Evidence for the Elevation to Family Status of the Angelfishes (Pomacanthidae), Previously Considered to be a Subfamily of the Butterflyfish Family, Chaetodontidae[1]

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MOST AUTHORS have classified the butterflyfishes and angelfishes as two subfamilies, Chaetodontinae and Pomacanthinae, of the family Chaetodontidae (Woods and Schultz *in* Schultz et al 1953, Greenwood et al 1966, and Böhlke and Chaplin 1968). Ahl (1923), Weber and de Beaufort (1936), and Marshall (1964) included subfamilies, as Scatophaginae, Drepaninae, etc., within the Chaetodontidae along with Chaetodontinae and Pomacanthinae, which are presently considered as families. Smith (1953, 1955) and Munro (1955, 1967) preferred to use family Chaetodontidae and family Pomacanthidae. None of the above authors gave sufficient supporting evidence to justify their use of a particular classification.

Fraser-Brunner (1945) recognized some of the distinguishing characteristics of the angelfishes (frontal bones forming a concavity between the orbits, the presence of a strong spine at the angle of the preoperculum, the absence of the pelvic axillary process, the distal portions of the ribs normally formed, and a forward ventral expansion of the first interhaemal bone) but continued to use subfamily Pomacanthinae and subfamily Chaetodontinae.

A few workers dealing with certain aspects of the anatomy of fishes have mentioned particular differences between the two groups. Some of them, such as Cockerell (1915, 1916) and Freihofer (1963), were of the opinion that the differences might be enough to warrant full family distinction.

On the basis of the following anatomical and life history differences the two subfamilies should be considered as separate and distinct families.

SCALES

Cockerell (1915, 1916) investigated the form of the scales in the genera *Chaetodon, Heniochus, Chelmon, Chaetodontoplus, Pomacanthus, Centropyge (Holacanthus bicolor = Centropyge bicolor),* and *Microcanthus*. In his analysis of scale structure he divided these fishes into three distinct groups which happen to correspond to the currently accepted families Chaetodontidae, Pomacanthidae, and Scorpididae.

Cockerell (1915) found the scales of the butterflyfish genera similar and remarked, "It is impossible to find satisfactory characters for the separation of the species of *Chaetodon, Chelmon,* and *Heniochus*. The ctenoid elements of *Chelmon* are coarser than those of *Heniochus,* but the structure is the same." I have examined scales from all genera and subgenera of the family Chaetodontidae and have found that, although the scales are variable in size and shape, the basic structure is the same. The chaetodontids have scales in which the ctenii extend in a band along the apical margin with the elements separate and striated (Fig. 1*B*).

Pomacanthids have scales in which the median ribs of apical teeth extend as continuing rods to the base of the apical field (Fig. 1*A*). Cockerell (1915) reported this for the genera *Chaetodontoplus, Pomacanthus,* and *Centropyge*. I have examined scales from the other genera of the family Pomacanthidae and found all of them to be similarly structured.

Cockerell also reported that the scales of *Microcanthus* were similar to those of

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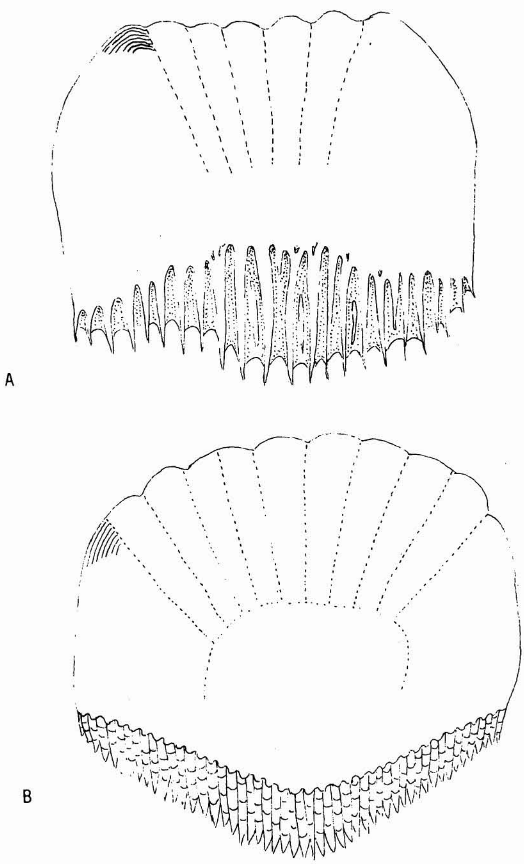


FIG. 1. Body scales. *A*, *Centropyge* (Pomacanthidae); *B*, *Chaetodon* (Chaetodontidae).

Chaetodon, *Heniochus*, and *Chelmon*. They differed, however, in general shape and the genus was placed in a third group apart from the pomacanthids and chaetodontids mentioned above. Although *Microcanthus* was considered to be a genus of the family Chaetodontidae in Cockerell's time, it was placed in the family Scorpididae by Fraser-Brunner in 1945.

AXILLARY SCALES

Regan (1913) and Norman (1957) made their primary division of percoid families on the basis of the presence or absence of a scaly process in the axil of the pelvic fins. They placed the Chaetodontidae (including Pomacanthidae) with the families that have this feature. Gosline (1966) discussed this character and pointed out that the "axillary process is not an all or none character; it can be and frequently is rudimentary or practically transitional between a ridge and a process."

However, Gosline said that the scaly axillary process in the great majority of percoid families is either consistently absent or consistently present. I have examined all genera of both families and found as Fraser-Brunner (1945) reported that, although variable in size and shape, the axillary process is consistently present in the Chaetodontidae (Fig. 2*B*, *C*) but consistently absent in the Pomacanthidae (Fig. 2*A*).

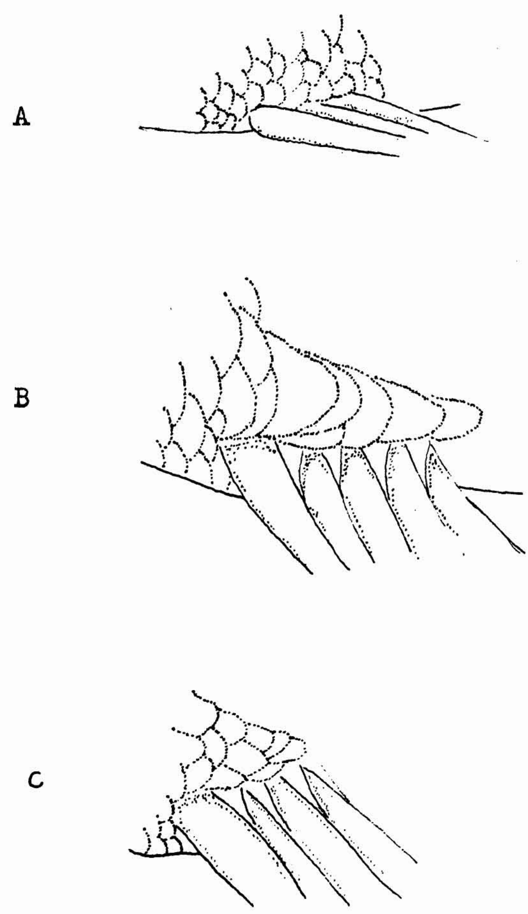


FIG. 2. *A*, Base of pelvic fin of *Pomacanthus* (Pomacanthidae); *B*, base of pelvic fin showing axillary scaly process of *Chaetodon* (Chaetodontidae); *C*, base of pelvic fin showing axillary scaly process of *Heniochus* (Chaetodontidae).

RAMUS LATERALIS ACCESSORIUS NERVE

Freihofer (1963), in dealing with the patterns exhibited by the *Ramus lateralis accessorius,* discovered that the arrangement of these nerves in genera of the family Chaetodontidae is different from that of the pomacanthid genera. He stated, "Although still incomplete, the survey for RLA in chaetodontid (sensu latro) genera indicates that pattern 8 is characteristic of the Chaetodontinae (two genera examined) and pattern 9 the Pomacanthinae (three genera examined). Judging from the apparent significance RLA has in other groups, such a distribution in the Chaetodontidae raises serious doubts that the two subfamilies are correctly classified."

AUXILIARY SCALES

Auxiliary scales (small scales at the base of the larger ones) occur in adult specimens of all pomacanthid genera and are absent in all genera of chaetodontids (personal observations).

Fraser-Brunner (1933) used the presence or absence of these scales in his generic keys to help separate various groups of species. I have examined several of the species which were reported by him as lacking auxiliaries (e.g., *Chaetodontoplus melanosoma, Pomacanthus imperator, Apolemichthys xanthurus*) and found that these small scales are present in large specimens, particularly in the areas below the anterior dorsal spines and on the chest.

OSTEOLOGY

Skeletons of the following species were examined in an attempt to determine differences between the family Chaetodontidae and the family Pomacanthidae: *Chaetodon ornatissimus, C. multicinctus, C. trifasciatus, C. auriga, C. lunula, C. lineolatus, Chelmon rostratus, Forcipiger flavissimus, Hemitaurichthys polylepis,* and *Heniochus acuminatus* of the family Chaetodontidae; *Pomacanthus imperator, Apolemichthys arcuatus, Pygoplites diacanthus,* and *Centropyge potteri* of the family Pomacanthidae. Some of the above species were represented by articulated skeltons. Abbreviations used in the illustrations are as follows: FR, frontal; V, vomer; PS, parasphenoid; OP, opercle; IO, interopercle; EX, exoccipital; EP, entopterygoid; HY, hyomandibular; Q, quadrate; CLT, cleithrum; SCA, scapula; AR, articular; FM, foramen magnum; PF, prefrontal; ME, mesethmoid; SO, supraoccipital; BO, basioccipital; PO, preopercle; SO, subopercle; P, palatine; MP, metopterygoid; PT, pterygoid; S, symplectic; COR, coracoid; DN, dentary. Illustrations were prepared by Lourdes A. Burgess.

Within each family the skeltons are essentially similar, although variations do exist, e.g., greater or lesser spination of certain bones (both chaetodonts and pomacanthids), proportional differences due to prolongation of the snout (chaetodontids), and varying body depths (both families). The differences between the families, however, are much more extensive.

The form of the preopercle has served as the most useful and distinctive character to differentiate the two groups. In pomacanthids there is a large spine at the angle of the preopercle and smaller spines on the preopercle, lacrymal, and interopercle (Fig. 3*D*). The chaetodontids lack the spine at the angle and have, at most, small serrations on the preopercle and lacrymal; the interopercle is smooth (Fig. 3*C*).

The opercles, although somewhat variable within the two families, are similar. This is also true of the subopercles but with one major exception. The process on the upper edge of the subopercle in the chaetodontid genera is perpendicular to the long axis of the bone but forms an acute angle with the long axis in the pomacanthids (arrows in Figs. 3*Ca* and 3*Da*). The interopercles are not only shaped differently, but their relative position is not the same in the two families. In the chaetodontids the long axis of the interopercle is set at about an angle of 45° with the horizontal. The broad anterior end of this bone is curved inward toward the mid-ventral line where it meets the one from the opposite side (Figs. 3*C* and 9*A*). The interopercle of the pomacanthids

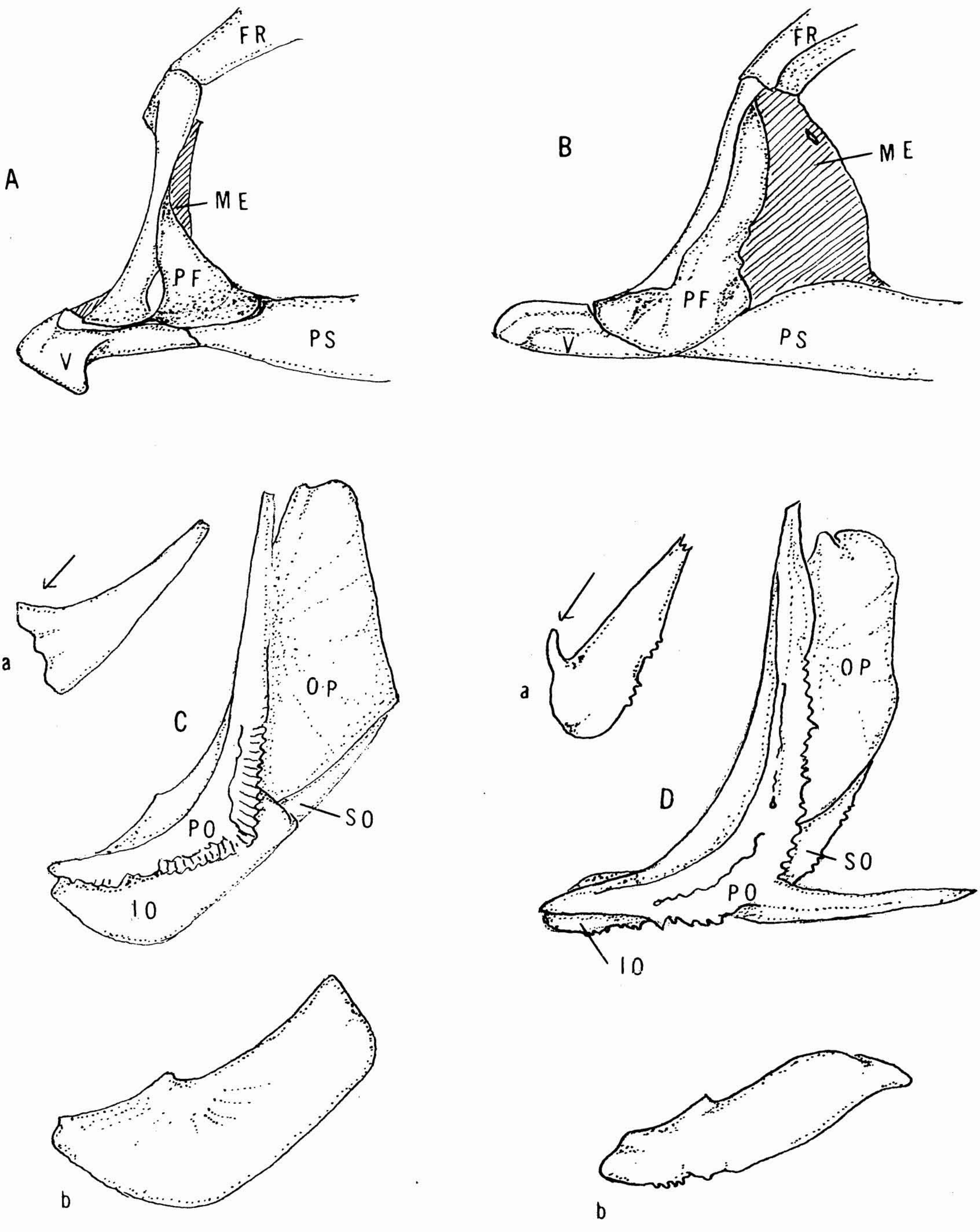


FIG. 3. *A*, lateral view of the ethmoid region of *Chaetodon; B*, lateral view of the ethmoid region of *Pomacanthus; C*, opercular bones of *Chaetodon; a*, interopercle of *Chaetodon; b*, subopercle of *Chaetodon; D*, opercular bones of *Holacanthus; a*, interopercle of *Holacanthus; b*, subopercle of *Holacanthus*.
See page 59 for definitions of symbols.

is relatively flat, the longest axis almost horizontal or only slightly inclined; the narrow anterior ends of the right and left interopercle approach each other but do not touch midventrally (Figs. 3*D* and 9*B*).

Except for differences in spination, the lacrymal and orbital bones are similar. A subocular shelf is present in both families.

The supraoccipital crest is comparatively shorter and not as well developed in the pomacanthids as it is in the chaetodontids (Fig. 4*A*, *B*). This is true even when compar-

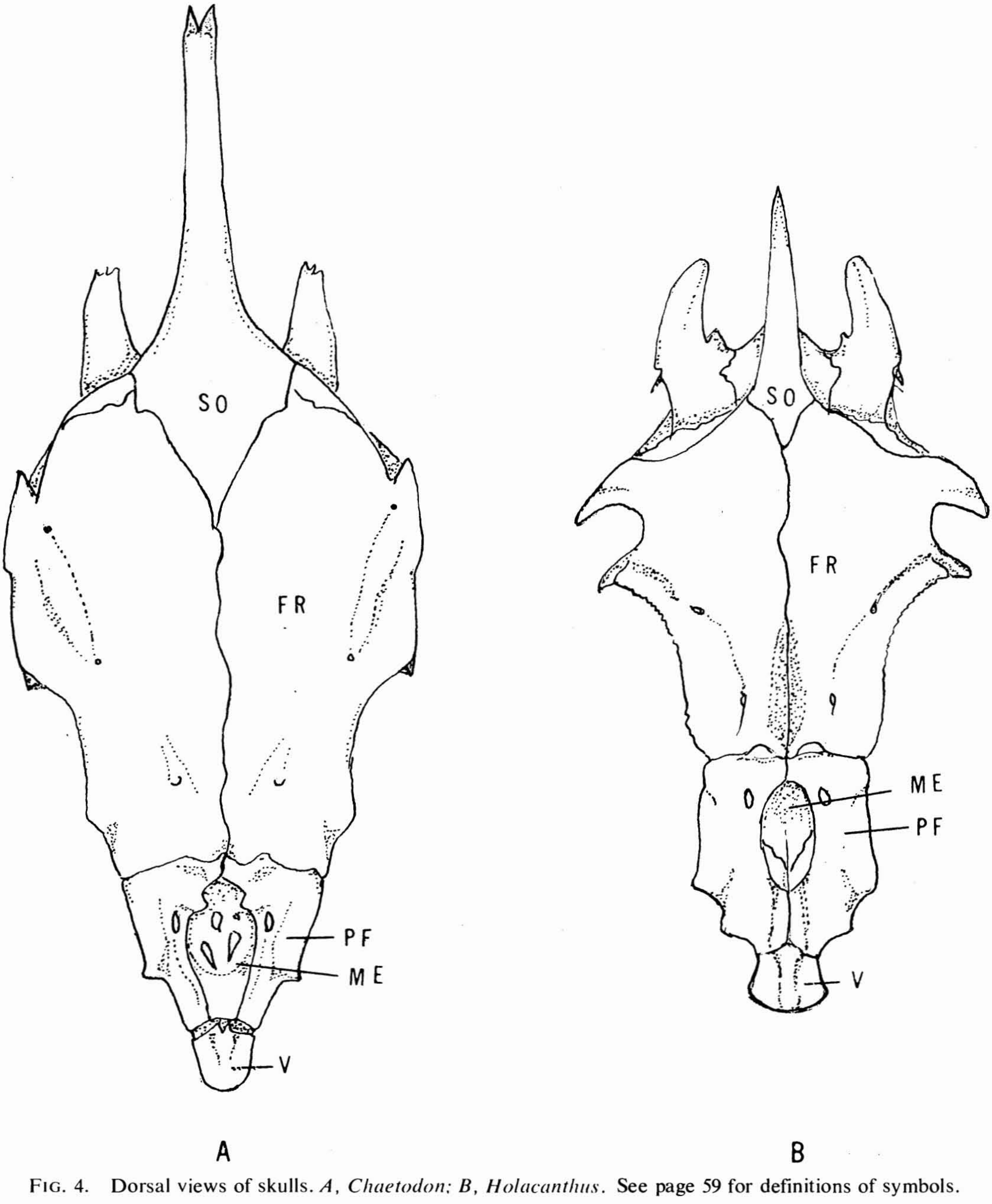


FIG. 4. Dorsal views of skulls. *A*, *Chaetodon*; *B*, *Holacanthus*. See page 59 for definitions of symbols.

ing such deep-bodied angelfishes as *Pomacanthus imperator* with shallow-bodied butterflyfishes such as *Chaetodon trifascialis*. In addition the tip of the supraoccipital crest of the chaetodontids has a distinct bifurcation (Fig. 4*A*). By contrast, in the pomacanthids, it has a single point (Fig. 4*B*). The bifurcation of the chaetodontids accepts the first predorsal (Fig. 5*C*). The first predorsal just touches the point of the occipital crest in the pomacanthids (Fig. 5*D*).

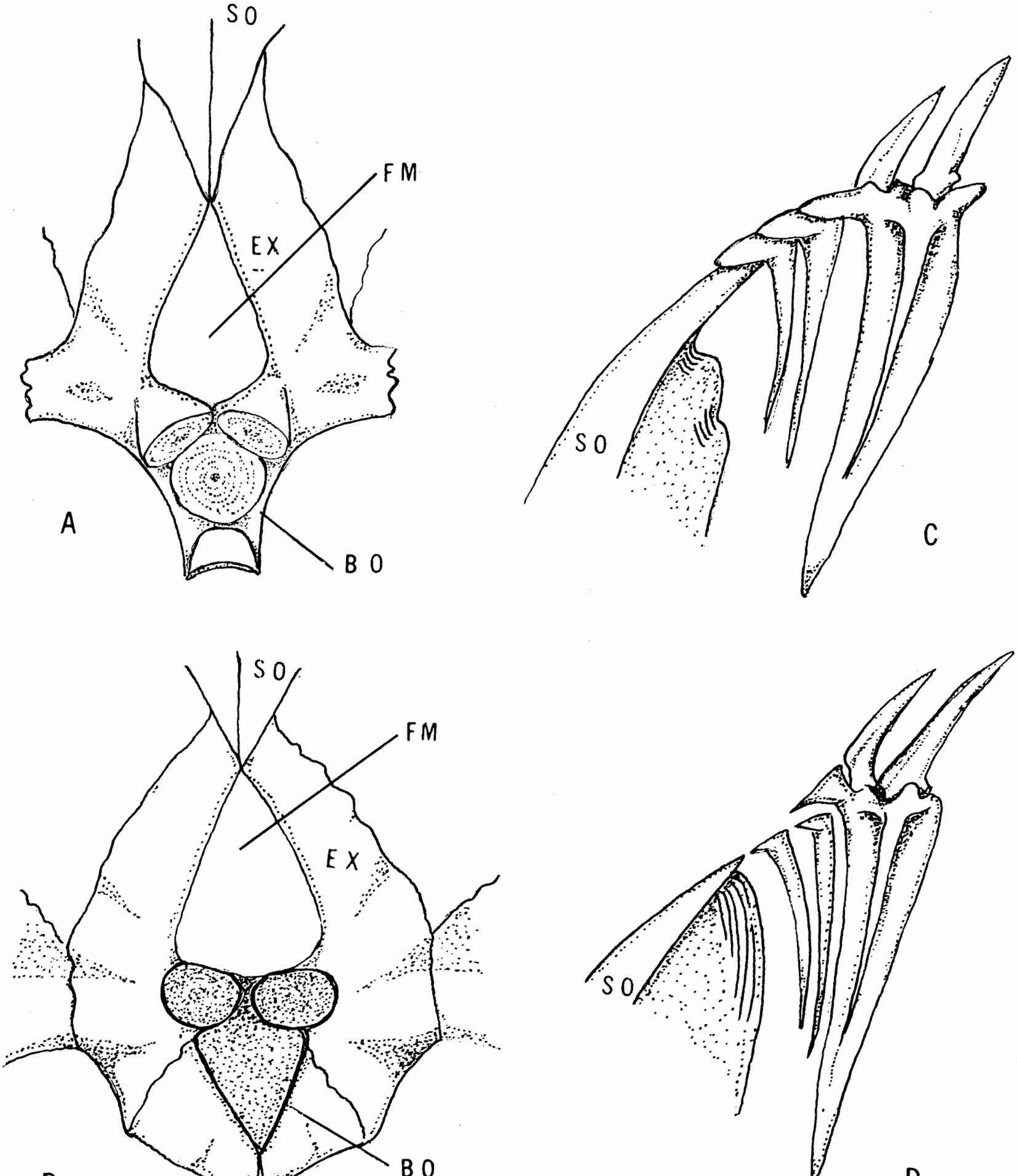


FIG. 5. *A*, occipital region of *Chaetodon*; *B*, occipital region of *Holacanthus*; *C*, predorsal and first interneural of *Chaetodon*. *D*, predorsal and first interneural of *Pomacanthus*.
See page 59 for definitions of symbols.

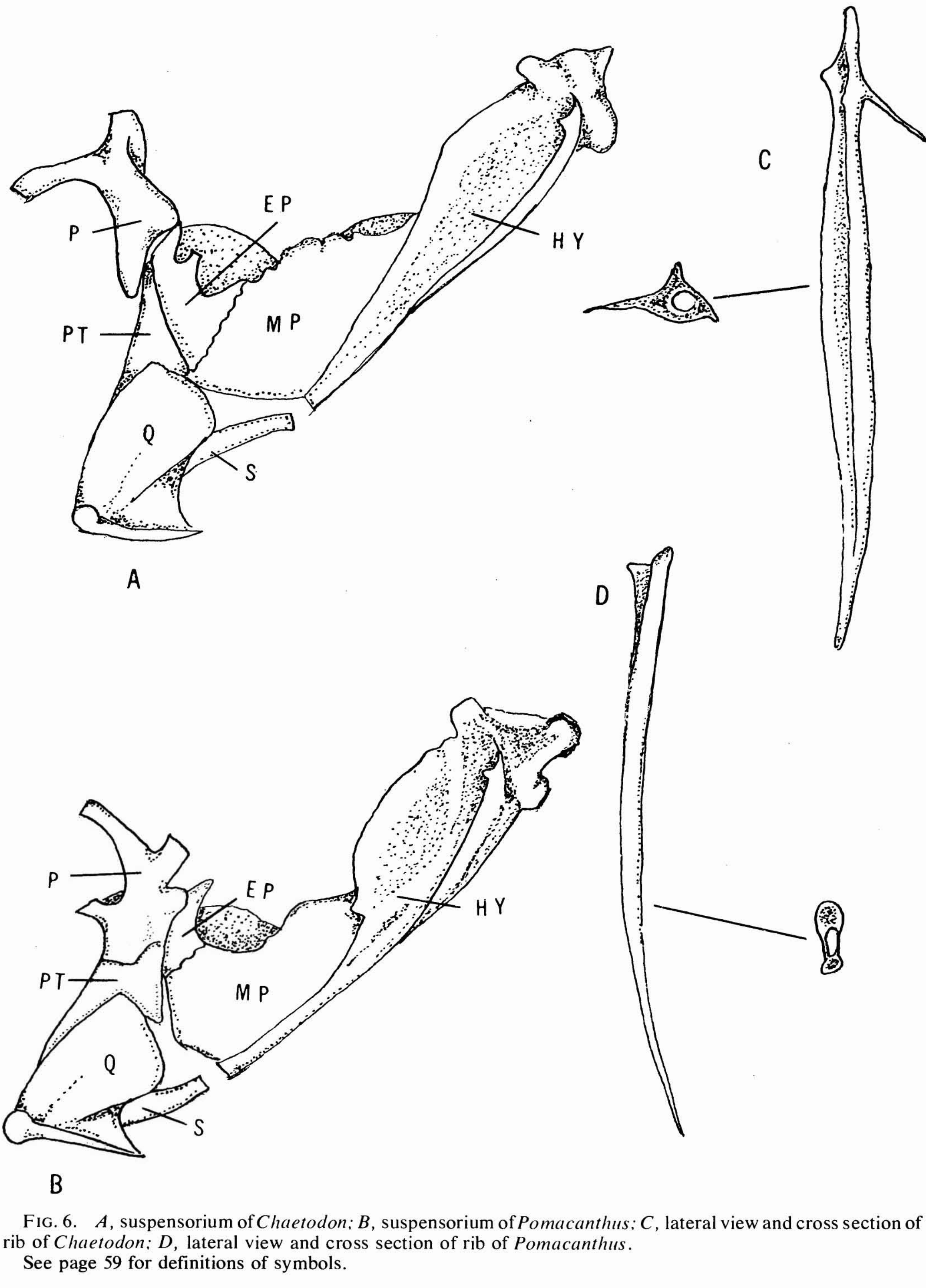


FIG. 6. *A*, suspensorium of *Chaetodon; B*, suspensorium of *Pomacanthus; C*, lateral view and cross section of rib of *Chaetodon; D*, lateral view and cross section of rib of *Pomacanthus*.
See page 59 for definitions of symbols.

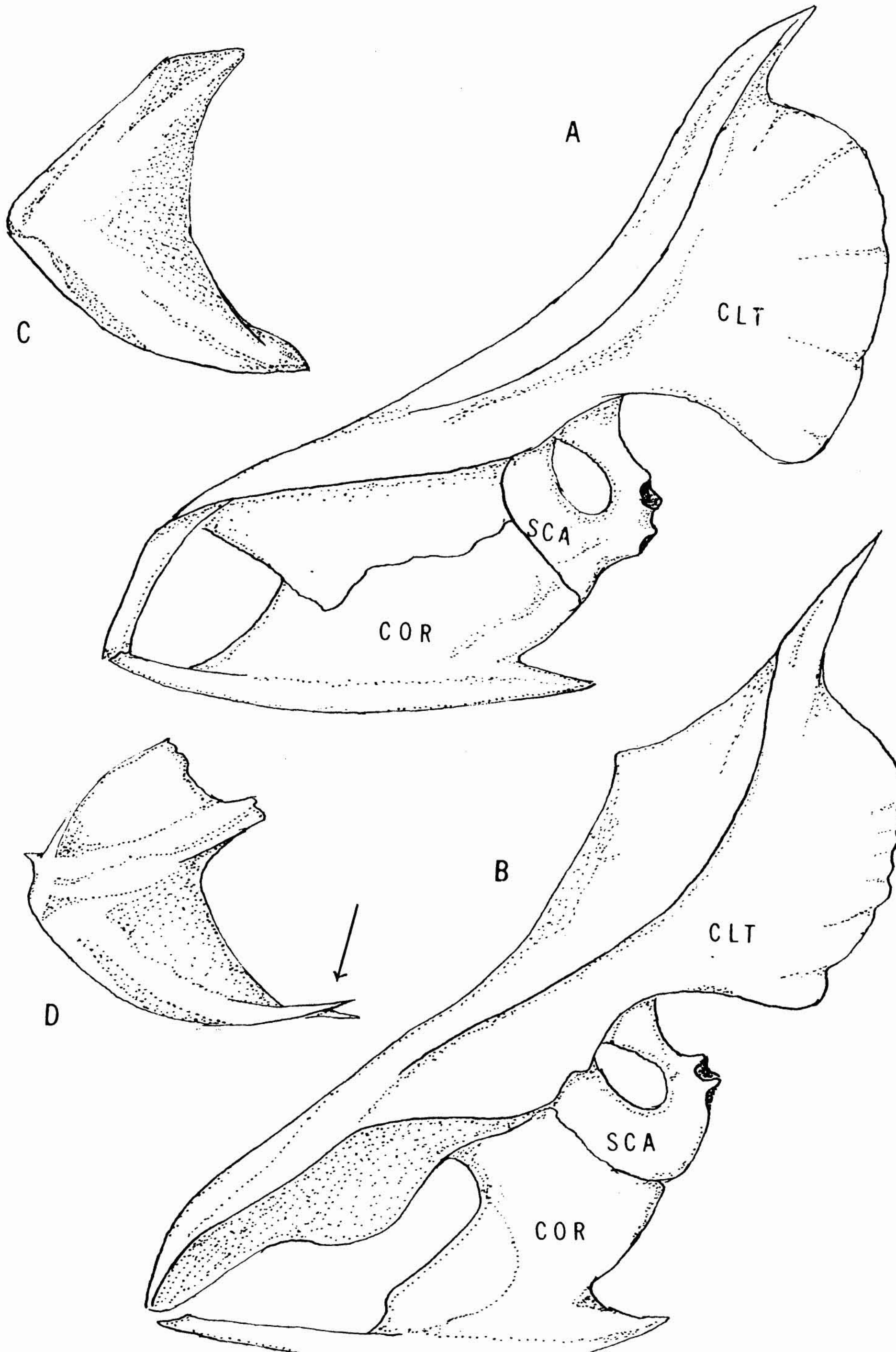


FIG. 7. *A*, pectoral girdle of *Chaetodon; B*, pectoral girdle of *Holacanthus; C*, urohyal of *Chaetodon; D*, urohyal of *Holacanthus*.
See page 59 for definitions of symbols.

The urohyals of the two families are similarly shaped (Fig. 7*C*, *D*), that of *Hemitaurichthys* resembling the pomacanthids more than other chaetodontid genera but is still distinctly chaetodontid in form. The pomacanthids have a peculiar double-pronged arrangement at the end of the ventral process of the urohyal (arrow, Fig. 7*D*). The forward edge of the cleithrum fits into the fork and is braced by it. The chaetodontids do not have this connection.

The bracing between head and axial skelton in the chaetodontids then is between the supraoccipital and the predorsals (Fig. 5*C*). The brace in the pomacanthids is between the urohyal and the pectoral girdle (Fig. 5*D*).

The shape of the vomer is quite different in the two families (Figs. 3*A*, *B*; 4*A*, *B*). That of the pomacanthids is depressed with the anterior end wider than the posterior. The vomer of the chaetodontids is not depressed but hoof-shaped (Figs. 3*A* and 4*A*), the anterior end narrower than the posterior.

The bones of the ethmoid region have been discussed by Starks (1926). The specimens of angelfishes he examined (*Angelichthys ciliaris*, *Holacanthus tricolor*, and *Pomacanthus paru*) were found to be "strikingly similar to *Drepane*." According to Starks, and confirmed by me on specimens of additional genera, "the inner edges of the prefrontals are turned backward (not visible in illustration) and attached to the side walls of the mesethmoid, which is in the form of two converging walls enclosing a wedge-shaped cavity between them" (Fig. 3*B* and 4*B*). In the butterflyfishes, the prefrontals are not turned back but "there is a deep cavity that occupies the greater part of the mesethmoid and extends back somewhat into the interorbital region behind the prefrontals. It is more or less completely walled behind by very open, lace-like bone, that occasionally is nearly absent, and the cavity becomes simply a large foramen through the mesethmoid." The cavity, instead of being wedge-shaped as in *Holacanthus* et al., is cup-shaped (Figs. 3*A* and 4*A*).

There is a depression or groove at the anterior half of the median suture of the frontals in the pomacanthids that is absent in the chaetodontids (Fig. 4*A*, *B*). The anterior wedge of the supraoccipital that extends between the posterior part of the frontal is much more developed in the chaetodontids, being a pointed wedge (Fig. 4*A*); that of the pomacanthids is short and sometimes irregular (Fig. 4*B*).

The posterior ventral section of the skull in the Chaetodontidae is narrower than in most pomacanthids, where it is slightly inflated (Fig. 5*A*, *B*). The basioccipital has a more-or-less rounded area for attachment of the lower edge of the vertebral centrum in the chaetodontids; in the pomacanthids this area is triangular (Fig. 5*A*, *B*). The butterflyfishes, in addition to the foramen magnum above, have an opening or canal immediately below the basioccipital. This canal is pinched off in the angelfishes (Fig. 5*A*, *B*). The first vertebra is firmly wedged into the skull in pomacanthids, that of the chaetodontids is not.

No important differences were seen between the postemporal and supracleithra of the two families.

The hyomandibular bones are somewhat different. The pomacanthids have a hyomandibular that is laterally flared in the upper portion, becoming abruptly a strut, which is sometimes flattened below (Fig. 6*B*). The condyles are low and almost continuous (not evident in view in Fig. 6). In the chaetodontids the flared portion of the hyomandibular reaches to, or almost to, the lower end of the bone (Fig. 6*A*). The condyles are better differentiated and well separated (also not evident in view in Fig. 6).

Starks (1930) studied the primary shoulder girdle in several species of butterflyfishes and angelfishes and pointed out that the pomacanthids, as opposed to the genus *Chaetodon*, "do not have the interosseus space [between the coracoid and the cleithrum] divided, and in the latter genus (*Angelichthys*) the cleithrum does not send a process back to meet the tip of the coracoid." The coracoid in the pomacanthids has a lesser amount of thin bone filling the space between the coracoid and scapula (Fig. 7*A*, *B*). The lower tip of the cleithrum is curved posteriorly to meet the tip of the

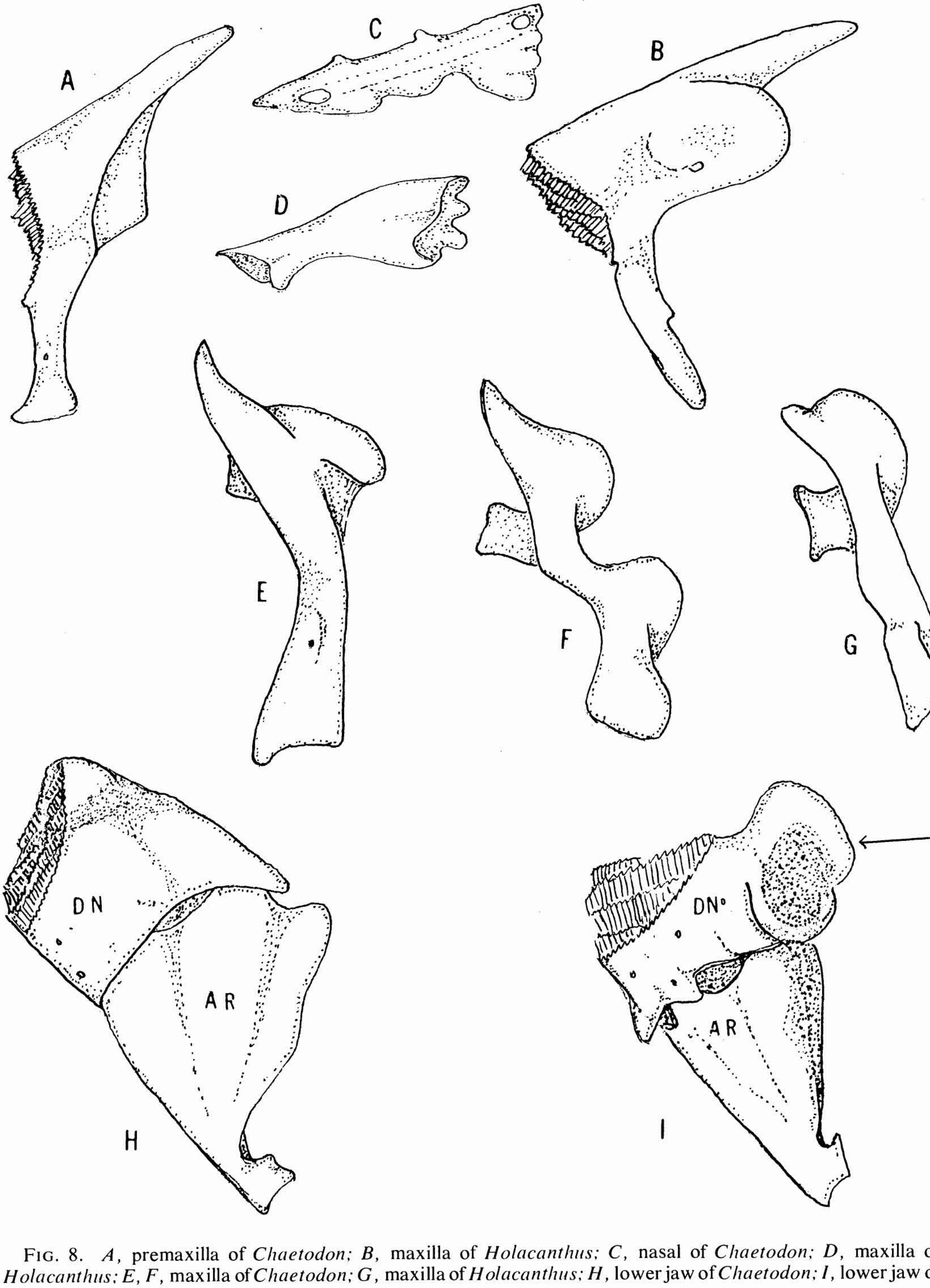


FIG. 8. *A*, premaxilla of *Chaetodon; B*, maxilla of *Holacanthus; C*, nasal of *Chaetodon; D*, maxilla of *Holacanthus; E, F*, maxilla of *Chaetodon; G*, maxilla of *Holacanthus; H*, lower jaw of *Chaetodon; I*, lower jaw of *Holacanthus*.

See page 59 for definitions of symbols.

coracoid in the chaetodontids but is almost straight in the pomacanthids, the coracoid extending forward to meet it (Fig. 7*A*, *B*).

The suspensorium is similar in both families except for minor differences in the shapes of the various bones and the differences mentioned above in the hyomandibular (Fig. 6 *A*, *B*).

The maxillaries of both the chaetodontids and pomacanthids are twisted and irregular in shape (Fig. 8*E*–*G*). Although most chaetodontids have an extra flared portion (Fig. 8*F*) some species, such as *Chaetodon ornatissimus* and *C. trifasciatus*, do not (Fig. 8*E*). The premaxilla of the chaetodontids has a long, slender, median, ascending process (Fig. 8*A*); the premaxilla of the pomacanthids has a broader base to the median ascending process and a straight, pointed, lateral process (Fig. 8*B*).

The nasal bones of the butterflyfishes are irregular in shape but heavier than those of the pomacanthids; the nasal includes a slender tube through the center (Fig. 8*C*). The angelfishes have a shorter, stubbier, nasal bone which is practically hollow, the tube being much wider (Fig. 8*D*).

The lacrymal bone is irregular in both families, a comparison not revealing anything that can be construed as important as a family distinction. The spination was mentioned above.

The dentary and articular bones are similar when using a short-snouted chaetodontid such as *Chaetodon ornatissimus* for the comparison (Fig. 8*H*, *I*). The pomacanthids do have an extra process (arrow, Fig. 8*I*) that the chaetodontids lack.

No important differences were noted in the pelvic girdles of these families.

The first interneural has an anteriorly directed spine (procumbent spine at the base of the first dorsal spine) in the pomacanthids (Fig. 5*D*), whereas in the chaetodontids this is a blunt, flattened, spade-shaped process (Fig. 5*C*). The predorsals in the chaetodontids are incorporated into the connection between the supraoccipital crest and the first interneural; those of the pomacanthids are separate (Fig. 5*C*, *D*). The first interhaemal of the pomacanthids has a prominent anteriorly directed process at the base of the first anal spine; in the chaetodontids this process is blunt (Fig. 9*C*, *D*).

The ribs of the butterflyfishes are distinctive in having flattened, expanded, medial and distal portions, giving extra protection to the visceral area (Fig. 6*C*). The ribs of the angelfishes are without these expansions (Fig. 6*D*). In both families the ribs are attached to transverse processes.

OTOLITHS

Mr. John Fitch, Marine Resources Region, California State Fisheries Laboratory, examined the otoliths of various genera of butterflyfishes and angelfishes at my request. He found significant differences in size and configuration between those of the chaetodontids and pomacanthids, and considers the otolith to be a "good tool at the family level" (personal communication). Mr. Fitch will report on the specific differences in his own papers.

SWIM BLADDER

The swim bladder in the Chaetodontidae has two anteriorly directed processes or "horns." That of the Pomacanthidae lacks such anterior horns but may have posteriorly directed extensions.

NUMBER OF VERTEBRAE

Both the chaetodontids and pomacanthids have 24 vertebrae. The angelfishes, however, have a formulae of 10+14; the butterflyfishes 11+13. Scorpidids, on the other hand, have 10+15.

LARVAE

One of the main arguments for retaining the angelfishes as a subfamily of the Chaetodontidae is that they are considered to have a "tholichthys" stage similar to that of the butterflyfishes (Lütken 1880, Fraser-Brunner 1933). The tholichthys larva is highly modified with large bony plates extending from the posterior portion of the head; the head itself is encased in a bony armor (Fig. 10*A*). Lütken (1880) described

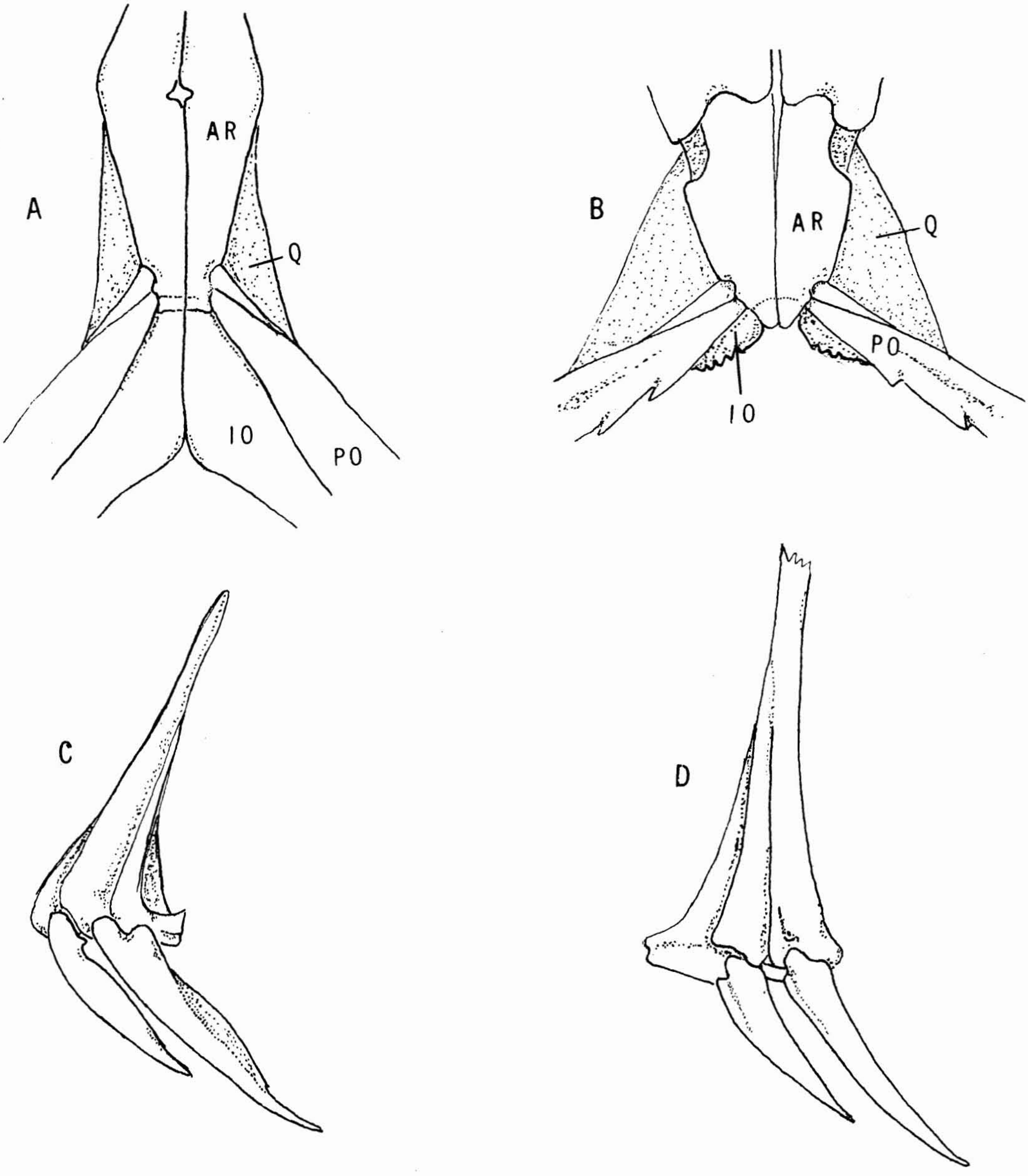
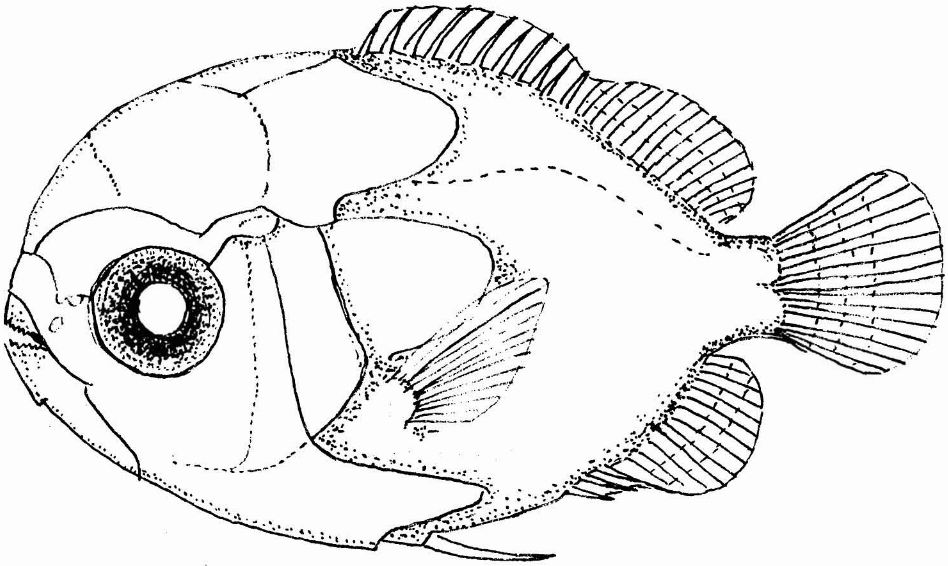
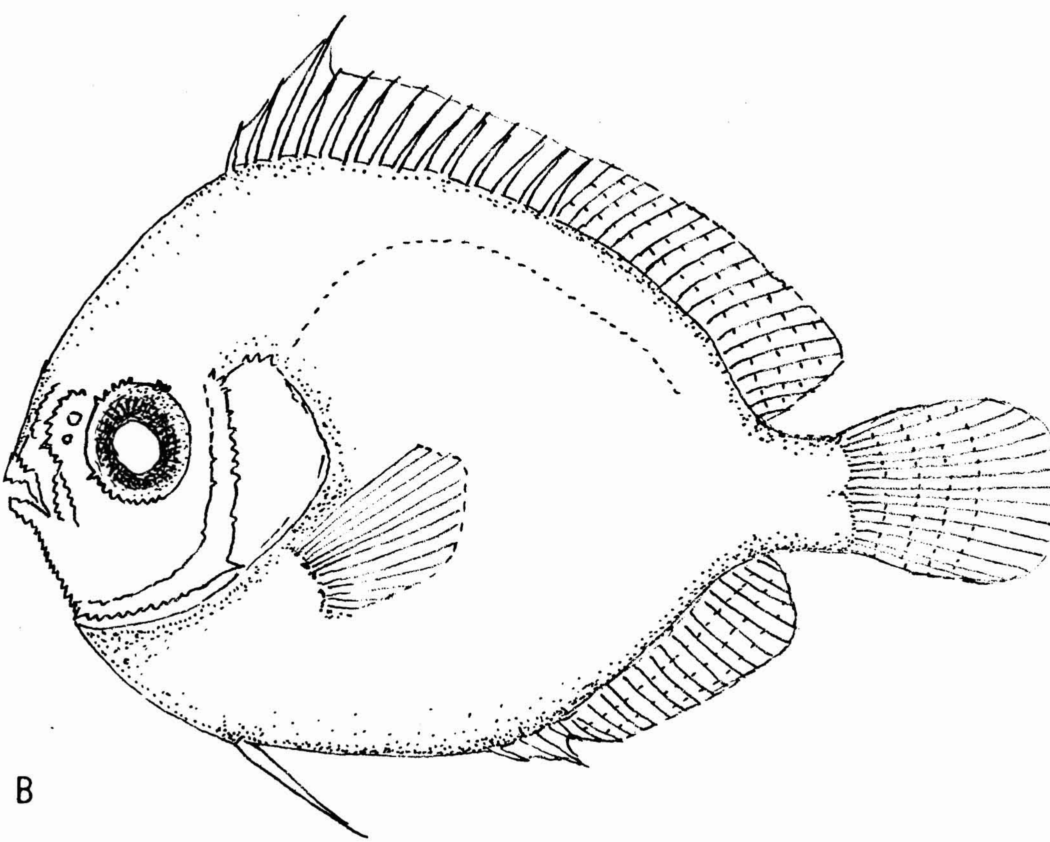


FIG. 9. *A*, ventral view of opercular region of *Chaetodon; B*, ventral view of opercular region of *Holacanthus; C*, first interhaemal of *Chaetodon; D*, first interhaemal of *Pomacanthus*.
See page 59 for definitions of symbols.

and figured several of these forms. One of them he identified as a larval stage of *Pomacanthus*. This specimen, from the South Atlantic, was even more peculiarly developed. In addition to the bony development of the head it had two "horns" projecting from the supraorbital region. Fraser-Brunner (1933) followed Lütken in referring this type of tholichthys to the pomacanthids. I have studied many larvae of both the Pomacanthidae and Chaetodontidae, including most of the Atlantic species, in prep-



A



B

FIG. 10. *A*, larval stage (tholichithys) of a 10-mm chaetodontid; *B*, larval stage of a 12-mm pomacanthid.

aration for papers describing the larval forms of these families. The larvae of the pomacanthids, including those of the Atlantic species of the genus *Pomacanthus*, do not pass through a tholichthys stage. They are compressed, round to oval, and lack the characteristic head armature (Fig. 10*B*).

The form illustrated by Lütken and Fraser-Brunner (1933, text fig. 3) as belonging to the genus *Pomacanthus* is typical of that occurring in *Chaetodon ornatissimus* and *C. meyeri*. It is not a pomacanthid larva and apparently was erroneously recorded from the Atlantic Ocean. Günther (1871) illustrated a larger specimen of the same type of tholichthys larva and correctly identified it as a chaetodontid.

The larvae of the family Scatophagidae are the only other tholichthys-like form (see Weber and de Beaufort 1936, fig. 3 *a–d*).

SUMMARY

Several morphological characters of the butterflyfishes and angelfishes were presented and the differences between them were pointed out. Many of these characters were of such a magnitude that it is surprising the two groups were never separated on a more stable basis before this time. The false impression that a tholichthys state was present in the Pomacanthidae, however, probably had much to do with repressing any further investigation into the matter.

Once I had established that the larvae were completely different, I made a close examination of the external morphology and pointed up some differences between the two groups, particularly in the structure and arrangement of the scales. The major differences, however, that completely nullified the possibility of these fishes being in the same family were internal. Aside from the discoveries of the divergent types of swim bladders and the patterns of certain nerves, the most significant findings were made in the investigation of the skeletal system. Again, although major differences were noted in such things as otoliths and number of vertebrae, the most important finding was that of the completely different relationship between the skull and axial skeleton. The dissimilar basioccipitals and atlas combination, together with the two types of bracing, dorsally in the Chaetodontidae and ventrally in the Pomacanthidae, leave no doubt that these two groups of fishes deserve separate families.

It is even questionable whether the butterflyfishes and angelfishes are closely related and further osteological studies are being conducted to discover the extent of the relationship between the groups of fishes variously united with the Chaetodontidae (Scatophagidae, Platacidae, Ephippidae, etc.).

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