Ecolsonia cutlerensis, an Early Permian dissorophid amphibian from the Cutler Formation of north-central New Mexico

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New Mexico Bureau of Mines & Mineral Resources

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Abstract

Recently discovered specimens of the temnospondyl labyrinthodont amphibian *Ecolsonia cutlerensis* Vaughn (1969) from the Lower Permian (Wolfcampian) Cutler Formation of north-central New Mexico allow a more complete description of its anatomy and a re-evaluation of its familial position. E. *cutlerensis* was originally assigned to the Trematopsidae primarily on the basis of its possession of an elongate external naris, a characteristic feature of the family, *yet* it was also recognized as possessing features characteristic of the Dissorophidae. Although the new materials of *Ecolsonia* clearly indicate the presence of a trematopsid-like naris, numerous other cranial features, particularly the otic notch, firmly establish its dissorophid affinities. *Ecolsonia* appears to be the only nontrematopsid labyrinthodont definitely known to possess an external naris identical to that of trematopsids. The postcranial skeleton of *Ecolsonia*, on the other hand, does not possess features that are diagnostic of either family. The absence in *Ecolsonia* of the highly specialized dorsal dermal "armor" that characterizes the great majority of dissorophids is unexpected in light of its otherwise highly advanced structural grade of organization. The probable functions of the typical dissorophid dermal "armor," that of providing strength and immobility to the vertebral column and protection from body-moisture loss and from predators, are believed to have been assumed in great part in *Ecolsonia* by several structures not seen in other dissorophids: (1) greater ossification of presacral intercentra to form ring-like structures; (2) neural spines with a pair of lateral tubercles or with bifid or nodular-like expanded summits that very likely accommodated a greatly increased development of the system of tendinous attachment of the dorsal axial musculature; and (3) well-developed, sculptured osteoderms that formed a dense, armor-like covering over much of the body. The possession by *Ecolsonia* of numerous unique derived features indicates that it represents a distinct lineage that separated from all other dissorophid lines before the Early Permian. Further, its possession of several primitive features not seen in other dissorophids suggests that the branching may have occurred as early as the Middle Pennsylvanian.

Introduction

Until very recently, the labyrinthodont amphibian *Ecolsonia cutlerensis* was known only by a partial skull collected and described by Vaughn (1969) from the well-known VanderHoof quarry in the Lower Permian Cutler Formation near the village of Arroyo de Agua, north-central New Mexico (Fig. 1). The discovery of additional specimens of this species was reported by Eberth and Berman (1983) from a site about 2.5 km northwest of, and at essentially the same stratigraphic level as, the type locality. They presented some important additional information about

FIGURE 1—Map showing the VanderHoof quarry and Morfin bonebed, the localities of the type (UCLA VP 1734) and referred specimens (CM 38017 and CM 41703) of *Ecolsonia cutlerensis*, respectively. Also shown are other well-known localities (see Langston, 1953): Anderson quarry (A), Baldwin bonebed (B), Camp quarry (C), Miller bonebed (M), and Welles quarry (W).

the cranial anatomy of *Ecolsonia,* **but** a **thorough** description had to await further preparation. Although *Ecolsonia* was assigned by Vaughn (1969) to the family Trematopsidae, he emphasized its apparent affinities with the family Dissorophidae, thereby reinforcing earlier studies that recognized a close relationship between the two families (Olson, 1941; DeMar, 1966a). Members of both families show the greatest degree of adaptation among labyrinthodonts to a terrestrial existence. The Dissorophidae is one of the largest Paleozoic amphibian families, including as many as 18 genera that occur over a time span **from the Late Pennsylvanian to the Late Permian.** The family Trematopsidae, on the other hand, is more restricted both in the number of genera (only four well-established genera) and the time span over which they occurred (Late Pennsylvanian to Early Permian).

Vaughn's (1969) decision to assign *Ecolsonia* to the Trematopsidae was apparently based mainly on the presence of a very elongate external naris. At that time this feature, seen in all trematopsid species, had been noted only in one other non-trematopsid, the advanced Early Permian dissorophid *Longiscitula houghae* (DeMar, 1966a). *Actiobates peabodyi* was later described (Eaton, 1973) from the Late Pennsylvanian as a dissorophid with a trematopsid-like naris. The occurrence of an elongate naris in *Longiscitula,* however, has been questioned (Bolt, 1974a), and it is argued here that *Actiobates* should be considered a trematopsid. The new material of *Ecolsonia* clearly documents the presence of a trematopsid-like narial opening, but all other features of the skull strongly indicate dissorophid affinities. Its possession of an elongate narial opening is, therefore, judged as an unique feature for a dissorophid. In a detailed comparative study of the narial region of dissorophids and trematopsids Bolt (1974a) argued, however, that their unique possession of a narial **flange would allow**

for the parallel development of an elongate naris to accommodate a large structure such as a gland—possibly a salt gland like that found in most living reptiles—lateral to the flange. Thus, he contended that an elongate external naris is not a diagnostic character for the family Trematopsidae.

Aside from the elongate narial opening, *Ecolsonia* can be distinguished from all other dissorophids by several unique derived characters of the skull and postcranial skeleton, whereas still other shared derived characters indicate an advanced stage of organization within the family. In view of its otherwise advanced level of structural organization, the absence of typical dissorophid "armor" of serially arranged, dorsal dermal plates that are intimately associated with the vertebral column is unexpected, because it occurs in all members of the family except two of the most primitive and earliest genera. In an analysis of the functions of the armor in dissorophids DeMar (1966b, 1968) concluded that it served several different adaptive roles in a terrestrial existence; primarily it strengthened and restricted movement of the vertebral column, while secondarily providing protection from drying by evaporation through the skin and from predators. It is argued here that in *Ecolsonia* these functions were performed in great part by structures otherwise unknown in dissorophids: (1) a greater ossification of the presacral intercentra so as to form ring-like structures surrounding the notochordal canal; (2) a pair of lateral tubercles or processes of the presacral neural spines, nodular expansion of the spine summits of anterior presacrals, and bifurcation of the spines of anterior caudals very likely accommodated an increased development of the tendinous attachment of the dorsal axial musculature; and (3) an extensive, armor-like body covering of closely spaced, well-developed, sculptured dermal ossifications or osteoderms.

Ecolsonia does possess several primitive features of the skull and postcranial skeleton which are not known in the other dissorophids. Those of the postcranial skeleton are restricted to the humerus and are also typical of trematopsids. The combination of the primitive features of the humerus and the trematopsidlike features of an elongate external naris and ring intercentra, and the absence of typical dissorophid dorsal "armor" might be construed as possibly indicating trematopsid affinities of *Ecolsonia.* The alter

native conclusion reached here is that *Ecolsonia* represents a widely divergent lineage that may have been distinct from the central line or lines of dissorophids by as early as the Middle Pennsylvanian. The few features of *Ecolsonia* that are considered unique within the Dissorophidae, but also characteristic of the Trematopsidae, are interpreted as probably reflecting a tendency toward parallel evolution between closely related families that became highly adapted to a terrestrial existence.

Acknowledgments

Abbreviations

CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; KU, Museum of Natural History, University of Kansas; MCZ, Museum of Comparative Zoology, Harvard University; UCLA VP, University of California, Los Angeles.

Geology

General

The Cutler Formation occurs throughout north-central New Mexico as a thick, southwestward-thinning, elastic wedge. The sediments are derived from the ancient Uncompahgre highland to the north and northeast that extended from Colorado into New Mexico. Although there is no doubt that Cutler deposition took place across the Pennsylvanian-Permian boundary, biostratigraphic (Langston, 1953) and lithostratigraphic (Eberth, in prep.) data strongly indicate a Lower Permian (Wolfcampian) assignment for the fossiliferous exposures in the Arroyo de Agua region of Rio Arriba County. Here the Cutler exposures are 150-200 m thick (Fig. 2). The base of the formation is not exposed and a northeast-dipping, angular unconformity marks the contact between the Cutler and the overlying Triassic sediments of the Chinle Formation. In general the Cutler Formation sediments represent the remains of an extensive fluvial system that includes alluvial fans (Mack and Rasmussen, 1984), and low-sinuosity and anastomosed rivers (Eberth and Berman, 1983). In the Arroyo de Agua region the Cutler sediments consist of several different lithofacies, including feldspathic quartz-channel sands, crevasse channel fills composed of reduced gravels, sands, silts, and shales, crevasse splays, and caliche-rich paleosols. Though fossil vertebrates have been collected from all of these lithofacies, the majority of specimens have come from the crevasse-channel and splay deposits that predominate in the lowermost 75 m of the exposures. Langston (1953) incorrectly interpreted these richly fossiliferous deposits as "pond deposits."

Type and referred localities

The VanderHoof quarry and Morfin bonebed (Fig. 1), respectively the type and referred localities of *Ecolsonia cutlerensis,* are at essentially the same stratigraphic level near the base of the exposed section of the Cutler Formation (Fig. 2). The VanderHoof quarry is a U-shaped, cut-and-fill deposit, with a maximum depth of 7.5 m and a width of 40 m (measured perpendicular to paleoflow). The base of the deposit consists of sandy, lime-pebble conglomerate lag. Above this is a grossly fining-upward sequence of complexly interbedded, reduced lenses of sands, silts, shales, and marls, which have yielded numerous disarticulated, associated, and articulated specimens of fish, amphibians (including the holotype of *E. cutlerensis),* and reptiles, as well as coprolites, plants, and a variety of discoid, calcium-carbonate nodules (see Langston, 1953, p. 358). The upper half of the deposit is dominated by shales that produce only occasional coprolites.

The VanderHoof quarry is interpreted as a crevasse, channel-fill deposit. This is based on its U-shaped morphology, vertically accreted sediments, and erosive-based, thin sandstone lenses and interbedded marls. The latter feature denotes alternating periods of shallow, high-velocity flows with periods of stag-

TRIASSIC

METERS

CI CLAY
S SILT
F FINE SS
M MEDIUM SS
C COARSE SS
G GRANULES
P PEBBLES
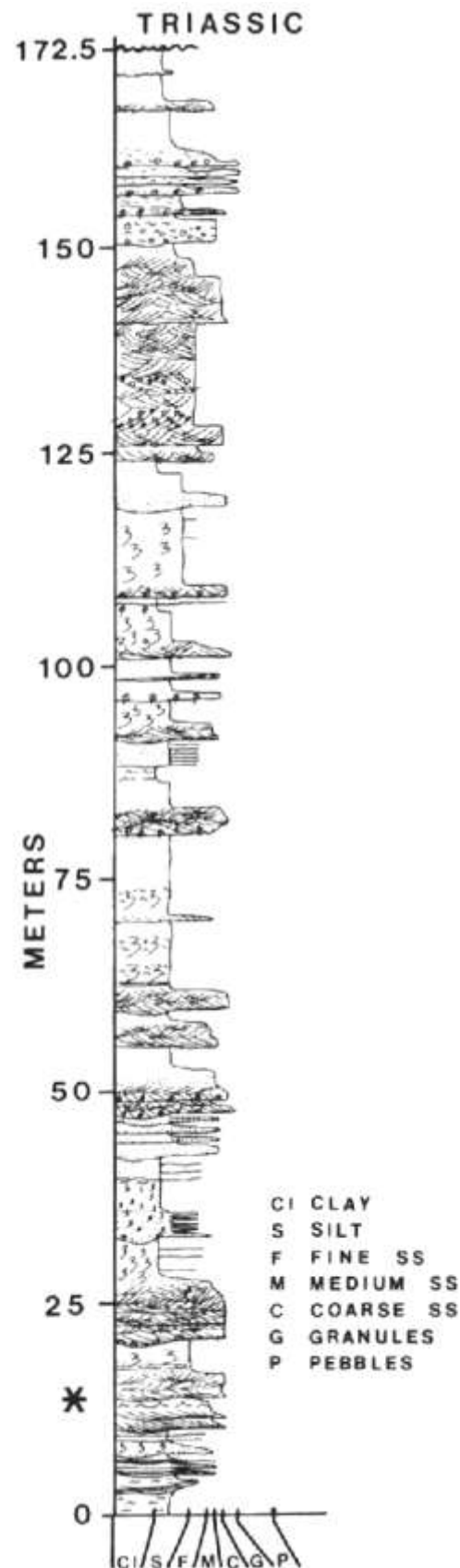
FIGURE 2—Generalized stratigraphic section of Cutler Formation exposures in Arroyo de Agua region. Asterisk marks approximate level of the VanderHoof quarry and Morfin bonebed localities.

nation and calcium-carbonate precipitation. The overall fining-upwards lithology of the deposit and the dominance of shales in the upper half indicate that the channel was eventually cut off from its source of bed load and that infilling continued largely from settling of suspended sediments. The occurrence of coprolites throughout the deposit and finely preserved seed-fern fronds in the lower half of the deposit suggest that some of the articulated vertebrates may have been in-situ faunal elements, whereas most of the disarticulated and partially articulated specimens are considered to have been washed in.

The Morfin bonebed, described here for the first time, occurs in the lower 1 m of a 5 m, overall fining-upwards sequence (Fig. 3). From the base of this sequence a laterally extensive, 25 cm thick, basal lime-pebble conglomerate fines upward into a 75 cm thick unit of dull red—brown, sandy shales and silts that contain caliche nodules, a few laterally limited, medium- to coarse-grained sandstone lenses that exhibit medium scale, trough crossbedding and some horizontal stratification. The sandy-shale and silt unit in turn fines upward into a 4 m thick unit of red—brown, silty clay and clay that contains abundant caliche-nodule horizons. Bone fragments are common throughout the basal conglomerate, but articulated and associated elements of vertebrates (including the referred specimens of *E. cutlerensis)* are found only in the overlying sandy-shale and silt unit. Adjacent (to the west) to the fossiliferous sandy-shale and silt unit of the Morfin bonebed and overlying the extensive basal conglomerate is a lens-shaped deposit contain

ing 5-10 cm thick, laminitic-limestone sheets and interbedded lenses of pebbly sandstone, silt, and marl (Fig. 3). It has a maximum thickness of 1.75 m and a traceable lateral extent of 23 m. The deposit (to be described in a future paper) is ascribed a fresh-water, cryptalgal origin. Although we have compiled over 40 measured vertical sections and conducted extensive sedimentological and paleontological investigations in the region, this is the only deposit of this type in the Cutler Formation of north-central New Mexico known to us.

The Morfin bonebed deposit does not exhibit the distinct, U-shaped morphology of the channel-fill deposit of the VanderHoof quarry. Yet, its possession of a sequence of sandstone lenses and sheets with interbedded silts and muds is indicative of repeated cycles of shallow, ephemeral flow and deposition from suspension, which are characteristics of crevasse-splay deposits. The adjacent algal-laminite deposit indicates that this locality was a topographic low. The apparent absence of other algal-laminite deposits and the ubiquitous occurrence of seed ferns at other fossiliferous localities in the Cutler beds of Arroyo de Agua suggest that at the Morfin bonebed seasonal wetness was sufficient for algal blooms, but longer periods of aridity and desiccation prevented colonization by seed ferns. A similar explanation for the occurrence of algal laminites on the supratidal marshes in Florida and the Bahamas has been given by Monty and Hardie (1976). The absence of higher plants and reduced sediments, shales, and coprolites indicates that standing water was not a common feature at the Morfin bonebed. Thus, in contrast to the VanderHoof quarry, it is unlikely that many of the fossil vertebrates in this bone-bed represent in-situ occurrences.
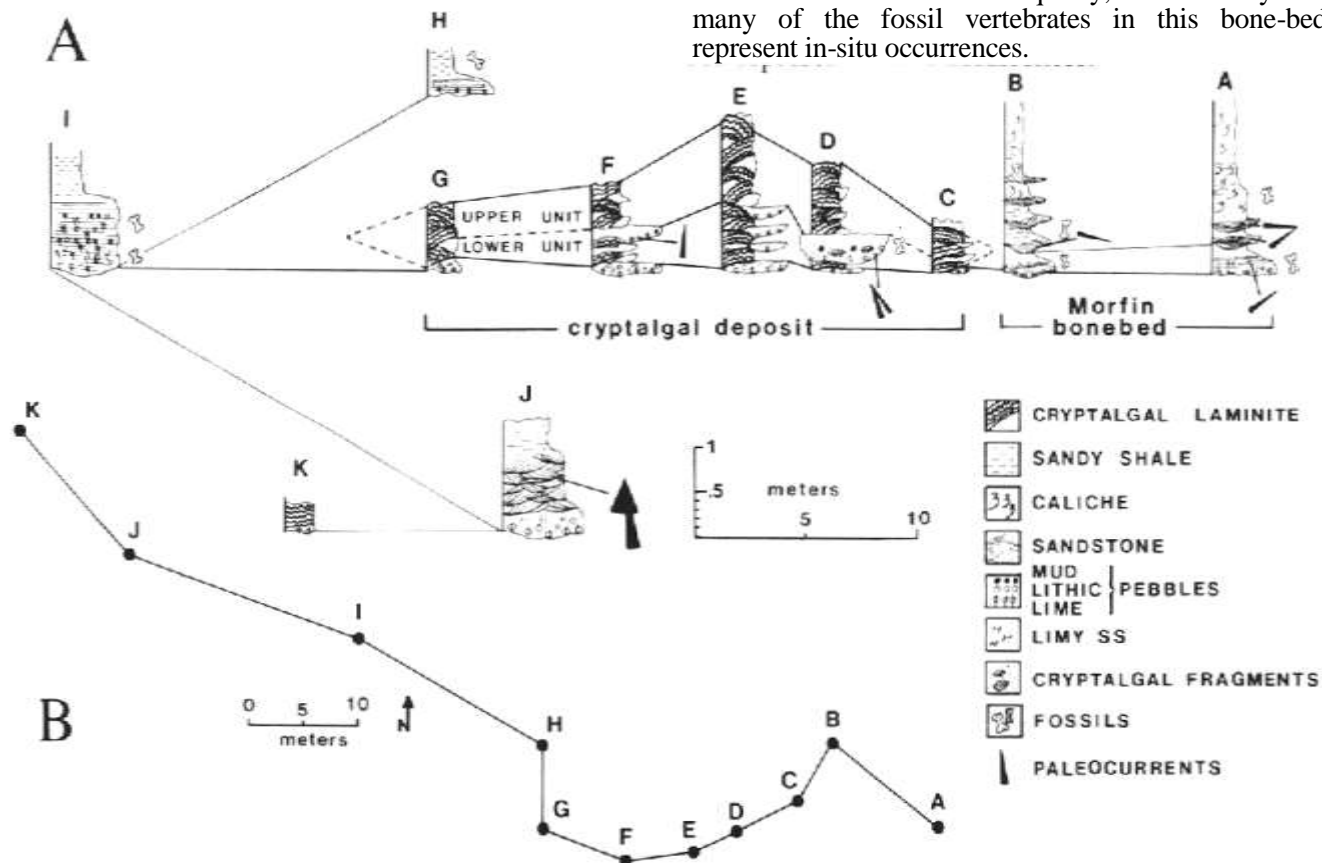
FIGURE 3—A, Microstratigraphic relationships at Morfin bonebed locality; B, plan view and relative positions of the microsection localities of A.

Systematic **paleontology**

Type species— *Ecolsonia cutlerensis* Vaughn, 1969.

Revised diagnosis—Large dissorophid temnospondyl that differs from all other members of the family in the following features: elongate, partially subdivided external naris; otic notch closed posteriorly by contact between tabular and well-developed posterodorsal processes of quadratojugal and quadrate; quadratojugal very large, and its posteroventral corner joined medially to posterodorsal process by a narrow, saddle-shaped neck of bone; presacral neural spines possess a pair of asymmetrically positioned, lateral tubercles; nodular or papillose expansion of neural-spine summits of anterior presacrals; spines of anterior caudals bifurcated; ring intercentra of pre-sacral column; dense body covering of well-developed, non-overlapping dermal ossifications or osteoderms. The following combination of characters distinguishes *E. cutlerensis* from other dissorophids: lateral exposure of palatine on ventral rim of orbit very narrow; 35-39 relatively large, slightly recurved marginal teeth on either side of **skull; large,** medial exposure of articular; dorsal, expanded portion of cleithrum very small. Primitive features not seen in other dissorophids include: open, mobile basicranial joint; contact between pterygoid and vomer; humerus with well-developed supinator process, distinct separation between deltoid and pectoralis components of deltopectoral tuberosity, and dorsolateral projection of large ectepicondyle from a level dorsal to the radial condyle.

ECOLSONIA CUTLERENSIS Vaughn, 1969

Holotype—UCLA VP 1734, a partial skull that includes a greater part of the roof and the anterior portion of the palate.

Referred specimens—CM 38017: posterior half of skull with part of left mandible; series of closely associated far-anterior presacral vertebrae and ribs, and loosely articulated right scapulocoracoid and clavicle preserved immediately behind skull; loosely articulated elements of two probable mid-presacral vertebrae; associated and partly articulated vertebral series that includes elements of posterior presacrals with rib fragments and a sacral neural arch; several isolated presacral intercentra; left pleurocentrum; neural arch of an anterior presacral; two isolated neural arches of anterior caudals; left caudal rib and isolated rib fragments; left scapulocoracoid; left clavicle (closely associated with skull CM 41703); proximal end of left and distal end of right humeri; proximal end of right ulna; right pelvis; proximal and distal ends of left femur.

CM 41703: complete skull with left mandible; portions of right mandible; four articulated neural arches

of anterior caudals with associated central elements and ribs; articulated last 12 caudal vertebrae; articulated left scapulocoracoid and cleithrum; left clavicle and interclavicle closely associated with skull; right clavicle; proximal end of left humerus; left radius; proximal and distal ends of right and proximal end of left ulnae; greater portions of pelves; associated left femur, fibula, proximal and distal ends of tibia, and partial pes; distal end of right tibia; isolated phalanges.

Dermal ossifications or osteoderms of various dimensions occur with most of the skeletal materials of both specimens.

Horizon and locality—All specimens are from essentially the same stratigraphic level in the lower part of the exposed section of the Cutler Formation near Arroyo de Agua, Rio Arriba County, north-central New Mexico (Fig. 2). An Early Permian, Wolfcampian, age is widely accepted for this level of the section (see Langston, 1953). The holotype was collected from the VanderHoof quarry in SW 1/4 SW 1/4 NE 1/4 sec. 8, T. 22 N., R. 3 E., whereas the referred specimens were collected in 1982 (Eberth and Berman, 1983) from the Morfin bonebed in SE 1/4 NE 1/4 NW 1/4 sec. 6, T. 22 N., R. 3 E. (Fig. 1). The Morfin bonebed is described here for the first time and named in recognition of Mr. Randy Morfin, on whose property it is located. Eberth and Berman (1983) misidentified this site as the well-known Miller bonebed, located about 0.7 km farther to the southeast. This confusion arose, in part, from a map showing the collecting sites near Arroyo de Agua by Romer (1960, p. 48), in which the Miller bonebed is erroneously located near the Morfin bone-bed. What he designated as the site of the Miller bone-bed does not correspond to any specific locality known to us. Further, in Romer's map the designation "p" indicates the southeasternmost point in which most of the fossils in the Cutler exposures along the northeastern side of the Salitral Creek valley have been found. As correctly shown in Langston's locality map (1953, p. 355), this designation is the site of the Miller bonebed. The histories and vertebrate assemblages of the well-known localities of the Arroyo de Agua region have been discussed in detail by Langston (1953).

Description

Skull and lower jaw

The referred skulls CM 41703 and CM 38017 are excellently preserved, and Figs. 4-8 eliminate the need for a detailed description of all aspects of the skull anatomy. CM 41703 is complete, but has suffered some dorsoventral crushing, particularly in the cheek region. As seen in the partial skull CM 38017, the cheek area posterior to the orbit meets the skull table at nearly a right angle, giving at least the posterior half of the skull a box-like configuration. In dorsal view the skull is triangular in outline, with a rounded snout and a deeply concave occipital margin. Pertinent **skull** measurements of CM 41703 are as follows: total length
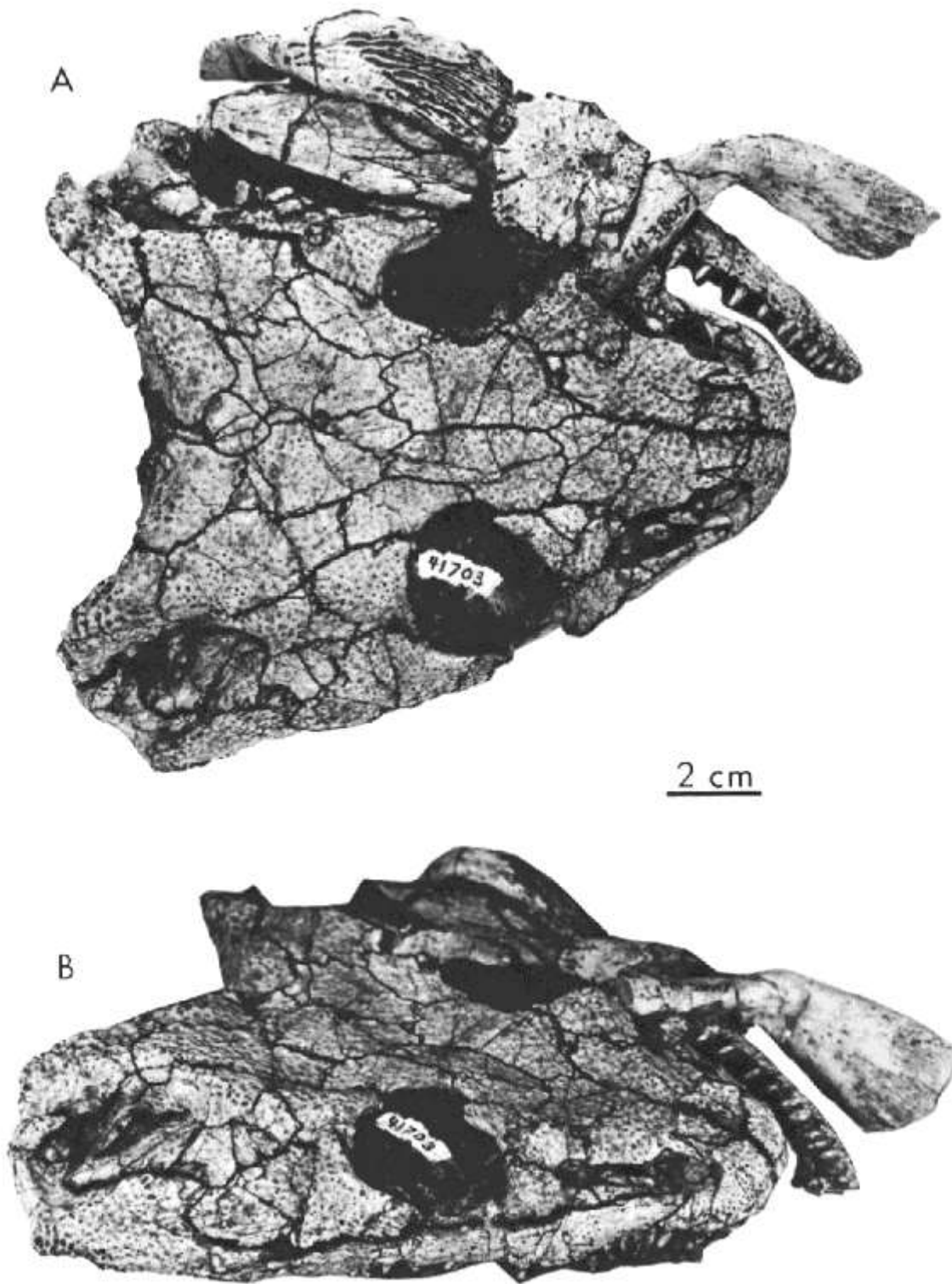
FIGURE 4—*Ecolsonia cutlerensis*, CM 41703. A, Dorsal view of skull with partial lateral view of left mandible; B, dorsolateral view of skull. Adhering to left side of skull are the left clavicle and interclavicle of CM 41703, and left clavicle of CM 38017.
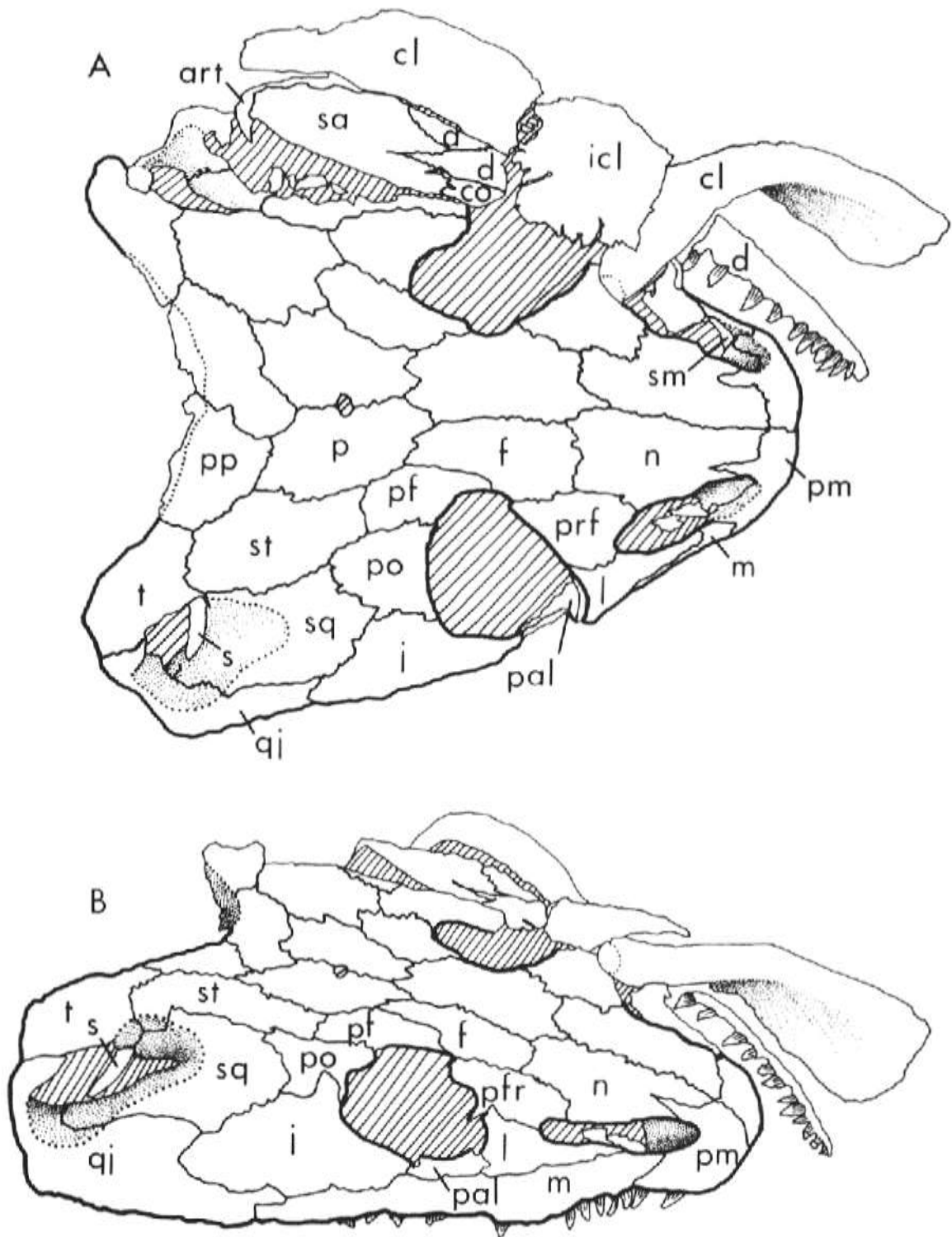
FIGURE 5—A, B, Outline sketches of views A and B of Fig. 4 to indicate individual elements and other structures of *Ecolsonia cutlerensis*, CM 41703. Abbreviations: **a**, angular; **art**, articular; **cl**, clavicle; **co**, coronoid; **d**, dentary; **f**, frontal; **icl**, interclavicle; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal, **pal**, palatine; **pf**, postfrontal; **po**, postorbital; **pp**, postparietal; **prf**, prefrontal; **qj**, quadratojugal; **s**, stapes; **sa**, surangular; **sm**, septomaxilla; **sq**, squamosal; **st**, supratemporal; **t**, tabular.

along midline, 135 mm; preorbital length, 48 mm; postorbital length along midline, 48 mm; width of skull roof between posterolateral tips of tabulars (somewhat exaggerated by crushing), 115 mm; minimum interorbital width, 34 mm; longitudinal and transverse diameters of orbit approximately 38 and 36 mm, respectively. The total length/postorbital length ratio is consistent with those of other dissorophids (DeMar, 1968; Berman, Reisz, and Fracasso, 1981). Of the above measurements, only the postorbital length, 46 mm, and the width between the posterolateral tips of the tabulars, 124 mm, are available from the partial skull CM 38017. The dermal sculpturing of the skull roof is of the typical labyrinthodont amphibian pattern, consisting of a reticulate network of ridges surrounding pits. It exhibits its greatest development along the lateral and posterior margins of the skull table and over most of the postorbital cheek region, particularly on the tabular and quadratojugal. The sculpturing is least developed on the central area of the skull table. There are no prominent exostoses or tubercles as are often seen in large dissorophids, but there is, as Vaughn (1969) noted in the holotype UCLA VP 1734, a low, sculptured ridge along the occipital margin of the postparietal which merges with the coarse sculpturing of the tabular. The prefrontal and postorbital are both greatly thickened into broadly rounded, roughly anteroposteriorly oriented, ridge-like swellings that become very pronounced toward the orbital margin.

The structure of the skull roof is with only a few exceptions quite typical of dissorophids. The premaxilla forms the anterior and anteromedial margins of the external naris. Its posterodorsal process is a narrow, sharply pointed splint of bone that projects into the anterolateral margin of the nasal. The right premaxilla possesses five teeth with spaces for four more, and the left has six teeth and spaces for two more. The teeth in both elements increase in size posteriorly from a basal diameter of just under 2 mm and a length of about 5 mm to about 3 and 9 mm, respectively. The teeth are sharply pointed and slightly recurved distad. The maxillary tooth row extends posteriorly to just beyond the level of the posterior orbital margin. It is estimated that the maxilla possessed, or had spaces for, about 27-30 teeth. The teeth are like those of the premaxilla and gradually decrease in size posteriorly. The first two teeth are equal in size to the largest and posteriormost premaxillary tooth.

Probably the most interesting feature of the skull of *Ecolsonia* is the structure of the external naris. It is like that of trematopsids in being greatly elongated and partially subdivided into a shorter anterior and a longer posterior portion by a broadly triangular, lateral projection of the nasal. The narial opening may have been divided at the same level by a septomaxilla. What is undoubtedly this element is preserved in the left naris of CM 41703. Here the small, triangular septomaxilla is supported by the otherwise very narrow contribution of the maxilla to the ventral narial rim. The slightly thickened posterior edge of the septomaxilla is smoothly finished and straight for most of its length, curving strongly anteriorly at its dorsal end. The septomaxilla extends anteriorly from its pos-

terior border as a narrow flange that dorsally becomes depressed into an anterolaterally facing, trough-like concavity. It is quite likely that the septomaxilla has tilted forward on its base about 45° from its correct orientation. If so, then its posterior border would have been vertical and the dorsal end would have closely approached, possibly even contacted, the apex of the laterally projecting flange of the nasal. The anterior portion of the external narial opening, undoubtedly the true external naris, is floored by the vomer, and the posterior portion directly overlies the internal naris as described by Olson (1941) and Bolt (1974a). Small fragments of bone lying in the right naris of CM 41703 probably represent a portion of the displaced septomaxilla. The lacrimal extends anteriorly along the ventral border of the posterior portion of the external naris as a long, narrow, tapering process; it reaches, or nearly reaches, the septomaxilla.

In CM 41703 there appears to be a dorsoventrally narrow, sculptured element along the ventral border of the right orbit that excludes the maxilla from the orbital margin. This element most likely represents a lateral exposure of the palatine on the skull surface, a feature which Bolt (1974c) has shown to be common in dissorophids and trematopsids, but very rare in other labyrinthodonts.

The sutural pattern of the skull roof is similar to that of dissorophids in general, but the relative positions of the sutural contacts between the supratemporal, postfrontal, and frontal series on the right side of the CM 41703 exhibit an anomalous pattern. Here, in contrast to the left side of the skull, the supratemporal extends farther anteriorly at the expense of the postfrontal, which in turn encroaches more extensively upon the posterolateral margin of the frontal and its contribution to the orbital rim. The sutural relationships of these elements on the left side of the skull are considered normal, because they are identical to those in CM 38017 and UCLA VP 1736 and are typical of dissorophids.

The otic notch of *Ecolsonia* is typical of dissorophids in most of its features except that in most species it is not closed posteriorly. In lateral view its outline is that of a right-angled triangle with the dorsal and posterior margins forming the horizontal and vertical sides of the right angle, respectively. The well-defined, smooth area bordering much of the otic notch is widest along the broad, flat, shelf-like ventral rim formed by the squamosal and quadratojugal. The smooth border narrows somewhat as it curves around the anterior corner of the notch on the squamosal; it then terminates at about the midlength of the dorsal rim of the notch in a dorsally arching border that incorporates a small, ventral portion of the supratemporal and the anteroventral corner of the tabular. A contact between the squamosal and tabular excludes the supratemporal from the otic-notch margin. At the level of this contact the smooth dorsal border of the notch projects ventrally a short distance as a semilunar flange. This flange is identical to the otic-notch flange described by Carroll (1964) and DeMar (1968) in most dissorophids. The most remarkable feature of the otic notch is the manner in which it is closed posteriorly. The tabular is greatly elongated postero-
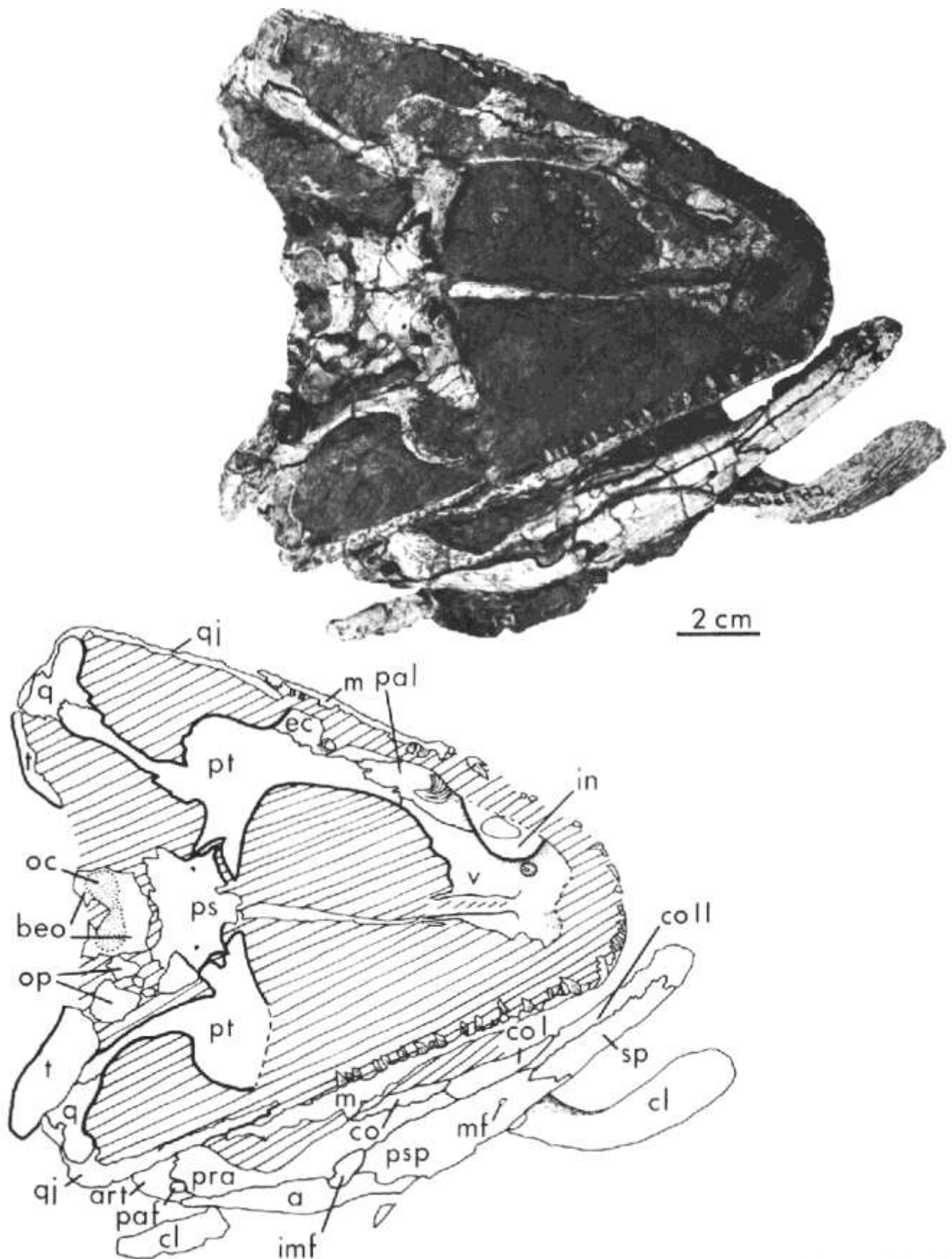
FIGURE 6—*Ecolsonia cutlerensis*, CM 41703. Ventral view of skull and medial view of left mandible with outline sketch indicating individual elements and other structures. Abbreviations: **a**, angular; **art**, articular; **beo**, basioccipital–exoccipital complex; **cl**, clavicle; **co**, coronoid; **co I**, intercoronoid; **co II**, precoronoid; **ec**, ectopterygoid; **in**, internal naris; **imf**, inframeckelian fossa; **m**, maxilla; **mf**, mandibular foramen; **oc**, occipital condyle; **op**, opisthotic; **paf**, para-articular foramen; **pal**, palatine; **pra**, prearticular; **ps**, parasphenoid; **psp**, postsplenial; **q**, quadrate; **qj**, quadratojugal; **sp**, splenial; **t**, tabular; **v**, vomer.
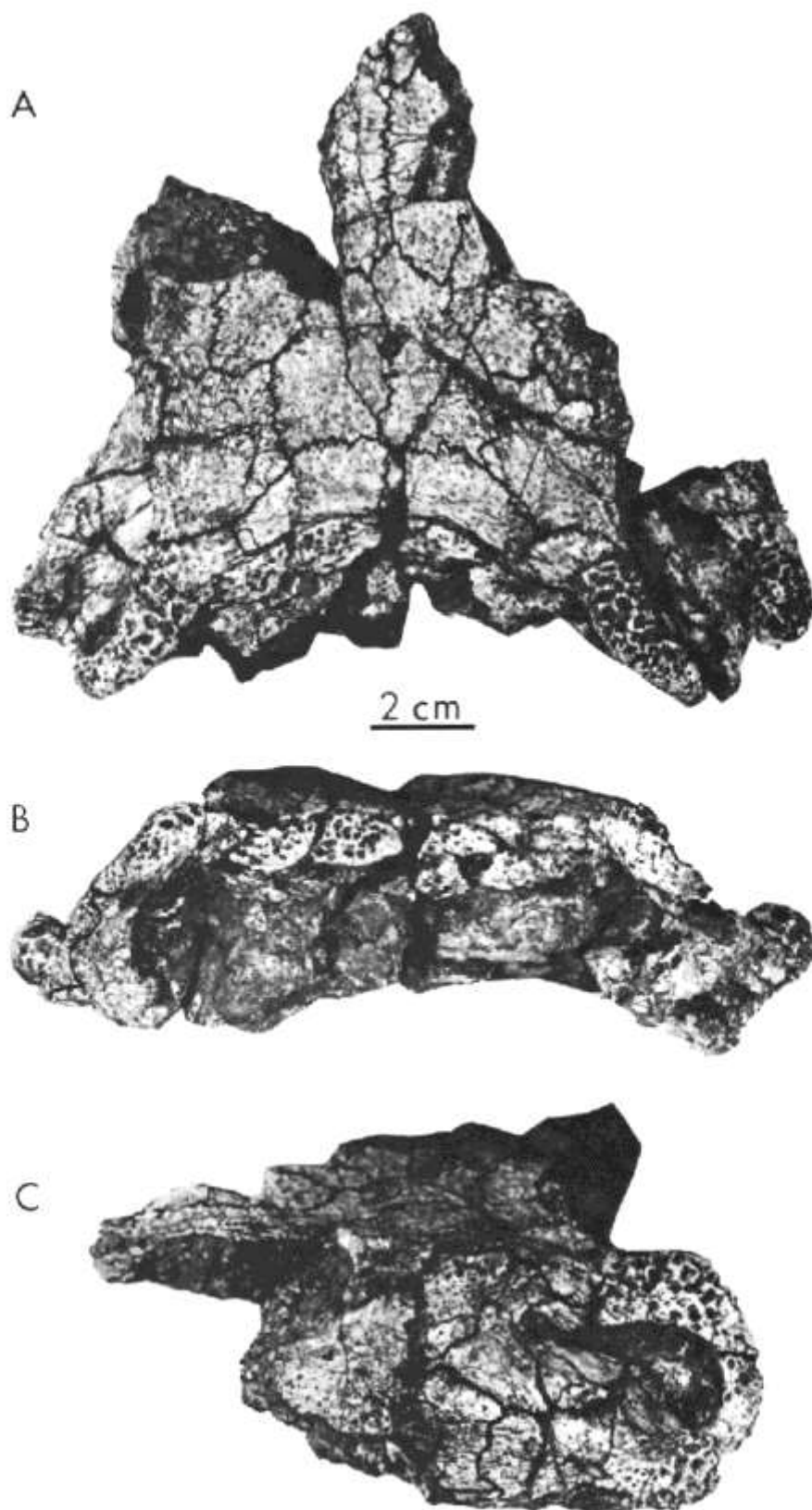
FIGURE 7—*Ecolsonia cutlerensis*, CM 38017. Dorsal (A), occipital (B), and left lateral (C) views of posterior portion of skull.
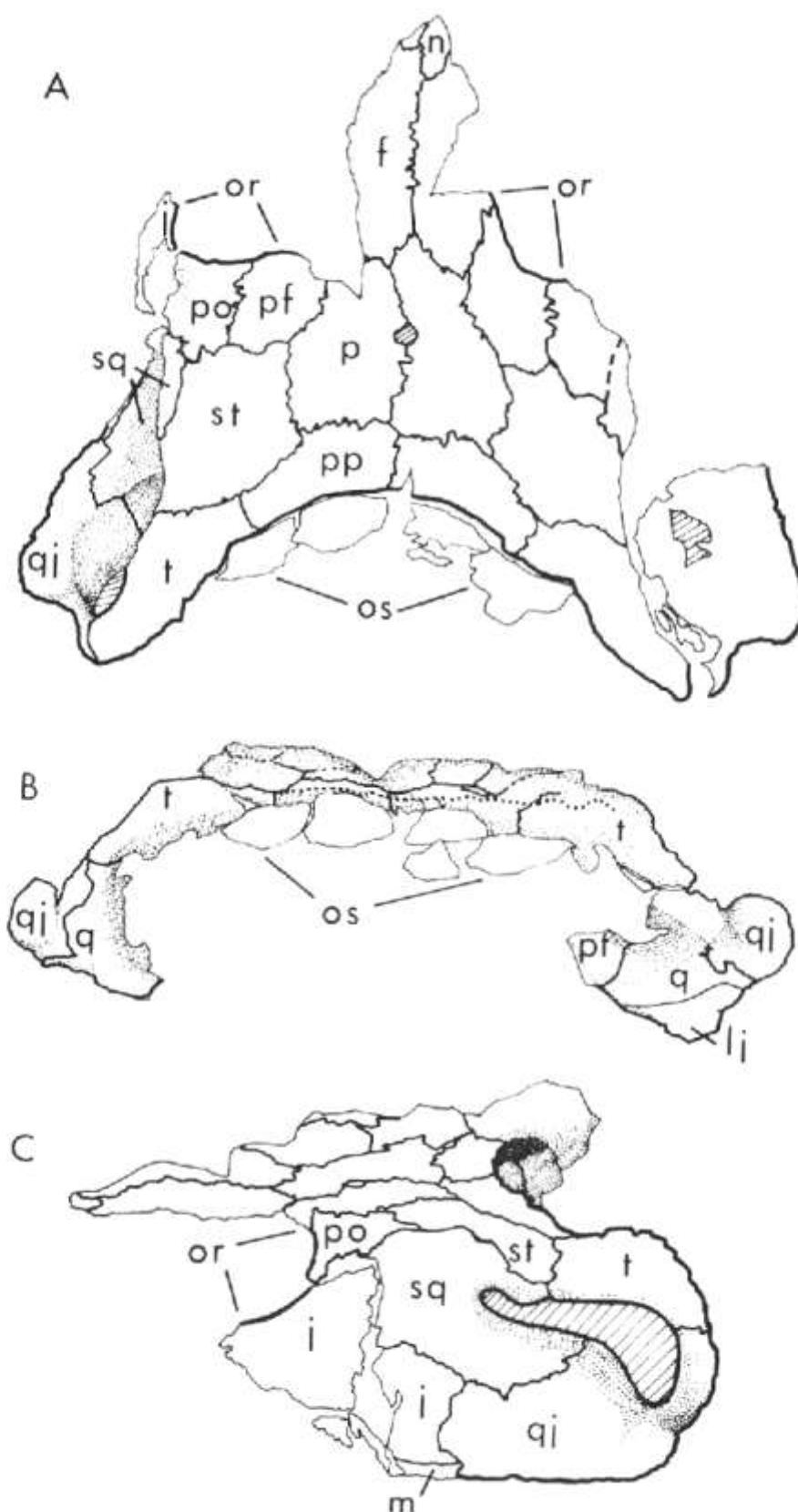
FIGURE 8—Outline sketches of views A, B, and C of Fig. 7 to indicate individual elements and other structures of *Ecolsonia cutlerensis* CM 38017. Abbreviations: f, frontal; j, jugal; lj, lower jaw; m, maxilla; n, nasal; or, orbit; os, osteoderm, p, parietal; pf, postfrontal; po, postorbital; pp, postparietal; q, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal.

laterally and in lateral view bends abruptly postero-ventrally at nearly a right angle to the skull table. The ventral surface of the distal end of the horn-like extension of the tabular contacts the essentially vertical posterodorsal process of the quadratojugal. A posterodorsal process of the quadrate extends along the medial surface of the posterodorsal process of the quadratojugal and also contacts the ventral surface of the distal end of the tabular; the posterior margins of both processes are coarsely sculptured. Medial exposure of both quadrates of CM 38017 reveals that the posterodorsal process possesses an anterior, flange-like expansion like that described by Bolt (1977a) in *Cacops* and as probably occurring in other dissorophids having closed otic notches. The quadratojugal is very large, and the posteroventral corner is set off laterally from the posterodorsal process by a narrow, saddle-shaped neck of bone. This is best exemplified in CM 38017 where the posteroventral corner of the quadratojugal, particularly in posterior view, has a nearly spherical appearance.

The postparietal and tabular have well-developed, posteroventrally projecting occipital flanges; the occipital margin of the dorsal surface of both bones projects posteriorly as a small lip over the occiput. The occipital flange of the postparietal contacts the upper end of the dorsal process of the exoccipital. The occipital flange of the tabular can be divided into two distinct components: a small dorsomedial flange and a large ventrolateral flange. The dorsomedial flange contacts the lateral margin of the occipital flange of the postparietal. Its ventral margin projects postero-ventrally as a well-developed ridge over the dorsal margin of the larger, ventrolateral flange. The ventrolateral flange projects medially from the postero-lateral edge of the tabular and undoubtedly joined the distal end of the paroccipital process of the opisthotic. This arrangement is similar to that described in the dissorophid *Platyhystrix* (Berman, Reisz, and Fracasso, 1981).

Only the right side of the palate of CM 41703 was prepared. The interpterygoid vacuities are greatly expanded. The greater portions of the oral surfaces of the palatal bones are covered by fine denticles. A small tusk-and-socket *pair* is located at about the midlength of the ectopterygoid and near the anterolateral border of the vomer, whereas a very large tusk-and-socket pair is located about midlength along the palatine. A very long, splint-like palatine process of the vomer narrowly contacts the pterygoid to exclude the palatine from the interpterygoid vacuity. Both the vomer and palatine make a substantial contribution to the medial border of the internal naris. The vomers form a large, deep, concave internarial depression along their anteromedial union. An extremely thin, short process projects posteriorly from the posteromedial corner of the vomer; the distal end of the parasphenoid rostrum, slightly displaced to the left, was undoubtedly clasped between the posteromedial processes of the vomers. The contact between the vomers and the rostrum was misinterpreted by Vaughn (1%9); re-examination of the holotype shows this contact to be identical to that in CM 41703.

The braincase of *Ecolsonia* is quite similar to that of

Platyhystrix (Berman, Reisz, and Fracasso, 1981). Due to crushing, the main body of the braincase in CM 41703 has been displaced dorsally relative to the plane of the palate, and the fused basioccipital—exoccipital complex has been somewhat rotated anteriorly so that the articular surfaces of the distinctly double occipital condyle face mainly ventrally rather than posteriorly. The parasphenoid forms a long, narrow cultriform process that thins to a knife-like edge anteriorly and a large, smooth, subrectangular plate that underlies most of the posterior portion of the braincase. The stout, wedge-shaped basipterygoid process fits snugly into a V-shaped socket on the pterygoid to form a mobile joint between the palate and braincase. The central area of the main body of the parasphenoid is depressed into a broad, shallow basin. Posterior to the basipterygoid processes, the lateral margins of the parasphenoid curve dorsally, whereas on either side of the midline the posterior border is arched ventrally away from the fused basioccipital—exoccipital complex as the thin, feathered edges of the cristae ventrolaterales. Although sutures of the basioccipital—exoccipital complex cannot be discerned, it is assumed that the basioccipital forms much of the narrow, raised area on the ventral midline. The foramina for the internal carotids are clearly visible behind the basipterygoid processes near the lateral edges of the parasphenoid. Only the badly broken and slightly displaced left opisthotic is exposed. Undisturbed, its flat, plate-like paroccipital process would have joined with the medial edge of the ventrolateral component of the occipital flange of the tabular in a smoothly continuous plate of bone. In occipital view, the exoccipitals form almost the entire margin of the foramen magnum; the basioccipital presumably makes a small contribution to the ventral margin. Above the occipital condyles, the exoccipitals constrict to a narrow neck before expanding to contact dorsally the occipital flanges of the postparietals, giving the foramen magnum a teardrop outline. A bluntly pointed, slightly curved, rod-like bone that projects laterad through the right otic notch of CM 41703 is probably the stapes.

The lower jaw is represented by a complete left ramus adhering to the left margin of the skull roof of CM 41703; it is partially exposed in lateral view and almost entirely in medial view. Isolated posterior and midlength portions of a right ramus are presumed to belong to CM 41703. Preserved with the partial skull of CM 38017 is a portion of the left ramus; it has not been completely prepared due to its inaccessibility and the recalcitrant matrix. Almost the entire lateral surface of the jaw is sculptured in the same manner as the skull roof; only the dorsal margin of the surangular and coronoid appear to be free of pitting. There is no disruption in the continuity of the ventral curvature of the angular by a pronounced ventral projection of this bone as described in *Broiliellus* (Carroll, 1964) and *Dissorophus* (DeMar, 1968).

The only possibly distinctive feature of the lateral sutural pattern of the lower jaw worth noting is the narrow exposure of the articular. In the only other dissorophids in which the posterior end of the jaw has been described in detail, this area is covered by

the surangular *in Tersomius* (Carroll, 1964) and the angular in *Dissorophus* (DeMar, 1968); in neither genus is the articular exposed laterally. The articular of *Ecolsonia,* however, has an unusually large, medial exposure. According to Carroll's (1964) description of *Tersomius,* the articular is covered medially by the surangular, prearticular, and angular. DeMar (1968), on the other hand, illustrates *Dissorophus* as having a very narrow exposure of the articular along the medial edge of its articular surface; below this the articular is covered almost entirely by the angular *except* for a small exposure of the surangular at the posterior edge of the jaw. A large foramen, generally thought to transmit the chorda tympani branch of the seventh cranial nerve, pierces the articular near the ventral end of its contact with the prearticular. A similar, large foramen was described by Romer and Witter (1942) in the primitive rhachitome *Edops.* They reasoned that the large size of the foramen probably indicates the additional passage of blood vessels and, therefore, referred to it by the noncommittal term of Para-articular foramen. The name was chosen by analogy with the closely comparable paraquadrate, or quadrate, foramen of the upper jaw. The three narrow coronoids are covered by a shagreen of teeth. The prearticular extends anteriorly as a narrow strip that contacts the posterior margin of the intercoronoid. The dentary held approximately 33 teeth like those of the upper jaw; it is not possible to discern their variation in size.

Vertebrae and ribs

CM 38017 and CM 41703 were preserved in very close association with sections of their vertebral columns intermingled, and therefore it has not been possible to sort out all of the axial materials of these two specimens without the likelihood of error. As a consequence, some assignments were made arbitrarily or with little evidence of direct association. In addition, it was not always possible to distinguish between cervical, dorsal, and lumbar vertebrae, and therefore only the very general regional terms such as anterior presacral or midpresacral have been used. Axial material assigned to CM 38017 includes: loosely associated series of far-anterior presacral vertebrae and ribs preserved immediately behind the skull; loosely articulated elements of two probable midpresacral vertebrae with rib fragments and a sacral neural arch; several isolated presacral intercentra; left pleurocentrum; anterior presacral neural arch; two isolated neural arches of anterior caudals; and left caudal rib and isolated ribs fragments. Axial material assigned to CM 41703 includes: articulated series of four neural arches of anterior caudals with closely associated central elements and ribs; and articulated last 12 caudals.

The neural arches illustrated in Fig. 9A—C are believed to be from the anterior, middle, and posterior regions of the presacral column; they differ mainly in the structure of the neural spine and in the orientation and structure of the transverse process. The spine summit of the probable anterior presacral **is** expanded noticeably by a very coarse, nodular or papillose sculpturing. A small but distinct tubercle projects laterally from about midheight of the right side of the spine, whereas a similar, more distally positioned projection on the left side is confluent with the sculpturing of the spine summit. The neural spines of the far-anterior presacral vertebrae preserved immediately behind the skull CM 38017 (Fig. 13) are very similar in structure to that of the above noted arch of a probable anterior presacral. The spine of the probable midpresacral neural arch is higher, more laterally flattened, rectangular in outline, and without any noticeable sculpturing at its summit. Distinct lateral tubercles are present in approximately the same positions on the right and left sides of the spine as in the spines of anterior presacrals except for being nearer the posterior edge of the spine. The neural spine of the posterior presacral is reduced to a narrow, rod-like structure. It appears to possess only a single lateral tubercle near the base of its right side, yet in another closely associated neural arch of a posterior presacral (not illustrated) a pair of asymmetrically positioned tubercles is present as in the more anterior presacrals. In all three presacral neural arches the lower parts of the fore and aft edges of the spine bifurcate into divergent ridges which form the lateral walls of a deep, suboval pit as they pass ventrolaterad into the zygapophyses. The articular surfaces of their zygapophyses are tilted about 30° from the horizontal. The blade-like transverse processes of the arches from the anterior and middle regions of the presacral column are well developed, projecting posterolaterad in the former and ventrolaterad and slightly anteriorly in the latter. The distal ends of the processes are beveled ventromediad in both arches so that the articular surfaces face ventrolaterad and slightly posteriorly in the anterior presacral arch and ventrolaterad and slightly anteriorly in the midpresacral arch. The narrow articular surface of the process widens slightly dorsally in both arches, and that of the mid-dorsal is weakly constricted into dorsal and ventral portions. The ventrolaterally directed transverse process of the arch of posterior presacrals differs noticeably from those of the anterior and middle regions of the presacral column in its much shorter lateral extent; its articular surface faces ventrolaterad.

The sacral neural arch (Fig. 9D) is easily distinguished from those of the rest of the column. The summit of the short, narrow neural spine is divided into right and left lobes; the left is slightly larger and more anteriorly positioned. As is typical of sacral neural arches, the zygapophyseal planes are very steeply inclined, and the anterior zygapophyses are much more greatly developed and separated than the posterior zygapophyses. The transverse process is massive and directed posterolaterad, and its large rib facet is roughly an inverted teardrop in outline.

The neural arches of the caudal vertebrae exhibit numerous differences from those of the presacrals. **A** neural arch from the anterior region of the tail and the last 12 articulated caudal vertebrae are illustrated (Figs. **9E, 10A)** and described to demonstrate these differences. The spines of the caudal neural arches are low and vertical except **for those of the far-posterior** region, which are strongly inclined posteriorly. In anterior and posterior views the spine of the anterior caudal widens distally to form right and left lobe-like
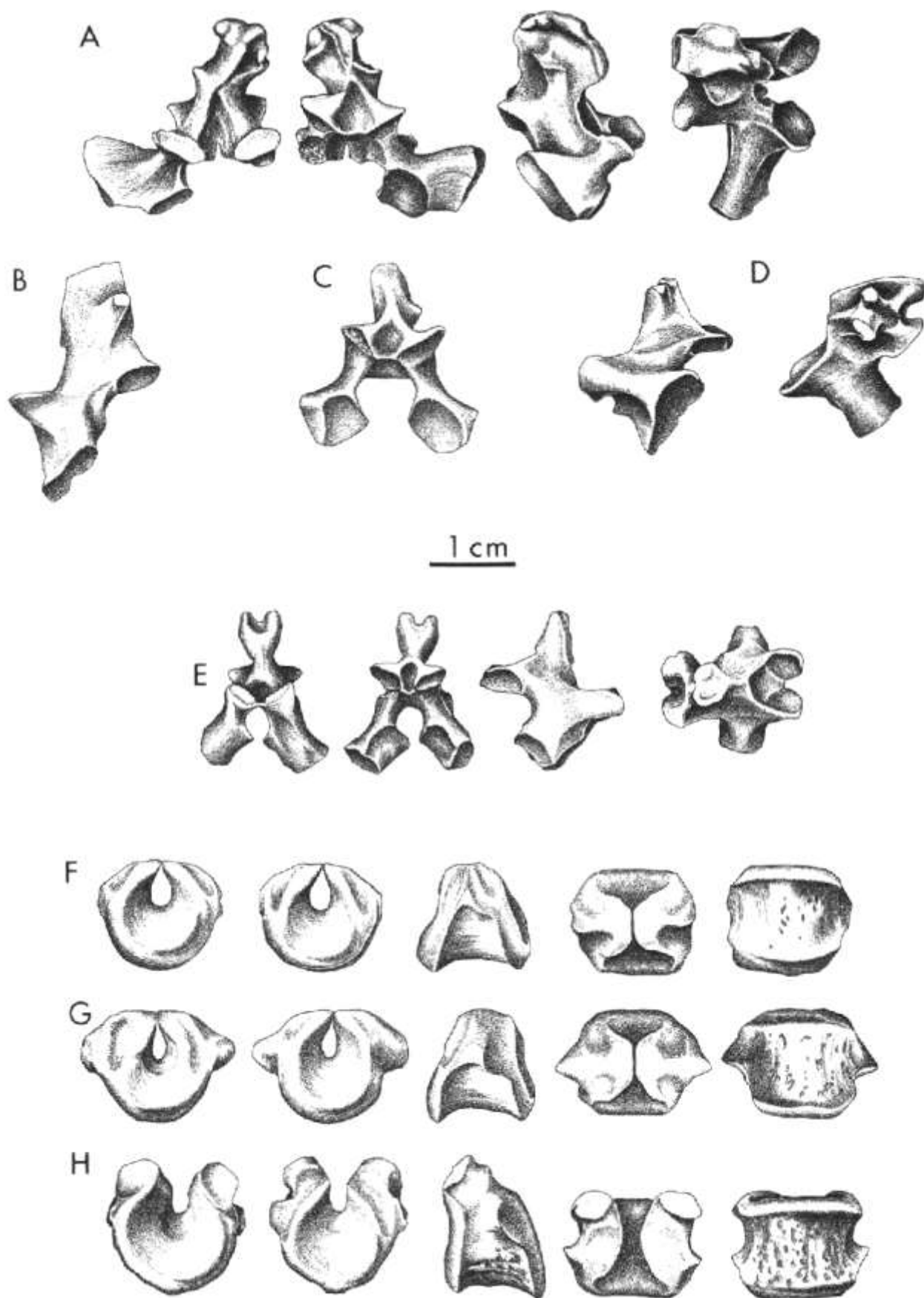
FIGURE 9—Vertebral elements of *Ecolsonia cutlerensis*, CM 38017. **A,** Anterior, posterior, lateral, and dorsal views of a probable neural arch (missing left pedicle) of anterior presacral; **B,** lateral view of a probable midpresacral neural arch; **C,** anterior view of a probable neural arch of posterior presacral; **D,** lateral and dorsal views of sacral neural arch (right pedicle not shown); **E,** anterior, posterior, lateral, and dorsal views of a neural arch of anterior caudal; **F, G,** anterior, posterior, left lateral, dorsal, and ventral (anterior toward top of page) views of presacral intercentra; **H,** fused pleurocentrum and intercentrum in same views as F and G.
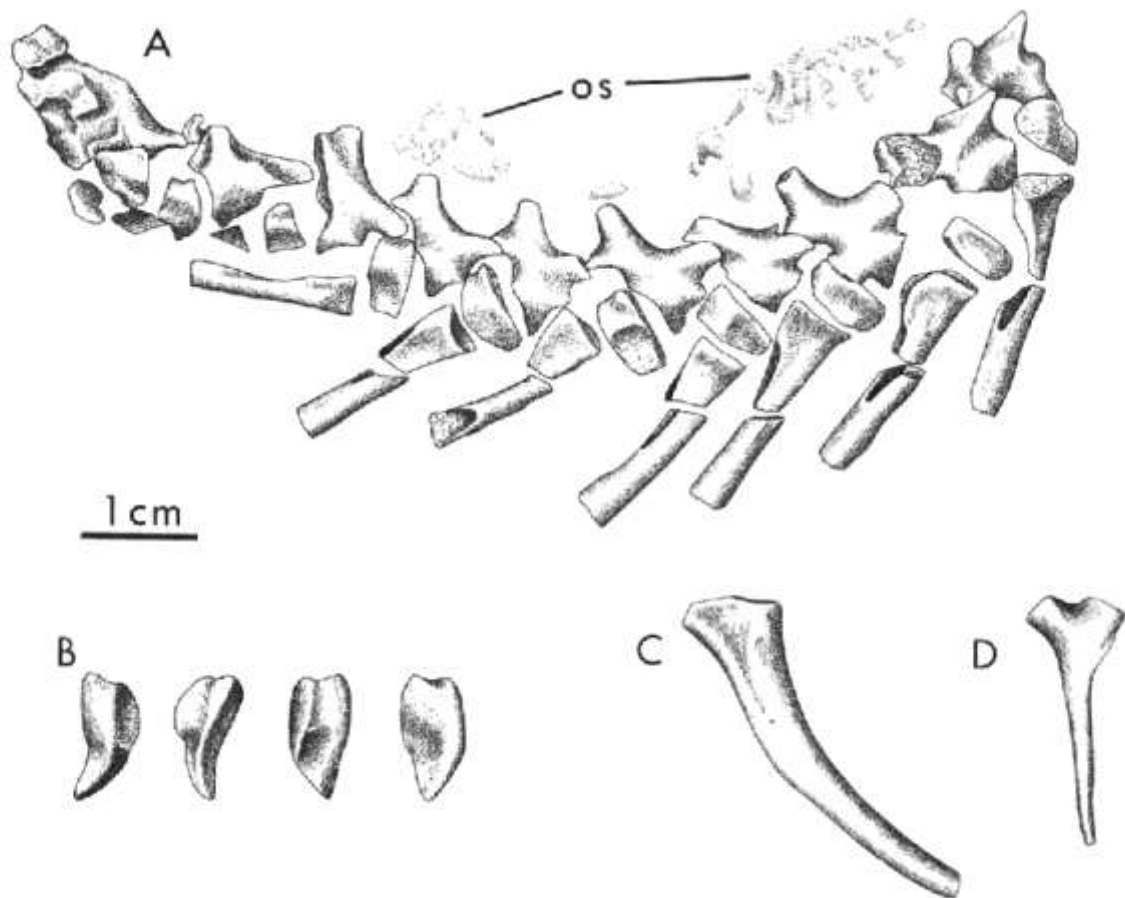
FIGURE 10—Vertebral elements of *Ecolsonia cutlerensis.* A, Last 12 caudal vertebrae of CM 41703; B, anterior, posterior, lateral, and medial views of left pleurocentrum of CM 38017; C, D, left caudal ribs of CM 38017 and CM 41703, respectively. Abbreviation: os, osteoderm.

processes that are separated dorsally by a small cleft. Bifid caudal neural spines are not unique among labyrinthodonts; they were described by Moulton (1974) in *Eryops,* and White (1939) described the irregular occurrence of bifid neural spines along the presacral column of *Seymouria.* The reduced spines of the posterior caudals of *Ecolsonia* are simple. The zygapophyses of the caudals are closer together than those of the presacrals, and their articular surfaces are more tilted, about 40-45° from the horizontal. The transverse processes of the anterior caudals are directed strongly ventrolaterad and slightly posteriorly. The outline of the rib facet, as well as the cross section of the process, is subcircular to oval.

The presacral intercentra (Fig. 9F-H) are of the typical rhachitome pattern except that the dorsal apices of the lateral ascending processes curve mediad and abut, or nearly abut, dorsally to essentially enclose a small notochordal canal. In lateral view the intercentra are wedge-shaped, and, because the external surface is slightly concave, the anterior and posterior margins curve outward to form lip-like rims. The greater part of the external surface is of finished bone that exhibits small, scattered pits. Near the apices of the ascending wings of the intercentra is a small, rounded, laterally projecting process. Its anterior surface is convex and covered by finished bone, whereas its posterior surface is slightly concave and of unfin

ished bone, and is undoubtedly the site of the rib-capitulum articulation. The intercentra of the anterior caudals are like those of the presacrals except that they do not appear to form a ring around the notochordal canal. The intercentra of posterior caudals possess heamal arches that in lateral view are long and narrow, expanding slightly toward their proximal end.

The pleurocentra are not unlike those of other rhachitomes; an isolated left pleurocentrum illustrated in Fig. **10B** in lateral view can be divided into an upper portion that is subrectangular in outline, and a lower, sharply pointed, wedge-shaped portion. The finished bone that covers most of the lateral surface extends onto the convex, dorsal edge. The outer surface is concave in horizontal section, whereas the internal surface is broadly concave in transverse section. The pleurocentrum thickens anteriorly in horizontal section, particularly the upper portion, and its anterior surface has a large, nearly flat, subcircular facet for articulation with the neural arch. The pleurocentra in the articulated series of the posteriormost 12 caudals of CM 41703 (Fig. **10A)** are visible only in lateral view; their outline varies from lozenge-shaped to subrectangular. Worth noting is an isolated intercentrum co-ossified with the pleurocentra of the preceding vertebra which is assigned to CM 38017 (Fig. 9H). Moulton (1974) reports identical cases of co-os-

sification in *Eryops.* The intercentrum is slightly opened dorsally, but can still be considered a ring intercentrum.

Only a few complete, or nearly complete, ribs have been found; others are either very fragmentary or can be only partially exposed. In CM 38017 a series of about five pairs of partially exposed, closely stacked ribs is associated with the disarticulated series of far-anterior presacral vertebrae preserved immediately behind the skull (Fig. 13). The rib heads are greatly expanded, with a distinct division or constriction separating the capitulum and tuberculum. The proximal halves of the rib shafts are expanded into broad, sub-rectangular, plate-like structures with the anterior edge being slightly concave and the posterior nearly straight except for a very weakly developed, triangular uncinate process. The distal halves of the shafts are claw-shaped in outline, tapering to a point as they abruptly curve posteriorly. An isolated rib (Fig. IOC) appears to be the left rib of a far-anterior caudal vertebra. It is about 3.5 cm long, but may be missing as much as 1 cm of its distal end. It is moderately curved and narrows gradually distad from 1 cm at its proximal *end* to 5 mm and 3.5 mm in distances of 1 and 2 cm, respectively. The capitulum and tuberculum are sub-equally developed and separated by a modest depression on the external surface of the rib. Several ribs are also associated with the series of four anterior caudal vertebrae assigned to CM 41703; a complete, moderately curved left rib (Fig. 10D) is 2.3 cm long. Its triangular head quickly narrows distad from just under 9 mm to 3 mm in a distance of 7 mm; the shaft then narrows very gradually to its distal end. A shallow depression on the external surface of the head separates the capitulum from the slightly larger tuberculum.

Appendicular elements

Only a few elements of the appendicular skeleton of CM 38017 and CM 41703 were found articulated or closely associated. Specimen assignments were made on the basis of size. Elements assigned to CM 38017 include: loosely articulated right scapulocoracoid and clavicle; left scapulocoracoid; left clavicle; proximal end of left and distal end of right humeri; proximal end of right ulna; right pelvis; and proximal and distal ends of left femur. Elements assigned to CM 41703 include: articulated left scapulocoracoid and cleithrum; clavicles; interclavicle; proximal end of left humerus; left radius; proximal and distal ends of right and proximal end of left ulnae; greater portions of pelves; associated left femur, fibula, proximal and distal ends of tibia, and partial pes; distal end of right tibia; and isolated phalanges. Figs. 11 and 12 are intended to supplement the descriptions given below.

The scapulocoracoid has a large, expanded dorsal blade that slopes posteriorly so that its anterodorsal corner is at a level directly above the posterior edge of the glenoid. The glenoid has the strap-shaped, spiral curve characteristic of primitive tetrapods. The dorsal, expanded portion of the cleithrum is very small, contacting only the anterodorsal corner of the scapular blade. In dissorophids such as *Dissorophus* and

Cacops the dorsal portion of the cleithrum is greatly expanded and extends along almost the entire dorsal margin of the scapular blade. The ventral stem of the cleithrum extends to nearly the level of the glenoid. **The** clavicle conforms to the typical rhachitome pattern. In external view the angle formed between the posterior margin of the ventral plate and the dorsal shaft is slightly greater than a right angle. The external surface of the ventral plate is strongly sculptured with transversely oriented ridges and grooves except for a narrow area along the posterior border. The dorsal one-third of the dorsal shaft has an elongate groove on its posteromedial surface that receives the ventral one-third of the ventral stem of the cleithrum. The interclavicle of CM 41703, preserved on the left margin of the skull of the same specimen (Figs. 4, 5), is exposed in ventral view. The interclavicle is diamond-shaped with rounded corners. It lacks a posterior stem, and the transverse width slightly exceeds the antero-posterior length. The sculpturing, restricted mainly to the anterior and central areas, is weakly developed and consists of small, circular pits.

As in primitive tetrapods generally, the humerus of *Ecolsonia* is tetrahedral in shape, having a distinct shaft and expanded proximal and distal ends that are twisted about the shaft so that their planes are at approximately right angles to one another. The proximal end of the humerus is subrectangular in dorsal view, with the proximal articular surface extending along one side and the deltopectoral tuberosity at one corner and the shaft at another. The proximal articular surface is band-shaped and curves from the dorsal to the ventral surface as it passes posteriorly across the proximal end of the bone. The edge of the bone that extends between the posterior termination of the articular surface to the deltopectoral tuberosity is a single ridge covered by finished bone. The deltopectoral tuberosity is a distinctly bipartite structure, having a dorsad projecting deltoid tuberosity and a ventrad projecting pectoralis tuberosity. The more massive pectoralis tuberosity is bulbous and continuous with the proximal margin of the bone, whereas the deltoid tuberosity, complete only in the proximal end of the left humerus of CM 41703 (not figured), is cone-shaped. The distal end of the humerus lacks both the ectepicondylar and entepicondylar foramina. A large, distinct supinator process is located just proximal to the radial condyle. The large ectepicondyle projects dorsolaterad from a level dorsal to the radial condyle. The radial condyle is damaged, so its shape is uncertain.

The ulna conforms to the general rhachitome pattern. It possesses a distinct semilunar notch and a well-developed olecranon process. The olecranon process of the smaller referred specimen CM 41703 is incompletely ossified and a depressed area of unfinished bone at its apex is continuous with an only partially formed notch. On the other hand, the olecranon of the larger CM 38017 ulna is more fully developed; a similar unfinished area at its apex is separated by a band of finished bone from a fully formed notch. The olecranon process is apparently one of the last skeletal elements to ossify fully. The distal end of the ulna is far more slender than the
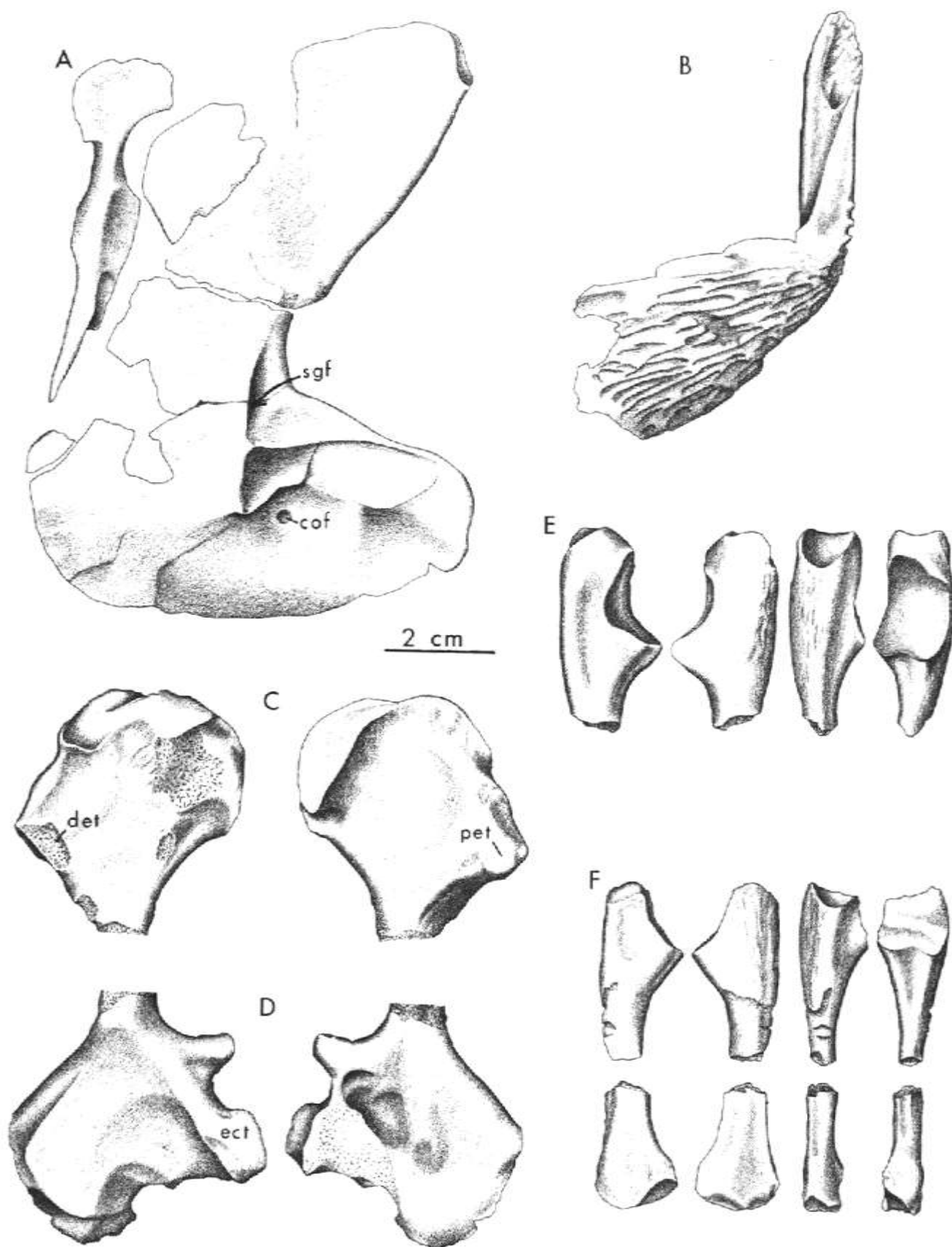
FIGURE 11—Appendicular elements of *Ecolsonia cutlerensis*. **A,** Lateral view of left scapulocoracoid and cleithrum of CM 41703; **B,** external view of right clavicle of CM 41703; **C,** dorsal and ventral views of proximal end of left humerus of CM 38701; **D,** dorsal and ventral views of distal end of right humerus of CM 38017; **E,** anterior, posterior, lateral, and medial views of proximal end of right ulna of CM 38017; **F,** proximal and distal ends of right ulna of CM 41703 in same views as in E. Abbreviations: **det,** deltoid tuberosity; **ect,** ectepicondyle; **cof,** coracoid foramen; **pet,** pectoralis tuberosity; **sgf,** supraglenoid foramen.
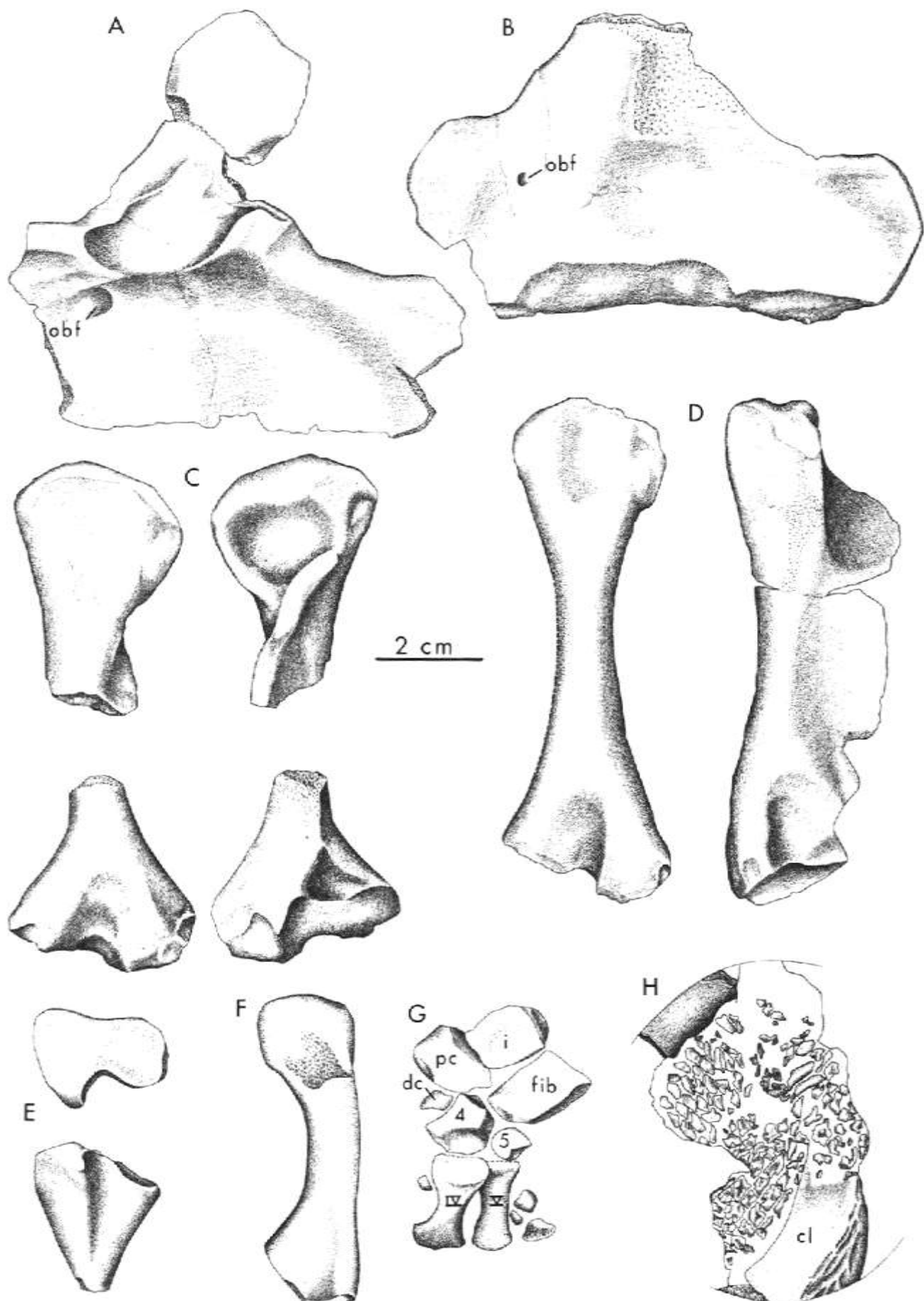
FIGURE 12—Appendicular elements of *Eocisoma cutlerensis*. **A,** Lateral view of left pelvis of CM 41703; **B,** medial view of right pelvis of CM 38017; **C,** dorsal and medial views of proximal and distal ends of left femur of CM 38017; **D,** dorsal and posterior views of left femur; **E,** articular surface and anterior view of proximal end of left tibia; **F,** anterior view of left fibula; **G,** partial pes of CM 41703; **H,** patch of osteoderms covering portion of right pectoral girdle of CM 38017 as seen in Fig. 13. Abbreviations: **cl,** clavicle; **dc,** distal centrale,; **fib,** fibulare; **i,** intermedium; **obf,** obturator foramen; **4, 5,** distal tarsals; **IV, V,** metatarsals.

proximal end and is divided into lateral and medial articular facets for the ulnare and intermedium. The radius (not figured) is a stout element, but with a rather narrow shaft connecting the expanded proximal and distal ends; the distal end exceeds the proximal end in mediolateral width by almost 40%. The bone is equally concave on its medial and lateral margins. The proximal end is subcircular in cross section and its articular surface is concave for the reception of the radial condyle of the humerus. The distal articular surface has distinct facets for the radiale and centrale.

The pelvis and hind-limb elements of *Ecolsonia* exhibit little or no deviations from the typical rhachitome pattern. None of the pelves are complete, but together they illustrate most features of the element. The pelvic bones are well fused and faint sutures can be discerned only on the left of CM 41703. The iliac blade is best represented in the left pelvis of CM 41703; though the edges are incomplete and its full extent is unknown, it could not have been greatly expanded. The pubis is substantially shorter anteroposteriorly than the ischium. The symphyseal surface is large, with the widest area of contact at the level of the acetabulum. The obturator foramen is distinct.

The moderately expanded proximal and distal ends of the femur are joined by a long, slender shaft. The proximal articular surface is widest anteriorly, where it extends slightly onto the dorsal surface of the head. A distinct intertrochanteric fossa is present and is partially bordered anteriorly by the internal trochanter. The internal trochanter is not a distinct process but rather a thickened area at the proximal end of the adductor crest. The adductor crest is greatly developed and thins to a sharp, free edge. The crest extends distad in a midventral position on the shaft to a well-defined popliteal depression. The distal articular surface is divided into two distinct areas for the tibia and fibula. The tibial surface is dumbbell-shaped and faces ventrolaterad and slightly anteriorly; the oval fibular surface faces posterolaterad. The intercondylar groove is short, but becomes very deep distally.

The proximal articular surface of the tibia is divided into a medial oval area with the long axis oriented anteroposteriorly, and a somewhat smaller, lateral circular area. The medial condyle expands anteriorly to form the proximal end of a cnemial crest. The distal articular surface of the tibia (not figured) is oval in outline and has two subequal articular areas for the centrale and tibiale. They are set at an angle of approximately 60° to one another, giving the distal end of the tibia a wedge-shaped appearance in anterior or posterior view. The fibula is stoutly constructed, with greatly expanded ends. The shaft has a straight lateral margin and a strongly concave medial margin. The proximal articular surface is oval-shaped and faces mediad and slightly proximad. The distal articular surface is slightly more expanded than the proximal surface and has two articular areas; a small lateral facet for the fibulare faces distad, and a larger medial facet for the intermedium faces mediodistad. The partial, articulated pes is represented by the fibulare, intermedium, proximal centrale, distal centrale (probably third), fourth and fifth distal tarsals, and the fourth and fifth metatarsals. Poor preservation prevents a detailed description of the tarsus.

Dermal ossifications or osteoderms

An unusual and striking feature of *Ecolsonia* is its possession of well-developed dermal ossifications or osteoderms that must have encased most of the body in a pavement-like "armor." The osteoderms vary considerably in size and shape regionally, and exhibit a sculpture pattern of circular pits, like that of the skull roof. The dermal ossifications of *Ecolsonia* differ in several significant ways from the gastralia or scale types seen in many aquatic or semiaquatic Paleozoic labyrinthodonts (i.e. *Eryops,* Romer and Witter, 1941; *Trimerorhachis,* Olson, 1979; *Greererpeton,* Romer, 1972; *Colosteus,* Hook, 1983) in that (1) they are not arranged in distinct chevron-shaped rows, (2) do not overlap each other, and (3) their entire outer surface is sculptured, rather than having a crenulate to punctate pattern of ornamentation limited to the posterior border. Carroll (1964) has described, however, the presence of quite large fragments of pitted bone lying between the lower jaw rami of a specimen of the dissorophid *Tersomius.* In *Ecolsonia* four regional types of osteoderms can be roughly distinguished on the basis of size and shape; regional differences are, however, blurred by transitional varieties.

A series of four very large, irregularly shaped osteoderms extends along the occipital margin of the skull roof of CM 38017 (Figs. 7, 8, 13); their anterior borders closely conform to the occipital curvature of the skull roof. These strongly sculptured, plate-like occipital osteoderms are complete, or nearly complete, and are transversely elongate, with a greatest width of about 2 cm. The fact that the plates are positioned on either side of the axial midline and are not bilaterally symmetrical provides convincing evidence that they are not intimately associated or connected with the vertebral neural spines as in dissorophids (DeMar, 1966a). Lying just posterior to some of the occipital osteoderms are large fragments of what were probably similarly sized plates. Somewhat smaller osteoderms, exhibiting the same degree of sculpturing as the above occipital osteoderms, are also found in CM 38017, where they are scattered throughout the matrix adhering to the ventral surface of the skull and densely packed around the closely associated axial elements of the anterior end of the vertebral column preserved a short distance behind the skull (Fig. 13). Their sizes and shapes are difficult to discern, but most appear to measure about 1.0 to 1.5 cm in greatest diameter and vary in shape from ovoid to narrowly rectangular. A patch of small osteoderms, which appear to have retained their original relationships to each other, is preserved in a thin layer of matrix covering part of the external surfaces of the loosely articulated right scapulocoracoid and clavicle of CM 38017, also preserved behind the skull of that specimen (Figs. 12H, 13). These osteoderms measure from 3 to 6 mm in greatest diameter, are sculptured with minute pits, vary in shape from rectangular to rhomboidal to diamond, and have interposing spaces of at most only a few millimeters. Finally, small patches of
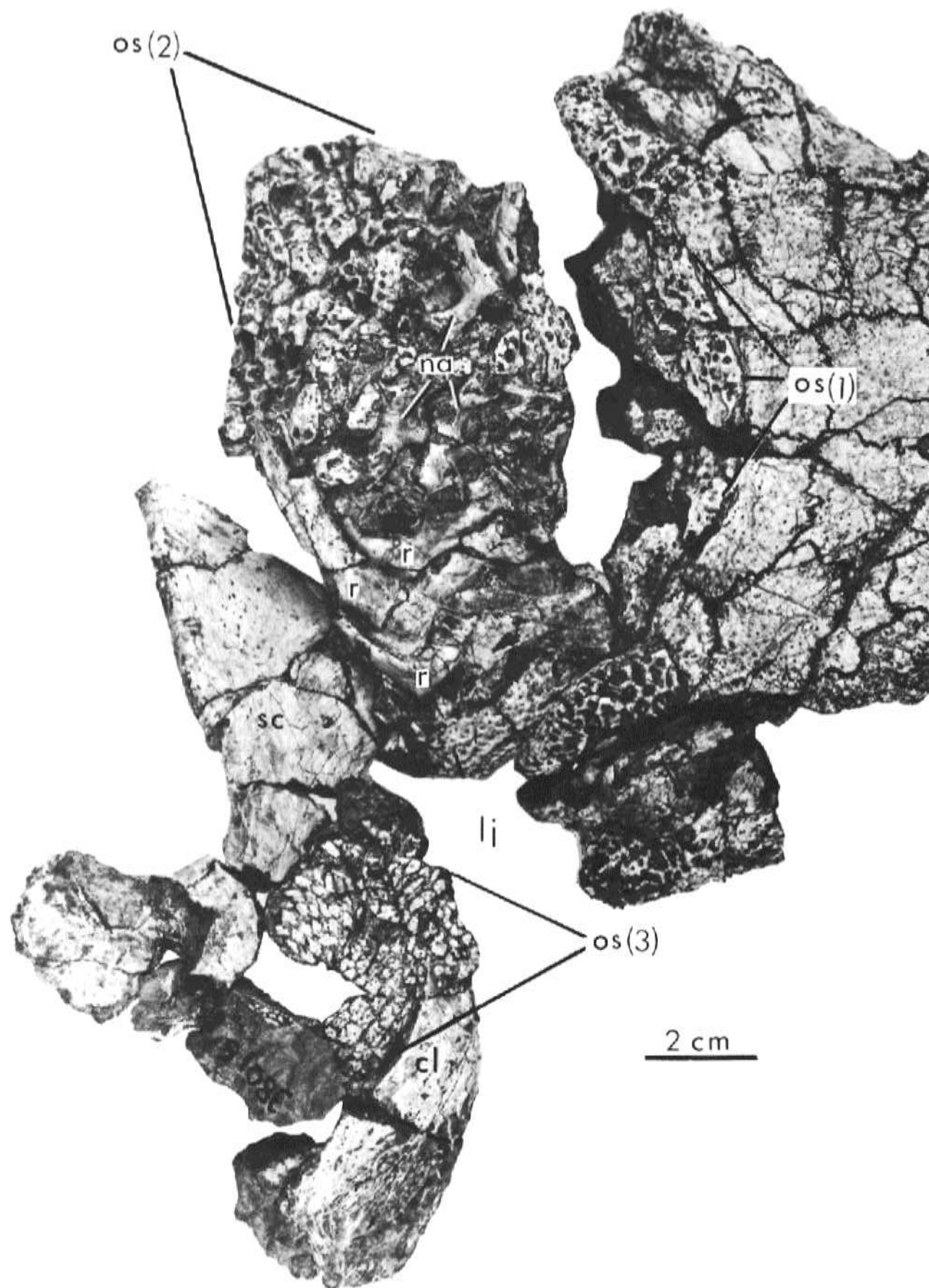
FIGURE 13—*Ecolsonia cutlerensis*, CM 38017. View showing posterior portion of skull and closely associated postcranial elements in order to illustrate regional types of osteoderms: (1) osteoderms along occipital margin of skull; (2) osteoderms surrounding anterior end of the vertebral column; and (3) osteoderms covering portion of external surface of pectoral girdle. Abbreviations: cl, clavicle; lj, lower jaw; na, neural arch; os, osteoderm; r, rib; sc, scapulocoracoid.

minutely sculptured osteoderms, ranging from 1 to 3 mm in greatest diameter and having very irregular outlines, are closely associated with the neural spines of the articulated last 12 caudal vertebrae of CM 41703 (Fig. 10A). It seems quite probable that most of the integument of *Ecolsonia* was armored with a pavement of sculptured, non-overlapping osteoderms; the skull roof and limbs are the only regions in which the presence of an integumentary "armor" cannot be demonstrated.

Ecolsonia as a dissorophid

The discovery of excellent specimens of *Ecolsonia* permits a thorough comparison of its anatomy with those of dissorophids and trematopsids, and a reassessment of its familial assignment. Although Vaughn (1969) described the partial, holotypic skull of *Ecolsonia cutlerensis* as possessing a combination of dissorophid and trematopsid features, his decision to assign it to the Trematopsidae was undoubtedly influenced mainly by the presence of an elongate narial opening. The elongate, partially subdivided narial opening certainly has to be judged as an important feature of trematopsids, because it occurs in all members of that family. Its reported occurrences outside the family are otherwise limited to the dissorophids *Longiscitula houghae* and *Actiobates peabodyi.* As discussed below (Discussion section), however, the presence of an elongate narial opening is not demonstrable in the former (Bolt, 1974a), and the latter is probably a trematopsid rather than a dissorophid. Further, strong doubts have been raised by Bolt (1974a) as to the value of the long narial opening as a diagnostic feature of the Trematopsidae. In a detailed description and discussion of the trematopsid narial region he argued that the posterior portion of the naris probably resulted in response to the development of a large gland, possibly a salt gland similar to that found in most living reptiles. If, as he explains, enlargement of the gland at this position was restricted to lateral expansion, it could have been accommodated only by the development of the posterior portion of the elongated naris. Important to Bolt's theory is the concomitant development of a nasal flange with the posterior expansion of the external naris. The fully developed nasal flange of trematopsids is described as a shelflike structure that projects downward from the ventral surfaces of the nasal and prefrontal, and extends parallel to, and nearly the entire length of, the external narial opening; the flange was, therefore, positioned medial to the nasal capsule and the hypothesized gland. A transversely oriented extension of the lacrimal just behind the posterior border of the external naris contributes to the posteroventral portion of the flange. According to Bolt, as the antorbital bar narrowed due to the posterior expansion of the external naris, the possible loss of its structural integrity by forces acting mainly on the tooth row was prevented by the development of the nasal flange. In essence, the nasal flange became an anterior, strut-like extension of the antorbital bar and, thereby, served to divert some stresses from the bar. Bolt was also able to dem

onstrate the presence of a nasal flange, though considerably less developed than in the trematopsids, in the dissorophids *Broiliellus* and *Tersomius,* and in the very closely related, probable dissorophid (Bolt, 1977b), *Doleserpeton.* Despite an admittedly limited survey, he believed this structure to be not only confined to, but a primitive character of, trematopsids and dissorophids (including *Doleserpeton).* These observations led Bolt to infer that in any labyrinthodont possessing a nasal flange like that of dissorophids an enlargement of a structure lateral to the nasal capsule, such as a gland, would be expected to produce the elongate naris and the much more fully developed nasal flange of the trematopsids. If it is accepted that *Ecolsonia* is a dissorophid, rather than a trematopsid, then the above interpretation would seemingly provide a logical explanation for its possession of a trematopsidlike external naris. However, Bolt's conclusion (p. 28) that "The elongate external naris, even if accompanied by a trematopsid-like nasal flange, is not a diagnostic character for the family Trematopsidae" may be too cautious, inasmuch as *Ecolsonia* appears to be the only known example of a non-trematopsid labyrinthodont possessing an elongate external naris. Further, the trematopsids, which can be characterized by other features (see below), all possess elongate external nares.

Vaughn (1969) noted two other trematopsid-like features in the holotypic skull of *Ecolsonia,* both of which are undoubtedly misinterpretations due to incomplete preservation: (1) the small size of the tabulars, and (2) the great length of the frontals relative to the parietals. It is obvious from Figs. 4, 5, 7, and 8 that the tabulars of the referred skulls CM 38017 and CM 41703 are not only very large, but larger than those of most dissorophids. The tabular of the holotypic skull UCLA VP 1734 obviously represents only a small remnant of the original element. In contrast to the holotype, in which the frontals are one and half times as long as the parietals, the greatest lengths of the frontals of the referred skulls exceed only slightly those of the parietals. Where measurements are available from published illustrations of trematopsid skulls (Olson, 1941), the frontals exceed the parietals in length by as much as 42%, whereas in dissorophids the frontals are either slightly longer than, or subequal in length to, the parietals. The frontals of the holotype, as in the referred skulls, are, however, of normal dissorophid length in extending from about the posterior to the anterior levels of the orbital margins; in trematopsids, on the other hand, the frontals typically extend well beyond the level of the anterior orbital margins. The parietals of the holotype, therefore, are proportionately too short to conform to either the dissorophid or trematopsid pattern. This discrepancy is probably due to a transverse break through the parietals near their posterior margins. A considerable amount of bone has been lost along the break, and the remaining portions of the parietals were joined via a very narrow, tenuous contact. The loss of even a small amount of bone at this contact would account for the proportionately shorter parietals.

Whereas an elongate external naris is a hallmark feature of the trematopsids, *Ecolsonia* possesses no

other cranial features that can be interpreted as characteristic of that family. On the other hand, an extensive list of its dissorophid-like features can be compiled. Considering the size and the well-ossified condition of the referred specimens of *Ecolsonia,* none of their dissorophid-like features can be interpreted as larval or juvenile trematopsid features (see Discussion section). An important and readily recognizable dissorophid feature of *Ecolsonia* is the short preorbital length of the skull. Its preorbital length is about 35% of the skull length measured along the midline, which falls well within the range of available measurements for dissorophids, about 30-45%, and well below that for the trematopsids, about 44-57% (Berman, Reisz, and Fracasso, 1981). In the sculpturing pattern of the skull roof, *Ecolsonia* is clearly dissorophid-like. In trematopsids the dermal sculpturing of the skull roof is typically uniform throughout its extent and is never coarse. In *Ecolsonia,* on the other hand, the ridge-like swellings of the prefrontal and postorbital, the strongly accentuated pit-and-ridge sculpturing along the margins of the skull table and the postorbital cheek region, and the sculptured, ridge-like structure along the occipital margin of the postparietal are all features typical, or reminiscent, of the skull-roof ornamentation of moderate- to large-sized dissorophids (Carroll, 1964; DeMar, 1967, 1968; Berman, Reisz, and Fracasso, 1981). The premaxilla of *Ecolsonia, as* in dissorophids, is far less massively constructed than that of trematopsids. Further, the snout of *Ecolsonia* is like that of dissorophids in being pointed, rather than having the very broadly rounded, sometimes nearly transversely truncated, termination seen in trematopsids. It has already been noted above that the frontals of *Ecolsonia* are dissorophid-like and can be contrasted with those of trematopsids in their shorter length relative to the parietals and their very limited extent beyond the level of the anterior orbital margins. To this it can be added, as Vaughn (1969) pointed out, that the frontals of *Ecolsonia* are somewhat dissorophid-like in their broad entrance into the orbital margin.

That *Ecolsonia is* a dissorophid and not a trematopsid is most strongly supported by the structure of its otic-notch region. Though the otic-notch regions of dissorophids and trematopsids are unusual, if not unique, among labyrinthodonts, and are very similar in their overall structure, DeMar (1968) and Bolt (1974b, 1977a) described numerous characters that can be used to distinguish between them. In *Ecolsonia* and dissorophids the sculpturing of the skull table extends onto portions of the cheek region dorsal to the otic notch, an area composed of the squamosal, supratemporal, and tabular, and referred to as the supratympanic flange by Bolt (1974b). In contrast, the entire supra-tympanic flange in trematopsids is smooth. Bolt also described the sculptured skull table of trematopsids as extending a short distance laterad above the smooth supratympanic flange to form a ventrally smooth shelf termed by him as the supratympanic shelf. This shelf is poorly developed or absent in dissorophids and absent in *Ecolsonia.* DeMar (1968) noted that, with the exception of the primitive and early *Tersomius* and *Amphibamus,* in all other dissorophids where the dor

sal margin of the otic notch is preserved there is a ventrad directed "half-moon-shaped" flange that narrows the notch from above. Bolt (1974b) pointed out that this feature is the result of a semilunar curvature of the squamosal along the ventral border of the supratympanic flange, and, most importantly, that it is probably unique to dissorophids. Though Bolt also tentatively concluded that the presence of a supratympanic flange without the ventral semilunar curvature of the squamosal is a shared derived character of the Trematopsidae, he conceded that the dissorophid condition may be more derived than that of trematopsids. The possession by *Ecolsonia* of a ventral, semilunar curvature of the squamosal identical to that in dissorophids is, therefore, a strong indication of its dissorophid affinities.

In comparing the otic-notch regions of dissorophids and trematopsids with closed otic notches, Bolt (1977a) described several other apparent differences between the two families. Although these differences are based on a very limited sample (three dissorophids and one trematopsid), they are nevertheless significant. In dissorophids that have a closed otic notch, the horn-like process of the tabular bends sharply posteroventrad at about a right angle to the skull table to contact an essentially vertically oriented posterodorsal process of the quadrate; the resultant enclosure is greatly expanded posteroventrad to form an opening that has the outline of a right-angled triangle. The same features appear to be present in the recently described (Gubin, 1980) dissorophids from the Late Permian of Russia, *Kamacops acervalis* and *Iratusaurus vorax.* In these features the closed otic notch of *Ecolsonia* conforms exactly to the dissorophid pattern and can be contrasted with that of trematopsids in which: (1) the horn-like process of the tabular bends downward at about 45° to the skull table to contact a posterodorsal process of the quadrate that is inclined anterodorsad at about 35° from the horizontal; and (2) the enclosed otic notch is a horizontal, slit-like opening. It should also be noted that the anterior expansion of the posterodorsal process of the quadrate, described by Bolt (1977a) as present in all dissorophids having a closed otic notch, is also present in *Ecolsonia;* the anterior expansion of the quadrate is absent, however, in the one species of trematopsid *(Trematops miller')* with a closed otic notch for which Bolt had adequate material for examination. Gubin's (1980) illustration of *Kama-cops* (fig. 1, p. 85) indicates that it possessed a similar anterior expansion of the quadrate. Bolt cautions, however, that an isolated trematopsid-like quadrate recovered by him from the Early Permian Fort Sill locality in Oklahoma has an anteriorly expanded posterodorsal process.

The palate of *Ecolsonia* exhibits two features that are typical of dissorophids. The widely expanded interpterygoid vacuities of *Ecolsonia* are characteristic of dissorophids and are in marked contrast to the moderate or narrow vacuities that characterize trematopsids. The contact between the cultriform process of the parasphenoid and the vomers in *Ecolsonia* is also found in dissorophids, whereas in trematopsids such a contact appears to be lacking (Olson, 1941).

The possession of ring intercentra and the absence

of typical dissorophid dorsal dermal armor are features of *Ecolsonia* which on initial consideration might suggest a closer alliance with trematopsids than with dissorophids. The intercentra of all dissorophids in which the vertebrae are known, which includes the majority of known genera, are of the typical rhachitomous pattern. Among the trematopsids ring intercentra are present in *Trematops,* even in immature specimens, but are absent in all known specimens of *Acheloma* (Olson, 1941); of the few known trematopsid genera, these are the only ones in which the axial skeleton is adequately known. Dorsal dermal armor is present, though exhibiting some variation in form, in all dissorophids except two of the most primitive and earliest forms, the Late Pennsylvanian *Amphibamus* and the Early Permian *Tersomius;* Bolt (1974d) suggested that the absence of armor in these genera may not necessarily be related to primitiveness, but possibly to immaturity or small size. In no instance, however, has dorsal dermal armor like that of dissorophids been reported in trematopsids. Dissorophid "armor" has been described in detail (DeMar, 1966a); in general it consists of sculptured dermal plates that are not only serially arranged along the dorsal midline, but also intimately associated with the vertebral column. Although lacking this type of armor, *Ecolsonia* nevertheless possesses an equally impressive, armor-like structure consisting of well-developed, sculptured dermal ossifications or osteoderms that were densely distributed over much of the body.

In *Ecolsonia* the ring intercentra, the unusual features of the neural spines, and the body covering of osteoderms undoubtedly served many of the same functions as the dorsal dermal "armor" that typifies the great majority of dissorophids. In a detailed phylogenetic and functional analysis of the armor of the dissorophids, DeMar (1966b, 1%8) concluded that the armor had several functions which were clearly related to a highly terrestrial habit; it appears to have served primarily to strengthen and restrict movements of the vertebral column, whereas secondarily it could have aided in reducing water loss by evaporation through the skin and in providing protection from predators. The greater ossification of the pre-sacral intercentra in *Ecolsonia* so as to form ring-like structures would have provided additional support and rigidity to the vertebral column. The pair of asymmetrically positioned, lateral tubercles of the presacral neural spines, the nodular or papillose expansion of the neural-spine summits of anterior presacrals, and the bifurcation of the neural spines of anterior caudals very likely represent structures that served to accommodate a greatly increased development of the system of tendinous attachment of the dorsal axial musculature (Olson, 1936). In a detailed study of the dorsal axial musculature of certain primitive Permian tetrapods, Olson (1936) demonstrated that the tendons functioned primarily to support the axial column. In reference to Olson's study, Moulton (1974, p. 6) reasoned that the bifurcated caudal spines of Eryops suggest "a tail of reasonable length which may have been held off the ground." Olson's investigation also offers a plausible explanation for the apparent restriction of the nodular expansion of the neural-spine summits to the anterior presacral vertebrae in *Ecolsonia.* As he points out, in the far-anterior region of the column additional support may have been required because of the weaker articulation between certain specialized cervical vertebrae, and the heavy skull and the pull of occipital muscles. The possession of an extensive body covering of well-developed ossifications or osteoderms undoubtedly reduced moisture loss through the skin and may have had some value in protection from predators.

Of the appendicular skeleton of *Ecolsonia* only the humerus exhibits noticeable similarities with those of trematopsids; all other elements show no significant similarities with either family. As in trematopsids, but in contrast to dissorophids, *Ecolsonia* possesses a well-developed supinator process and a distinct division of the deltopectoral tuberosity into a dorsal deltoid and a ventral pectoralis tuberosity. The dorsolateral projection of the large ectepicondyle from a level dorsal to the radial condyle in the humerus of *Ecolsonia is similar* to the condition in trematopsids, but unlike that in dissorophids where the ectepicondyle projects directly laterad. The above characters shared by *Ecolsonia* and trematopsids have no value as indicators of phylogenetic relationship, however, because they can be interpreted as primitive among labyrinthodonts generally.

Discussion

The families Dissorophidae, Trematopsidae, Doleserpetonidae, Branchiosauridae, and Micromelerpetontidae have been included in the superfamily Dissorophoidea Bolt (1969). The latter two families include branchiosaurs and are interpreted by Boy (1972) as representing secondarily aquatic, partially neotenic offshoots of an unknown amphibian group which adapted rapidly to a riparian and other terrestrial habitats and were probably ancestral to the other dissorophid families. Doleserpetontidae Bolt (1969) is a monotypic family erected for the Early Permian *Doleserpeton annectens,* which Bolt (1977b) now believes may be a junior synonym of the dissorophid genus *Tersomius* of the same age. Among the labyrinthodont amphibians the Dissorophidae and Trematopsidae include the species most highly adapted for terrestrial existence. A close relationship between the two families was first proposed by Olson (1941). While noting fundamental differences between dissorophids and trematopsids, he also recognized several similarities, mainly in their postcranial skeletons. However, as Olson rightly cautioned, these similarities may reflect in great part parallelism due to similar adaptive responses or general evolutionary trends within the rhachitomes. In a series of detailed, comparative studies of the cranial anatomy of both families, Bolt (1974a, b, c, 1977a) pointed out numerous features of the nasal and otic-notch regions and the sutural pattern of the skull roof that are unique among the labyrinthodonts and, therefore, greatly reinforce the concept of their close relationship. The most compelling evidence of a close alliance, however, has come from the descriptions of three dissorophid species which re-

portedly possess a combination of features that are characteristic of both families: *Longiscitula houghae* DeMar, 1966a, *Actiobates peabodyi* Eaton, 1973, and *Ecolsonia cutlerensis* Vaughn, 1969.

The dissorophid *Longiscitula houghae* from the Early Permian of Texas was described by DeMar (1966a) as possessing very elongate external naris like that of trematopsids. However, Bolt's (1974a) re-examination of the nasal region of the holotype (FMNH UR 430), the only specimen in which this region is preserved, revealed it to be too poorly preserved to demonstrate either the presence or absence of this feature. DeMar also judged the elongation of the skull of *Longiscitula as* a trematopsid-like feature, but it is not much more elongate than that of the dissorophid *Platyhystrix* (Berman, Reisz, and Fracasso, 1981); further, the poor preservation of the type material does not allow an accurate determination of the skull proportions. All other features of *Longiscitula,* particularly the otic notch, are consistent with its inclusion in the Dissorophidae.

On the basis of an essentially complete skull and partial postcranial skeleton from the Late Pennsylvanian of Kansas, Eaton (1973) briefly described a new genus and species of amphibian, *Actiobates peabodyi,* which he believed to be a dissorophid with a trematopsid-like narial opening. However, it can be far more effectively argued that *Actiobates* is a trematopsid and that the few dissorophid-like features exhibited by the holotype (KU 17941) reflect a juvenile, probably early postmetamorphic, stage of development. This is supported in part by Olson's (in press) description of a larval trematopsid (UCLA VP 3861) from the Early Permian of Texas. Several of the cranial features exhibited by the larval trematopsid are not only identical to those that have been considered dissorophid-like relative to trematopsids, but also either relied on by Eaton in his diagnosis of *Actiobates as* a dissorophid, or can be noted in his illustrations of the skull. These features include: (1) widely expanded interpterygoid vacuities; (2) very short preorbital portion of skull, about 34% of the midline length of the skull; (3) premaxillae relatively delicate; (4) frontals with wide entrance into orbital rim; and (5) frontals about the same length as the parietals and extending anteriorly to about the level of the anterior orbital margins. Several other cranial features of *Actiobates* can be cited as indicating a probable early postlarval stage of development: (1) orbits are relatively very large, with an anteroposterior diameter of nearly one-third the mid-line length of skull; (2) frontals have an unusually large entrance into the orbital rims; (3) maxillae enter orbital rims, preventing a lacrimal—jugal contact; and (4) postorbital region of skull roof is relatively short. And lastly, *Actiobates* exhibits several trematopsid-like features, discussed in the previous section, which are not attributable to a larval or subadult stage of growth: (1) external naris is elongate and partially subdivided; (2) dermal sculpturing of the skull roof is uniformly developed and without any indications of protuberances or ridge-like swellings; (3) tip of the snout is very broad and blunt, giving it a nearly truncated appearance; and (4) tabulars are very small.

It is unfortunate that Eaton (1973) did not give a detailed description of the otic notch of *Actiobates,*

inasmuch as that structure, if well preserved, would provide a firmer basis for familial assignment. Eaton noted (p. 3) that "Four small bones are present anteriorly [behind the skull] that look like double-ended paddles" and suggested that "these are probably units of the dorsal armor, but they lack attachment to the neural spines." If these elements represent portions of a vertebral armor, then they are, of course, of taxonomic significance. However, they are quite unlike the dorsal-armor units described in any dissorophid (DeMar, 1966b), and it seems unlikely that they pertain to that structure; perhaps they represent portions of the hyoid apparatus or cervical ribs. Until the holotype of *Actiobates peabodyi* is thoroughly described (it is presently unavailable for study), it seems best to view it as a trematopsid.

The above comments are intended to demonstrate that *Ecolsonia* is presently the only dissorophid definitely known to possess a trematopsid-like narial opening; in this derived feature the skull of *Ecolsonia* can be distinguished from those of all other dissorophids. There are also no detailed features of its narial opening that would differentiate it from those of trematopsids. However, it should be noted that the long, narrow, anterior extension of the lacrimal along the entire ventral border of the posterior portion of the naris in *Ecolsonia is* a feature that has been shown in only one specimen of trematopsid. Discussing the trematopsid nasal region, Bolt (1974a) illustrated, but did not comment on, an identical, long, anterior process of the lacrimal in a specimen of *Acheloma* (MCZ 1485) believed by him to possibly represent a new species. In other trematopsid species in which this region is adequately preserved, the anterior process of the lacrimal is greatly abbreviated so that the maxilla forms most of the ventral border of the posterior portion of the narial opening. A lacrimal with a long anterior process like that in *Ecolsonia* is also present in a yet undescribed trematopsid (CM 41711) recently discovered by two of us (D.S B. and D.A.E.) at a very low horizon, possibly Upper Pennsylvanian, of the Cutler Formation in El Cobre Canyon, Rio Arriba County, New Mexico. A long anterior process of the lacrimal is surely a primitive feature, particularly if it is accepted that the anterior portion of the narial opening represents the true external naris and that in the primitive state the lacrimal reached the posterior border of the external naris.

Ecolsonia is advanced over the Late Pennsylvanian and contemporaneous, earliest Permian, Wolfcampian, dissorophids in its possession of a closed otic notch. A closed otic notch has been positively identified in only the later Early Permian, Leonardian, *Longiscitula* (DeMar, 1966a), *Dissorophus multicinctus* (DeMar, 1968), and *Cacops* (Williston, 1910), and in the Late Permian *Kamacops* and *Iratusaurus* (Gubin, 1980). In these forms, as in *Ecolsonia,* the otic notch is closed posteriorly by a contact between the distal end of a horn-like tabular and a posterodorsal process of the quadrate. In *Ecolsonia,* however, the otic notch is closed posteriorly by an additional contact between the distal end of the tabular and a posterodorsal process of the quadratojugal; in fact, the posterodorsal process of the quadratojugal appears to form a more

substantial contact with the tabular than does that of the quadrate. A tabular—quadratojugal contact that encloses the otic notch posteriorly can only be interpreted as a unique derived condition.

The upper marginal dentition of *Ecolsonia* is considered somewhat more advanced than that of other dissorophids of the same age. The marginal dentitions of dissorophids are adequately known in about nine genera, and the teeth exhibit a general trend toward becoming relatively larger, less numerous, and slightly recurved. In the Late Pennsylvanian and earliest Permian, Wolfcampian, forms the premaxillary-maxillary tooth counts range from 45 to 70 or more, and the teeth are relatively very small, simple, pointed pegs (Carroll, 1964; Berman, Reisz, and Fracasso, 1981). The same counts for the later Early Permian, Leonardian, *Dissorophus multicinctus* and *Cacops* are about 45 and 30, respectively (Williston, 1910; DeMar, 1968), whereas the Late Permian *Kamacops* possesses only about 25-28 relatively large, slightly recurved teeth on either side (Gubin, 1980). The possession by *Ecolsonia* of 35-39 relatively large and slightly recurved upper marginal teeth is therefore viewed as a feature advanced over its Wolfcampian dissorophid contemporaries.

The vertebrae of *Ecolsonia* exhibit several features which are interpreted as having provided greater support of the column and as derived among the dissorophids. Obvious among these is the greater ossification of the intercentra so as to form ring-like structures that surrounded a small notochordal opening. Unique derived features of the neural spines believed to be related to an increased tendinous support of the column include: (1) asymmetrically positioned pair of lateral tubercles of the presacral spines; (2) nodular or papillose expansion of spine-summits of anterior presacrals; and (3) bifurcated spines of anterior caudals. The extensive, densely distributed body covering of well-developed sculptured osteoderms of *Ecolsonia* is also considered a unique derived feature within the dissorophids. It is quite likely that some dissorophids possessed at least a partial body covering of thin dermal scales or osteoderms such as has been reported in several aquatic or semiaquatic Paleozoic amphibians (Romer and Witter, 1941; Olson, 1979; Romer, 1972; Hook, 1983). Yet, if other members of the Dissorophidae had a body covering of dermal ossifications of the same degree of development as in *Ecolsonia,* it seems highly unlikely that it would have gone unnoticed in this large family whose members are often well represented.

There are at least two prominent, primitive cranial features of *Ecolsonia* that are apparently absent in other dissorophids: (1) retention of a contact, though very narrow, between the pterygoid and vomer, and (2) an open, mobile basicranial joint. A pterygoid—vomer contact is definitely absent in the primitive dissorophids *Amphibamus, Tersomius,* and *Broiliellus.* The situation in more advanced dissorophids is unknown except that this contact appears to be absent in *Platyhystrix* (Berman, Reisz, and Fracasso, 1981). The mobile joint between the palate and braincase in *Ecolsonia* cannot be judged as simply representing the retention of a primitive feature, however, even though this

interpretation would be true for labyrinthodonts generally and all other dissorophids have an immobile joint. In the early, primitive dissorophids, such as *Amphibamus* and *Tersomius,* the joint is not firmly fused, but movement was nevertheless unlikely (Carroll, 1964). In later, more advanced dissorophids, such as *Dissorophus multicinctus, Cacops,* and *Kamacops,* there was solid fusion with no possibility of movement. The basicranial joint in *Ecolsonia,* instead of being weakly fused or sutured, exhibits a construction that, while emphasizing strength in its stoutly built palatal and braincase components, obviously permitted considerable freedom of movement through its simple, pegand-socket design. Despite what may be an instance of selection toward maintaining and emphasizing a mobile basicranial joint, this feature in *Ecolsonia* is viewed as primitive.

Only the humerus of the postcranial skeleton of *Ecolsonia* exhibits primitive features which have not been noted in other dissorophids. These features, as already noted in the previous section, are also present in trematopsids and include: (1) a distinct supinator process, (2) distinct dorsal and ventral components of the deltopectoral tuberosity, and (3) the dorsolateral projection of the ectepicondyle from a level dorsal to the radial condyle. They are assessed as primitive for trematopsids and dissorophids on the basis of their presence in primitive amphibians such as Edops and *Trimerorhachis,* and because of their wide distribution among temnospondyls.

In the previous section it was argued that the functions performed by the dorsal dermal "armor" that characterizes the great majority of dissorophids were likely taken over, at least in great part, in *Ecolsonia* by a greatly increased development of the system of tendinous attachment of the dorsal axial musculature as indicated by various unusual structures of the neural spines (lateral tubercles and bifurcation or nodular expansion of the spine summits), an increased ossification of the presacral intercentra so as to form ring-like structures, and an extensive, dense, body covering of well-developed osteoderms. Also having an important bearing on this subject is DeMar's (1966b, 1968) convincing argument that the "armor" of dissorophids had developed independently in two, or possibly three, different lineages during the Late Pennsylvanian or Early Permian. The unusual armor of *Platyhystrix* and *Astreptorhachis* (Lewis and Vaughn, 1965; Vaughn, 1971) also suggests, along with other evidence (Berman, Reisz, and Fracasso, 1981), that they may represent still another independent dissorophid lineage. If "armor" arose independently as many as three or four times within the Dissorophidae, then it seems reasonable to expect that there may have also existed a lineage in which adaptation to a terrestrial habitat was manifested in structures other than the dorsal dermal armor that typifies the Dissorophidae. The thesis that *Ecoisonia* represents a distinct lineage well separated from the main line or lines comprising the other dissorophids before the Early Permian is supported by its possession of numerous unique derived features. In addition, the possession by *Ecolsonia* of several primitive features not seen in other dissorophids indicates that the separation occurred very

early in the history of the family, perhaps as early as the Middle Pennsylvanian.

As an alternative approach to resolving the question of the familial affinities of *Ecolsonia,* a cladistic analysis is presented here (Fig. 14) to test two hypotheses of relationships. The first is that *Ecolsonia* shares a more recent common ancestor with *Trematops* than with *Dissorophus,* and the second is that *Ecolsonia* shares a more recent common ancestor with *Dissorophus* than with *Trematops.* In this analysis *Dendrerpeton* is chosen as the primitive out-group for comparison because it is a well-described, unspecialized primitive temnospondyl generally considered near the ancestral stock of the dissorophids. *Trematops* and *Dissorophus* were selected as reference genera for the Trematopsidae and Dissorophidae because they are among the best known representatives of the families and exhibit the greatest number of characters in common with *Ecolsonia.*

Shared derived characters considered as uniting the three dissorophoid genera are:
  (1) laterally exposed palatine on skull roof;
  (2) greatly expanded otic notch;
  (3) supratympanic flange;
  (4) posterodorsal process of quadrate;
  (5) limb elements long, slender, and well ossified.
The hypothesis that *Ecolsonia* shares a more recent common ancestor with *Trematops* than with *Dissorophus* is tested by the following derived characters:
  (6) ring intercentra;
  (7) elongate, partially divided external naris;
  (8) absence of typical dissorophid dermal armor.
The hypothesis that *Ecolsonia* shares a more recent common ancestor with *Dissorophus* than with *Trematops* is tested by the following derived characters:
  (9) box-like configuration of skull roof, with abrupt right-angled union between cheek and table areas;
  (10) greatly variable development of skull-roof sculpturing;
  (11) very short preorbital length of skull;
  (12) greatly expanded interpterygoid vacuities;
  (13) tabular horn bends sharply posteroventrad at

about a right angle to skull table to contact a vertically oriented posterodorsal process of quadrate;
  (14) semilunar curvature of squamosal that narrows the otic notch from above;
  (15) posterodorsal process of quadrate possesses an anterior expansion.

The latter hypothesis, suggesting that *Ecolsonia* is more closely related to *Dissorophus* than to *Trematops,* is the preferred one, because it requires the fewest number of parallel events. Most importantly, it supports the contention that *Ecolsonia is* best considered a member of the Dissorophidae.
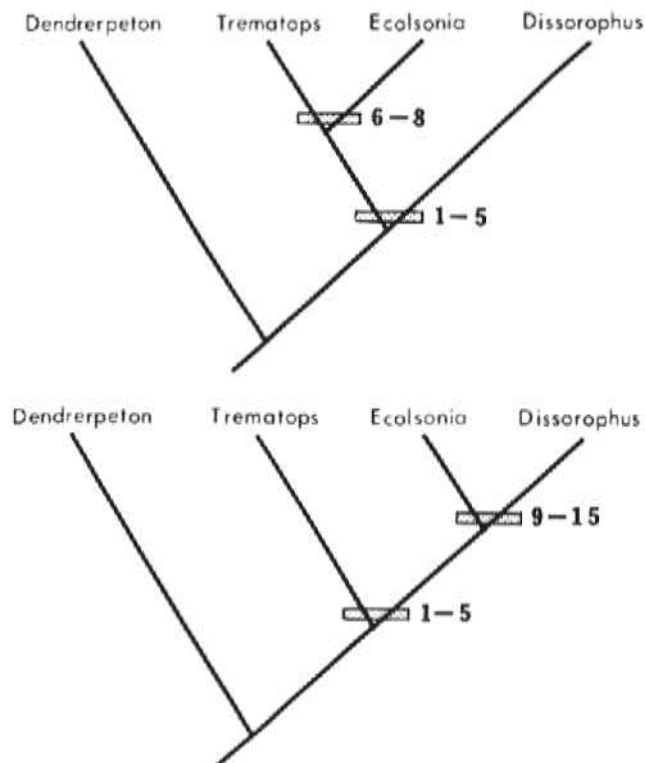
FIGURE 14—Cladogram illustrating two hypotheses of relationships of *Ecolsonia.* Shared derived characters 1–15 are listed in text.

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Selected conversion factors*

TO CONVERT	MULTIPLY BY	TO OBTAIN
Length		
inches, in	2.540	centimeters, cm
feet, ft	3.048×10^{-1}	meters, m
yards, yds	9.144×10^{-1}	m
statute miles, mi	1.609	kilometers, km
fathoms	1.829	m
angstroms, Å	1.0×10^{-8}	cm
Å	1.0×10^{-4}	micrometers, μm
Area		
in²	6.452	cm²
ft²	9.29×10^{-2}	m²
yds²	8.361×10^{-1}	m²
mi²	2.590	km²
acres	4.047×10^{3}	m²
acres	4.047×10^{-1}	hectares, ha
Volume (wet and dry)		
in³	1.639×10^{1}	cm³
ft³	2.832×10^{-2}	m³
yds³	7.646×10^{-1}	m³
fluid ounces	2.957×10^{-2}	liters, l or L
quarts	9.463×10^{-1}	l
U.S. gallons, gal	3.785	l
U.S. gal	3.785×10^{-3}	m³
acre-ft	1.234×10^{3}	m³
barrels (oil), bbl	1.589×10^{-1}	m³
Weight, mass		
ounces avoirdupois, avdp	2.8349×10^{1}	grams, gr
troy ounces, oz	3.1103×10^{1}	gr
pounds, lb	4.536×10^{-1}	kilograms, kg
long tons	1.016	metric tons, mt
short tons	9.078×10^{-1}	mt
oz mt⁻¹	3.43×10^{1}	parts per million, ppm
Velocity		
ft sec⁻¹ (= ft/sec)	3.048×10^{-1}	m sec⁻¹ (= m/sec)
mi hr⁻¹	1.6093	km hr⁻¹
mi hr⁻¹	4.470×10^{-1}	m sec⁻¹

TO CONVERT	MULTIPLY BY	TO OBTAIN
Pressure, stress		
lb in⁻² (= lb/in²), psi	7.03×10^{-2}	kg cm⁻² (= kg/cm²)
lb in⁻²	6.804×10^{-2}	atmospheres, atm
lb in⁻²	6.895×10^{3}	newtons (N)/m², N m⁻²
atm	1.0333	kg cm⁻²
atm	7.6×10^{2}	mm of Hg (at 0° C)
inches of Hg (at 0° C)	3.453×10^{-2}	kg cm⁻²
bars, b	1.020	kg cm⁻²
b	1.0×10^{6}	dynes cm⁻²
b	9.869×10^{-1}	atm
b	1.0×10^{-1}	megapascals, MPa
Density		
lb in⁻³ (= lb/in³)	2.768×10^{1}	gr cm⁻³ (= gr/cm³)
Viscosity		
poises	1.0	gr cm⁻¹ sec⁻¹ or dynes cm⁻²
Discharge		
U.S. gal min⁻¹, gpm	6.308×10^{-2}	l sec⁻¹
gpm	6.308×10^{-5}	m³ sec⁻¹
ft³ sec⁻¹	2.832×10^{-2}	m³ sec⁻¹
Hydraulic conductivity		
U.S. gal day⁻¹ ft⁻²	4.720×10^{-7}	m sec⁻¹
Permeability		
darcies	9.870×10^{-13}	m²
Transmissivity		
U.S. gal day⁻¹ ft⁻¹	1.438×10^{-7}	m² sec⁻¹
U.S. gal min⁻¹ ft⁻¹	2.072×10^{-1}	l sec⁻¹ m⁻¹
Magnetic field intensity		
gausses	1.0×10^{5}	gammas
Energy, heat		
British thermal units, BTU	2.52×10^{-1}	calories, cal
BTU	1.0758×10^{2}	kilogram-meters, kgm
BTU lb⁻¹	5.56×10^{-1}	cal kg⁻¹
Temperature		
°C + 273	1.0	°K (Kelvin)
°C + 17.78	1.8	°F (Fahrenheit)
°F − 32	5/9	°C (Celsius)

*Divide by the factor number to reverse conversions.
Exponents: for example 4.047×10^{3} (see acres) = 4,047; 9.29×10^{-2} (see ft²) = 0.0929.

ECOLSONIA (AMPHIBIA, EARLY PERMIAN)

New Mexico Bureau of Mines & Mineral Resources