THE EDOPOID AMPHIBIAN *COCHLEOSAURUS* FROM THE MIDDLE PENNSYLVANIAN OF NOVA SCOTIA

by OLIVIER RIEPPEL

ABSTRACT. A new species of the edopoid genus *Cochleosaurus*, *C. florensis*, has been found in the Westphalian D deposits of Nova Scotia. It differs from the Czechoslovakian species *C. bohemicus* in the sculpture pattern of dermal bones and in skull proportions. Morphologically, the skull of *Cochleosaurus* is intermediate between those of the edopoid genera *Dendrerpeton* (Westphalian B of Nova Scotia) and *Chenoprosopus* (Lower Permian of New Mexico).

IN 1956, a field party from the Museum of Comparative Zoology, Harvard, under the direction of the late Dr. A. S. Romer, excavated four of five fossil tree stumps at a new locality near Florence, Nova Scotia. Vertebrate fossils were found embedded in upright *Sigillaria* stumps that have been exposed by strip mining. The tree stumps are rooted above the Lloyd Cive seam of the Morian group, corresponding in age to the Westphalian D of Europe (Carroll *et al.* 1972). Stump number three produced most of the primitive captorhinomorph *Palaeothyris acadiana* (Carroll 1969), the limnoscelid amphibian *Limnostygis relictus* (Carroll 1967*b*) and several genera of primitive pelycosaurs (Reisz 1972), as well as two skulls of *Cochleosaurus*.

SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA
Subclass LABYRINTHODONTIA Owen, 1860
Order TEMNOSPONDYLI Zittel, 1887
Suborder RHACHITOMI Cope, 1882
Superfamily EDOPOIDEA Romer, 1945
Family COCHLEOSAURIDAE Broili, 1923
Genus COCHLEOSAURUS Fritsch, 1885
Cochleosaurus florensis n. sp.

Etymology. From the locality near Florence, Nova Scotia.

Holotype. MCZ 4343. Almost complete skull.

Referred specimen. MCZ 4344. Partial skull with well-preserved palate.

Horizon and locality. Morien group, equivalent to Westphalian C and D of Europe. Dominian Coal Co., strip mine No. 7, 2 miles north of Florence, Cape Breton County, Nova Scotia.

Diagnosis. An edopoid labyrinthodont assignable to the genus *Cochleosaurus* based on the presence of postparietal lappets, but distinct from the Czechoslovakian species *C. bohemicus* Fritsch, 1885, by smaller over-all size and by shorter postparietal lappets. The orbits are smaller, the snout is shorter, and the skull table is wider in *C. florensis* than in *C. bohemicus*.

Known distribution. Middle Pennsylvanian of eastern North America.

The edopoids are considered to represent a primitive stage in the evolution of rhachitomous amphibians (Romer 1947, 1966). They are characterized by the retention of the intertemporal, a movable palatobasal articulation, a single occipital condyle, and the absence of lateral line canals. The genus

Cochleosaurus Fritsch, 1885, is characterized by the development of distinct posterior lappets on the postparietals. The pineal opening is present in juvenile specimens but is closed during subsequent growth (Steen 1938).

Both specimens of *C. florensis* (text-figs. 1 and 4) show a narrow, anteriorly rounded snout. The cheeks show a slight swelling, so that the lateral outline of the skull is fairly sigmoidal. The same is observed in the latex cast of the specimen of *C. bohemicus* (HMB 1902.1386b) available for study (text-fig. 4), but it is not shown in Steen's (1938) reconstruction of the skull of the latter species. Measurements taken from *C. florensis* (MCZ 4343) and *C. bohemicus* (HMB 1902.1386b) (Table 1) indicate the orbits of *C. florensis* to be somewhat smaller, the snout to be somewhat shorter in relation to the skull table but the skull table to be somewhat wider posteriorly.
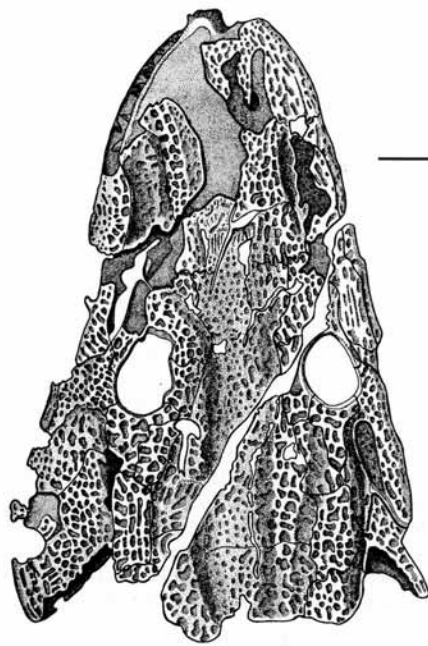
In *C. florensis* the sculpturing of the dermal roofing bones of the skull consists of deep, rounded pits separated by high, narrow ridges the thickness of which is less than the diameter of the pits (text-fig. 1). Several depressed areas with subdued sculpturing are observed on the skull roof. Along the midline of the skull runs a band with less distinct sculpturing. The pits of this area are shallow, small, and rounded in outline and widely separated from each other. Elevated areas with strongly expressed sculpturing cover the temporal series of bones, surround the orbits, and continue anteriorly on the lateral halves of the nasals up to the posterior margins of the external nares. On the skull table, a level of intermediate height between the temporal bones and the mesial depression covers the lateral parts of the parietals and postparietals with an intermediate intensity of sculpturing. In the preorbital region, a depression with subdued sculpturing covers much of the lacrimal on either side. A high ridge running on the lateral parts of the nasal separates the lacrimal depression from the midline depression.

TABLE 1. Measurements taken on the specimens of *Cochleosaurus florensis* (MCZ 4343) and *C. bohemicus* (HMB 1902.1386b). All measurements in mm. Length of skull: from posterior margin of postparietal lappets to tip of snout; length of snout: from anterior border of orbit to tip of snout; length of skull table: from posterior margin of postparietal lappets to posterior margin of orbits; width of skull table: lateral edges of tabulars at posterior border; diameter of orbit: measured longitudinally.

|	*C. florensis*	*C. bohemicus*
Length of skull	124	111
Length of snout	61	52·5
Length of skull table	44	39·5
Diameter of orbit	16	18
Width between orbits	25	17
Width of skull table	45	37
Index skull length:diameter of orbit	7·75	6·17
Index snout length:length of skull table	1·16	1·33
Index skull length:width of skull table	2·75	3
Index skull length:width between orbits	4·96	6·53

TEXT-FIG. 1. The skull of *Cochleosaurus florensis* (Holotype, MCZ 4343) in dorsal (*left*) and in ventral (*right*) view. ×$\frac{3}{4}$. Abbreviations: ang, angular; ar, articular; cl, cleithrum; ec, ectopterygoid; f, frontal; fi, fibula; it, intertemporal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pf, postfrontal; pl, palatine; plf, palatine fang; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; rb, ribs; sang, surangular; sp, splenial; sph, sphenethmoid; spp, postsplenial; sq, squamosal; st, supratemporal; t, tabular; ti, tibia; v, vomer; HMB, Museum für Naturkunde der Humboldt-Universität zu Berlin (DDR); MCZ, Museum of Comparative Zoology, Harvard University.

TEXT-FIG. 2. The reconstruction of the skull of *Cochleosaurus florensis* in dorsal (*left*) and in ventral (*right*) view. The interorbital space is interpreted as being vaulted, which accounts for a 10% loss in interorbital width as compared to text-fig. 1. ×$\frac{3}{4}$. Abbreviations as in text-fig. 1.
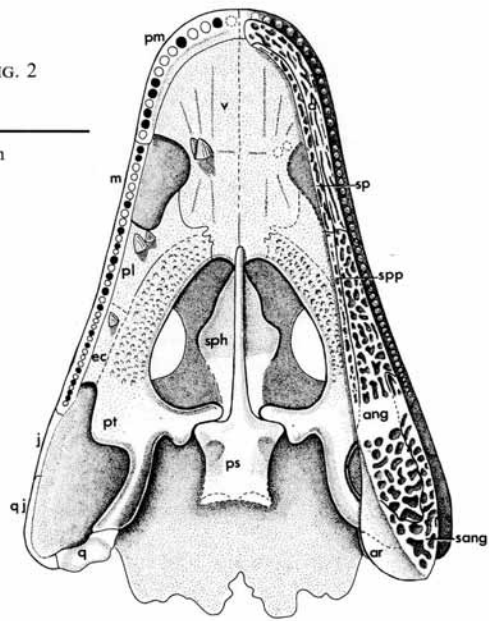
TEXT-FIG. 1

5 cm
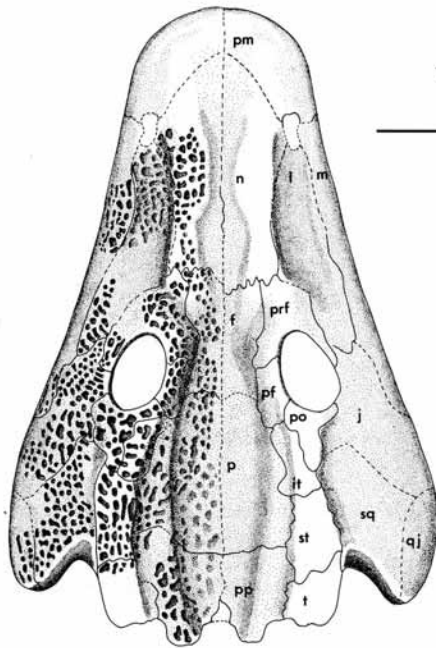
TEXT-FIG. 2

5 cm

In *C. bohemicus* (HMB 1902.1386b) (text-fig. 4) the sculpturing of the dermal bones is also most pronounced on the temporal series of bones, around the orbits, and across the ossification centre of the nasals. There is subdued sculpturing along the midline of the skull roof, on the lateral margin of the parietal, and on the lacrimal. The ossification centre of the parietal is coarsely sculptured.

Thus a comparable pattern of intensified and subdued sculpturing exists in the two species of *Cochleosaurus*, but the specimen of *C. bohemicus* at hand lacks the depressions of the areas with subdued sculpturing. On the other hand, Fritsch (1885, table 60) figures another specimen of *C. bohemicus* with ridges running along the temporal series of bones and dorsal to the orbits, as well as on the lateral parts of the parietals and postparietals. The midline of the skull shows a somewhat weaker ridge. No difference between coarse and subdued sculpturing can be made out on Fritsch's (1885) plate, however. Somewhat similar ridges as those figured by Fritsch (1885) for *Cochleosaurus* are found in the genus *Zatrachys* (Langston 1953), although in a different arrangement.

One major difference between the two species of *Cochleosaurus* is that *C. florensis* shows uniformly shaped and distributed pits throughout, whereas *C. bohemicus* shows an elongation of the pits towards the margins of the dermal bones, most prominent in a longitudinal direction in the pre-orbital region and in a radial pattern on the cheeks. The elongate pits correspond to zones of intensive growth (Bystrow 1935) and indicate that the snout grows strongly in a longitudinal direction while the cheeks increase in width. The elongate pits are distinct in juvenile specimens but become obscured by subdivision when the animal is fully grown (Bystrow 1935). Thus it may be assumed that *C. florensis* was mature with a skull length of 124 mm (MCZ 4343), whereas the skull of *C. bohemicus* (HMB 1902.1386b) represents a still-growing juvenile at the length of 111 mm. *C. bohemicus* grows to 210 mm skull length at which size it has lost the juvenile pattern of ornamentation (Milner, pers. comm.). It appears that *C. bohemicus* would have reached a larger over-all size. This is considered as a species difference.

The postparietal lappets of *C. bohemicus* (HMB 1902.1386b) are more prominent than in *C. florensis* (MCZ 4343). Steen (1938) was able to show that the postparietal lappets show positive allometric growth during ontogeny. It thus appears that the adult *C. bohemicus* is characterized by much more prominent postparietal lappets than the smaller adult *C. florensis*.

The sculpturing of the lower jaw of *C. florensis* is characterized by large, irregular pits separated by high, narrow ridges on the angular and surangular. On the splenials, the pits tend to be smaller and shallower. On the dentaries, the sculpturing changes to a pattern of longitudinal ridges very different from the pitting on the other dermal bones. No lower jaw of *C. bohemicus* is available or well-enough figured to be used for comparison. In *Dendrerpeton* (Carroll 1967a), a condition similar to that of *C. florensis* is observed. Deep but elongate pits radiate to the margins of the angular bone. Pits on the splenial tend to be smaller. On the dentary, only shallow ridges are observed. In *Caerorhachis* (Holmes and Carroll 1977), evenly coarse sculpturing covers the lateral side of the lower jaw. The same appears to be true for *Chenoprosopus* (Langston 1953).

Because of the uniformity of the sculpturing, suture-lines separating the dermal elements of the skull are often difficult to follow in *Cochleosaurus florensis*. The pattern appears to be closely comparable to that in *C. bohemicus* (text-figs. 1 and 4). The lacrimal is excluded from the orbit by a narrow ventral process of the prefrontal which contacts the jugal. The jugal enters the lower margin of the cheek in *Cochleosaurus* but not in *Dendrerpeton* (Carroll 1967a). The postorbital typically consists of a broad anterior part bordering the orbit and a narrow, elongated posterior part lying between the intertemporal and the jugal which may reach the supratemporal bone posteriorly. The same arrangements are found in *Caerorhachis* (Holmes and Carroll 1977) and in *Dendrerpeton* (Carroll 1967a). Of the temporal series of bones, the supratemporal is the largest.

The palate of *Cochleosaurus bohemicus* is very poorly known (Broili 1905). It is well preserved in *C. florensis* (MCZ 4344), however, which serves as the basis for the following description (text-fig. 3).

The interpterygoid vacuities are wide, about one-sixth of the snout-quadrate length, but become narrower anteriorly. The palatine rami of the pterygoids converge anteriorly, but they do not meet in the midline anterior to the interpterygoid vacuities. They are bordered anteriorly by the vomers which
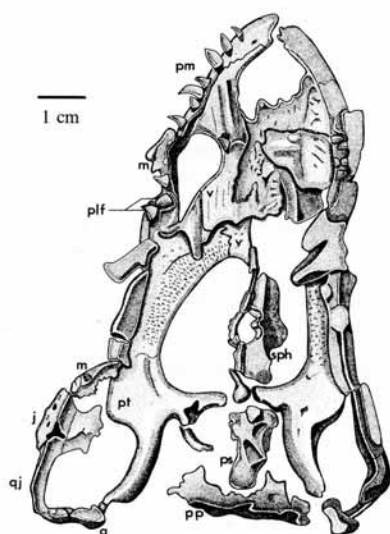
TEXT-FIG. 3. The palate of *Cochleosaurus florensis* (MCZ 4344) in ventral view. Natural size. Abbreviations as in text-fig. 1.
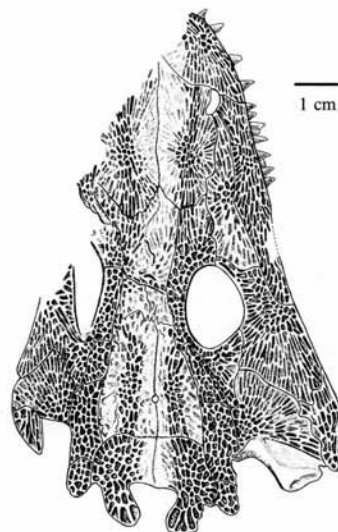
TEXT-FIG. 4. The skull of *Cochleosaurus bohemicus* (HMB 1902.1386b) in dorsal view. ×¾.

form an interdigitating suture with the tips of the pterygoids and which enclose between them the tip of the cultriform process of the parasphenoid. In *Caerorhachis* (Holmes and Carroll 1977), a primitive edopoid with a shorter snout, the pterygoids meet anterior to the relatively narrow interpterygoid vacuities. This is probably the primitive condition. *Dendrerpeton* is generally considered to be somewhat more primitive than *Cochleosaurus* (Carroll 1967*a*). As restored by Carroll (1967*a*), the pterygoids in *Dendrerpeton* are less convergent anteriorly, which results in wider interpterygoid vacuities. However, in the text, Carroll (1967*a*) mentions the impossibility of determining the exact shape of the pterygoids. In *Chenoprosopus* (Langston 1953), the pterygoids form an interdigitating suture with the broadened tip of the cultriform process. This could be a secondary condition to reinforce the snout by bringing the anterior parts of the pterygoids near to the midline. *Cochleosaurus* is intermediate between *Dendrerpeton* and *Chenoprosopus* with respect to this character.

The quadrate ramus of the pterygoid is a high, blade-like structure with a narrow ventral edge. The jaw articulation lies between the occipital condyle and the occipital plane of the skull roof. The quadrate ramus of the pterygoid, the quadrate, the quadratojugal, the jugal, and the posterior part of the maxilla bordering the subtemporal fossa, all have their ventral edges on the same plane.

Of the braincase, only the anterior part of the parasphenoid showing grooves for the internal carotid arteries and vidian nerves, and the long, narrow cultriform process are preserved. Associated with the cultriform process in both specimens of *Cochleosaurus florensis* are parts of the ossified sphenethmoid. It seems to be broadest in its middle portion but tapers anteriorly, barely reaching the vomers. The posterior part of the sphenethmoid is lacking. The parasphenoid articulates with large processes of the pterygoids. The right pterygoid of MCZ 4344 bears a notched process against which fitted the antero-lateral edge of the parasphenoid. The posterior parts of the braincase are lacking.

The palate of *C. florensis* shows four to five irregular longitudinal rows of small denticles on the palatine rami of the pterygoids. Each vomer bears several ridges, on each of which runs one row

of small denticles. These ridges radiate from the vomerine fangs, three anteriorly, one transversely, and two posteriorly on each vomer. In *Caerorhachis* (Holmes and Carroll 1977) and in *Dendrerpeton* (Carroll 1967*a*), a shagreen of small denticles is evenly distributed over all palatal bones, a primitive condition. With reference to specimen MCZ 4343, the premaxilla of *Cochleosaurus florensis* bears thirteen or fourteen tooth positions, with seven teeth *in situ*. The maxilla shows thirty-six tooth positions with twenty-one teeth *in situ*. This results in a total of forty-nine or fifty teeth for each upper jaw ramus of *C. florensis*. Fritsch (1889) estimated a total of fifty teeth for each upper jaw ramus of *C. bohemicus*.

A lateral view of the left mandibular ramus is shown in MCZ 4343. A large angular extends far anteriorly. The posterior end of the lower jaw is formed by the surangular. The splenial and the postsplenial appear to be of about equal length, the splenial extending to the angular as in *Chenoprosopus* (Langston 1953). The suture between the splenial and the postsplenial in *Cochleosaurus florensis* (MCZ 4343) lies on a crack, and there is some suspicion that it may lie further anteriorly, which would result in a shorter splenial.

A tibia and a fibula as well as a clavicle can be identified, lying across the lower surface of the palate of *C. florensis* (MCZ 4343) (text-fig. 1). The association of these elements with *Cochleosaurus* is questionable. Other elongated elements may represent ribs.

DISCUSSION

Palaeogeography

During the Middle Pennsylvanian, the genus *Cochleosaurus* inhabited Europe (*C. bohemicus* Fritsch, 1885) and, as far as presently known, eastern North America (*C. florensis* n. sp.), the two populations being distinct at the specific level. According to Milner and Panchen (1973) and Panchen (1977), the locality near Florence lies on the European side of the Appalachian Mountain Chain of Laurasia. These authors believe that *Cochleosaurus* represents an aquatic animal which was unable to migrate across the Appalachian Mountains. However, on the basis of the absence of lateral-line canals on the dermal skull bones, *Cochleosaurus* could be interpreted as a predominantly terrestrial genus, and indeed *Cochleosaurus* might also occur at Linton, Ohio, on the North American side of the Appalachian Mountain Chain (Milner, cited in Panchen 1977). A terrestrial habit of *Cochleosaurus* would fit the character of the Florence locality, which otherwise yielded predominantly terrestrial reptiles (Carroll 1969; Reisz 1972).

Relationships

A typical feature of *Cochleosaurus* is a pattern of strong and subdued sculpturing of dermal skull bones, associated with the depression of certain areas in *C. florensis*. The two species of *Cochleosaurus* can readily be distinguished by zones of intensive growth (Bystrow 1935), resulting in elongated pits in the sculpturing of *C. bohemicus* which are lacking in *C. florensis*. This is, however, a matter of maturity.

Within the closely related edopoid genera *Dendrerpeton*, *Cochleosaurus* and *Chenoprosopus*, a successive lengthening of the snout is observed. Although the snout of *Cochleosaurus florensis* is slightly shorter than in *C. bohemicus*, the snout of the genus *Cochleosaurus* in general is longer than in *Dendrerpeton* but shorter than in *Chenoprosopus*. *Cochleosaurus* is also morphologically intermediate between *Dendrerpeton* and *Chenoprosopus* with respect to the size of the interpterygoid vacuities.

Chenoprosopus is considered to be more advanced than *Cochleosaurus* and possibly a descendant of the latter by Langston (1953), although he places the genus in a distinct family. Romer (1966) includes *Chenoprosopus* within the Cochleosauridae. Significant similarities between *Cochleosaurus* and *Chenoprosopus*, as noted by Langston (1953), include the size and the shape of the internal nostrils as well as of the interpterygoid vacuities and the loss of the parietal foramen in adult specimens of both genera. To this list of similarities between *Cochleosaurus* and *Chenoprosopus* may be added the depressed area with subdued sculpturing in the preorbital region of *Chenoprosopus*

covering the lacrimal bone, as well as a similar depression lying between the external nares. A primitive feature of *Chenoprosopus* is the single occipital condyle. The vomers do not enter the interpterygoid vacuities but are excluded from them by the pterygoids which turn inwards to contact the tip of the cultriform process in an interdigitating suture. This might represent a secondary specialization of *Chenoprosopus* rather than a primitive feature.

Dendrerpeton resembles Cochleosaurus in the shape and position of the postorbital and temporal series of bones. The lacrimal bone broadly enters the orbit in *Dendrerpeton*, however, a primitive feature that has been lost in *Cochleosaurus*. The jugal does not enter the lower margin of the cheek in *Dendrerpeton* as it does in *Cochleosaurus*. The pineal foramen is persistently large in *Dendrerpeton*, another primitive feature of the genus. The palate of *Dendrerpeton* appears to be more primitive than the palate of *Cochleosaurus*. Denticles are found on all palatal bones of *Dendrerpeton*, while in *C. florensis* they are restricted to the pterygoids and vomers. The vomers of *Dendrerpeton* lack the ridges described above for *C. florensis*.

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DR. OLIVIER RIEPPEL

Paläontologisches Institut und Museum der Universität
Künstlergasse 16
8006 Zürich
Switzerland