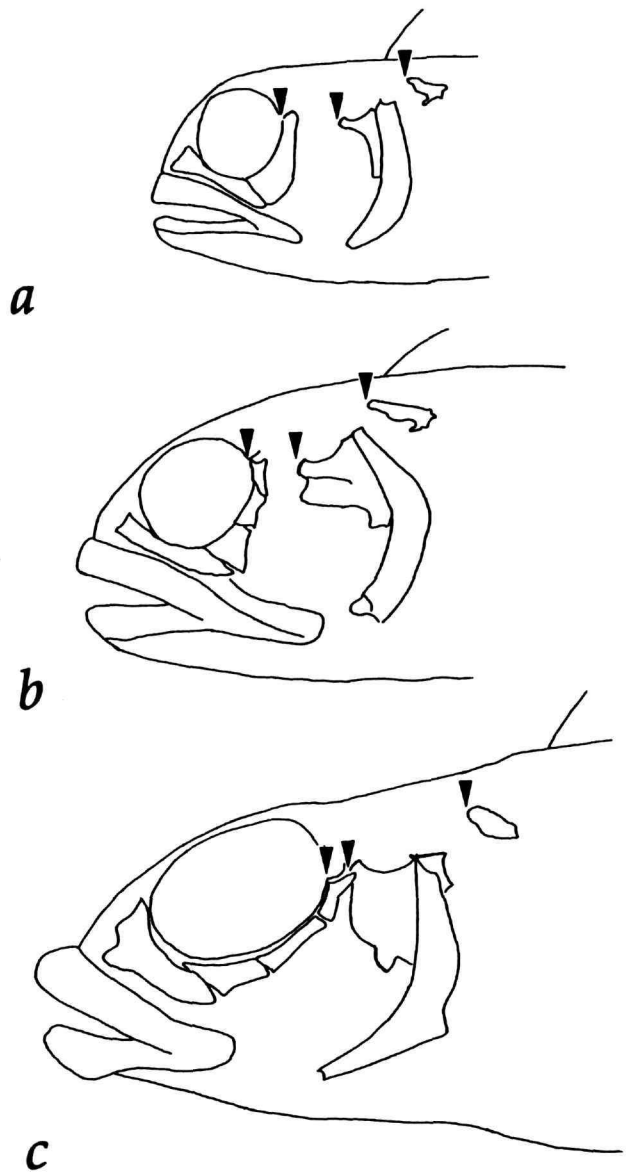


FIGURE 24.—Hyomandibular insertion relative to infraorbital and posttemporal insertions in three blennioids. *a*, *Ekemblemaria myersi* (UAZ 69-48-8); *b*, *Neoclinus bryope* (UAZ uncat.); *c*, *Labrisomus pomaspilus* (UAZ 63-25-9). Arrows, from left to right, indicate insertion of dorsalmost infraorbital, anterior insertion of hyomandibula, and anterior insertion of posttemporal.

Neoclinus, in which the spine may be pointed, a broad flange, or apparently absent (e.g., *N. stephensae*). In *Mccoskerichthys*, the sphenotic spine is fan-shape, expanding distally. In most other blennioids, a bony ridge extends from the orbital region posteriorly along the otic canal crossing the sphenotic (state 0). However, a sphenotic spine is not restricted to the Chaenopsidae, as it also is seen in the Blenniidae (Springer, 1968) and some species of the labrisomid tribe Starksiini (see below).

Character 8: In *Stathmonotus*, all chaenopsins, and most species of *Neoclinus*, the dorsal portion of the scapula is thin and well separated from the cleithrum (state 1; Figure 23*c*). In most other blennioids, this arm is

broad and closely applied to the posterior margin of the cleithrum (state 0). However, the upper scapular arm of *Neoclinus nudus* is stout and closely applied to the cleithrum, and that of *Mccoskerichthys*, although short, is closely applied to the cleithrum (Figure 23*b*).

A behavioral character, use of shelters, also may support the monophyly of the Chaenopsidae. Members of the Chaenopsinae are well-known for occupying vacant invertebrate tests (Stephens, 1963), as are species of *Neoclinus* (Fukao, 1980, 1987) and *Mccoskerichthys* (Rosenblatt and Stephens, 1978). Although the microhabitats of *Stathmonotus* species are not well-known, James C. Tyler (pers. comm.) recently collected a specimen of *S. hemphilli* from a hole in a coral, and *S. sinuscalifornici* has been collected from the osculum of a sponge (SIO 68-176), indicating that some members of this genus may also inhabit such shelters. Among other blennioids, the habit of shelter-dwelling is common only among the Blenniidae. If the outgroup of the Chaenopsidae lies within the Labrisomidae (see below), then the habit of shelter-dwelling is also a synapomorphy of the Chaenopsidae.

A recent study using allozyme data from a limited number of taxa (Stepien et al., 1993) indicated that *Neoclinus* is the sister group of a clade containing the Clinidae and a paraphyletic Labrisomidae, and that the Chaenopsinae (as defined herein) is the sister group of that clade. Although not fully supporting our results, the placement of *Neoclinus* outside of the Labrisomidae and close to the Chaenopsinae would be consistent with our results if the trees presented by Stepien et al. (1993) were rooted differently. Additional allozyme data, especially on *Mccoskerichthys* and *Stathmonotus*, are needed for a more direct comparison of these hypotheses.

The taxa we include in the Chaenopsidae, with the exception of *Mccoskerichthys* and a few chaenopsin genera, which were unknown at the time, and *Stathmonotus* (*Auchenistius*) *stahli*, which was considered to be a clinid, were included by Hubbs (1953a) in the Blenniidae as the subfamily Chaenopsinae. Within our redefined Chaenopsidae, we recognize the same lineages as did Hubbs, except as noted below.

By including *Stathmonotus* in the Chaenopsidae, we have revived an hypothesis of its relationships first presented by Jordan (1923). Although Kotrschal (1988) recently noted a similarity in the jaw morphology between *Stathmonotus* and chaenopsins, most recent authors have placed *Stathmonotus* in the Labrisomidae, hypothesizing that it is closely related to *Paraclinus* (Hubbs, 1952; Springer, 1955). Two character states support this hypothesis. First, *Stathmonotus* and some species of the Paraclinini are unique among blennioids in having only spines in the dorsal fin (see character 38); however, some species of *Paraclinus* have a single segmented dorsal-fin ray. Second, *Stathmonotus*, the Paraclinini, and the Starksiini are unique in having a deep notch in the dorsal margin of the upper lip (see character 36). However, our parsimony analysis does not support this hypothesis of relationships; rather it indicates that *Stathmonotus* is indeed a chaenopsid.

TAXA OF UNCERTAIN AFFINITIES.—Another possible member of the Chaenopsidae is the enigmatic blennioid *Haptoclinus* Böhlke and Robins, 1974. Its only species, *H. apectolophus*, shares with the Chaenopsidae a free ventral posttemporal process (character 2, state 1), loss of the posterior lateral line (3, state 1), and a long upper jaw, at least in males (4, state 1). It also shares several character states with selected lineages within the Chaenopsidae, but it is unlike chaenopsids in having a relatively short palatine (1, state 0) and in having the hyomandibular inserted just behind the orbit (6, state 0). We were unable to score several characters for *Haptoclinus* (Table 1); consequently, until additional material of this genus becomes available and its morphology is better known, its relationship to chaenopsids cannot be fully analyzed.

The blennioid genus, *Nemaclinus* Böhlke and Springer, 1975, shares some character states with all or portions of the Chaenopsidae: loss of the posterior portion of the lateral line (character 3), a nonautogenous ventral hypural plate (see character 14), and simple head pores (see character 15). However, it does not share the remaining chaenopsid apomorphies (characters 1, 2, 4–8). Although apparently not a chaenopsid, we consider its phylogenetic relationships otherwise unresolved.

OUTGROUP RELATIONSHIPS OF THE CHAENOPSIDAE

No known apomorphy unequivocally unites the Chaenopsidae with any other currently recognized family or clade of blennioid fishes. Consequently, its outgroup relationships remain unresolved. Several factors have contributed to our continued inability to resolve these relationships. First, the interrelationships of the other families of the Blennioidei are unresolved and essentially unhypothesized (Springer, 1993). Second, the monophyly of the Labrisomidae, recently split from the Clinidae (Springer and Freihofer, 1976; George and Springer, 1980), is in doubt (Springer, 1993; Stepien et al., 1993). Third, it is clear that homoplasy is common in these fishes and may be obscuring their relationships.

A parsimony analysis of intrarelationships of the Blennioidei is beyond the scope of our study. However, in searching for clues to the outgroup relationships of the Chaenopsidae, we have discovered some new characters that may provide information of blennioid intrarelationships. Rather than attempt a parsimony analysis of all blennioids, we present a brief discussion of some of the evidence for blennioid intrarelationships as it pertains to chaenopsids.

Böhlke (1957) and Stephens (1963) considered chaenopsids to be related to *Neoclinus*, and, by implication, to other "clinid" blennies, which then included *Neoclinus*, the Clinidae, and the Labrisomidae. George and Springer (1980) defined a restricted Clinidae (essentially the Clininae of Hubbs, 1952), and its monophyly subsequently has been supported by Stepien (1992) and Springer (1993). Stepien et al. (1993), using allozyme data,

also confirmed the monophyly of the Clinidae and hypothesized that (1) the Labrisomidae is paraphyletic, (2) the Clinidae plus all labrisomid tribes form a monophyletic group, (3) *Neoclinus* is that clade's sister group, and (4) the Chaenopsidae (= Chaenopsinae) is the sister group to that entire clade.

We have identified one morphological character that may support the second assertion of Stepien et al. (1993), that the Clinidae and Labrisomidae form a monophyletic group. The ventral postcleithrum is thin and slightly curved posteriorly in most blennioids including tripterygiids, dactyloscopids, blenniids, and all chaenopsids (sensu lato; Figure 23*d,e*). In at least some members (e.g., *Clinitrachus, Heterostichus,* and *Gibbonsia*) of the apparently specialized clinid tribe Myxodini (whose monophyly has not been hypothesized based on morphological characters), and at least some members of all tribes of the Labrisomidae, the ventral tip of the ventral postcleithrum is expanded into a broad blade (Figure 23*f,g*). However, the ventral postcleithrum is slender in the clinid tribes Clinini and Ophiclinini, in at least two species of the Paraclinini (*P. cingulatus* and *P. infrons*), in one species of the Starksiini (*Starksia nanodes*), and in the cryptotreminin labrisomids *Auchenionchus* and *Calliclinus* (but it is expanded in the cryptotreminin genera *Alloclinus* and *Cryptotremus*). Considering the apparent monophyly of the Clinidae (Stepien, 1992; Springer, 1993), it may be that an expanded ventral postcleithrum is a synapomorphy of the clinid-labrisomid clade that has reversed within the Clinidae and repeatedly within labrisomids. The alternative is that an expanded ventral postcleithrum evolved independently in the Myxodini and probably repeatedly in the paraphyletic labrisomids.

We have identified two characters that support the sister group relationship of the Chaenopsidae sensu lato with the Clinidae and Labrisomidae. However, this interpretation is dependent upon the monophyly of the Chaenopsidae sensu lato (node A, Figure 21). The first character concerns the distribution of sensory pores on the ramus of the lower jaw (see character 20). In all blennioids, the mandibular canal extends from the preopercular canal anteriorly through the angulo-articular and dentary, ending near the dentary symphysis, where a single pore (M1A) is located. In labrisomids, at least some clinids (e.g., *Gibbonsia*), *Neoclinus,* and *Mccoskerichthys* (Figure 25*a*), a second pore (M1B) opens on the medial side of the canal directly posterior to the first pore (state 1). M1B is absent (state 0) in *Stathmonotus* and all chaenopsins (Figure 25*b*). Tripterygiids and dactyloscopids also appear to lack M1B. The mandibular pores of blenniids are difficult to compare with those of labrisomids and chaenopsids because of the relatively short dentary and high degree of variation in number and position of mandibular pores in blenniids. Nevertheless, the presence of M1B in at least some chaenopsids (*Neoclinus* and *Mccoskerichthys*), in all labrisomids, and in some clinids, supports the monophyly of a clade containing the Labrisomidae, Clinidae, and Chaenopsidae. The absence of M1B in *Stathmonotus* and the Chaenopsinae apparently represents a secondary loss (Figure 26*a*).

The second character supporting the sister group relationship of the Chaenopsidae sensu lato with the Clinidae and Labrisomidae involves the shape of the proximal-middle dorsal-fin pterygiophores supporting spines (see character 29). In all blennioids, these pterygiophores bear a cartilage-tipped, rod-shape ossification near their anterior margin (Figure 27). A second ossified ridge, lacking a cartilage tip, is present posterior to the cartilage-tipped rod (state 1) in labrisomids, clinids, and *Stathmonotus*. In *Neoclinus* and *Mccoskerichthys,* this second ridge is present on at least some pterygiophores, although it is always much weaker than the anterior ridge (Figure 27*a,b*). This second ridge is absent (state 0) in blenniids, tripterygiids, dactyloscopids, and all chaenopsins (Figure 27*c,d*). Assuming the monophyly of the Chaenopsidae sensu lato, this character supports its sister group relationship

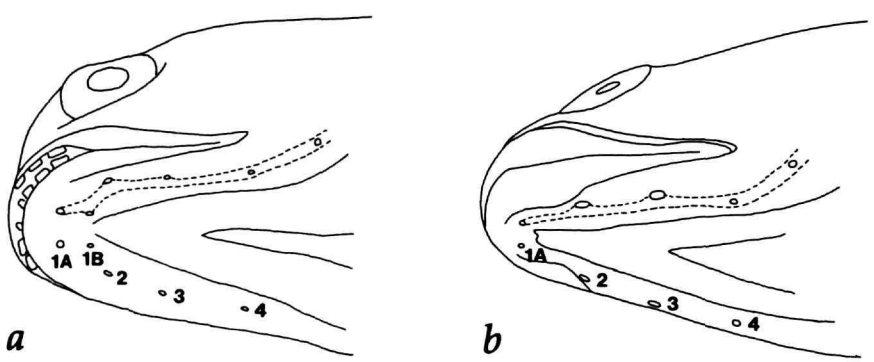


FIGURE 25.—Ventrolateral view of head of two chaenopsids. *a, Mccoskerichthys sandae* (USNM 317709); *b, Ekemblemaria myersi* (UAZ uncat., PAH 8222). Mandibular sensory pores on right side are numbered; dotted line on left side indicates relationship of pores and underlying sensory canal.

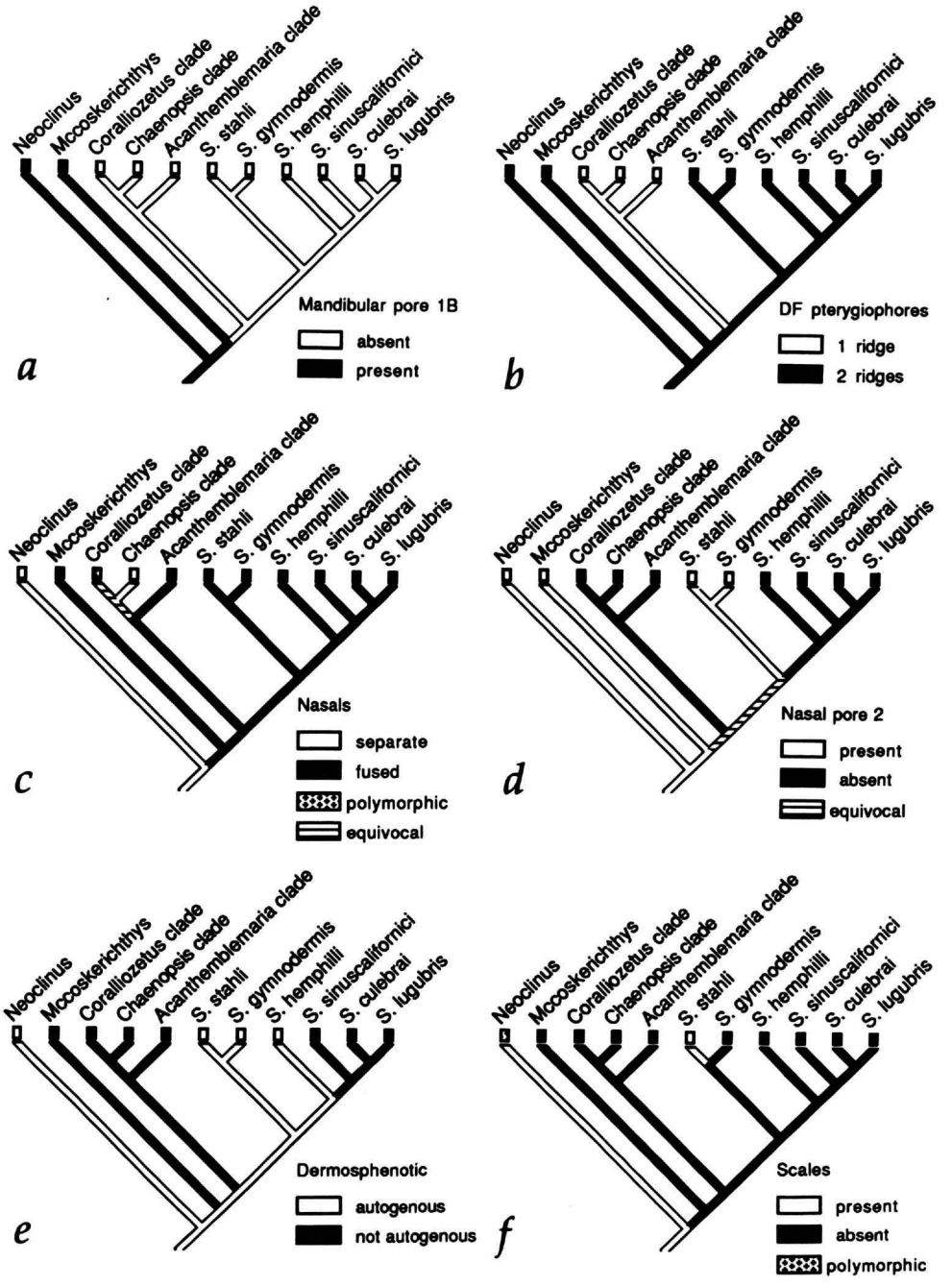


FIGURE 26.—Character maps for six characters on one of the most parsimonious topologies. *a*, Presence or absence of mandibular sensory pore 1B (character 20). *b*, Number of lateral ridges on dorsal-fin pterygiophores supporting spines (character 29). *c*, Nasals separate or fused (character 10). *d*, Presence or absence of nasal pore 2 (character 55). *e*, Dermosphenotic autogenous or not (character 57). *f*, Presence or absence of scales (character 61).

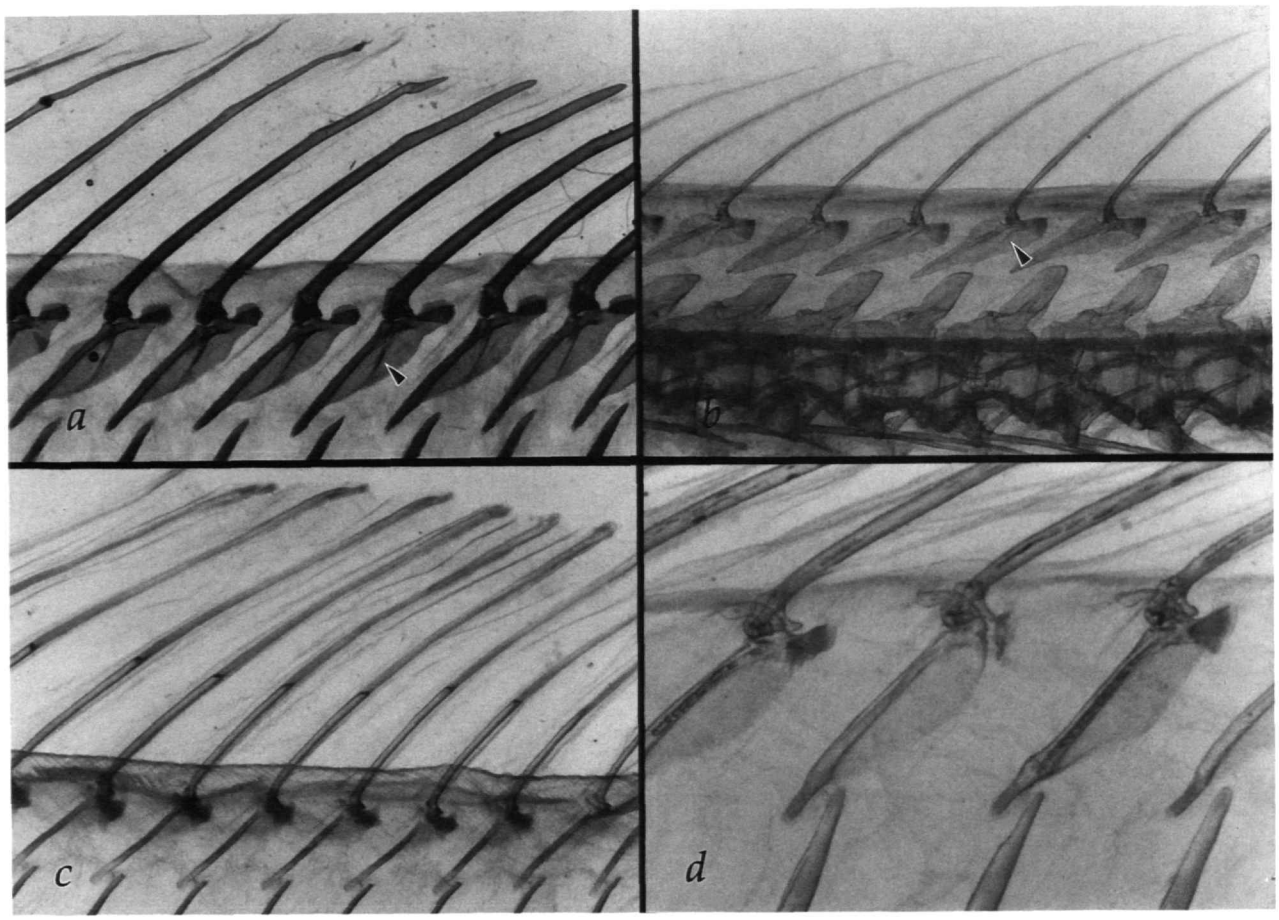


FIGURE 27.—*a–c*, Lateral views of left side of middle of spinous dorsal fin for three chaenopsids (*a* = *Neoclinus stephansae*, LACM 38626; *b* = *Mccoskerichthys sandae*, USNM 214706; *c* = *Coralliozetus micropes*, UAZ 84-17). *d*, Lateral view of dorsal-fin pterygiophores of *Protemblemaria bicirris* (UAZ uncat., PAH 8320). Arrows in *a* and *b* indicate second lateral ridge on proximal pterygiophores (absent in *c* and *d*).

with the Clinidae and Labrisomidae, with the absence of this ridge in the Chaenopsinae representing a secondary loss (Figure 26*b*). This seems plausible; although the ridge is well-developed in *Stathmonotus*, it is weak, at best, in *Neoclinus* and *Mccoskerichthys* and could well have been lost in the Chaenopsinae.

Because the Labrisomidae may not be monophyletic (Stepien et al., 1993), one or more of its included lineages could be the sister group of the Chaenopsidae. Among the currently recognized tribes of labrisomids, the Starksiini share the greatest number of apparent apomorphies with chaenopsids. These include a posterior insertion of the hyomandibula (character 6, state 1; also seen in the Dactyloscopidae and Blenniidae) and presence of a sphenotic spine (character 7, state 1; also present in many blenniids). The Chaenopsidae without *Neoclinus* shares four apparent apomorphies with Starksiini: a single epural (see character 13), a nonautogenous ventral hypural plate (see character 14), relatively simple cephalic sensory pores (see character 15), and a spur on the lateral surface of the hyomandibula (see character 16). However, these four characters exhibit a high degree of homoplasy within these and other blennioids, suggesting that they may not be reliable indicators of relationships at this level.

Hubbs (1953a) considered chaenopsins, together with *Neoclinus* and *Stathmonotus* (but not the scaled *Auchenistius stahli*), to be a subfamily of the Blenniidae. He based this on their high, anterior eyes, stout suborbitals (= infraorbitals), incisor-like recurved teeth, and reduced or absent scales. However, the homology of eye position in these fishes is difficult to assess, the infraorbitals of blenniids and chaenopsids are quite different, the teeth of *Neoclinus* and most chaenopsins are not incisor-like, and scales may have been lost

(or regained) more than once in blennioids (see character 61). Hubbs' (1953a) hypothesis is not supported by his listed characters, and it has received little subsequent empirical support. We have found other character support for the sister group relationship of chaenopsids and blenniids, however, and cannot confidently exclude Hubbs' hypothesis.

Blenniids and chaenopsids share apparently derived states of two characters, a posterior insertion of the hyomandibula (character 6, state 1; also present in the Starksiini and Dactyloscopidae) and presence of a sphenotic spine (character 7, state 1; also present in the Starksiini). The Chaenopsidae without *Neoclinus* shares one apomorphy with some members of the Blenniidae (e.g., *Plagiotremus, Entomacrodus*): presence of a neural spur on the anterior precaudal vertebrae (see character 9). The Chaenopsidae without both *Neoclinus* and *Mccoskerichthys* (i.e., Chaenopsinae and *Stathmonotus*) shares one apparent apomorphy with some of the Blenniidae: muscles of the adductor mandibularis A2 complex (sensu Winterbottom, 1974) cover the dorsal portion of the neurocranium (see character 17 and figures in Kotrschal, 1988). Finally, the median-fin spines of chaenopsins are not ossified to their tip (see character 27), a condition also present in a few blenniids (e.g., *Hypsoblennius, Salarias*) and in dactyloscopids.

Resolution of the outgroup relationships of chaenopsids unfortunately must await a phylogenetic analysis of the entire suborder Blennioidei. Until that task is accomplished, further speculation is unwarranted.

Ingroup Relationships of the Chaenopsidae

Neoclinus.—Our phylogenetic analysis indicates that the genus *Neoclinus* is the sister group of the remainder of the Chaenopsidae. *Neoclinus,* which includes nine species (Fukao, 1980, 1987), has not been well-diagnosed morphologically but has been defined by a combination of character states present in a variety of other blennioids (Hubbs, 1953a; Fukao, 1980). Although we have not studied *Neoclinus* in detail, we have identified one possible apomorphy of this genus. All species of *Neoclinus* have a strongly recurved flange on the dorsal margin of the metapterygoid (Figure 28*a*). A similar flange is present in labrisomids and chaenopsins (Figure 28*b*), but it is always relatively smaller in these groups than in *Neoclinus*. This flange is very small or absent in *Mccoskerichthys* (Figure 28*c*) and *Stathmonotus* (Figure 28*d*).

Node B.—*Mccoskerichthys, Stathmonotus,* and the Chaenopsinae are hypothesized to form a monophyletic group (Figure 21). In our study, we found eight apomorphies (characters 9–16) supporting this relationship.

Character 9: In *Mccoskerichthys, Stathmonotus,* and the Chaenopsinae, lateral spurs are present on the neural arches of some or all precaudal vertebrae (state 1). These "neural spurs," illustrated for *Acanthemblemaria* by Hastings (1990, figure 3a,b), are well developed and present on several of the precaudal vertebrae in *Mccoskerichthys* and most chaenopsins. In *Stathmonotus* (Figure 5*d*), neural spurs are present only on the first few precaudal vertebrae and may be difficult to see without dissection. In *Neoclinus* and most other blennioids, the lateral surfaces of the neural arches are simple and lack lateral projections (state 0). Similar neural spurs are, however, present in some blenniids, such as *Plagiotremus* and *Entomacrodus*. Neural spurs are absent from some chaenopsins, including some species of *Ekemblemaria* and *Chaenopsis* (Hastings, 1992a,b), but we infer that they represent secondary losses.

Character 10: The left and right nasals are fused medially (state 1) in *Mccoskerichthys* (Figure 29*a*), *Stathmonotus* (Figure 29*b*), and many members of the Chaenopsinae. In other blennioids, the left and right nasals are completely separate (state 0). The nasals are separate in most species of *Neoclinus*, but those of *N. toshimaensis* and *N. lacunicola* lie close together and may be weakly ankylosed (Fukao, 1980); however, this weak ankylosis does not approximate the strongly fused condition in *Mccoskerichthys, Stathmonotus,* and many chaenopsins. Although once considered a derived condition within chaenopsins (Stephens, 1963), the occurrence of this character state within the outgroups of the Chaenopsinae indicates that "fused nasals" is plesiomorphic within chaenopsins and that "separate nasals" is apomorphic within this clade (Figure 26*c*). This character could plausibly reverse via paedomorphosis because the nasals in chaenopsins are separate in early ontogeny, and separate nasals are seen in paedomorphic females of *Coralliozetus* (Hastings, 1991, in prep.).

Character 11: In *Mccoskerichthys, Stathmonotus,* and most chaenopsins, two branchiostegals attach to the lateral surface of the posterior ceratohyal, two attach to the lateral surface of the anterior ceratohyal, and two lie below and attach to the ventral surface of the anterior ceratohyal (state 1; Figure 29*c*). In most blennioids, one branchiostegal attaches to the lateral surface of the posterior ceratohyal, three attach to the lateral surface of the anterior ceratohyal, and two attach to the ventral side of the anterior portion of the anterior ceratohyal (state 0; Figure 29*d*). The inferred derived condition also is seen in some cryptotreminins (Labrisomidae), tripterygiids, and clinids.

Character 12: The lateral extrascapular is not autogenous (state 1) in *Mccoskerichthys, Stathmonotus,* and chaenopsins. It is autogenous (state 0) in most blennioids, including *Neoclinus*, but may be autogenous or not in the Blenniidae (Springer, 1968).

Character 13: Mccoskerichthys, Stathmonotus, and chaenopsins have only one epural in the caudal fin (state 1). Most other blennioids have more than one (state 0), except for the Starksiini (Labrisomidae), *Notoclinus* (Tripterygiidae), and some blenniids (Springer, 1968, 1993).

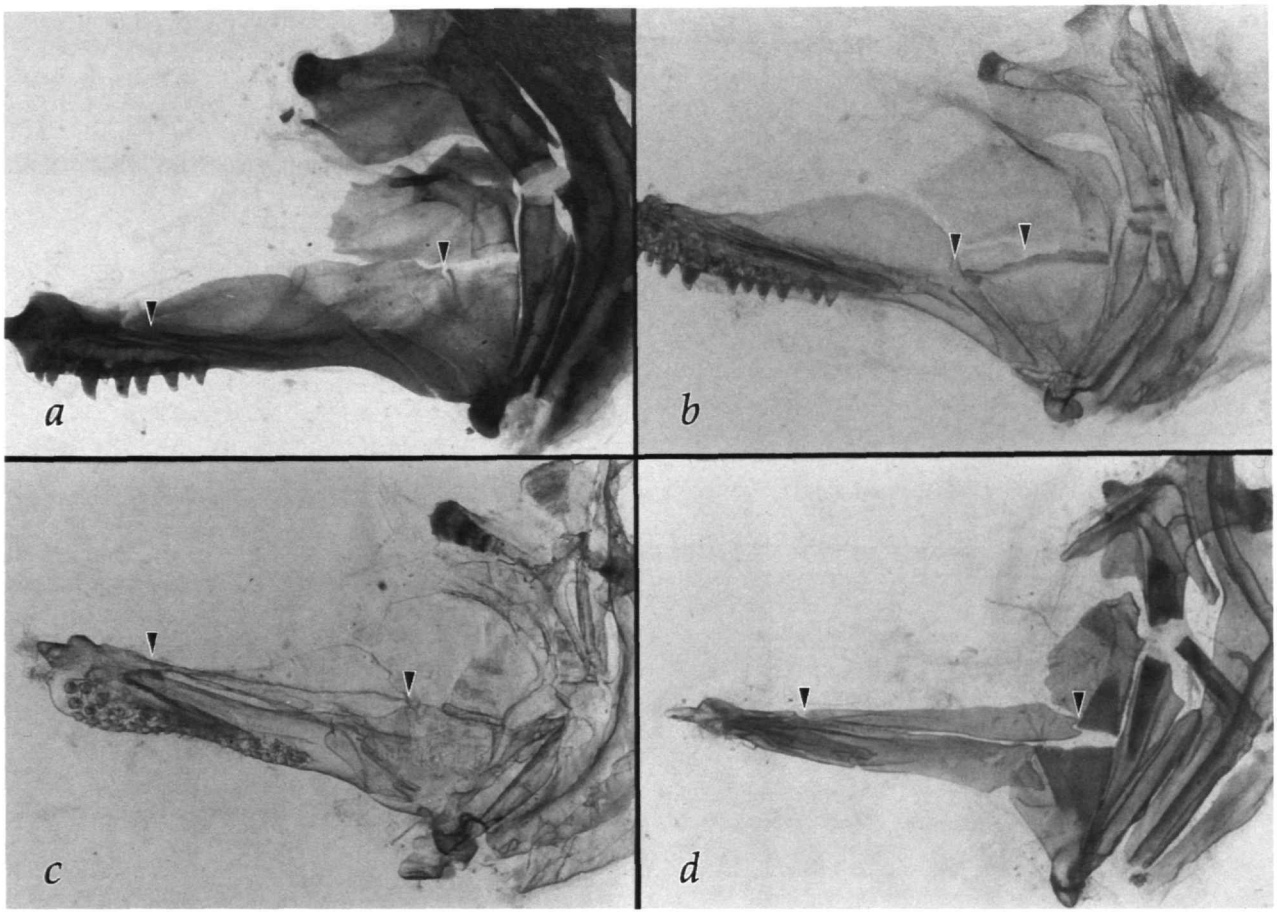


FIGURE 28.—Lateral views of left suspensorium of four blennioids. In each, left and right arrows indicate, respectively, anterior and posterior extent of mesopterygoid. *a, Neoclinus lacunicola* (UAZ uncat.); *b, Protemblemaria bicirris* (UAZ uncat., PAH 8417); *c, Mccoskerichthys sandae* (LACM 32551); *d, Stathmonotus sinuscalifornici* (UAZ 71-36).

Character 14: Mccoskerichthys, Stathmonotus, and the Chaenopsinae have the ventral hypural plate fused to the urostylar vertebra (state 1). The ventral hypural plate, however, is autogenous (state 0) in *Neoclinus* and many other blennioids. The ventral hypural plate is nonautogenous in a variety of blennioids, including the Starksiini, Paraclinini, *Nemaclinus* (Labrisomidae), *Notoclinus* (Tripterygiidae), all clinids, all dactyloscopids, and many blenniids (Springer, 1968, 1993).

Character 15: The cephalic sensory system of *Mccoskerichthys, Stathmonotus,* and chaenopsins is relatively simple in that secondary canals are rare and few pores open along the primary canals (state 1). In many blennioids, including *Neoclinus* and most labrisomids, the cephalic sensory system, especially on the dorsal portion of the head, is more complex with multiple secondary and tertiary canal branches, and numerous small pores opening along these branches (state 0). Simple pores, however, occur also in the Starksiini, *Nemaclinus, Haptoclinus* (Labrisomidae), some clinids, and many blenniids.

Character 16: Mccoskerichthys, Stathmonotus (Figure 3), and most chaenopsins (the sole exception is *Coralliozetus;* Hastings, in prep.) have a spur on the lateral surface of the hyomandibula (state 1). Although absent (state 0) from most blennioids, this spur also is present in some labrisomids, including several species of the Paraclinini, *Labrisomus, Malacoctenus,* and *Nemaclinus* (Böhlke and Robins, 1974).

Mccoskerichthys.—Our phylogenetic analysis indicates that

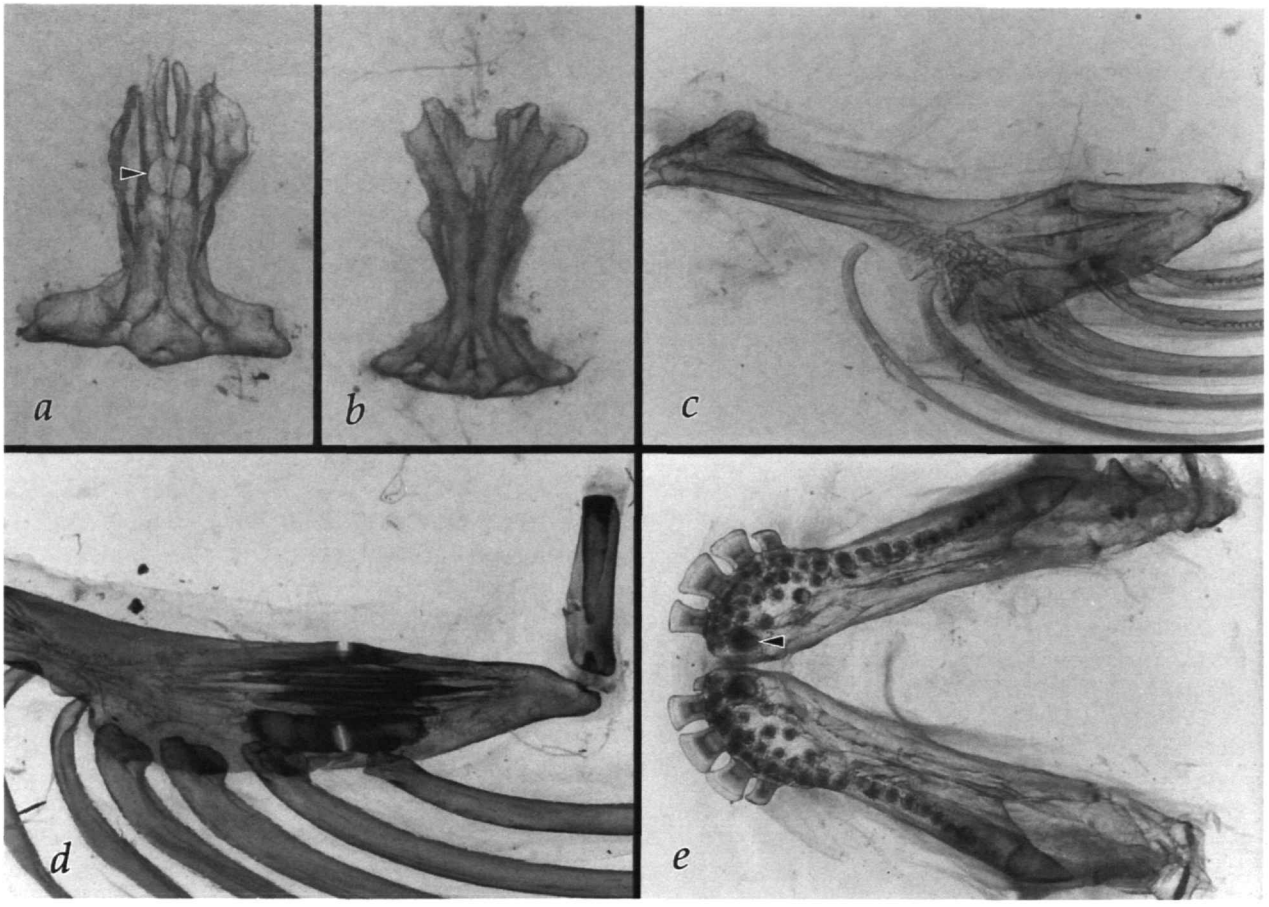


FIGURE 29.—*a*, Fused nasals of *Mccoskerichthys sandae* (LACM 32551); arrow indicates nasal pore 2. *b*, Fused nasals of *Stathmonotus sinuscalifornici* (UAZ 71-36). *c*, Lateral view of left ceratohyals of *Ekemblemaria myersi* (UAZ uncat., PAH 8222); note two branchiostegals inserting on posterior ceratohyal and simple suture between ceratohyals. *d*, Lateral view of left ceratohyals of *Neoclinus stephansae* (LACM 38626); note one branchiostegal inserting on posterior ceratohyal and complex suture between ceratohyals. *e*, Dorsal view of lower jaw of *Mccoskerichthys sandae* (LACM 32551); arrow indicates an enlarged symphyseal tooth.

Mccoskerichthys is the sister group of the remainder of the Chaenopsidae (Figure 21). Rosenblatt and Stephens (1978) commented on the unique morphology of the monotypic *Mccoskerichthys*, and we concur. We report 12 autapomorphies of *Mccoskerichthys*. (1) *Mccoskerichthys* is unique within the Blennioidei in having teeth on the ectopterygoid (Rosenblatt and Stephens, 1978; Figure 28*c*). (2) *Mccoskerichthys* is unusual in having five pairs of highly branched supraorbital cirri (Rosenblatt and Stephens, 1978). The only blennioids with similar elaboration of the supraorbital cirri are several Japanese species of *Neoclinus* (Fukao, 1980, 1987). (3) The left and right premaxillaries of *Mccoskerichthys* are fused medially. (4) The upper jaw of *Mccoskerichthys* is largely immobile, with essentially nonprotrusible premaxillaries that are strongly bound to the maxillaries. (5) *Mccoskerichthys* has broad, spatulate teeth on the outer rows of the premaxilla and dentary (Rosenblatt and Stephens, 1978; Figure 29*e*). Similar teeth occur in some species of the chaenopsin genus *Acanthemblemaria* (Hastings, 1990). (6) *Mccoskerichthys* has a pair of enlarged symphyseal teeth (one on each side) on the dentary (Figure 29*e*). Similar, but not nearly so large, symphyseal teeth occur in some species of *Acanthemblemaria* (Hastings, 1990). (7) *Mccoskerichthys* has ossified gill rakers on the hyoid arch. (8) *Mccoskerichthys* has lateral spurs on the hemal spines of the anteriormost caudal vertebrae. Similar spurs are present on the neural spines of *Mccoskerichthys*, *Stathmonotus*, and most chaenopsins (see character 9), but only *Mccoskerichthys* has them on the hemal spines. (9) In *Mccoskerichthys*, the dorsal

scapular arm is short and does not extend distally as far as the pectoral-fin radials (Figure 23*b*). (10) In *Mccoskerichthys*, the dorsal postcleithrum is triangular rather than elongate. (11) The ventral process on the posttemporal is short and round in *Mccoskerichthys* (see character 2; Figure 23*b*). In other blennioids, the ventral process is finger-like (Figure 23*a*). (12) *Mccoskerichthys* has two pairs of nasal cirri, one on the anterior and one on the posterior margins of the anterior nostril tube. Only the posterior cirrus is present in most other blennioids, although some species of the blenniid genera *Ecsenius*, *Mimoblennius*, and *Cirrisalarias* (Springer, 1968, 1976; Springer and Spreitzer, 1978) have more than one cirrus on the anterior nostril.

NODE C.—Our phylogenetic analysis indicates that *Stathmonotus* and the Chaenopsinae form a monophyletic group (Figure 21). We have identified six apomorphies (characters 17–22) shared by these taxa.

Character 17: In *Stathmonotus* and most chaenopsins, muscles of the adductor mandibularis A2 complex (sensu Winterbottom, 1974) insert on the dorsal portion of the neurocranium (state 1). The few chaenopsins lacking the dorsal extension of these muscles, *Lucayablennius* and female *Coralliozetus* species, are clearly paedomorphic (Hastings, 1991, 1992b). Most other blennioids, including *Neoclinus* and *Mccoskerichthys*, lack these muscles on the dorsal portion of the neurocranium (state 0), although these muscles are present in some blenniids (see illustrations in Kotrschal, 1988).

Character 18: In *Stathmonotus* and chaenopsins, the branchial arches are thin, rod-like bones without lateral flanges (state 1). In most other blennioids, including *Neoclinus* and *Mccoskerichthys*, the branchial arches are heavy and stout, with distinct lateral flanges that are evident when viewed from above (state 0). These flanges are especially prominent on the basibranchials and hypobranchials.

Character 19: In *Stathmonotus* (Figure 8) and chaenopsins, the third basibranchial is unossified (state 1). In other blennioids, including *Neoclinus* and *Mccoskerichthys*, the third basibranchial is fully ossified (state 0).

Character 20: *Stathmonotus* and chaenopsins lack mandibular sensory pore 1B (state 0; Figure 25*b*). This pore is present (state 1) in *Neoclinus*, *Mccoskerichthys* (Figure 25*a*), labrisomids, and clinids, and it may represent a synapomorphy of these groups. If so, the loss of this pore is shared by *Stathmonotus* and chaenopsins (Figure 26*a*).

Character 21: *Stathmonotus* and chaenopsins also lack an otic pore (state 1). One or more pores are present along the otic canal (state 0) in *Neoclinus*, *Mccoskerichthys*, tripterygiids, and most labrisomids. An otic pore also is absent in *Haptoclinus* (Labrisomidae), some clinids, dactyloscopids, and some blenniids.

Character 22: *Stathmonotus* and most chaenopsins have a relatively simple suture between the anterior and posterior ceratohyals; fewer than six total interdigitations are present on the lateral and medial faces (state 1; Figures 6, 29*c*). In most other blennioids, including *Mccoskerichthys* and *Neoclinus* (Figure 29*d*), the junction between the anterior and posterior ceratohyals is more complex, with seven or more total interdigitations on the lateral and medial faces (state 0). Exceptions include many blenniids, which have a simple suture, and some chaenopsins (some species of *Acanthemblemaria* and *Protemblemaria*), which have a complex suture (Hastings, 1990, in prep.).

NODE D: CHAENOPSINAE.—We include 11 genera and approximately 60 species in the Chaenopsinae (= Chaenopsidae sensu Stephens, 1963). Stephens (1963) diagnosed his Chaenopsidae as having two infraorbitals and a unique combination of other traits, such as absence of scales and absence of a lateral line on the body. In our study, we found three unequivocal and four homoplastic apomorphies (characters 23–29) supporting the monophyly of the Chaenopsinae.

Character 23: The Chaenopsinae is unique among the Blennioidei in having the mesopterygoid, when present, oval and restricted posteriorly to a position just dorsal to the quadrate (state 1; Figure 28*b*). In other blennioids, including *Neoclinus* (Figure 28*a*), *Mccoskerichthys* (Figure 28*c*), and *Stathmonotus* (Figures 4, 28*d*), the mesopterygoid is elongate and extends from the quadrate anteriorly along the medial margin of the ectopterygoid to the region of the palatine (state 0). In most chaenopsins, the ectopterygoid is expanded medially, occupying the approximate position of the anterior portion of the mesopterygoid of other blennioids (Figure 28*b*).

Character 24: The Chaenopsinae is unique among the Blennioidei in the distribution of the testicular tissue. In all chaenopsins, the testicular tissue is in a single lobe on the right side of the coelom (state 1; Patzner, 1992; Hastings and Patzner, in prep.). In other blennioids, including *Neoclinus*, *Mccoskerichthys*, and *Stathmonotus*, the testis is bilobed, with a lobe on each side of the coelom and germinal tissue in each lobe (state 0).

Character 25: The Chaenopsinae is unique among the Blennioidei in having a testicular accessory organ that is in a single lobe on the left side of the coelom and not closely applied to the testis (state 1; Patzner and Seiwald, 1988; Patzner, 1992; Hastings and Patzner, in prep.). In other blennioids, the accessory organ, when present, is bilobed and closely associated with both testicular lobes (state 0). *Mccoskerichthys* apparently lacks an accessory organ (Hastings and Patzner, in prep.).

Character 26: As noted by Stephens (1963), virtually all chaenopsins have two (state 1) infraorbitals (IOs). The only known exceptions are rare specimens with three or four IOs (Stephens, 1963), females of *Coralliozetus*, which typically have three IOs (Hastings, 1991), and rare specimens with the IOs fused into a single bone (e.g., observed in specimens of *Ekemblemaria nigra* and *Emblemariopsis diaphana*). Other blennioids, including the other members of the Chaenopsidae (*Neoclinus*, *Stathmonotus*, and *Mccoskerichthys*), have three or more IOs. The only known exception is the blenniid *Medusablennius*, which has two IOs (Springer, 1966).

Three lines of evidence indicate that the chaenopsin condition of two IOs has resulted from the fusion of IOs 2, 3, and 4. First, the anteriormost IO (lacrimal) is similar in size, shape, and position and typically bears three anterior infraorbital (AIO) pores in chaenopsins, *Neoclinus*, *Mccoskerichthys*, and the subgenus *Auchenistius* of *Stathmonotus* (Figure 5*a* and Table 2). Second, in *Neoclinus*, *Mccoskerichthys*, and *Auchenistius* (Figure 5*a* and Table 2), at least three posterior infraorbital pores (PIO) are present, one between IO 1 and 2, one between IO 2 and 3, and one between IO 3 and 4. Chaenopsins typically have three primary PIO pores that appear to be homologous with the PIO series of other chaenopsids. Finally, examination of the cleared and stained larval and postlarval chaenopsins of the genera *Acanthemblemaria*, *Coralliozetus*, and *Protemblemaria* reveals three IOs. All have an elongate IO 1 (lacrimal) with three pores, a short IO 2 with a single pore at its ventral margin, and a moderately long IO 3 with two pores, one at its ventral margin and the other near its midpoint. IO 2 is presumably homologous with IO 2 of other blennioids. The long IO 3 of postlarval chaenopsins is presumably homologous with the fused IOs 3 and 4 of other blennioids, but no suture is evident in it, even prior to its complete ossification.

Character 27: In all chaenopsins, both the dorsal-fin and anal-fin spines are thin and incompletely ossified (state 1; Figure 27*c*). These spines are ossified proximally, but the ossification ends abruptly and the distal portion is a flexible tissue that retains alcian blue stain. The fin spines of dactyloscopids and a few blenniids (e.g., *Hypsoblennius*, *Salarias*) also have an unossified extension like that of chaenopsins, but we believe this condition is convergent. In other blennioids, the fin spines are ossified to their tips (state 0). In nonchaenopsin blennioids with thin and flexible spines, the fin-spine ossification is either a central ossified core that decreases in diameter toward the tip of the spine (e.g., *Mccoskerichthys* and *Neoclinus*, Figure 27*a,b*) or the degree of ossification (as determined by the intensity of staining with alizarin red) decreases gradually toward the tips of the spines and no central core is evident (e.g., some blenniids).

Character 28: In all but one genus of the Chaenopsinae, the posteriormost branchiostegal is expanded or blade-like and, unlike the remaining five branchiostegals, is at least twice as wide near its midpoint as at its proximal portion (state 1). In the chaenopsin genus *Tanyemblemaria* (Hastings, 1992b), as well as most other blennioids, the posteriormost branchiostegal, like the remaining ones, is little if any wider distally than proximally (state 0). A broad, blade-like, posteriormost branchiostegal, similar to that of chaenopsins, also is present in the Dactyloscopidae.

Character 29: Chaenopsins lack the secondary lateral ossified ridge on the proximal dorsal-fin pterygiophores (state 0; Figure 27*c,d*). This ridge, discussed above, is well developed in labrisomids, clinids, and *Stathmonotus*, and weak, but present, in *Neoclinus* and *Mccoskerichthys* (Figure 27*a,b*). Its absence in chaenopsins is hypothesized to be a reversal (Figure 26*b*). This ridge also is absent in blenniids, tripterygiids, and dactyloscopids.

NODE E.—The Chaenopsinae may be divided into three, apparently monophyletic, lineages. The *Acanthemblemaria* clade includes *Acanthemblemaria* (17 species) and *Ekemblemaria* (3; see Hastings, 1990, 1992a). The *Chaenopsis* clade includes *Chaenopsis* (9), *Lucayablennius* (1), *Hemiemblemaria* (1), *Emblemaria* (13), and *Tanyemblemaria* (1; see Hastings, 1992b). The *Coralliozetus* clade includes *Coralliozetus* (6), *Protemblemaria* (3), and *Emblemariopsis* (9; Hastings, in prep.). The *Chaenopsis* clade and the *Coralliozetus* clade are hypothesized to be sister groups (Figure 21) based on a single apomorphy.

Character 30: Members of both of these clades have the epural well separate from the urostylar vertebra (state 1; Hastings, in prep.). In most members of the *Acanthemblemaria* clade, as well as in other blennioids, the epural is inserted in a slot in the urostylar vertebra (state 0).

NODE F: *Stathmonotus*.—Our study provides strong support for the monophyly of *Stathmonotus* as defined by Springer (1955). These six species share the apparently derived condition of 15 characters (characters 3 and 31–44).

Character 3 (state 2): The lateral line of five species of *Stathmonotus* is represented by a single tubular bone posterior to the posttemporal (Figure 5*c*) and a series of mid-lateral ossified placodes (state 2); a single tubular bone also is present in the fully scaled *S. stahli*, and the placodes are evident on some midlateral scales. Although considerable variation exists in the lateral line of other blennioids, this configuration otherwise is present only in a few blenniids.

Character 31: The number of anterior anal-fin pterygiophores is reduced in *Stathmonotus* such that one or more of the anterior hemal spines usually lacks an

associated pterygiophore (state 1; Figures 10, 11*c*). In other blennioids, there are more anal-fin pterygiophores than hemal spines in the anterior region of the anal fin (state 0).

Character 32: The first anal-fin pterygiophore in *Stathmonotus* is open, with a strut extending ventrally, anterior to the insertion of the first spine (state 1; Figure 11*c*). In other blennioids, the first anal-fin pterygiophore is closed, forming a ring-joint with the first spine (state 0).

Character 33: In five species of *Stathmonotus*, the lateral surface of the metapterygoid bears a well-developed bony flange (state 1; Figure 3). In the sixth species, *S. hemphilli*, this flange is small or sometimes absent. The lateral surface of the metapterygoid lacks a similar flange (state 0) in all other blennioids examined.

Character 34: The number of dorsal and ventral procurrent caudal-fin rays is reduced in *Stathmonotus*, usually to one, two, or occasionally three (state 1; Figure 10). In virtually all other blennioids, at least three and usually four or more procurrent rays are present both dorsally and ventrally (state 0). One exception is the blenniid *Xiphasia*, which also has reduced numbers of procurrent rays (Springer, 1968).

Character 35: The epineurals of *Stathmonotus* are large, and those on the precaudal vertebrae (except the anteriormost) articulate on the ventral prezygopohyses (state 1; Figure 11*a,b*). In other blennioids, the epineurals on the precaudal vertebrae are thin and usually contact the vertebrae via a ligament (state 0).

Character 36: The upper lip of *Stathmonotus* is deeply incised medially (state 1). A similar incision or notch is present in the labrisomid tribes Paraclinini and Starksiini, but it is absent (state 0) from other blennioids.

Character 37: In all species of *Stathmonotus*, the posterior margin of the preopercle is not free, rather it is obscured by skin (state 1). In most other blennioids, the skin covering the preopercle tucks under the posterior margin such that the posterior margin of the preopercle is evident externally (state 0). The posterior margin of the preopercle of blenniids is similar to that of *Stathmonotus*.

Character 38: The dorsal fin of *Stathmonotus* is composed of only spines (state 1). The dorsal fin of other blennioids (except the labrisomids *Exerpes* and some species of *Paraclinus*) has one or more segmented rays (state 0).

Character 39: In *Stathmonotus*, the insertion of the anteriormost dorsal-fin pterygiophore is relatively far posterior. In two species (*stahli* and *gymnodermis*), the first pterygiophore inserts posterior to the neural spine of the second vertebra (state 1; Figure 11*d*). In the remaining four species (*hemphilli, sinuscalifornici, culebrai,* and *lugubris*), the first pterygiophore inserts posterior to the neural spine of the third or fourth vertebra (state 2; Figure 10). In other blennioids (except for the clinids of the tribe Ophiclinini), one or more dorsal-fin pterygiophores typically insert anterior to the first neural spine (state 0).

Character 40: A single, slender (dorsal) postcleithrum is present in *S. hemphilli* (state 1; Figure 5*c*), but all other species of *Stathmonotus* have none (state 2). Although a number of specialized blenniids lack one or both postcleithra (Smith-Vaniz and Springer, 1971; Springer and Smith-Vaniz, 1972), all other blennioids have both dorsal and ventral postcleithra (state 0).

Character 41: All species of *Stathmonotus* have only two pelvic-fin rays (state 1). Other blennioids typically have three or four pelvic-fin rays (state 0). The blenniid tribe Omobranchini and many tripterygiids also have only two pelvic-fin rays (Springer, 1972; Springer and Gomon, 1975; Hardy, 1987).

Character 42: The basisphenoid of *Stathmonotus* lacks a belophragm (state 1). A belophragm generally is present (state 0) in other blennioids, with the exception of a few species of chaenopsins (Hastings, 1990) and some Omobranchini.

Character 43: Hypobranchial 3 of *Stathmonotus* is absent (i.e., not ossified and not represented by cartilage; state 1). Hypobranchial 3 of most blennioids is fully ossified (state 0). Exceptions include the chaenopsins *Lucayablennius* and some species of *Chaenopsis*, which also lack hypobranchial 3 (Hastings, 1992b).

Character 44: Basibranchial 2 of *Stathmonotus* is absent (i.e., not ossified and not represented by cartilage; state 1). In most blennioids, basibranchial 2 is present and fully ossified (state 0), with the exception of some genera of chaenopsins (Hastings, 1992b).

NODE G: SUBGENUS *Auchenistius*.—*Stathmonotus stahli* and *S. gymnodermis* form a monophyletic group (Figure 21) that corresponds to the subgenus *Auchenistius* as defined by Springer (1955). These species share two apparent apomorphies (characters 45, 46).

Character 45: Both species have a fleshy flap or cirrus on the margin of a preopercular sensory pore (state 1; Figure 12*a*). No flap or cirrus is present (state 0) on the preopercular pores in all other blennioids except for a few blenniids (Smith-Vaniz, 1976).

Character 46: *Stathmonotus stahli* and *S. gymnodermis* also share loss of the anteriormost pleural ribs (state 1). The first vertebra bearing both epineurals and pleural ribs is the fourth or fifth in *S. stahli* and the seventh in *S. gymnodermis*. In other blennioids, including the remaining species of *Stathmonotus*, the first vertebra bearing both epineurals and pleural ribs is typically the third (state 0).

NODE H.—The remaining four species of *Stathmonotus* form

a monophyletic group (Figure 21), sharing as many as 10 apomorphies (characters 39, 47–55).

Character 39 (state 2): In these species, the first dorsal-fin pterygiophore inserts posterior to the neural spine of the third or fourth vertebra (state 2). In other blennioids, except ophiclinin clinids, the first dorsal-fin pterygiophore inserts posterior to the neural spine of the second vertebra (state 1), or more anteriorly, usually over the neurocranium (state 0). In all or most ophiclinin clinids, the dorsal-fin pterygiophores begin well posterior to the third or fourth neural spine.

Character 47: In these species, the proximal end of the epineurals is expanded (state 1; Figure 11*b*). In other blennioids, the proximal end of the epineurals is slender (state 0).

Character 48: These species have a prominent lateral spur (Figure 5*b*) on the anguloarticular near its articulation with the quadrate (state 1). This spur is not present (state 0) in other blennioids.

Character 49: These species lack the third mandibular pore (state 1; Table 2; Figure 12). This pore is present (state 0) in labrisomids and all other chaenopsids.

Character 50: These species typically have two (state 1) preopercular (POP) sensory pores (Table 2; Figure 12*b,c*). Other chaenopsids and the labrisomids have three or more (state 0) POP pores.

Character 51: These species typically have two (state 1) anterior infraorbital (AIO) sensory pores (Table 2; Figure 12*b,c*). Other chaenopsids and the labrisomids have at least three (state 0) AIO pores.

Character 52: These species typically have two (state 1) posterior infraorbital (PIO) sensory pores (Table 2; Figure 12*b,c*). Other chaenopsids and the labrisomids have four or more (state 0) PIO pores.

Character 53: These species typically lack a commissural (CM) sensory pore (state 1; Table 2; Figure 12*b,c*). Other chaenopsids and the labrisomids typically have a single CM pore (state 0).

Character 54: These species are also unique within *Stathmonotus* in having dark color morphs, at least in males (state 0). (Dark morph females have been confirmed only in *S. sinuscalifornici*.) Dark morphs appear to be absent (state 0) in the two species of *Auchenistius*. (This character was scored as unknown for all other taxa; Table 1.)

Character 55: One character, the presence of nasal pore 2 (N2), has two equally parsimonious resolutions, one of which supports this clade (Figure 26*d*). N2 is absent (state 1) in these four species (Table 2; Figure 12*b,c*), as well as in chaenopsins. N2 is present (state 0) in *Neoclinus, Mccoskerichthys* (Figure 29*a*), and *Auchenistius* (Figure 12*a*). In one most-parsimonious resolution of this character, N2 is lost independently at this node (node H, Figure 21) and at the base of the Chaenopsinae (node D). In the second equally parsimonious resolution, N2 is lost at node C and regained in the subgenus *Auchenistius* (node G).

NODE I: Subgenus *Parastathmonotus*.—In one of the two equally parsimonious trees (Figure 21), *S. hemphilli* is the sister group of the remaining three species. The subgenus *Parastathmonotus*, as delineated by Springer (1955), comprises three species, *S. sinuscalifornici, S. culebrai*, and *S. lugubris*. We have identified two possible apomorphies of *Parastathmonotus* (characters 56, 57).

Character 56: These three species all lack teeth on the vomer (state 1). Vomerine teeth are present (state 0) in the other species of *Stathmonotus* and in most other blennioids. Many species of blenniids also lack vomerine teeth.

Character 57: These three species all lack an autogenous dermosphenotic (state 1), whereas the dermosphenotic is autogenous (state 0) in the other 3 species of *Stathmonotus* (Figure 5*a*). However, the dermosphenotic is not autogenous in *Mccoskerichthys* and the Chaenopsinae (Figure 26*e*), and there are three other equally parsimonious resolutions for the character.

NODE J.—Within *Parastathmonotus, S. culebrai* and *S. lugubris* are hypothesized to be sister species (Figure 21). They share only one apparent apomorphy.

Character 58: Both *S. culebrai* and *S. lugubris* have a low number of dorsal-fin spines (36 to 40; state 1) relative to the other species of the genus (Table 3). The other species of *Stathmonotus* usually have 40 or more dorsal-fin spines (state 0). This character was not scored for taxa other than the species of *Stathmonotus* because they all have both spines and rays in the dorsal fin and could not be directly compared to *Stathmonotus*, which has only spines.

NODE K.—One of the two most-parsimonious topologies places *S. hemphilli* and *S. sinuscalifornici* as sister species (Figure 21, dashed line). This is supported by a single apparent apomorphy.

Character 59: Stathmonotus hemphilli and *S. sinuscalifornici* have three (state 1) postemporal (PT) sensory pores (Figure 12*b,c*). The other species of *Stathmonotus* have four (state 0) PT pores (Table 2; Figure 12*a*). This could, however, represent independent losses of one of the PT pores.

ALTERNATIVE TOPOLOGIES.—Topologies that are one and two steps longer than the most parsimonious, regardless of the outgroup used, differ from that depicted in Figure 21 in the relationships within the Chaenopsinae (above node D) and within *Stathmonotus* (above node F), except for node H which

is stable. This result is not surprising because relationships within these portions of the topology are supported by relatively few characters (Figure 21).

One character (see character 40) supports the sister group relationship of *S. hemphilli* with the remainder of the genus *Stathmonotus*. All species of *Stathmonotus* except *S. hemphilli* have no postcleithra (state 2), whereas a single postcleithrum (state 1) is present in *S. hemphilli*, and two postcleithra are present (state 0) in most other blennioids. The presence of a postcleithrum in *S. hemphilli* is unexpected because this species has by far the most reduced pectoral fin in the genus (Figure 5*c*). The topology placing *S. hemphilli* as the sister group of the remainder of the genus is eight steps longer than the most-parsimonious topologies. Consequently, it is more likely that both postcleithra were lost at the base of *Stathmonotus* (node F) and that a single one was regained in *S. hemphilli*.

Character 60: One character, originally described by Rosenblatt and Stephens (1978), supports the sister group relationship of *Mccoskerichthys* and the Chaenopsinae. In both of these taxa, the maxillary is not exposed laterally but slips into a fold of skin below and posterior to the orbit (state 1). In virtually all other blennioids, including *Neoclinus* and *Stathmonotus*, the maxillary is exposed laterally, clearly visible externally, and does not slip into a fold of skin (state 0). The only exception is the labrisomid genus *Malacoctenus* in which the maxillary also slips under the suborbital region (Springer, 1959). Topologies placing *Mccoskerichthys* as the sister group of the Chaenopsinae are five or more steps longer than the most parsimonious.

Character 61: One final character, the presence or absence of scales, also is not congruent with the most-parsimonious topologies. Within the Chaenopsidae, scales are absent (state 1) in *Mccoskerichthys* and the Chaenopsinae (Stephens, 1963; Rosenblatt and Stephens, 1978). Scales are present (state 0) in eight of the nine species of *Neoclinus* (*N. nudus* lacks them; Stephens and Springer, 1971). Scales are present in *Stathmonotus stahli*, but absent in the other five species of the genus (Springer, 1955). Scales are present in most other blennioids with the exception of all Blenniidae and the monotypic clinid genus *Clinoporus*, which also lack them (Springer, 1968; Penrith, 1969). Assuming that the presence of scales is plesiomorphic for *Neoclinus* (i.e., the absence of scales in *N. nudus* is derived), the most parsimonious resolution of this character implies that scales were lost above *Neoclinus* (node B, Figure 21) and regained in *S. stahli* (Figure 26*f*).

Classification of the CHAENOPSIDAE

We present a classification of the Chaenopsidae that recognizes only monophyletic groups identified in our phylogenetic analysis (Figure 21). We have given subfamilial rank to the Chaenopsinae (= Chaenopsidae of Stephens, 1963), in accordance with the long-standing recognition of this speciose clade of tube blennies. However, we have not chosen to elevate the other lineages (*Neoclinus*, *Mccoskerichthys*, and *Stathmonotus*) related to the Chaenopsinae to subfamilial rank because we anticipate that this phylogeny, and any classification derived from it, may change as further evidence of the relationships of chaenopsids to other blennioids becomes available. Family-group names have been published for *Neoclinus* and *Stathmonotus* by Hubbs (1953a) and Jordan and Evermann (1898), respectively, but none is available for *Mccoskerichthys*. The appropriate taxonomic level accorded chaenopsids and other blennioids has been the focus of long and often heated debate (e.g., Hubbs, 1953a; Böhlke, 1957; Stephens, 1963, 1970; Böhlke and Robins, 1974; Böhlke and Springer, 1975; Acero, 1984). This debate is certain to continue.

CHAENOPSIDAE Gill, 1865
- *Neoclinus* Girard, 1865 (9 species)
- *Mccoskerichthys* Rosenblatt and Stephens, 1978 (1 species)
- *Stathmonotus* Bean, 1885 (6 species)

CHAENOPSINAE Gill, 1865
- *Acanthemblemaria* clade
  - *Acanthemblemaria* Metzelaar, 1919 (17 species)
  - *Ekemblemaria* Stephens, 1963 (3 species)
- *Chaenopsis* clade
  - *Chaenopsis* Poey in Gill, 1865 (8 species)
  - *Lucayablennius* Böhlke, 1957 (1 species)
  - *Hemiemblemaria* Longley and Hildebrand, 1940 (1 species)
  - *Emblemaria* Jordan and Gilbert, 1883 (14 species)
  - *Tanyemblemaria* Hastings, 1992 (1 species)
- *Coralliozetus* clade
  - *Coralliozetus* Evermann and Marsh, 1899 (6 species)
  - *Protemblemaria* Stephens, 1963 (3 species)
  - *Emblemariopsis* Longley, 1927 (9 species)

Biogeography of *Stathmonotus*

The closing of the transisthmian seaway across Central America has had a significant effect on the evolution of the marine biota of the tropical Western Hemisphere (Woodring, 1966; Rosen 1975; Jones and Hasson, 1985). This appears to be true for *Stathmonotus*, but the pattern only partially resembles that seen in other chaenopsids.

Three chaenopsin genera (*Acanthemblemaria*, *Ekemblemaria*, and *Coralliozetus*) include four sister-species pairs isolated by the isthmus (Smith-Vaniz and Palacio, 1974; Hastings, 1990, 1992a, in prep.). In three of these, the Pacific member is restricted to Central America or the Galapagos, whereas in three, the Caribbean member is restricted to Central

or northern South America (exceptions in both oceans are *E. myersi* in the Pacific and *C. cardonae* in the Caribbean, which have widespread distributions). This distributional pattern, together with the morphological similarity within each species pair, has been interpreted as evidence of their isolation by the emergence of the isthmus and their subsequent speciation (Hastings, 1990, in prep.).

In contrast, the most recent speciation events within *Stathmonotus* appear to be unrelated to the emergence of the isthmus. Sister species are found within the same ocean (*S. stahli* and *S. gymnodermis* in the Caribbean, and *S. culebrai* and *S. lugubris* in the eastern Pacific) rather than on opposite sides of the isthmus. An alternative topology, with relatively weak character support, places the eastern Pacific *S. sinuscalifornici* and the Caribbean *S. hemphilli* as sister taxa (Figure 21, node K). However, unlike the species pairs of chaenopsins mentioned above, these species differ considerably in morphology.

Assuming the monophyly of *Parastathmonotus* (Figure 21, node I), the restriction of these three species to the eastern Pacific, together with the occurrence of their apparent sister group (*S. hemphilli*) in the Caribbean, implies that a transisthmian event was involved in earlier speciation events within this genus. A similar pattern, with a relatively derived, multiple-species clade restricted to the eastern Pacific, has been reported for the chaenopsin genera *Acanthemblemaria* (Hastings, 1990) and *Coralliozetus* (Hastings, in prep.), as well as for a genus of echinoids (Harold and Telford, 1990). These distributional patterns imply that speciation, especially within the eastern Pacific, may have occurred subsequent to speciation events associated with the rise of the isthmus.

The distributional limits of the three eastern Pacific species of *Stathmonotus* conform exactly to the faunal barriers discussed by Springer (1959). To the north, *S. sinuscalifornici* occurs along the outer coast of Baja California to at least Bahia Magdalena, within a region where the predominantly tropical Gulf of Californian fauna gradually gives way to a more temperate fauna (Springer, 1959; Walker, 1960; Stephens, 1963; Rosenblatt and Parr, 1969).

Stathmonotus sinuscalifornici is separated from *S. lugubris* by a faunal gap on the Mexican mainland between Guaymas and Mazatlán, an area largely devoid of rocky outcroppings (Springer, 1959; Walker, 1960). This faunal barrier is selective, affecting only some species of blennioids. It forms the northern or southern distributional limit of several species or subspecies, including both rocky-shore and sand-dwelling blennioids (Springer, 1959; Stephens, 1963; Dawson, 1975); however, many species of blennioids cross it without exhibiting noticeable morphological variation (Hubbs, 1953b; Springer, 1959; Stephens, 1963; Dawson, 1975).

The sister species, *S. lugubris* and *S. culebrai*, are separated by the "Pacific Central American Faunal Gap" (Springer, 1959:483), a stretch of coastline largely devoid of rocks between the Golfo de Tehuantepec, Mexico, and the Golfo de Fonseca, Nicaragua. This faunal barrier, like the one south of the Gulf of California, is selective, affecting only some species of blennioids (Springer, 1959; Stephens, 1963; Rosenblatt and Parr, 1969; Rosenblatt and Taylor, 1971; Dawson, 1975).

Assuming that these current zoogeographic boundaries were causally related to speciation events within *Stathmonotus*, a temporal sequence for the operation of these barriers may be inferred from the branching sequence hypothesized for the subgenus *Parastathmonotus* (Figure 21). This topology implies that the barrier south of the present Gulf of California first separated a northern species, *S. sinuscalifornici*, from a southern species (Figure 21, node J). Subsequently, this southern species became divided by a barrier (the Pacific Central American Faunal Gap), leading to the speciation of *S. lugubris* and *S. culebrai*.

The allopatric distributions of the eastern Pacific species of *Stathmonotus* stand in sharp contrast to the broadly overlapping distributions of the Caribbean species (Figures 15, 17). Consequently, little of the historical biogeography of the Caribbean can be inferred from the present-day distributions of these *Stathmonotus* species. Both *S. stahli* and *S. gymnodermis* exhibit noticeable geographic variation (Table 4), with the region west of Puerto Rico marking a zone of transition. However, no obvious biogeographic barriers in this region are known to us, and the significance of this geographic variation, if any, remains unknown. In neither instance do the forms exhibit what we consider to be species-level differences.

Valid names are available for the geographic forms (subspecies) of *S. stahli*, but not for *S. gymnodermis*. Considerable debate exists over the relative merits of recognizing subspecific categories (e.g., Rosen, 1979; Warren, 1992), and, although we wish to call attention to the pattern of geographic variation of these species, we do not choose to encumber the literature with additional subspecific names.

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