Microsaurs as possible apodan ancestors

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The specific ancestry and nature of the relationships of modern amphibians have not yet been established. Detailed comparisons of the anatomy of the skull roof, palate and braincase of living apodans and the Paleozoic microsaur *Goniorhynchus* demonstrate greater similarities than between apodans and any other group of amphibians, fossil or recent. Unlike any other amphibians, extensive pleurosphenoid ossifications are developed in the area of the Vth nerve, uniting the otic capsule with the sphenethmoid. Other important features that they share (although not uniquely) include the presence of all the primitive dermal elements of the palate, a solidly roofed temporal region, a row of palatal teeth parallel to the marginal dentition and a row of teeth on the medial surface of the lower jaw. The stapes has a similar configuration and position, totally different from that of frogs and salamanders. Such similarities do not necessarily prove close relationship, but indicate the necessity for considering that apodans may have an ancestry distinct from that of frogs and salamanders.

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INTRODUCTION

Despite extensive knowledge of a great variety of Paleozoic amphibians, the specific ancestry of the three living amphibian orders has not been established. On the basis of the fossil record of anurans, urodeles and apodans, there is nearly as great a possibility that each has a distinct ancestry as that they are more closely related to one another than to any Paleozoic groups.

Reviews by Eaton (1959), Szarski (1962), Parsons & Williams (1963) and Cox (1967) demonstrate that the modern amphibians have a large number of

anatomical and physiological features in common that distinguish them clearly from both reptiles and all groups of Paleozoic amphibians. Of particular significance is the common practice of cutaneous respiration and the presence of pedicellate teeth in the vast majority of species (Parsons & Williams, 1962). The operculum-"opercularis" complex in frogs and salamanders is a further feature suggesting a common ancestor (Monath, 1965).

Despite the similarities of the living amphibians, the fossil record clearly demonstrates that all three orders have a long, unquestionably separate history. Essentially modern frogs are known from the Lower Jurassic (Estes & Reig, 1973), rather specialized salamanders from the Upper Jurassic (Estes, 1965), and an apodan from the Paleocene (Estes & Wake, 1973). If *Triadobatrachus* (Estes & Reig, 1973) is accepted as a frog ancestor or ancestral frog, the record of this group is further extended without approaching the condition exhibited by either apodans or urodeles. The fossil record demonstrates that anurans and urodeles must have been separate since at least the Upper Triassic. The single apodan vertebra from the Paleocene is essentially modern in configuration, suggesting that this group also had a long period of prior evolution.

A possible ancestor for the living amphibians, *Doleserpeton,* has been described from the Lower Permian of Oklahoma (Bolt, 1969). This genus is a rhachitomous amphibian, related to dissorophids and trematopsids. Uniquely among Paleozoic amphibians, it possesses bicuspid, pedicellate teeth. Exceptionally for a temnospondyl, the pleurocentra are the dominant vertebral elements and have a spool-like configuration. The general body proportions are like those of salamanders, but like frogs, *Doleserpeton* has a typical labyrinthodont otic notch. The skull of *Doleserpeton* shows no specific similarities to any of the living groups, although the large orbits and palatal vacuities, common to small and larval temnospondyls, give it a generally frog-like appearance. The skull roof, palate and braincase are totally unlike those of living apodans, however.

Because of their strictly tropical distribution and generally cryptic habits, much less is known of the anatomy or biology of apodans than of either frogs or salamanders although Taylor (1968) has published a monumental taxonomic study of the order. For this reason, they have not figured prominently in considerations of the ancestry of modern amphibians as a whole. Where any distinction is made, they are considered more closely allied to urodeles than to anurans.

Although all apodans practise cutaneous respiration and possess pedicellate teeth, there are few other features that indicate close relationship to frogs or salamanders. The peculiarities of the ear that are so significant in considering the relationships of frogs and salamanders are not developed in apodans for there is neither operculum nor "opercularis" muscle, and the general configuration of the skull is totally different. The general tenor of recent papers has been to assume that if frogs and salamanders are closely related, apodans surely belong with them as well. In the absence of any fossil evidence to support the derivation of apodans from either frogs, salamanders or the common ancestors of these forms, it is profitable to consider the ancestry of apodans separately, without immediate consideration of their possible relationships with urodeles or anurans.

Paleontologists have repeatedly suggested (but with little elaboration) that

apodans had a distinct ancestry from one or another group of Paleozoic amphibians. Lysorophids have frequently been suggested, and microsaurs or lepospondyls in general have been assumed to be ancestral to this group alone, or in consort with urodeles. Sollas (1920), Romer (1945, 1950), Gregory, Peabody & Price (1956), Cox (1967) are among the authors who have suggested these associations.

In the course of a general review of microsaurs, now nearing completion, the possibility of their relationships with other Paleozoic and Recent tetrapods has been considered. In the case of the often suggested relationship with reptiles, no significant similarities could be discovered (Carroll & Baird, 1968). Although many broad similarities between microsaurs and urodeles could be cited, these may be attributable to similarities in habits, rather than indicating close taxonomic affinities. No forms even vaguely analogous to frogs have been found among the wide variety of microsaurs. There are, however, general resemblances between several microsaur families and apodans, and one genus in particular shows striking similarities with living members of that group.

Before enumerating the similarities, it is well to consider some general problems inherent in any such comparison. Approximately 250 million years separate the modern apodans from microsaurs. This is a greater span of time than the entire history of the Class Mammalia. An enormous amount of anatomical change could have occurred during this time that saw the evolution of such strikingly similar but phylogenetically distinct groups as ichthyosaurs and porpoises.

Apodans are small, elongate, burrowing forms, as were the specific microsaurs with which they are being compared. It is obvious that these characteristics could lead to the evolution of a generally similar pattern of cranial anatomy. Similarities may be expected to be proportionately greater in closely related groups, but the anatomical similarities exhibited by specialized groups of placentals and marsupials in relationship to common environmental factors demonstrate the difficulties of determining relationships between groups if there is no fossil record. Nevertheless, the similarities between some microsaurs and living apodans are sufficiently numerous to warrant considering the possibility that the two groups may be more closely related to one another than either is to frogs and/or salamanders.

The most important assumption that must be made in this comparison is that the general anatomy of the skull of living apodans (Figs 1, 2 and 3) is broadly representative of the ancestors of the group. In past comparisons of apodans with salamanders and frogs it was assumed that this was not the case, but that the solid "stegocephalian" configuration had been derived from an open skull roof, similar to that of frogs and salamanders as a result of the development of a burrowing habit. In the absence of any fossil apodan skulls, it is not possible to prove either of these alternatives.

Two features of the apodan skull, the small number of cranial bones and the variable occlusion of the orbital region, are definitely specializations from the condition seen in any Paleozoic amphibians or other possible antecedents. The restriction of the orbital opening is clearly the result of adaptation to burrowing life, and is related to partial or complete loss of vision. This factor, however, does not preclude evolution from forms exhibiting the typical stegocephalian skull pattern. Developmental studies by Marcus, Stimmelmayr &
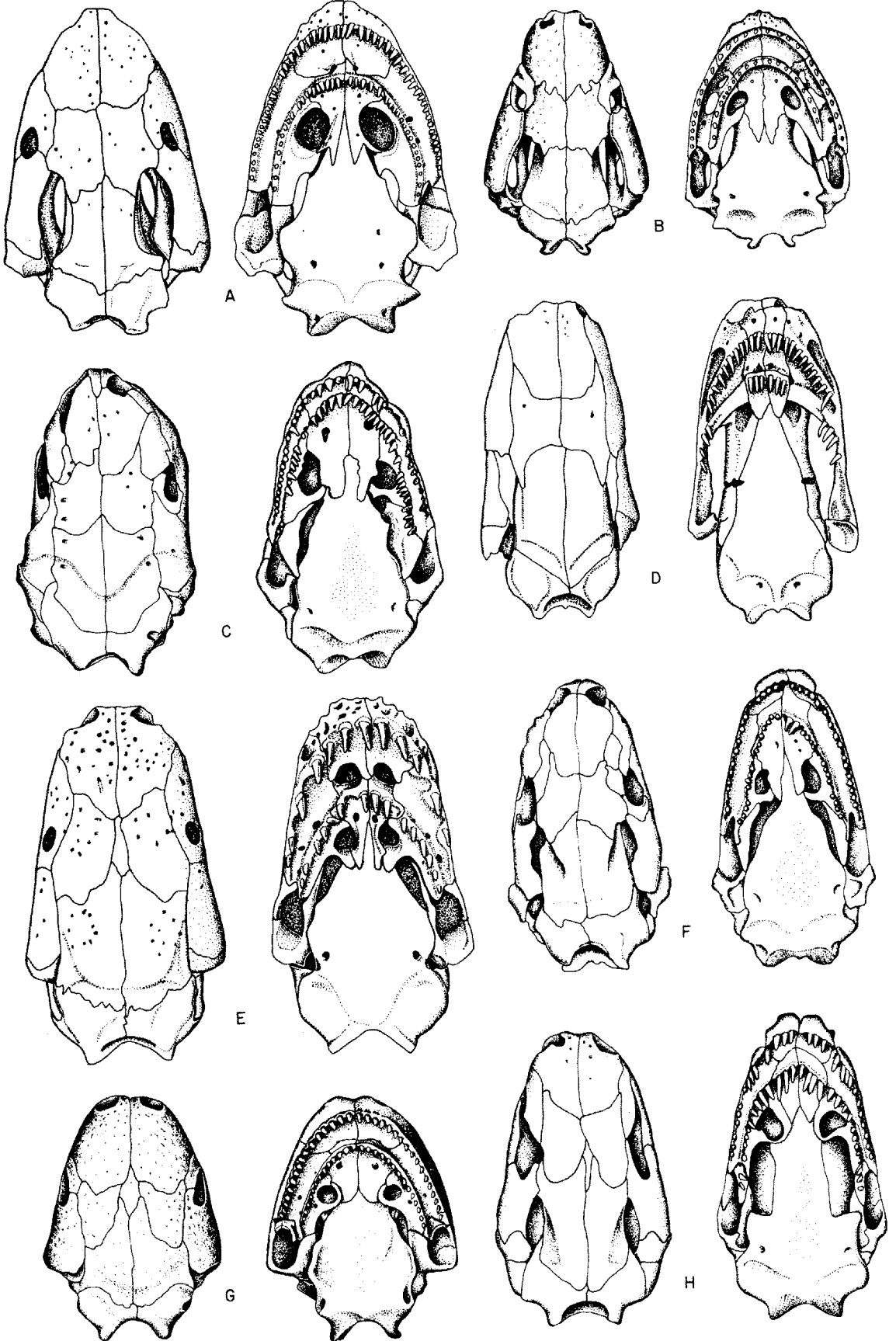
Porsch (1935), Peter (1898), Sarasin & Sarasin (1890) and Ramaswami (1948) all indicate that the reduced number of bones seen in modern genera result from the fusion of numerous separate centres of ossification. This conclusion is supported by consideration of a broad range of adult skulls of various species which show a great variety in the expression or fusion of individual centres of ossification (see Figs 1, 2 and 3).

In one or more genera, all of the following bones of the skull roof are present as discrete areas of ossification: parietal, frontal, nasal, premaxilla, prefrontal, one or more additional circumorbital bones, septomaxilla and/or lacrimal, squamosal and an additional "temporal" bone. The quadratojugal is suggested by Lawson (1963) and others as being incorporated into the quadrate-pterygoid complex, but it is apparently never expressed as a separate element. The only bone common to most Paleozoic amphibians that is never represented in any form is the postparietal. Although the otic-occipital region of the braincase is solidly fused in apodans, there is no difficulty in deriving this structure from the typical components in Paleozoic amphibians. The lower jaw similarly represents fusion from many, originally separate areas of ossification. The palate, in contrast, may retain all of the elements found in Paleozoic forms.

Thus, although there is some loss and fusion of bones in the apodan skull from the primitive Paleozoic pattern, there is no reason not to think that the generally complete roofing of the skull is primitive, rather than derived from the open condition seen in anurans and urodeles.

COMPARISON OF APODANS WITH THE MICROSAUR *GONIORHYNCHUS*
(LOWER PERMIAN OF OKLAHOMA)

Skull roof and palate

Comparison of the skulls of microsaurs with those of apodans is greatly facilitated by the work of Taylor (1969) who has recently published photographs of skulls belonging to 20 apodan genera. For the first time, we can see the total range of variation in cranial structure within the living members of the group. Taylor recognizes four families, one of which is further subdivided into two subfamilies: Ichthyophidae, Typhlonectidae, Scolecomorphidae, Caeciliidae, Caeciliinae, and Dermophinae. Each group can be defined on the

Figure 1. Skull roof and palate of apodans. A, *Typhlonectes natans* x 2.1, MCZ No. 24524. Colombia; B, *Chthonerpeton indistinctum* x 2.8. Brazil; C, *Ichthyophis glutinosus* x 4.5, BM(NH)1909.10.18.13. Ceylon; D, *Scolecomorphus kirkii* x 5.8, MCZ 27120. Nyasaland; E, *Caecilia albiventris* x 5, AMNH 49960. Colombia; F, *Uraeotyphlus oxyurus* x 5.2, BM(NH)1909.10.11.7. India; G, *Siphonops annulatus* x 2.3. Brazil; H. *Geotrypetes seraphini* x 4.6, BM(NH)1909.12.3.25. Cameroons.

A, D and E from Taylor (1969); B and G from Wiedersheim; C, F and H original.

A and B, Typhlonectidae; C, Ichthyophiidae; D, Scolecomorphidae; E, Caeciliidae, Caeciliinae, F-H, Caeciliidae, Dermophinae.

Abbreviations for institutions from which material has been cited: AMNH: American Museum of Natural History; BM(NH): British Museum (Natural History); FMNH: Field Museum of Natural History, Chicago; MCZ: Museum of Comparative Zoology, Harvard: MSU: Michigan State University Museum; RM: Redpath Museum, McGill University; UCLA VP: University of California, Los Angeles.
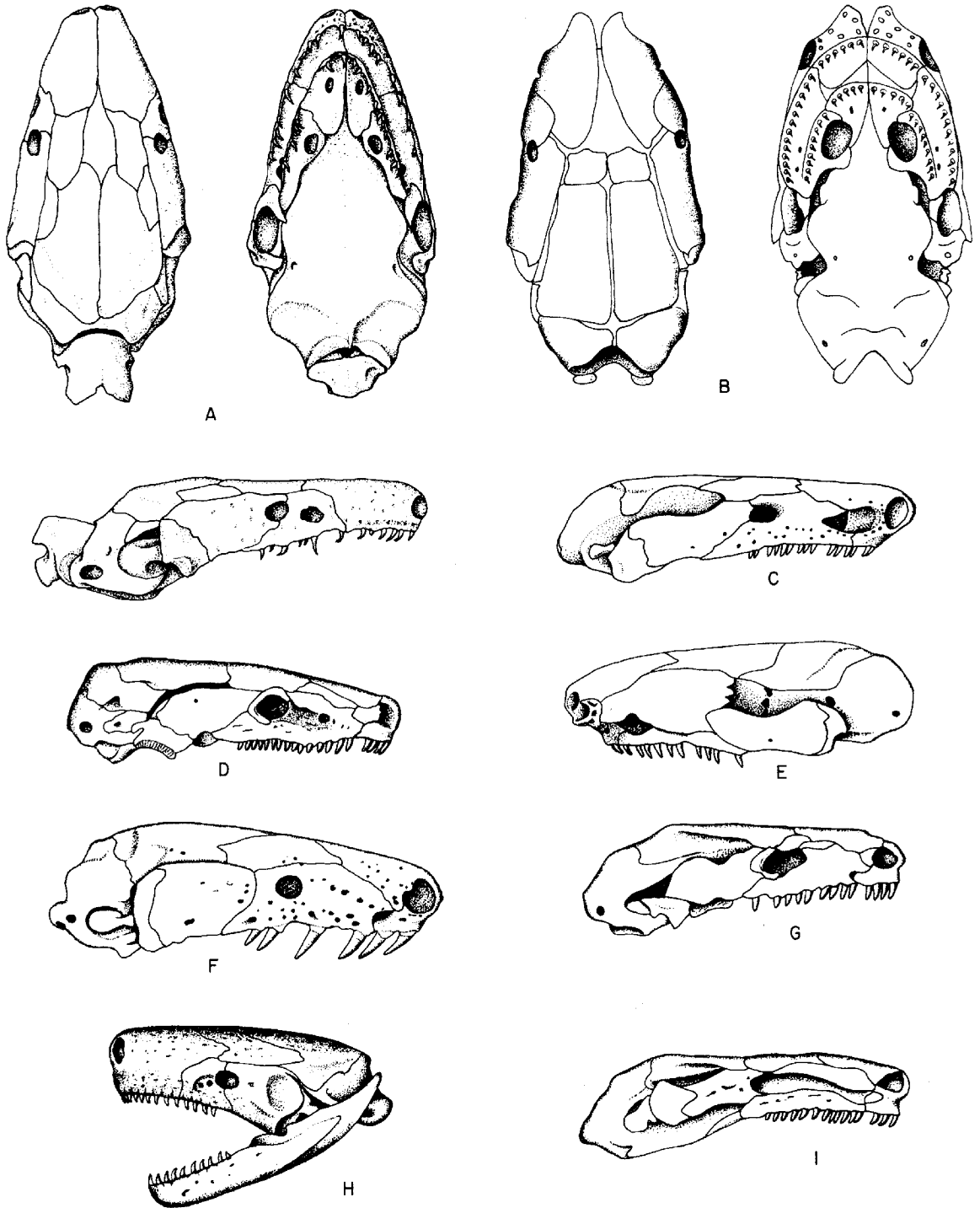
Figure 2. Skulls of apodans. A, *Schistometopum thomense* x 6, RM 13,653. Dermophinae, Gulf of Guinea; B, *Idiocranium russeli* x 10 (from Parker, 1936). Dermophinae, Cameroons: C, *Typhlonetes natans* x 2.1; D, *Ichthyophis glutinosus* x 4.5; E, *Scolecomorphus kirkii* x 5.8; F, *Caecilia albiventris* x 5; G, *Uraeotyphlus oxyurus* x 5.2; H, *Siphonops annulatus* x 2.3; I, *Geotrypetes seraphini* x 4.6.
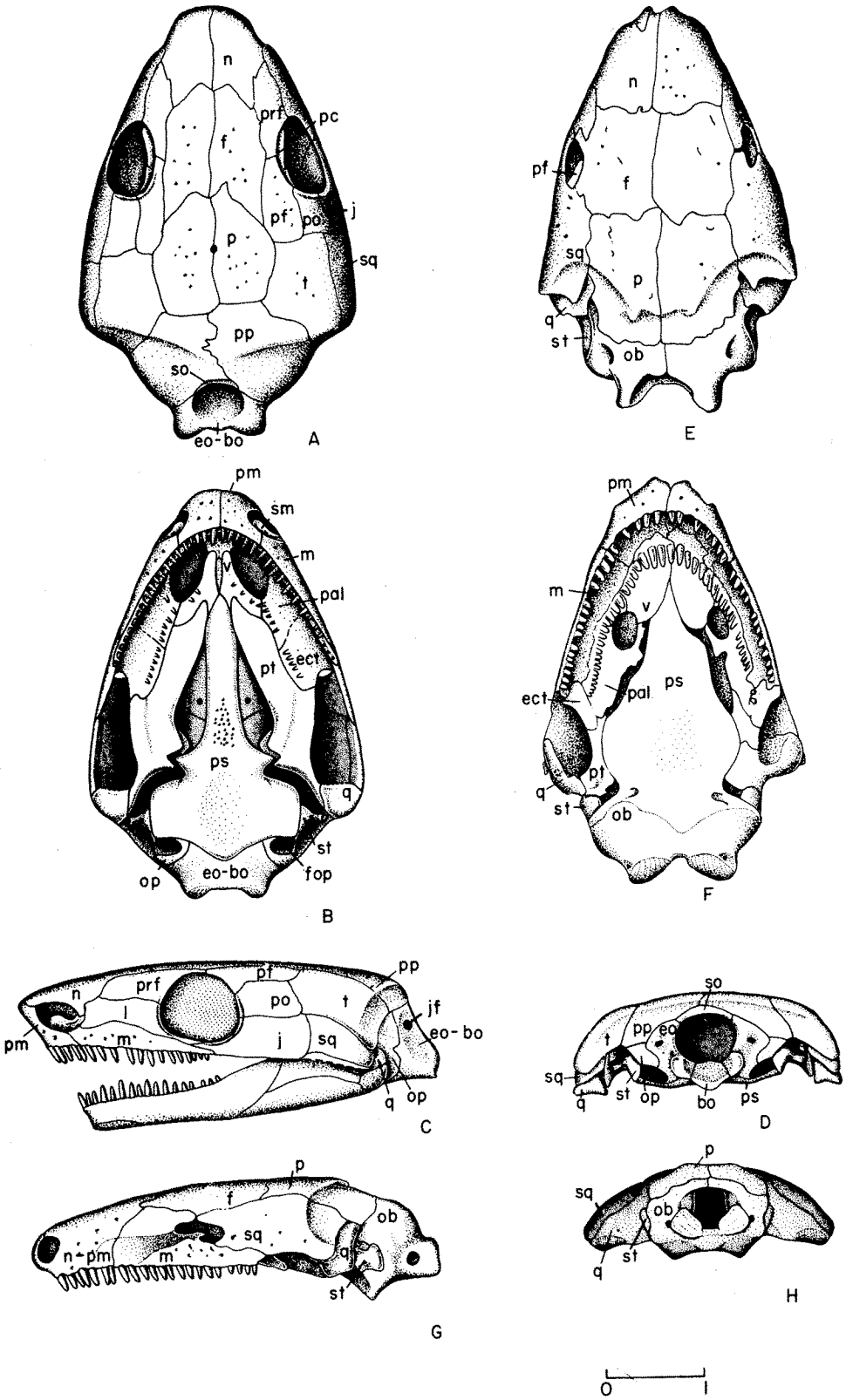
Figure 3. Comparison of skulls of microsaurs and apodans. A, B, C and D, Skull roof and palate, lateral and occipital views of the microsaur *Goniorhynchus stovalli,* based primarily on FMNH 1039 and 1040, x 3. Lower Permian, Oklahoma; E, F and G, *Grandisonia alternanas* BM(NH)1974.958, x 5. Seychelles; H, *Hypogeophis rostratus* (redrawn from Lawson) x 5.

basis of cranial characteristics and reproductive habits, as well as by broad habitat preference. The Scolecomorphidae (Figs 1D and 2E), containing only a single genus, is clearly the most specialized group, with complete loss of both orbits and stapes. Among other groups, it is difficult to determine which might be considered the most primitive on the basis of cranial structure. The overall configuration is basically quite stable. The variation is, in fact, much less extensive than is that which can be seen among modern salamanders, or even frogs. There do not appear to be any obvious trends in the groups as a whole. Fusion of originally separate centres of ossification occurs in a seemingly random fashion. The opening for the tentacle may be confluent with the orbit (presumably primitive) or more anterior in position. The orbital opening is always small and may be totally covered with bone. This feature is encountered in several genera in different geographical regions. The cheek (squamosal and quadrate) may be solidly attached to the skull roof, movable, or separated by a significant gap. Aside from this gap, the skull is always solidly roofed; the occipital condyle is always well behind the quadrate. The structure of the palate is particularly conservative. There are always two rows of teeth. In addition to the marginal series, a second is borne on the vomers, maxillo-palatines and occasionally the ectopterygoids. The internal narial opening is medial to the inner tooth row. The ventral margin of the cheek is never more than slightly emarginated. The quadrate is closely appressed to the ear region, and (except for *Scolecomorphus*) is in articulation with the stapes. The position of the quadrate and configuration of the jaw musculature are constant within the Apoda, and completely at variance with the pattern in either frogs or salamanders. The structure of this area is, however, very similar to that noted in the microsaur families Gymnarthridae (Gregory, Peabody & Price, 1956) and Goniorhynchidae.

The generally small size, the reduced number of bones in the skull roof, the absence of an otic notch and the relatively small size of the orbits and interpterygoid vacuities give microsaurs as a group a greater overall similarity to apodans than can be noted among any labyrinthodonts. Much more specific similarities with apodans can be seen in the latest known microsaur, *Goniorhynchus*. This genus was initially described by Olson (1970) on the basis of two very well preserved skulls in the collection of the Field Museum, Chicago (FMNH 1039 and 1040) from the Hennessey Formation, Lower Permian of Oklahoma. General similarities with apodans such as the small, triangular skull with an overhanging rostrum and the presence of a second row of teeth on the palate were evident from this description. Further preparation has indicated a number of other features in common (Figs 3, 4 and 5).

In apodans, as in microsaurs in general, the parietals, frontals and nasals are paired bones, making up most of the central portion of the skull roof. All apodans lack the postparietals, but these bones occupy a primarily superficial position in *Goniorhynchus*, overlying the otic capsule and supraoccipital. In apodans as a group, and in *Goniorhynchus*, there is a distinct groove in the posterior dermal elements marking the anterior extent of the cervical musculature; this suggests a similar functional relationship between the skull and the trunk. Apodans lack a pineal opening, but this is small in *Goniorhynchus* and is absent in some other microsaurs.

In the cheek region, the area of the quadratojugal is small in *Goniorhynchus*

and, in fact, the presence of this bone as a discrete centre of ossification cannot be demonstrated on the basis of available skulls. The squamosal extends ventrally to the articulating surface of the quadrate. The "supratemporal" or tabular is a large unit in microsaurs extending to the circumorbital bones anteriorly and covering the otic region posteriorly. (As recently pointed out by Romer (1969), Thomson & Bossy (1970) and by Panchen (1972), the bone commonly termed supratemporal in microsaurs has the same relationship to the braincase as does the tabular in labyrinthodonts and might better be referred to by the latter name.) A tiny separate bone covering part of this area is retained in a few apodans. An important difference between the microsaurian and apodan skull is the incorporation of the area primitively occupied by part of the tabular, the jugal and postorbital and typically the postfrontal with the squamosal into a single ossification in the latter group.

In apodans, the lacrimal is much reduced and/or fused to adjacent bones and the lacrimal duct is altered to provide for the development of the tentacle. In neither *Goniorhynchus* nor in any other microsaur is there evidence of a tentacle.

The similarity of the palatal structure of *Goniorhynchus* to that of apodans is especially striking. This is principally the result of the presence in many apodans of all the primitive palatal elements, ectopterygoid as well as palatine (although usually if not always fused to the maxilla), vomer and pterygoid. The parasphenoid is larger and the pterygoid is smaller (or may be incorporated into the quadrate) in apodans, but this can be attributed to the small size of the skull and the greater relative size of the braincase. Most apodans retain a movable articulation between the braincase and pterygoid similar to that seen in microsaurs. In both groups, the vomers extend posteriorly to make firm contact with the parasphenoid-sphenethmoid complex. In microsaurs the internal nares open lateral rather than medial to the medial tooth row, reflecting the much smaller size of the nasal capsule; and the rows of teeth on the two vomers do not unite at the midline.

One feature that might be expected in the ancestors of apodans that is definitely not expressed in this, or any other, microsaur, is pedicellate teeth. Despite this, the overall similarities between the dermal skull roof and the palate of *Goniorhynchus* and living apodans are greater than those with any frogs or salamanders living or fossil, or with any of the other Paleozoic amphibians.

Braincase

The similarity in structure of the braincase in *Goniorhynchus* and apodans is also striking (Fig. 4). Of greatest significance is the fact that uniquely among amphibians, an extensive pleurosphenoid joins the otic-occipital portion of the braincase with the sphenethmoid. The resulting braincase has fundamentally the same configuration in both groups, although the numerous discrete centres of ossification seen in microsaurs are fused into two large units in apodans (the os basale and the os sphenethmoidale). Developmental studies (Marcus *et al.*, 1935: De Beer, 1937; Ramaswami, 1948) have shown that the reduced number of bones in adult apodans results from the fusion of separate centres of ossification in the embryo. In *Hypogeophis rostratus,* the os basale forms from
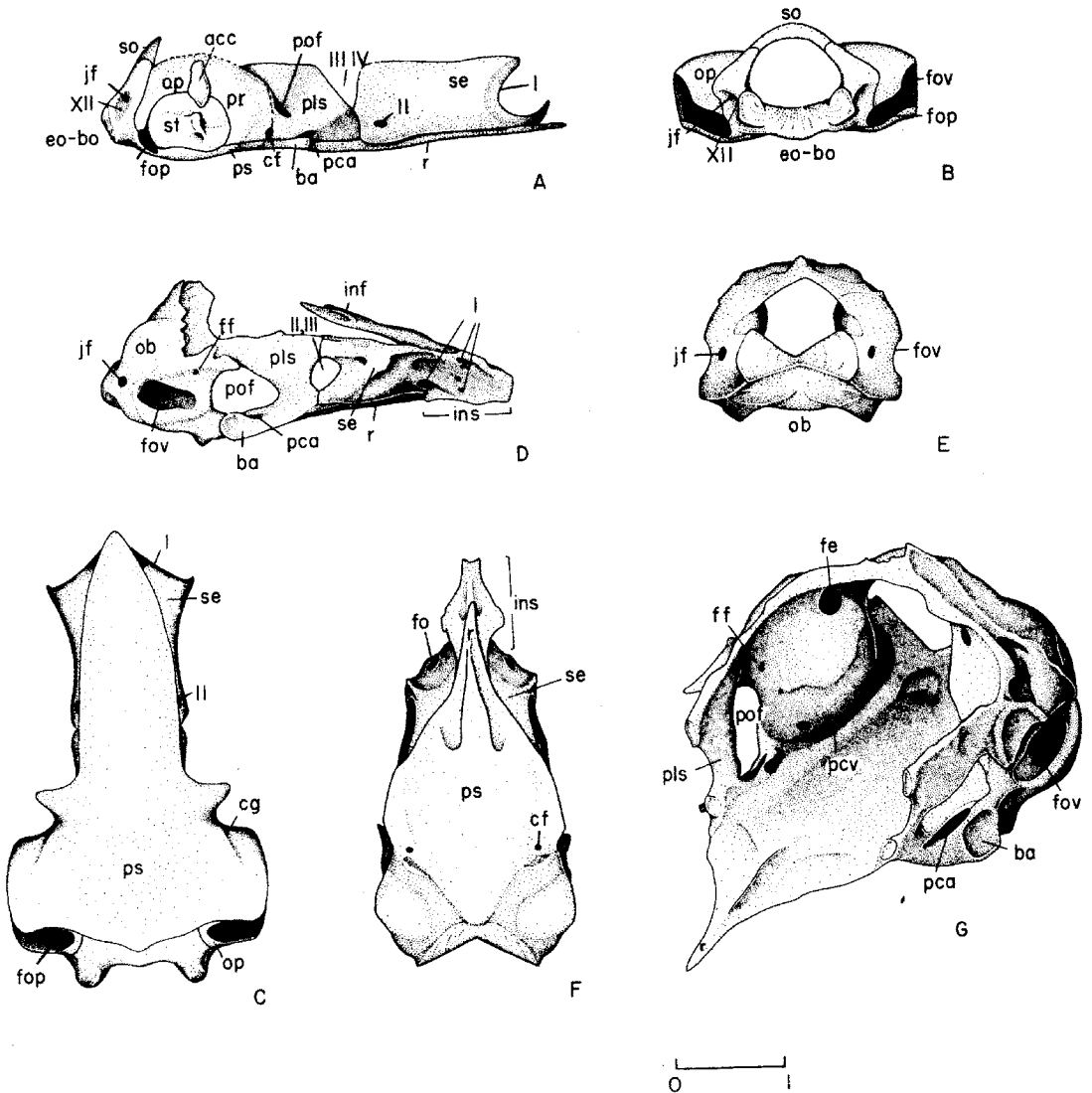
Figure 4. Comparison of braincase of microsaur and apodan. A, B, C, Lateral, occipital and palatal views of *Goniorhynchus stovalli*, based primarily on UCLA VP 2940, x 4.5; D, E, F, *Oscaecilia ochrecephala* x 7; G, oblique anterodorsal view of the os basale of *Oscaecilia ochrecephala* x 12, MSU 2846.

distinct elements identified as basioccipital, exoccipital, proötic, opisthotic and pleurosphenoid. The skeletal floor of the braincase is formed by the parasphenoid. The only primitive element not represented is the basisphenoid.

Double occipital condyles are found in both microsaurs and modern amphibians, but are quite variable in form in both groups. In the apodan *Oscaecilia*, the occipital condyles are linked by an articulating surface in the basioccipital area (Fig. 4). The condyles of *Hypogeophis* (Fig. 3) are more typical of apodans, with the knob-like processes separated medially. The occipital condyle of *Goniorhynchus*, like that of all microsaurs, is a wide arc, formed jointly by the exoccipitals and basioccipital. These bones are separate in small individuals, but fuse in more mature forms. In most genera, there is a more or less continuous, strap-shaped recess. In *Goniorhynchus*, the exoccipital portions are extended as double condyles, to form surfaces clearly distinct

from the recessed basioccipital. Among microsaurs, this pattern is closest to that seen in apodans.

Goniorhynchus differs from most other microsaurs in that the jugular foramen passes through the body of the exoccipital rather than between it and the opisthotic. A small hypoglossal foramen is seen externally, ventral and posterior to the jugular foramen; in some specimens these foramina are confluent medially. In apodans, the jugular foramen is located in the region of the exoccipital. It is interesting to note that Els (1963) reported that the exoccipital in *Schistometopum* encroaches onto the otic capsule and in all probability forms parts of the posterior wall. In most genera, the XIIth nerve originates posterior to the skull, although this is not true for all (Parsons & Williams, 1963).

In apodans, where the ontogenesis of the skull is known, a genuine supraoccipital is lacking. Marcus *et al.* (1935) reported a separate centre of ossification in membrane which becomes incorporated into the os basale of *Hypogeophis* above the foramen magnum. This, despite its dermal origin, was termed the "supraoccipital". In *Ichthyophis* and probably *Scolecomorphus* (Brand, 1956), this separate ossification is absent, and the exoccipitals extend toward the mid-dorsal line where they are suturally connected. In some individuals of *Oscaecilia ochrecephala* they become fused medially. In *Goniorhynchus,* there is a distinct supraoccipital, but this bone appears to be missing in a related microsaur family, the Gymnarthridae.

The otic capsule of apodans is fused solidly into the os basale, and the proötic and opisthotic are only distinct centres of ossification in some immature caecilians. The medial wall of the otic capsule is ossified. The fenestra ovalis is a large lateral opening, oriented slightly anteriorly. There have been no confirmed reports of the presence of an operculum in apodans, although Marcus (1935: 144) suggested that it had been incorporated into the footplate of the stapes. Apodans do not, in any case, have a fenestra opercularis distinct from the fenestra ovalis.

The proötic and opisthotic are distinct in *Goniorhynchus.* Most of the medial wall of the otic capsule was unossified. Laterally, there is a large fenestra ovalis. Continuous with this and oriented posteroventrally is a second opening, not covered by the footplate of the stapes, which appears in all specimens of this genus where the otic-occipital region is preserved. Such an opening is not present in apodans. Its significance in *Goniorhynchus* and other microsaurs has not been established.

The configuration of the stapes and its general relationship with the area of the quadrate in *Goniorhynchus* is similar to that seen in apodans, although actual articulation between these elements is not achieved. Some, but not all, specimens of this genus have a stapedial foramen. This opening is present in *Ichthyophis* among the apodans, but has not been reported in other genera.

The three microsaurs in which the braincase is adequately known, *Goniorhynchus, Pantylus* and the specimen Case (1929) attributed to *Ostodolepis,* have a large pleurosphenoid, occupying much of the area between the otic capsule and the sphenethmoid. The configuration in *Goniorhynchus* is particularly close to that in apodans. In both of these forms, the pleurosphenoid is continuous posteriorly with the otic capsule and ventrally with the parasphenoid. It extends dorsally to the dermal skull roof.

The proötic foramen is an extremely large opening in the pleurosphenoid dorsal to the basipterygoid articulation in most apodans. Most of the branches of the trigeminal and facial nerves pass through here, as does the abducens. Some apodans (such as *Siphonops*, see Wiedersheim, 1879) have several small foramina for the Vth and VIIth cranial nerves rather than a single large proötic foramen. In *Goniorhynchus*, there is a large proötic foramen piercing the pleurosphenoid midway in its height, anterior and medial to the otic capsule. It probably held most of the branches of the Vth and VIIth cranial nerves. A second small opening passes anterolaterally immediately dorsal to the basal articulation of the parasphenoid. A foramen in this position in *Pantylus* was, according to Romer, for the transverse vein. This vein has been lost in modern amphibians. The size and orientation of the foramen in *Goniorhynchus* would appear to suggest that a branch of the trigeminal passed through the pleurosphenoid here. A foramen in approximately the same location in those apodans which lack a single large proötic foramen, such as *Dermophis* (de Jager, 1939) and *Siphonops* (Wiedersheim, 1879) serves this function.

The pleurosphenoid region of the apodan os basale typically articulates with the sphenethmoid both above and below a large opening for the optic and oculomotor nerves. In *Goniorhynchus,* there is a wedge-shaped gap dorsal to the contact between pleurosphenoid and sphenethmoid; the optic nerve passed through a foramen near the posteroventral margin of the sphenethmoid.

In both groups, the rostral process of the parasphenoid extends far forward ventral to the sphenethmoid, and articulates anteroventrally with the vomers. In apodans, the parasphenoid is almost as broad in the region of the basal articulation as it is at the level of the otic capsules. The basipterygoid processes extend laterally from this area with concave facets directed dorsolaterally. The carotid foramen pierces the parasphenoid between the otic capsule and the basicranial articulation. In microsaurs the basicranial processes of the parasphenoid extend laterally from the base of the rostral process. The carotid foramina do not pierce the body of the parasphenoid in *Goniorhynchus*. Faint grooves on the ventral surface of the parasphenoid for this artery, posterior to the basipterygoid processes, extend dorsally and medially into the braincase at the anteroventral margin of the otic capsule.

The sphenethmoid is a similar, unitary structure in *Goniorhynchus* and apodans. Despite the apparent great length in lateral view, the portion of the sphenethmoid forming the lateral wall of the braincase in apodans is actually quite short. In contrast with other forms, the pila metoptica have been lost from the developing chondrocranium of apodans. Consequently, the optic nerve, when present, leaves the braincase with the oculomotor between the pleurosphenoid portion of the os basale and the sphenethmoid. Anteriorly, the bone is continued as an extensive medial nasal septum. Dorsally, an infrafrontal process articulates with the skull roof, often penetrating the dermal bones to take part in the skull roof itself. At the base of the nasal septum, the anterior portion of the sphenethmoid is ossified, except for a variable number of openings for branches of the olfactory nerve. In *Oscaecilia* five channels are present.

The sphenethmoid of *Goniorhynchus* lacks the specialized features seen in apodans, but is fundamentally a comparable structure. It resembles in outline that of *Eryops* (Sawin, 1941) and *Edops* (Romer & Witter, 1942), although it is

not so massive. It is relatively narrow posteriorly, but anteriorly it flares out laterally. The ventral plate extends medially beyond the remainder of the bone, narrowing to a point that may have continued in a cartilaginous nasal septum. There is no evidence of a dorsal infrafrontal extension. The anterior end of the sphenethmoid bone is widely open, although a lip of bone lateral and ventral to the opening suggests that the brain may have been enclosed anteriorly by a cartilaginous wall. The ventral surface of the sphenethmoid was recessed to articulate with the rostral process of the parasphenoid in both groups. The apodan sphenethmoid could have been derived from that of *Goniorhynchus* through ossification of the nasal septum and the development of an infrafrontal process.

There are no features of the braincase of *Goniorhynchus* which would exclude it as a possible antecedent to that of apodans. Fusion of the exoccipitals, basioccipitals, opisthotics, proötics, parasphenoid and pleurosphenoid, and the loss of the basisphenoid and supraoccipital would produce the os basale of apodans. The most significant feature is the presence of a large ossified pleurosphenoid in *Goniorhynchus*. Its presence results in the brain being almost completely surrounded by bone. This is a characteristic found in few Paleozoic tetrapods. A somewhat apodan-like single ossification in the otic-occipital region is present in aïstopods (McGinnis, 1967) but its specific configuration differs significantly. The sphenethmoid region is apparently entirely different, and the roof of the skull in that group is completely unlike that of apodans.

Lower jaw

The lower jaws in apodans (Fig. 5) are composed of only two or three bones in the adult, but, as with the bones in the skull, embryological development proceeds from numerous, smaller centres of ossification. In contrast with frogs and salamanders, the jaw of apodans always has a very extensive retroarticular process. A retroarticular process is also present in *Goniorhynchus*, although it is not a feature common to other microsaurs. A more striking similarity is the presence in *Goniorhynchus* and many, but not all, apodan genera, of a second row of teeth on the medial surface of the lower jaw. This is the only microsaur, and in fact the only Paleozoic amphibian known to have a single row of teeth in this position. It is borne on the coronoid of this genus. In apodans this area of ossification is indistinguishable from the dentary. The relative position of the teeth is very similar, however.

Vertebrae and ribs

There is very little of the postcranial skeleton of *Goniorhynchus* that is particularly close to the pattern of apodans. Like other microsaurs, this genus retains limbs, although they are very small relative to the length of the trunk. There are a minimum of 37 presacral vertebrae. Apodans rarely have fewer than 80 vertebrae, with the anus terminal or subterminal.

The individual vertebrae (Fig. 5) are similar to those of other microsaurs, but slightly closer to the apodan pattern in having very low neural arches and practically no expression of the neural spines. Primitive features that they share
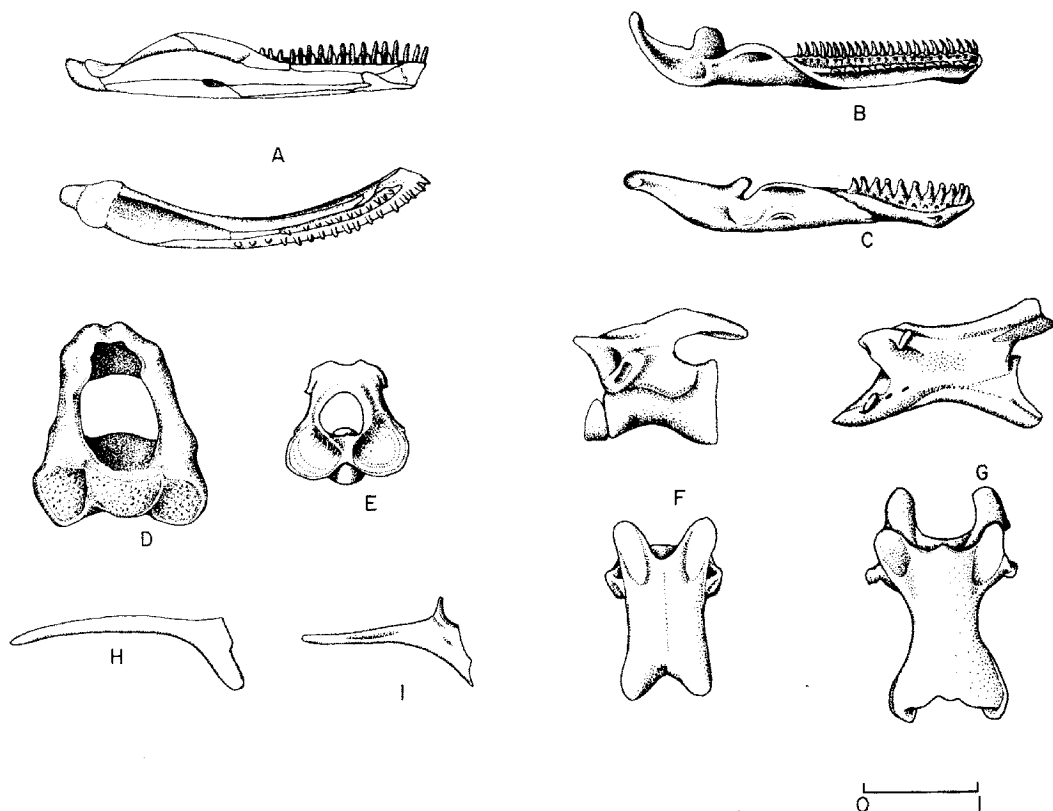
Figure 5. A, Lower jaws of *Goniorhynchus stovalli* FMNH 1243, x 3, in medial and dorsal views showing row of coronoid teeth; B, *Ichthyophis glutinosus* x 4.5 (from Wiedersheim) showing similar tooth row in medial view; C, *Siphonops annulatus* x 2.6 (from Wiedersheim). This genus lacks medial tooth row; D, anterior view of atlas of *Goniorhynchus* FMNH 1249, x 6; E, anterior view of atlas of *Hypogeophis rostratus* MSU 2341, x 6; F, lateral and dorsal views of posterior trunk vertebra of *Goniorhynchus* UCLA VP, x 4.5; G, lateral and dorsal view of trunk vertebra of *Hypogeophis rostratus* MSU 2341, x 6; H, anterior trunk rib of *Goniorhynchus* UCLA VP 2929, x 4.5; I, rib of *Hypogeophis rostratus* MSU 2341, x 6.

with apodans include deep, notochordal pits in the centra and short transverse process at the anterior end of the pedicle. It is hardly surprising that apodan vertebrae are more specialized, since the column must play the primary role in locomotion. Typically, the anterior margin of the centrum is extended in paired processes that underlie the posterior margin of the preceding vertebra. *Goniorhynchus* is among the few microsaurs with trunk intercentra. The apodan condition might have been achieved following fusion of an intercentrum with the anterior margin of the centrum.

The atlas of *Goniorhynchus* resembles in a general way that of apodans in the wide anterior face with paired lateral recesses for the condyles. The presence of a large median "odontoid" for articulation with the basioccipital is, however, not matched in that group. The atlas of both nectrideans and salamanders also follows this general pattern.

The ribs of apodans and *Goniorhynchus* are similar. They are short, pointed and have two distinct heads. Except for their unusual shortness, the ribs of *Goniorhynchus* are not exceptional among Paleozoic tetrapods. In fact, only the ribs of aïstopods and nectrideans are notably unlikely antecedents to those of apodans.

ANURANS, URODELES AND APODANS

Although this paper is not meant as a thorough evaluation of the possibility of close relationship between apodans and other living amphibians, the current tendency of herpetologists to accept the unity of the three orders requires some comments. In particular it is necessary to consider the skeletal resemblances of all three groups cited by Parsons & Williams (1963).

Of frogs and salamanders, Parsons & Williams (1963: 33) state: "Thus the type of skull fenestration or emargination found in the modern Amphibia, at least in the Anura and Urodela, seems distinctive. The orbit confluent with a lower temporal fenestra is a condition for which we have found no well-documented parallel in the known Paleozoic Amphibia; it may be a lissamphibian peculiarity." Nothing of this sort is found in any apodans. Parsons & Williams assumed that the complete covering of the cheek musculature is a secondary adaptation to burrowing, but there is no evidence among living apodans that this is the case and both snakes (which, according to Bellairs & Underwood (1951) arose from burrowing antecedents) and burrowing lizards have their jaw musculature "exposed", without a bony covering. Temporal openings do occur in apodans but they are of a type totally different from that seen in frogs and salamanders. Although not really comparable to the reptilian configuration, they could only be termed "upper" rather than lower openings, in contrast to the anuran and urodele condition. By analogy with the development of temporal openings in reptiles, it seems likely that the presence of a temporal opening in apodans is an advanced, rather than primitive characteristic. In any case, the structure of this region is vastly different from that known in frogs and salamanders, and can be readily derived from the condition seen in microsaurs.

Parsons & Williams refer to the palate in modern amphibians (but more particularly frogs and salamanders) as being derived from the "advanced" type of palate exhibited by Paleozoic amphibians, notably advanced temnospondyl labyrinthodonts. This is characterized by a firm union between the palate and the braincase and large interpterygoid vacuities. The palate of apodans does not fit this description. Although the small interpterygoid vacuities can be explained by the great relative size of the braincase in small skulls, the articulation which persists between the pterygoid and the braincase retains the essentially primitive configuration seen in microsaurs, the majority of lepospondyls and primitive labyrinthodonts. *Doleserpeton,* the suggested ancestor of modern amphibians, lacks the ectopterygoid, a bone present in several apodan genera.

Frogs and salamanders are unique among vertebrates in having an extra ear ossicle, the operculum, which is attached by an "opercularis" muscle to the shoulder girdle. Because apodans lack a shoulder girdle, it is not surprising that such a functional system is not present. Nor is the opercular bone reported in any adult apodans. Marcus (1935: 144) has reported a separate element that during development arises from part of the otic capsule and fuses to the base of the stem of the stapes, but there is no evidence that this ever was associated with a functional operculum-"opercularis" system.

The presence of pedicellate teeth is an unquestionable point of structural resemblance among all three amphibian orders. The apodans are the only forms

in which Parsons & Williams (1962) suggest that the division between the upper and lower portion of the tooth serves as a functional hinge. In this group alone can a selective advantage for this type of structure be noted.

Mentomeckelian bones are also cited as being a common heritage of the three living orders since they are typically found in all groups. The function of these structures is clearly different, however. In anurans in which respiratory function has been investigated, the mentomeckelian bones are movable structures associated with the closure of the internal nares. The elements termed mentomeckelian bones in apodans are fused to the dentary, and so cannot be used in this manner. This raises some questions as to the specific homology of the element, particularly since fused "mentomeckelian" bones are also seen in some lizards (de Beer, 1937; and R. Estes, pers. comm. cited by Parsons & Williams, 1963: 32).

Although there is a gross structural similarity among the vertebrae of living amphibians, the developmental patterns are very diverse both within and between groups. According to a recent study by Wake (1970: 33): "Nothing in the vertebral column of modern amphibians supports the concept of the Lissamphibia, and, in fact, the vertebral evidence offers no suggestion of relationship of the living amphibian orders." There is also a gross similarity between the vertebrae of frogs, salamanders, and apodans with the majority of Paleozoic lepospondyls. The similarities of the atlas and its relationship with the occipital condyle are particularly striking, but are shared to a variable extent by certain labyrinthodonts.

It is evident that apodans are exceptions to a greater or lesser degree in all of the skeletal characteristics (aside from pedicellate teeth) cited by Parsons and Williams for uniting the three living orders of amphibians. This is particularly evident in view of the features cited by them as being expected in the Paleozoic ancestors of these forms.

SUMMARY

Although there are numerous similarities in the anatomy and physiology of the three living amphibian orders, each has a long, separate fossil history. There is no fossil evidence of close relationship between these orders, nor with any Paleozoic amphibians. The apodans are typically assumed to be closely related to frogs and salamanders, but their position has never been discussed in detail since little is known of either their anatomy or biology. The general configuration of the apodan skull resembles that of Paleozoic amphibians, particularly microsaurs, much more than it does that of frogs or salamanders. This suggests that it may be profitable to consider the ancestry of apodans separately from that of other living amphibians.

The resemblance in cranial structure between a broad spectrum of living apodans and the microsaur *Goniorhynchus* (Lower Permian of Oklahoma) is particularly striking. In both, there is a row of palatal teeth borne on the ectopterygoid, palatine and vomer. There is also an extra row of teeth on the inside surface of the lower jaw. The jaw articulation is anterior to the occipital condyle and there is a retroarticular process. The stapes has a roughly similar configuration and position, and there is a comparable type of articulation between the braincase and the palate. The braincase of *Goniorhynchus* is

strikingly similar to that of apodans. The similarities noted between apodans and microsaurs may have resulted from similar adaptations among two distinct groups of small, burrowing amphibians, but they are sufficiently numerous that the possibility of relationship should be considered.

Evaluation of the numerous skeletal similarities cited by Parsons and Williams as uniting the three orders of living amphibians reveals that apodans are exceptional to a greater or lesser degree in most features. Consequently, the assumption of close relationship between apodans and frogs and salamanders is open to question. There is a strong possibility that apodans may have evolved separately since the Late Paleozoic, conceivably from microsaurs such as *Goniorhynchus*.

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ABBREVIATIONS USED IN FIGURES

acc	accessory ear ossicle	n	nasal
ba	basicranial articulation	ob	os basale
cf	carotid foramen	op	opisthotic
cg	carotid groove	p	parietal
ect	ectopterygoid	pal	palatine
eo-bo	exoccipital-basioccipital complex	pc	palpebral cup
f	frontal	pca	palatine canal
fe	foramen endolymphaticus	pcv	posterior cerebral vein canal
ff	facial foramen	pf	postfrontal
fo	foramen	pls	pleurosphenoid
for r.	ophthalmicus profundus	pm	premaxilla
fop	fenestra opercularis	po	postorbital
fov	fenestra ovalis	pof	proötic foramen
inf	infra frontal extension of sphenethmoid	pp	postparietal
ins	internasal septum	pr	proötic
j	jugal	prf	prefrontal
jf	jugular foramen	ps	parasphenoid
l	lacrimal	pt	pterygoid
m	maxilla	q	quadrate