

CRANIAL OSTEOLOGY OF *HYPSOGNATHUS FENNERI*, A LATEST TRIASSIC PROCOLOPHONID REPTILE FROM THE NEWARK SUPERGROUP OF EASTERN NORTH AMERICA

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ABSTRACT—Based primarily on two previously undescribed skulls, this paper presents a detailed description of the skull and mandible of the latest Triassic procolophonid reptile *Hypsognathus fenneri* Gilmore, 1928. One of the new skulls, belonging to a presumed juvenile, clearly establishes for the first time the sutural pattern, which differs significantly from that in *Procolophon* and more basal procolophonid taxa. A number of shared derived features in the structure of the skull and mandible indicate that *Hypsognathus* is closely related to *Leptopleuron* from the Upper Triassic Lossiemouth Sandstone Formation of Scotland. *Hypsognathus* had a wide geographic and stratigraphic distribution in eastern North America during the latest Triassic (Norian-Rhaetian).

INTRODUCTION

The Procolophonidae form a clade of small to medium-sized parareptiles of mainly Triassic age. Diagnostic apomorphies for this taxon include: postfrontal splint-like or splint-like with posterior portion fused with parietal; postparietal small or absent; and depression on anterolateral surface of maxilla immediately behind external naris (Spencer, 1994; Lee, 1995, 1997). Skeletal remains referable to procolophonid reptiles have been found on all continents including Antarctica and are locally very abundant. The best known representative is the nominal genus *Procolophon* Owen, 1876, which is represented by numerous well-preserved skulls and skeletons from the Lower Triassic *Lystrosaurus* Assemblage Zone of South Africa (Watson, 1914; Broili and Schröder, 1936; Kemp, 1974; Carroll and Lindsay, 1985) and the correlative Fremouw Formation of Antarctica (Colbert and Kitching, 1975).

Gilmore (1928) described the partial skeleton of a small reptile preserved as a natural mold (with some soft, chalky bone initially remaining in the impressions) in a block of sandstone (USNM 11643) from the Upper Triassic "Brunswick" (now upper Passaic) Formation, which was temporarily exposed at a construction site for an underpass in Clifton, New Jersey. He designated this fossil as the holotype of the new taxon, *Hypsognathus fenneri*, and suggested "cotylosaurian" affinities, comparing it primarily to forms now referred to the Procolophonidae. In 1939 and 1940, a second incomplete skeleton including a skull and mandible (AMNH 1676) as well as two partial skulls (AMNH 1677 and AMNH 1678) were collected from a quarry in the same formation on Paulison Avenue on the municipal boundary between Clifton and Passaic, some 2.6 miles (4.16 km) by air from the type locality. Colbert (1946) provided a detailed description of these specimens and referred them to *Hypsognathus fenneri*. He explicitly placed *Hypsognathus* in the Procolophonidae and interpreted it as the most highly derived member of this group then known. Colbert noted the much enlarged orbit (orbitotemporal opening sensu Huene [1912]), considerable transverse width of the skull, and the presence of prominent, spine-like bony processes on the quadratojugal. The localities yielding the holotype of *Hypsognathus*

fenneri and Colbert's referred material are located in the Newark basin of the Newark Supergroup (Fig. 1A).

Since the publication of Colbert's monograph, numerous skeletal remains of Procolophonidae have been discovered in the Late Triassic sedimentary strata of the Newark Supergroup of eastern North America (Baird, 1986; Sues and Olsen, 1993; Sues and Baird, 1998). Preparation of two previously undescribed skulls referable to *Hypsognathus fenneri* has revealed a wealth of new data concerning the structure of the skull and mandible. The cranial bones of AMNH 1676, described and figured by Colbert (1946), have poorly preserved external surfaces, which are traversed by numerous fine fractures. Few sutures can be definitely identified on the skulls of this and the other AMNH specimens. Thus Colbert reconstructed the pattern of cranial sutures based on that in *Procolophon*. However, a superbly preserved skull and mandible of *Hypsognathus* from the Blomidon Formation of Nova Scotia establishes numerous differences in the sutural pattern between *Hypsognathus* and *Procolophon*.

In view of the continuing debate concerning the interrelationships of parareptiles, especially the phylogenetic position of turtles (Laurin and Reisz, 1995; Lee, 1995, 1997), it is important to gain a better understanding of the skeletal structure of the Procolophonidae. To date, only the skulls of *Procolophon* (Carroll and Lindsay, 1985) and *Tichvinskia* (Ivakhnenko, 1973) have been described in detail. More recently, Spencer (in press) has studied the braincase of *Leptopleuron*. The present paper provides a detailed description of the skull and mandible of *Hypsognathus fenneri*. It is based primarily on two specimens, the skull and articulated mandible of a presumed juvenile individual (NSM 998GF45.1) from the basal portion of the Blomidon Formation of Nova Scotia and the skull and articulated mandible of a large, presumably adult individual (YPM 55831) from the upper part of the New Haven Formation of Connecticut. Some additional details were taken from casts of YPM-PU 21752, a natural mold of a skull found in a coping stone of a low wall on a residential property in Passaic, New Jersey, and reported by Baird (1986). This block was originally derived from strata of the upper portion of the Passaic Formation. At the time of its discovery, the specimen preserved the molds of the skull roof and of the dorsal surface of the palate. During preparation, Donald Baird took a synthetic-rubber im-

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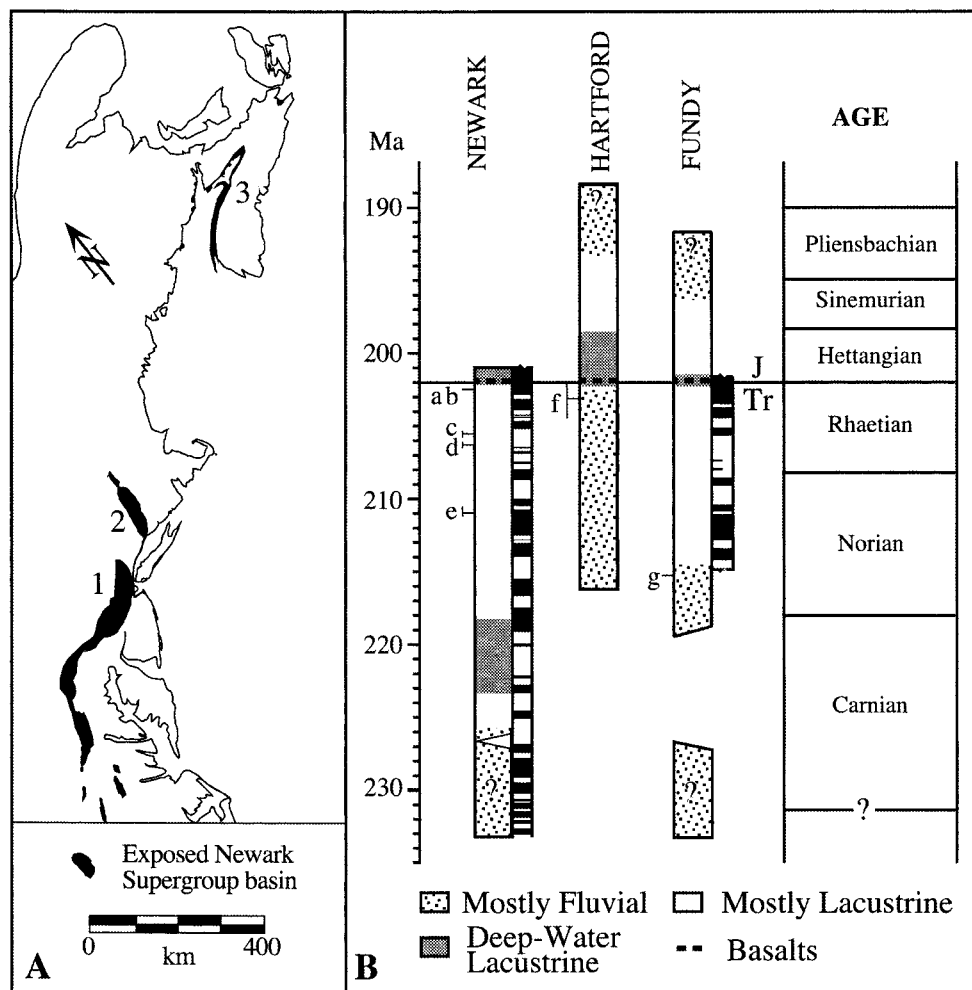


FIGURE 1. Geographic and stratigraphic distribution of *Hypsognathus fenneri* in eastern North America. **A**, Map of eastern North America with the rift basins of the Newark Supergroup that have yielded fossils of *H. fenneri*. 1, Newark basin; 2, Hartford basin; 3, Fundy basin. **B**, Stratigraphic positions of currently known localities yielding specimens referable to *H. fenneri*. **Abbreviations:** a, Jacksonwald syncline, Exeter Township, Pennsylvania; b, type locality of *H. fenneri* (USNM 11643), Clifton, New Jersey; c, Paulison Avenue quarry, Passaic, New Jersey (Colbert, 1946); d, YPM-PU 21752, Passaic, New Jersey; e, East Greenville, Pennsylvania; f, YPM 55831, Meriden, Connecticut; g, NSM 998GF45.1, Kings County, Nova Scotia. The stratigraphic profiles and magnetostratigraphic sequences are based on Olsen and Kent (in press).

pression of the palate before sacrificing it to expose the impression of the skull roof.

YPM 55831, comprising a partial skeleton including skull and mandible, was found by David Bazzano and Robert Baron in a block of sandstone in a backyard in Meriden, Connecticut, and was subsequently donated to the Peabody Museum of Natural History at Yale University (Ostrom, 1967). The more anterior region of the vertebral column, the pectoral girdle, and parts of both forelimbs were preserved as natural molds. Initially, there was no trace of the skull. However, subsequent preparation of the block by Peter Whybrow and Robert T. Bakker exposed an almost complete skull and mandible (Ostrom, 1969). The original provenance of the block containing YPM 55831 is unknown, but heavy-mineral analysis (Griggs, 1973) and the coarseness of the sandstone matrix indicate its derivation from the upper part of the New Haven Formation (formerly New Haven Arkose). This formation in the Hartford basin of the Newark Supergroup ranges in age from the Norian to the Hettangian (Fig. 1). Its upper portion can be correlated with the upper part of the Passaic Formation of the Newark basin in New Jersey (Olsen, 1980). The skull of YPM 55831 (Fig. 2) is

preserved with the mandible in tight occlusion and has been slightly distorted during fossilization. The external surfaces of the cranial bones are not well preserved and are crisscrossed by fractures in many places, making it difficult to trace various sutures. The left cluster of quadratojugal spines was only preserved in the form of impressions, which were filled in with epoxy resin during preparation. The posterior portion of the left mandibular ramus and much of the palate are not preserved. The length of the skull, measured along the midline from the tip of the snout to the posterior end of the parietals, is 75 mm, which is 50 percent longer than that of AMNH 1676 (50 mm).

NSM 998GF45.1 was discovered in 1983 by Anson Brown, a geologist working for ARCO Petroleum, in a seacliff southwest of Paddy's Island, West Medford, Kings County, Nova Scotia. The specimen was preserved in a massive, pebbly sandstone in the middle of a fining-upward sequence of beds made up of trough-cross-bedded gravel and pebbly sandstone that grades upwards into fine to medium tabular beds of sandstone, which are capped by red mudstone. The base of this sequence cuts about 1 m down into underlying red mudstone and sandstone. The sandstone layer containing the fossil shows no ob-

vious bedding and is poorly sorted, perhaps due to bioturbation. The skull of NSM 998GF45.1 (Fig. 3) was preserved with its dorsal side facing up. The mandible is preserved in tight occlusion, and it was not possible to separate the upper and lower teeth without incurring damage to the fossil. The rostral tip of the snout was accidentally destroyed at the time of discovery, and the apices of the spine-like bony processes on the quadratojugal were slightly rubbed during subsequent handling. The right paroccipital process and part of the posterior portion of the right mandibular ramus were apparently lost prior to burial. Most of the cranial sutures are clearly visible. The skull was associated with an incomplete interclavicle and small fragments of vertebrae and limb-bones. In places, small pebbles were pressed into the underlying bone, resulting in a distinctly "pock-marked" appearance of the external surfaces of the cranial bones. The estimated length of the skull (measured along the midline) is 36 mm. The juvenile nature of this specimen is not only indicated by its small size (compared to that of other known skulls referable to *Hypsognathus*) but also by the short spine-like bony processes on the quadratojugal. The skull of NSM 998GF45.1 shares numerous autapomorphies with other skulls referable to *Hypsognathus fenneri*, and, in the absence of contradictory evidence, we regard it as a juvenile specimen of the latter taxon rather than as a representative of a distinct species.

The Blomidon Formation forms part of the Fundy Group in the Fundy basin of the Newark Supergroup (Fig. 1A) and ranges in age from the Norian to the Hettangian. NSM 998GF45.1 was found in the basal portion of the Blomidon Formation, in the upper part of the Red Head Member, about 15 m below the base of the overlying undivided remainder of the formation. Based on stratigraphic correlation with the Newark basin and on the polarity stratigraphy in the GAV-3 core through the Blomidon Formation, the Red Head Member near Paddy's Island most likely correlates with polarity zone E15 and members R–U of the Passaic Formation (Olsen and Kent, in press). The occurrence of *Hypsognathus fenneri* in the Red Head Member represents the stratigraphically oldest record of this taxon known to date (Fig. 1B).

Lucas (1998) used the occurrence of *Hypsognathus fenneri* to define a "Cliftonian land-vertebrate faunachron (LVF)" in eastern North America. Given the current paucity of skeletal remains of continental tetrapods in the Norian-Rhaetian continental strata of the Newark Supergroup, formal designation of this biostratigraphic unit would appear premature.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; NSM, Nova Scotia Museum, Halifax; USNM, National Museum of Natural History (formerly United States National Museum), Washington, DC; YPM, Peabody Museum of Natural History, Yale University; YPM-PU, former Princeton University collection, now housed at the Peabody Museum of Natural History, Yale University.

SYSTEMATIC PALEONTOLOGY

PARAREPTILIA Olson, 1947 sensu Laurin and Reisz, 1995

PROCOLOPHONIDAE Seeley, 1888

LEPTOPLEURONINAE Ivakhnenko, 1979 emend.

HYPSONGNATHUS Gilmore, 1928

Type Species—*Hypsognathus fenneri* Gilmore, 1928 (by monotypy).

Diagnosis—As for the type and only known species, as diagnosed below.

Distribution—Late Triassic (Norian-Rhaetian), eastern North America.

HYPSONGNATHUS FENNERI Gilmore, 1928
(Figs. 2, 3)

Holotype—USNM 11643, natural mold of mandible and partial postcranial skeleton (in ventral view) in a block of sandstone. Upper portion of Passaic Formation, Newark basin (Newark Supergroup), Clifton, Passaic Co., New Jersey. Age: Late Triassic (late Norian–Rhaetian).

Referred Material—See Colbert (1946), Baird (1986), and this paper. Skeletal remains referable to *H. fenneri* are now known from Connecticut, New Jersey, Nova Scotia, and Pennsylvania. New material that can be assigned to this taxon has recently been collected by private collectors from various temporary exposures in the Passaic Formation of the Newark basin in southeastern Pennsylvania. The fossils come from East Greenville and the Jacksonwald syncline in Exeter Township. Detailed description of this material must await preparation and study by the authors. Along with the holotype, the specimens from the Jacksonwald syncline represent the stratigraphically youngest known records of *Hypsognathus*, occurring just below the Triassic–Jurassic boundary (Fig. 1B).

Diagnosis—Among the known taxa of Procolophonidae, *Hypsognathus fenneri* can be characterized by the following autapomorphies: anterolateral shelf of nasal roofing external naris; no distinct postorbital; thick ventral processes of parietals sutured to dorsomedial crest on supraoccipital; quadratojugal with large, anteroventrally curved process; no sutural separation between supratemporal and squamosal; ventral base of epipterygoid indistinguishably fused to pterygoid; basipterygoid articulation sutured; ventrolateral crests of parabasisphenoid developed as extensive alae in adult individuals; and crown of second premaxillary tooth labiolingually flattened and with distinct anterior and posterior carinae.

DESCRIPTION

Comparative information on the skull of *Procolophon* is primarily based on the detailed description by Carroll and Lindsay (1985). Data for *Leptopleuron* are based on the accounts by Huene (1912, 1920) and Spencer (in press) as well as on a latex cast of the skeleton reported by Huene (1920). Most of the material referable to *Leptopleuron* is represented by natural molds in sandstone and requires casting with flexible compounds; it is often difficult to identify cranial sutures with certainty.

The skull of *Hypsognathus* differs from that of *Procolophon* in its greater transverse width, the pronounced posterior extension of the orbit to form a large orbitotemporal opening, and the presence of a cluster of spine-like bony processes on the quadratojugal. The orbitotemporal opening faces almost directly dorsally. Posteriorly, it extends well behind the large pineal foramen, leaving only a narrow strip of bone (formed by the posterolateral process of the parietal) between the posterior margin of the orbitotemporal opening and that of the skull roof. The orbitotemporal opening has a length of 39 mm in the 75 mm long skull of YPM 55831 and 19 mm in the approximately 36 mm long skull of NSM 998GF45.1. In YPM 55831 and other specimens such as YPM-PU 21752, its outline is distinctly keyhole-shaped in dorsal view. The skull roof is almost flat between the openings. Most of the skull bones lack sculpturing. Only the quadratojugal "spines" on the larger skulls have textured surfaces with fine longitudinal grooves, which indicate a specialized, possibly keratinous covering of the bony processes in life.

The premaxilla forms much of the margin of the large, anterolaterally facing external narial fenestra. Its palatal portion is perforated by a large, round foramen prepalatinum (for the passage of A. nasalis inferior and associated neurovascular structures; Heaton, 1979). The foramen is surrounded by a de-

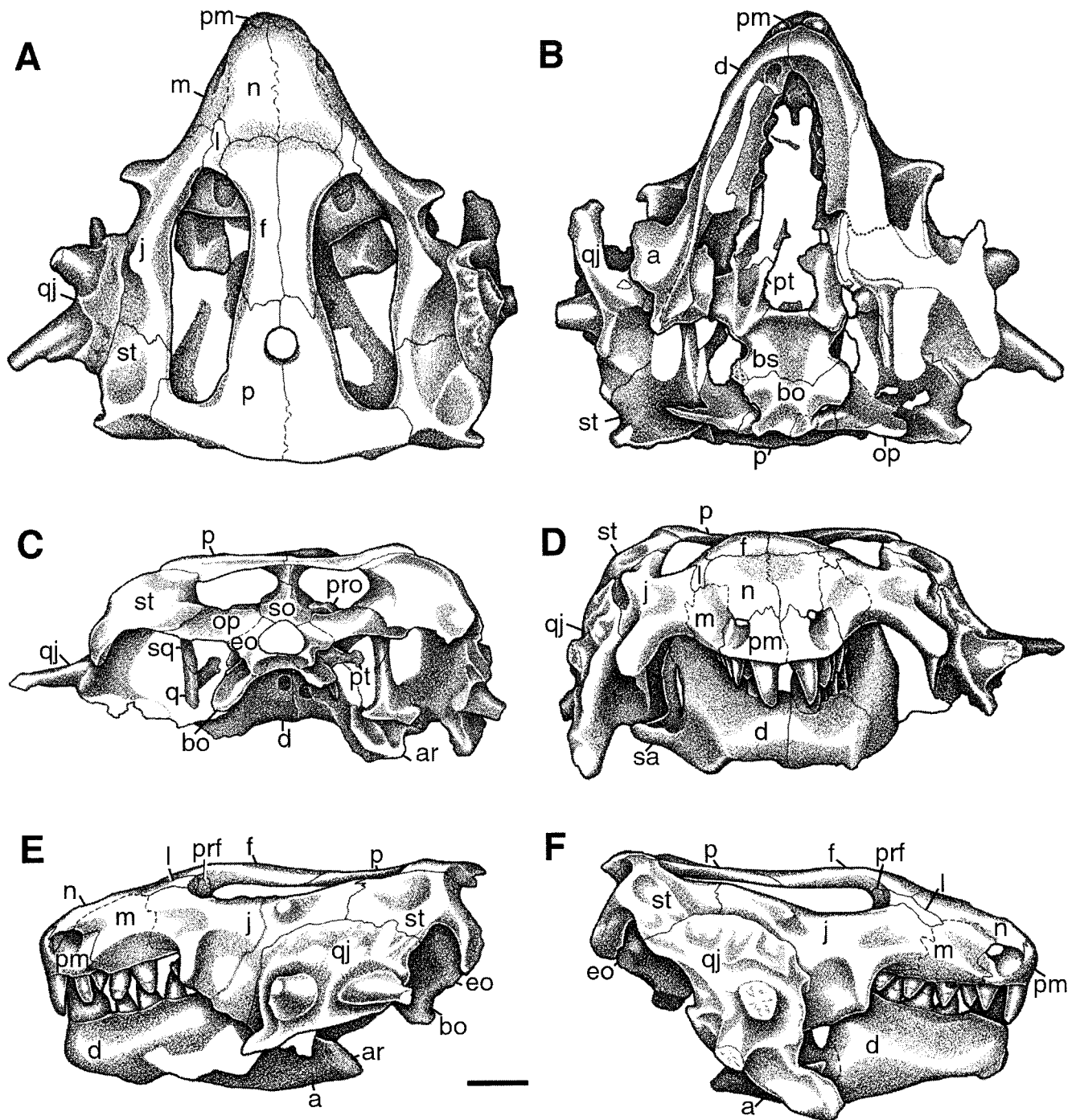


FIGURE 2. Skull and mandible of an adult specimen of *Hypsognathus fenneri* (YPM 55831) in (A) dorsal, (B) ventral, (C) occipital, (D) anterior, (E) left lateral, and (F) right lateral views. Unshaded areas indicate missing bone or matrix. Scale bar equals 1 cm. Due to the poor preservation of some bony surfaces, the course of some sutures remains somewhat uncertain. **Abbreviations used in Figures 2, 3:** a, angular; ar, articular; bo, basioccipital; bs, basisphenoid; co, coronoid; d, dentary; ec, ectopterygoid; eo, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pa, prearticular; pf, postfrontal; pl, palatine; pm, premaxilla; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; so, supraoccipital; sq, squamosal; st, supratemporal.

pression on the palatal surface of the premaxilla; this pit received the tip of the crown of the enlarged lower incisiform tooth. The transversely broad ascending processes of the premaxillae make up the robust internarial bar. The posterior ends of these processes are barely visible in dorsal view. The base of the internarial bar forms a median bony septum, which ex-

tends posterodorsally between the external nares. Each premaxilla bears two teeth. The crown of the first tooth is much larger than that of the second. It projects vertically over the anterior surface of the mandibular symphysis. The crown of the second tooth is labiolingually flattened and bears distinct anterior and posterior cutting edges. None of the available specimens shows

a distinct septomaxilla as in *Procolophon* (Carroll and Lindsay, 1985).

The maxilla is dorsoventrally deep above the tooth row. There are four maxillary teeth in NSM 998GF45.1 and five teeth in YPM 55831. Posteriorly, the tooth row terminates anterior to the orbit. The first maxillary tooth is conical, but all other teeth are molariform with transversely expanded crowns. The mandible is preserved in tight occlusion with the skull in both NSM 998GF45.1 and YPM 55831, and thus the upper and lower teeth could not be separated for more detailed examination. In ventral view, the maxillary tooth row is set in from the lateral margin of the snout, which bears a low ridge (particularly distinct on the left maxilla of YPM 55831). The dentary has a corresponding ridge and similarly inset tooth row. In YPM 55831, a shallow lateral depression is present just behind the external narial fenestra, unlike the more distinct "pocket" present in *Procolophon* and more basal procolophonid taxa. NSM 998GF45.1 has two small supralabial foramina on the lateral surface of the maxilla, one located above the second tooth and the other above the gap between the third and fourth teeth. The maxilla becomes transversely wider toward the posterior end of the tooth row, meeting the jugal posterolaterally in an extensive suture and forming a ventrally facing surface lateral to the posterior teeth. In NSM 998GF45.1, the facial portion of the maxilla is a thin sheet of bone that extensively overlaps the anterior portion of the jugal on the side of the snout; this sheet is completely preserved on the left side of this specimen, but it is incomplete on the right side, exposing the underlying jugal.

The nasal makes up the dorsal margin of the external narial fenestra. In YPM 55831, a small shelf of the nasal extends over the naris anterolaterally; the corresponding region in NSM 998GF45.1 is not preserved. The nasal forms a sutural contact with the maxilla laterally.

In *Procolophon*, the prefrontal is extensively exposed on the roof and on the side of the snout (Carroll and Lindsay, 1985). In *Hypsongnathus*, the prefrontal is restricted to the anterior bony wall of the orbit and forms a bony strut, which is sutured dorsally to the ventral surfaces of the lacrimal and nasal. A dorsomedially directed process extends from the ventromedial portion of the prefrontal to the frontal below the dorsomedial margin of the orbit in NSM 998GF45.1, and a foramen is enclosed between the frontal, lacrimal, and prefrontal. YPM 55831 has a shorter and more robust medial process, and there appears to be no foramen. This process may be homologous to the medially directed, freely ending process of the prefrontal in other procolophonid taxa. The posterior entrance of the orbitonasal canal (lateral orbitonasal foramen sensu Heaton, 1979; presumably for the passage for A. maxillaris, N. palatinus anterior, and a branch of N. maxillaris) lies at the anterior end of a deep groove formed by the lacrimal, palatine, and prefrontal; this groove is particularly pronounced in YPM 55831. The lacrimal is exposed on the skull roof between the jugal and the expanded anterior portion of the frontal. None of the specimens clearly shows the posterior entrance(s) of the lacrimal canal.

The frontals form the medial margins of the orbits. They are narrow between the orbits but greatly increase in width anteriorly. The dorsal surface of the interorbital region is flat.

Posteriorly, the postfrontal is fused to the parietal on the skull roof, but, more anteriorly, this element forms a thin bony splint along the orbital margin as in *Procolophon*. The parietal makes up the posterior and much of the medial margin of the greatly enlarged orbitotemporal opening. Its dorsal surface is flat. The large pineal foramen is situated well anterior to the posterior margin of the orbitotemporal opening and close to the suture between the frontals and parietals. Posteriorly, a steep angle marks the transition from the rather flat dorsal surface of the parietal to the narrow, nearly vertical occipital portion above

the large posttemporal fenestra. This transition probably reflects the anterior extent of the epaxial neck musculature (Carroll and Lindsay, 1985); it is marked by a distinct ridge in YPM 55831. The parietals overhang the occiput posteriorly, and the posteriormost point of the skull roof is located at the posterior end of the interparietal suture. There is no trace of a distinct postparietal.

The postorbital appears to be fused to the jugal; in NSM 998GF45.1, the narrow anterodorsal portion of the compound element occupies the same position as does the postorbital in *Procolophon*.

The jugal is much deeper dorsoventrally than in *Procolophon* and other procolophonid taxa. It forms the ventral margin of the orbit and anteriorly contacts the lacrimal, excluding the maxilla from participation in the anterior margin of the orbit. It extends anteromedial to the sheet-like posterior portion of the maxilla to contact the nasal in NSM 998GF45.1. The jugal is bowed out laterally, creating a considerable gap between it and the coronoid process of the dentary; this space presumably facilitated passage of part of M. adductor mandibulae (Carroll and Lindsay, 1985). The lateral surface of the deep suborbital process bears a broad embayment, which continues posteriorly onto the lateral surface of the quadratojugal. This embayment probably corresponds to a narrow, triangular depression on the lateral surface of the jugal in *Leptopleuron*. At the point where the orientation of the suborbital process changes from posterolateral to posterior, the ventral margin of this embayment is deflected anteroventrally to form the posterior edge of a ventral tubercle in NSM 998GF45.1. In YPM 55831, there is a distinct ridge, which terminates in a ventrolateral projection, rather than a ventral tubercle. The ventral margin of the jugal is convex, especially in YPM 55831, and faces anteroventrally.

The large quadratojugal makes up the posterolateral portion of the "cheek" region. It forms a robust, anteroventrally curved process in YPM 55831 and AMNH 1676 (Colbert, 1946:pl. 28); this projection is only developed as a tubercle in NSM 998GF45.1. Posterodorsally, the quadratojugal bears a conical, posterolaterally directed bony spine, which is obliquely oval in transverse section. Anteroventral to this process, another large, laterally projecting spine with an expanded, flange-like base is situated on the lateral surface of the central portion of the quadratojugal. In the larger specimens, the surfaces of the bony spines bear fine grooves suggestive of a specialized, perhaps keratinous covering in life. The base of each spine, especially the anterior one, is encircled by a sulcus. The lateral surface of the quadratojugal is slightly elevated around the bases of the spines and bears irregular grooves. Some of these grooves terminate in the sulci around the bases of the spines. These features may reflect the vascular supply to the specialized epidermal tissue covering the spines, similar to the condition in mammalian antlers (Bubenik, 1971). In NSM 998GF45.1, a low ridge connects a tubercle near the suture between the jugal and quadratojugal and the ventral rim of the orbitotemporal opening to the anteroventral spine. In YPM 55831, these two projections are widely separated, and the tubercle appears to be situated on the jugal. The transversely expanded anterior portion of the quadratojugal is excavated by a deep, anteriorly and slightly ventrally facing recess, which continues the embayment described above.

In lateral view, the quadratojugal largely covers the quadrate. The distal articular surface of the quadrate is much shorter anteroposteriorly than wide transversely and faces anteroventrally. It is gently concave transversely. The rather flat medial portion of the articular surface is shorter anteroposteriorly than the lateral portion, which has a convex surface and extends onto the posterior surface of the quadrate. More dorsally, the quadrate extends lateral to the distal articular surface to contact the quadratojugal. The medial portion of the quadrate forms a subtrian-

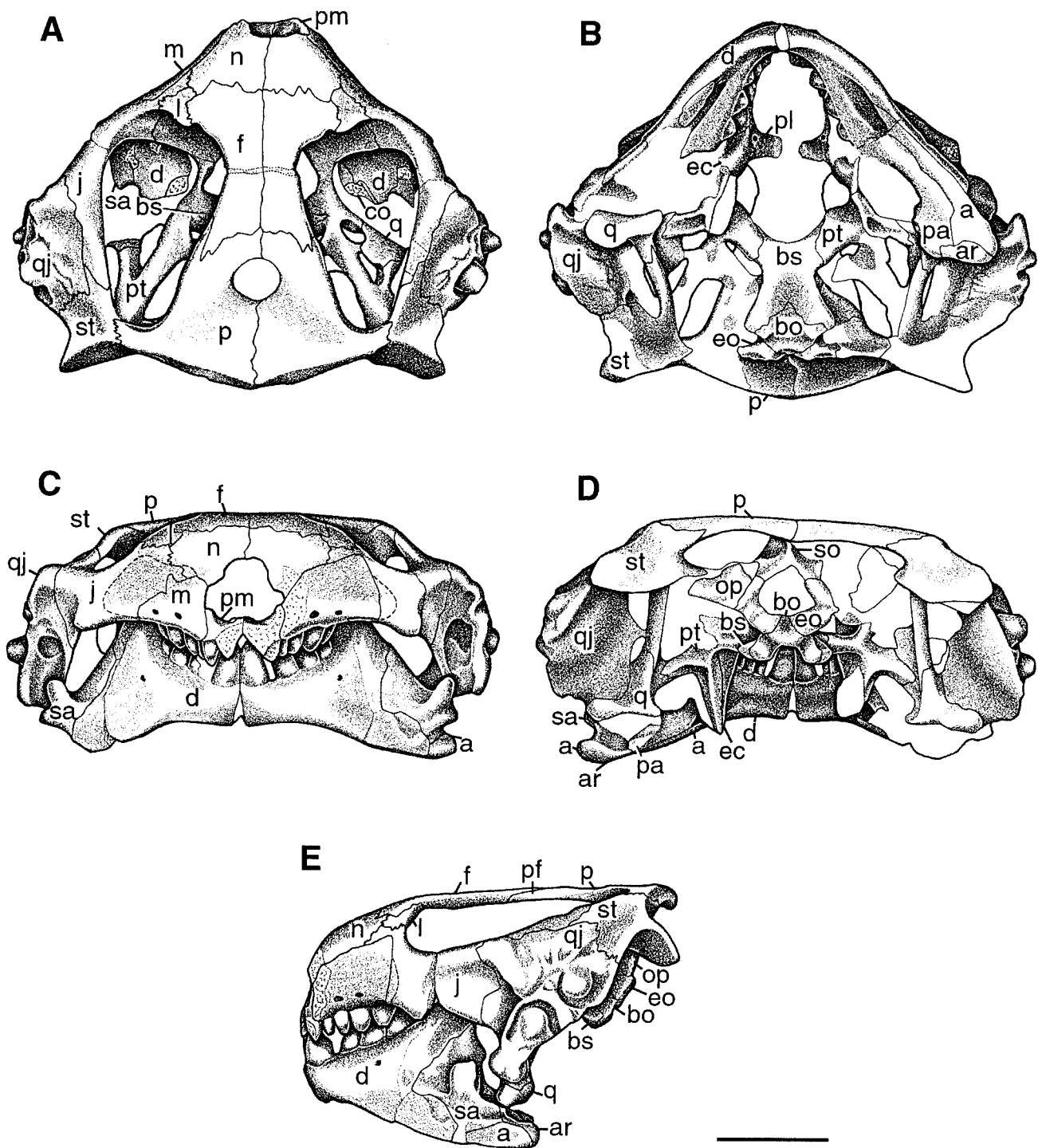


FIGURE 3. Skull and mandible of a juvenile specimen of *Hypsognathus fenneri* (NSM 998GF45.1) in (A) dorsal, (B) ventral, (C) anterior, (D) occipital, and (E) left lateral views. Unshaded areas indicate missing bone or matrix. Scale bar equals 1 cm.

gular, anteromedially projecting pterygoid process of the quadrate, which overlaps the posterolaterally directed quadrate flange of the pterygoid. Dorsally, it meets the long ventral process of the squamosal, which appears as a distinct, nearly vertical ridge in occipital view. This ridge forms the medial margin of a large, vertically more or less oval depression; the lateral margin of this depression is formed by the transversely expanded quadratojugal. Ventromedially, the depression houses

the quadrate foramen on the suture between the quadrate and quadratojugal. In NSM 998GF45.1, the paper-thin wall of the depression was apparently perforated post mortem (Fig. 3D).

There is no distinct suture between the supratemporal and squamosal. (The supratemporal was previously identified as a "tabular" by Colbert [1946] in *Hypsognathus* and by Kemp [1974] in *Procolophon*; however, the tabular is now known to be absent in Procolophonoidea [Carroll and Lindsay, 1985].)

The compound bone forms the pointed posterolateral corner of the skull roof, and its lateral edge defines the dorsal margin of the otic notch. Medially, it broadly enters into the posterolateral margin of the orbitotemporal opening. The occipital portion of the supratemporal is a thin but extensive flange, which contacts the distal end of the paroccipital process anteriorly. A long ventral process of the squamosal contacts a dorsal process arising from the medial condyle of the quadrate.

Only the anterior ends of the vomers are preserved in YPM 55831, and the bones have been lost in NSM 998GF45.1. They are exposed in dorsal view in YPM-PU 21752 where they form a long, narrow bar between the internal nares. The dorsal surface of this bar bears a distinct ridge, which presumably represented the base for a cartilaginous nasal septum. In contrast to *Procolophon* and *Leptopleuron*, vomerine teeth are absent.

The palatine is short and arched behind the internal naris. It is devoid of teeth.

In contrast to *Procolophon*, the pterygoid lacks teeth along its medial margin, which delimits the anteroposteriorly short interpterygoid vacuity. (Contrary to a claim by Lee [1997], an interpterygoid vacuity is present in *Hypsognathus*.) The transverse process of the pterygoid extends far ventrally into the oral cavity and forms a thin, more or less anteroposteriorly aligned flange. The concave ventrolateral surface of this flange may mark the area of origin of *M. pterygoideus posterior*. Most of the distal portion of the flange is developed as a more or less anteroposteriorly aligned, transversely narrow lappet, as in *Leptopleuron*. Posteromedial and dorsal to the transverse flange, the pterygoid forms a sutural contact with the distal end of the basiptyergoid process of the basisphenoid. The quadrate ramus of the pterygoid extends more or less vertically and almost transversely. It is deeply excavated behind its junction with the transverse flange. In contrast to the condition in more basal procolophonid taxa such as *Tichvinskia* (Ivakhnenko, 1973), the quadrate is situated more or less at the same level as the basiptyergoid articulation rather than posterolateral to it.

The ectopterygoid forms the anterolateral portion of the transverse flange.

The dorsal end of the narrow, strut-like, and posterodorsally inclined ascending process (columella) of the epiptyergoid is ossified, curved, and expanded, much as in *Leptopleuron* (Spencer, in press). It contacts the prootic as well as the anterolateral margin of the supraoccipital. The ventral base of the epiptyergoid appears to be indistinguishably fused to the pterygoid.

The plate-like supraoccipital forms the dorsal margin of the foramen magnum and posterior roof of the endocranial cavity. It contacts the prootic and epiptyergoid anterolaterally and the opisthotic along its lateral margin. The dorsal surface of the supraoccipital bears a pronounced median crest, which broadly contacts short ventral processes of the parietals well anterior to the posterior margin of the skull roof.

Few structural details of the prootic are visible in the specimens described here. Unlike the condition in *Procolophon* (Carroll and Lindsay, 1985), the prootic apparently does not enclose a foramen for *N. facialis* (VII).

The paroccipital process of the opisthotic is flattened anteroposteriorly and somewhat inclined anteroventrally. It extends more or less laterally from the braincase. As in *Leptopleuron* (Spencer, in press), its posterior surface forms a thin, nearly vertical lamina of bone that begins at a bulge near the lateral margin of the foramen magnum on the posterolateral surface of the opisthotic. The distal end of the paroccipital process was apparently not ossified. The ventral portion of the opisthotic forms a ventrally expanded plate as in *Leptopleuron*. The anteroventral surface of the opisthotic in NSM 998GF45.1 is notched to form part of the dorsal margin of the foramen jugulare anterior (presumably for the passage of cranial nerves IX–XI and V. cerebialis posterior) just above the suture between

the exoccipital and opisthotic. Anteriorly, the foramen jugulare anterior is confluent with the fenestra ovalis. There is an extensive unossified gap between the prootic and the basisphenoid, which probably forms the margin of the fenestra ovalis.

As in *Leptopleuron*, the roughly kidney-shaped occipital condyle is distinctly tripartite, with each exoccipital contributing the dorsolateral third of the articular surface of the condyle. It is transversely concave in NSM 998GF45.1, as in adult specimens of *Leptopleuron*. (The condylar region in YPM 55831 is damaged.) The exoccipitals form the lateral margins of the foramen magnum and greatly restrict the participation of the basioccipital in the ventral margin of the foramen magnum. Anteriorly, the exoccipital is pierced by the canal for the passage of *N. hypoglossus* (XII) just anterior to the proximal base of the paroccipital process. The condylar portion of the basioccipital faces posteriorly and slightly ventrally. The center of the condylar surface bears a notochordal pit. Anterior to the occipital condyle, the basioccipital forms a lateral recess at the posterior end of a pronounced lateral groove on the body of the basisphenoid (which appears to be indistinguishably fused with the parasphenoid). More anteriorly, well behind the basiptyergoid process, this sulcus contains the posterior entrance of the canal for *A. carotis interna* and possibly *ramus palatinus* of *N. facialis* (VII; Vidian nerve of authors). The paired basal tubera are separated medially by a deep notch. Their bases are linked by an arcuate ridge that forms the posterior border of the deep ventral depression on the basioccipital and basisphenoid. The basal tubera are largely formed by the basioccipital, with a ventrolateral contribution from the basisphenoid (and indistinguishably fused parasphenoid), and probably served as the points for insertion of *M. longissimus capitis, pars transversalis cervicis* (Heaton, 1979). They are set closely together in NSM 998GF45.1, but diverge considerably in YPM 55831.

It is not possible to distinguish the basisphenoid and parasphenoid, and the former term is applied here to the compound bone. The ventrolateral crests of the basisphenoid (cristae ventrolaterales of Heaton [1979]) form broad, ventrolaterally extending alae in YPM 55831. They project slightly anteromedially from the basal tubera and merge into the bases of the basiptyergoid processes anteriorly. As in *Leptopleuron* (Spencer, in press), the basisphenoid formed a robust, vertical pillar of bone in front of the sella turcica. None of the available specimens preserves any trace of an anteriorly projecting cultriform process, unlike the condition in *Procolophon*. The bony pillar anterior to the sella turcica in *Hypsognathus* and *Leptopleuron* may be homologous to the cultriform process in *Procolophon* and other tetrapods. Laterally, the basiptyergoid processes of the basisphenoid form sutural contacts with the pterygoids, rather than potentially mobile joints as in *Procolophon* (Kemp, 1974; Carroll and Lindsay, 1985) and *Tichvinskia* (Ivakhnenko, 1973).

The mandible is considerably shorter than the skull (27 mm vs. 36 mm in NSM 998GF45.1 and 54 mm vs. 75 mm in YPM 55831). In ventral view, its rami form a blunt, broadly rounded symphyseal region and diverge posteriorly.

The dentary is robust and becomes deeper toward its posterior end. It differs from that in *Libognathus* (Small, 1997) in that the alveolar margin extends almost parallel to the ventral margin for much of the length of the dentary, diverging only more posteriorly. (The dentary is deeper and its alveolar and ventral margins diverge much more posteriorly than Small [1997] inferred on the basis of Colbert's [1946] illustrations.) The ventral margin of the tooth-bearing ramus is slightly concave in lateral view. The tall coronoid process of the dentary steeply rises posterodorsally medial to the jugal. In NSM 998GF45.1, a mental foramen is present below the fifth tooth position on the lateral surface of the dentary. The mandibular symphysis is unfused. The symphyseal facet of the dentary is

vertically oriented and oval. Each dentary bears a single massive, slightly procumbent incisiform tooth, which is separated from the more posterior teeth by a short diastema (which is most pronounced in NSM 998GF45.1). The dentary of NSM 998GF45.1 bears four teeth and that of YPM 55831 six.

Little is visible of the coronoid because it is concealed by the transverse flange of the pterygoid in the specimens described here. It forms a transversely expanded, posteriorly concave apex of the coronoid process in YPM 55831.

The splenial only covers the more ventral portion of the lingual surface of the dentary, exposing much of the shallow Meckelian groove in medial view.

Posterolaterally, the surangular forms a prominent, dorsolaterally curving, and bifurcated process, which may correspond to the distinct, horizontal crest on the surangular of *Tichvinskia* (Ivakhnenko, 1973:fig. 6). The distal end of this process may have served as the point of insertion for a superficial portion of *M. adductor mandibulae*, which possibly originated from the deep anteroventral fossa on the quadratojugal.

The rather short retroarticular process is transversely expanded. The articular projects posteriorly beyond the adjacent bones and terminates in a blunt posterior end with an apparently unfinished bony surface. Its dorsal surface is transversely concave and forms a distinct postglenoid depression just behind the more or less transverse, shallow articular facet of the jaw joint. The jaw joint is situated well anterior to the occipital condyle and below the level of the alveolar margin of the dentary as in *Leptopleuron*.

The prearticular makes up much of the posteromedial surface of the lower jaw, including the ventral surface of the retroarticular process. It also forms the posterior and ventral margins of the adductor fossa. Its posterodorsal portion curves medially, presumably in relation to the transverse expansion of the articular facet for the jaw joint.

The angular forms an almost vertical plate covering the lateral surface of the retroarticular process. It wraps around the ventral margin of the lower jaw and extends forward to the foramen intermandibularis caudalis. Ventrally, the angular forms a pronounced vertical keel. The sharp ventral edge of this keel makes it unlikely that *M. pterygoideus* wrapped around the ventral margin of the posterior end of the mandibular ramus and inserted onto its posterolateral surface in the manner reconstructed by Ivakhnenko (1979:fig. 25).

Tooth Replacement—The adult specimen YPM 55831 is noteworthy for showing clear evidence of tooth replacement. As in *Libognathus* (Small, 1997) but unlike the condition reported in more basal procolophonid taxa (e.g., Gow, 1977), the pattern of tooth replacement appears to be typically odd–even alternating. Resorption pits formed lingual to the functional tooth, involving the root of the tooth (which appears to be fused to the alveolar bone) and the lingual wall of the respective alveolus. As new teeth erupted they presumably pushed out their predecessors. The pattern of tooth replacement is most obvious on the dentaries; little detail is apparent in the upper jaws. In the left dentary, a large resorption pit is present posterolingual to the lower incisiform tooth. The second and fourth molariform teeth have deep lingual resorption pits that affect both the root of the tooth and the lingual alveolar bone. A shallow depression is present just lingual to the third molariform. In the right dentary, the functional lower incisiform was lost, and a large replacement pit posterolingual to it contains apparent remnants of an erupting replacement tooth. The second and fourth molariforms have deep lingual resorption pits involving both the root of the tooth and lingual alveolar bone.

Functional Inferences—Various authors (Gow, 1977; Carroll and Lindsay, 1985) have suggested that at least the adult individuals of *Procolophon* and related taxa with molariform teeth may have fed on tough, high-fiber plant material. How-

ever, it cannot be ruled out that the diet also included other food items (e.g., arthropods with resilient cuticles) that required a powerful bite. Aside from the molariform posterior teeth (Colbert, 1946), the skull and mandible of *Hypsognathus* exhibit various features that are consistent with herbivorous habits. The greatly enlarged orbitotemporal opening, deep “cheek” region of the skull, and the tall, posterodorsally projecting coronoid process of the lower jaw all indicate much more extensive development of *M. adductor mandibulae* than in *Procolophon* and related taxa and are suggestive of a powerful bite. The jaw joint is situated well below the level of the alveolar margin of the dentary, which would have increased the moment arm of the adductor jaw muscles and also may have generated a posterodorsally directed bite-force component. As in *Procolophon*, the skull is solidly ossified and effectively akinetic, which is consistent with feeding on tough food items (Carroll and Lindsay, 1985). However, the absence of cranial kinesis might also reflect burrowing habits, which have been inferred for *Procolophon* (Groenewald, 1991). Jaw motion was primarily orthal. The interdigitating arrangement of the maxillary and more posterior dentary teeth, with the lower teeth biting behind the upper, would have precluded significant mandibular fore-and-aft motion. The lappet-like ventral portions of the transverse processes of the pterygoids would have restricted extensive medial excursion of the mandibular rami. However, the shape of the jaw joint implies slight medial movement of the ramus during jaw closing. The structure of the jaw joint indicates a simple, hinge-like motion. The tooth rows of the dentary and maxilla are inset from the lateral margins of the skull and mandible. Carroll and Lindsay (1985) interpreted this feature as indicating the possible presence of a “cheek” in *Procolophon*. There definitely exists evidence for the presence of an oral vestibule lateral to the maxillary and dentary tooth rows in *Hypsognathus*, but this space may have been enclosed laterally by epidermal structures such as enlarged labial scales rather than a muscular cheek in life.

The spine-like bony processes on the quadratojugal of *Hypsognathus*, which are particularly prominent in adult individuals, may have served as passive anti-predator defenses (Colbert, 1946; Baird, 1986), as has traditionally been suggested for the superficially similar cranial spines in the extant lizards of the genus *Phrynosoma* (Ditmars, 1936). Alternatively, they may have been used for intraspecific display and combat.

PHYLOGENETIC RELATIONSHIPS OF *HYP SOGNATHUS*

In his synopsis of Procolophonidae, Ivakhnenko (1979:21) proposed a subfamily Leptopleuroninae for the reception of *Hypsognathus*, *Leptopleuron*, *Paoteodon* and ?*Sphodrosaurus*. Of the constituent genera, *Paoteodon* is based on non-diagnostic material (Li, 1989) and *Sphodrosaurus* is not a procolophonid (Sues et al., 1993). However, a suite of synapomorphies in the skull and mandible clearly supports recognition of a clade comprising *Hypsognathus* and *Leptopleuron* (as well as other, as yet poorly known taxa; Spencer, 1994). *Leptopleuron* (= *Telerpeton*) is known only from the Upper Triassic Lossiemouth Sandstone Formation of Scotland (Huene, 1912, 1920; Sues and Baird, 1998; Spencer, in press).

A detailed review of procolophonoid interrelationships is beyond the scope of this study and is currently in preparation by Spencer and Sues. Among the better-known taxa of Procolophonidae, *Hypsognathus* and *Leptopleuron* share the following derived character-states in the structure of the skull and mandible:

1. Prefrontal exposed on skull roof and side of snout (0) or confined entirely to orbital wall (1). The derived condition is only known in *Hypsognathus* and *Leptopleuron*. Furthermore,

the medial process of the prefrontal contacts the skull roof in both taxa.

2. Jugal with concave or sigmoidal ventral margin (0) or with convex, anteroventrally facing ventral margin (1). *Hypsognathus* and *Leptopleuron* share the derived character-state.

3. Epipterygoid with unossified dorsal end (0) or with dorsal end ossified and in contact with prootic and supraoccipital (1). The derived condition is only known in *Hypsognathus* and *Leptopleuron* (Spencer, in press). In *Procolophon* and *Tichvinskia* (Ivakhnenko, 1973), the dorsal end of the rod-like epipterygoid was not ossified.

4. Vertical portion of transverse flange of pterygoid moderately expanded (0) or forming broad lappet distally (1). *Hypsognathus* and *Leptopleuron* share the derived character-state.

5. Palatine and pterygoid with teeth (0) or devoid of teeth (1). *Hypsognathus* and *Leptopleuron* both lack teeth on the palatine and pterygoid.

6. Basisphenoid without (0) or with robust, vertical pillar of bone between basiptyergoid processes (1). The derived character-state is currently known only in *Hypsognathus* and *Leptopleuron* (Spencer, in press).

7. Basal tubera of basioccipital exposed ventrally (0) or ventrally sheathed by basisphenoid (1). *Hypsognathus* and *Leptopleuron* (Spencer, in press) share the derived condition.

8. Occipital condyle uniform (0) or tripartite (1). The derived character-state is known only in *Hypsognathus* and *Leptopleuron* (Spencer, in press).

9. Dentary with several incisiform anterior teeth (0) or with only a single incisiform tooth (1). *Hypsognathus* and *Leptopleuron* both have only a single incisiform tooth in each dentary.

10. Facet for jaw joint on articular more or less level with (0) or situated well below alveolar margin of dentary (1). *Hypsognathus* and *Leptopleuron* share the derived character-state.

The aforementioned synapomorphies clearly support a sister-group relationship between *Hypsognathus* and *Leptopleuron*. *Hypsognathus* differs from *Leptopleuron* in the possession of a number of autapomorphies, which form the basis for the diagnosis provided in this paper. However, some of the character-states listed as synapomorphies for *Hypsognathus* and *Leptopleuron* and autapomorphies for *Hypsognathus* may well have a wider distribution among the derived taxa of Procolophonidae, most of which are still poorly known. *Libognathus* (Small, 1997) from the Upper Triassic (Norian) Cooper Canyon Formation (Dockum Group) of Texas and an unnamed procolophonid from Late Triassic fissure-fillings in southwestern Britain (Fraser, 1986) appear to be closely related to *Hypsognathus* and *Leptopleuron*. *Libognathus* is definitely known only from a partial mandibular ramus. The leptopleuronine material cited by Fraser has yet to be described in detail. Finally, several partial skulls and associated postcranial remains of a procolophonid very similar to *Hypsognathus* have been collected from the Owl Rock Member of the Chinle Formation (Norian) of Arizona and are currently under study by F. A. Jenkins, Jr. and H.-D. S.

ACKNOWLEDGMENTS

We are greatly indebted to J. A. Gauthier and M. A. Turner (Yale University) for the loan of YPM 55831 and D. Baird (Pittsburgh) for providing excellent casts of YPM-PU 21752. R. L. Carroll (McGill University) kindly lent us a cast of the skeleton of *Leptopleuron* described by Huene (1920). We thank A. Brown for discovering NSM 998GF45.1 and bringing it to the attention of P. E. O. The manuscript benefitted from reviews by R. L. Carroll and B. J. Small. Financial support for this study was provided by NSERC operating grant OGP138129 to H.-D. S. and NSF grant EAR-98-14475 to P. E. O. and H.-D. S.

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Received 15 May 1999; accepted 15 November 1999.