

CRANIAL MORPHOLOGY OF THE LATE TRIASSIC SOUTH AMERICAN ARCHOSAUR *NEOAETOSAUROIDES ENGAEUS*: EVIDENCE FOR AETOSAURIAN DIVERSITY

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Abstract: The cranial anatomy of *Neoaetosauroides engaeus* Bonaparte, 1969 from the upper part of the Los Colorados Formation, western Argentina, is addressed herein. This description is based on material collected recently, which permits a complete restoration of the skull; previously, a partial lower jaw and premaxillary and maxillary fragments were the only cranial remains known. Unlike other aetosaurs for which the premaxillary dentition is known, in *N. engaeus* the upper tooth row extends anteriorly to reach near the expanded tip of the snout; this condition is not compatible with

the presence of a keratinous beak previously suggested for other aetosaurs. The conical shape of the teeth of *N. engaeus* differs from the slightly compressed teeth of *Desmotosuchus*, *Stagonolepis* and *Typhothorax*, and the distinctly recurved teeth of *Aetosaurus* and *Aetosauroides*. This diversity of dental morphology suggests a variety of food-item preferences among aetosaurs.

Key words: Aetosauria, Archosauria, cranial anatomy, Crurotarsi, *Neoaetosauroides*, South America, Triassic.

AETOSAURIA is a well-corroborated clade of quadrupedal armoured crurotarsan archosaurs. Members of this clade were characteristic components of continental ecosystems during much of the Late Triassic in North America, Europe, North Africa, India and South America (Heckert and Lucas 1999, 2000). In this last continent aetosaurs are represented by *Aetosauroides* Casamiquela from Brazil and Argentina, *Chilenosuchus* Casamiquela from Chile, and *Neoaetosauroides* Bonaparte from Argentina.

Neoaetosauroides engaeus, the only known species of the genus, was first described by Bonaparte (1969) based on material discovered in the upper part of the Los Colorados Formation, Ischigualasto-Villa Union Basin, western Argentina. Subsequently, he presented a more complete description of the species (Bonaparte 1971a), although the partial lower jaw and fragmentary premaxilla and maxilla were the only skull remains known at that time. Since then, several field parties have recovered additional specimens referable to *N. engaeus* from the same beds (Desojo 2002). A revision of the postcranial skeleton of this species was addressed recently by Desojo and Báez (2005), whereas its cranial anatomy is described herein.

In general, postcranial remains and osteoderms outnumber cranial elements among aetosaurian fossils. Several taxa, such as *Paratyphothorax*, *Chilenosuchus* and *Lucasuchus*, are represented by armour and postcranial bones only, the skulls being unknown. To date, reasonably complete, well-described skull materials are known for the aetosaurs *Desmotosuchus haplocerus* (Cope 1892; Small 1985, 2002), *D. smalli* (Parker 2003, 2005), *Stagonolepis robertsoni* (Agassiz 1844; Huxley 1859, 1875; Walker 1961; Gower and Walker 2002) and *Longosuchus meadei* (Sawin 1947; Parrish 1994), most of them from the Northern Hemisphere. Skull elements of other taxa have been reported but they are either fragmentary or remain undescribed.

The highly specialized morphology of the aetosaurian skull and the scarcity of information on its taxonomic diversity have made it more difficult to interpret the interrelationships among aetosaurs as well as some aspects of their mode of life. Hence, the comparative description of the cranial anatomy of *Neoaetosauroides engaeus*, one of the latest representatives of the aetosaurian clade, is an important contribution to understanding the evolutionary history of this intriguing group of crurotarsan archosaurs. Also, this information might provide evidence to clarify

the conflicting position of aetosaurs within Crurotarsi (Sereno and Arcucci 1990; Parrish 1993; Juul 1994; Gower and Wilkinson 1996; Brochu 2001; Gower and Walker 2002).

Institutional abbreviations. PVL, Palaeontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; PULR, Paleontología Museo de Ciencias Naturales, Universidad Nacional de La Rioja, La Rioja, Argentina; TTUP, Museum of Texas Tech University, Lubbock, TX, USA.

Anatomical abbreviations. a, angular; af, antorbital fenestra; afq, articular facet for the quadrate; ar, articular; bo, basioccipital; bpt, basipterygoid process; bt, basal tuber; ch, choana; d, dentary; deb, deep excavation of the basisphenoid; ec, ectopterygoid; emf, external mandibular fenestra; eo, exoccipital; ept, ectopterygoid process of the pterygoid; f, frontal; fe, fenestra exonarina; fm, foramen magnum; fo, foramen for fibers of the mandibular branch of the trigeminal nerve (V3); if, infratemporal fenestra; imf, internal mandibular fenestra; j, jugal; l, lacrimal; m, maxilla; mf, Meckelian foramen; mr, medial ridge; n, nasal; o, orbit; op, opisthotic; p, parietal; pa, prearticular; pb, palpebral bone; pf, postfrontal; pl, palatine; pm, premaxilla; po, postorbital; pp, paraoccipital process; ppt, palatal process of the pterygoid; pr, prootic; prf, prefrontal; prt, protuberance; psf, posterior surangular foramen; ptf, posttemporal fossa; pv, palatal vacuity; q, quadrate; qf, quadrate foramen; qj, quadratejugal; qpt, quadrate process of the pterygoid; rp, retroarticular process; sa, surangular; sf, supratemporal fenestra; soc, supraoccipital; sof, suborbital fenestra; sp, splenial; sq, squamosal; v, vomer; XII, foramen for hypoglossal nerve.

SYSTEMATIC PALAEOLOGY

ARCHOSAURIA *sensu* Gauthier and Padian, 1986

CRUROTARSI Sereno and Arcucci, 1990

AETOSAURIA Marsh, 1884

Genus NEOAETOSAUROIDES Bonaparte, 1969

Type species. *Neoetosauroides engaeus* Bonaparte, 1969.

Diagnosis. As for type species.

Neoetosauroides engaeus Bonaparte, 1969

Text-figures 1–5

1969 *Neoetosauroides engaeus* Bonaparte, p. 283, figs 7–8.

1971a *Neoetosauroides engaeus* Bonaparte, p. 87, figs 34–42.

1971b *Neoetosauroides engaeus* Bonaparte, p. 171, fig. 17.

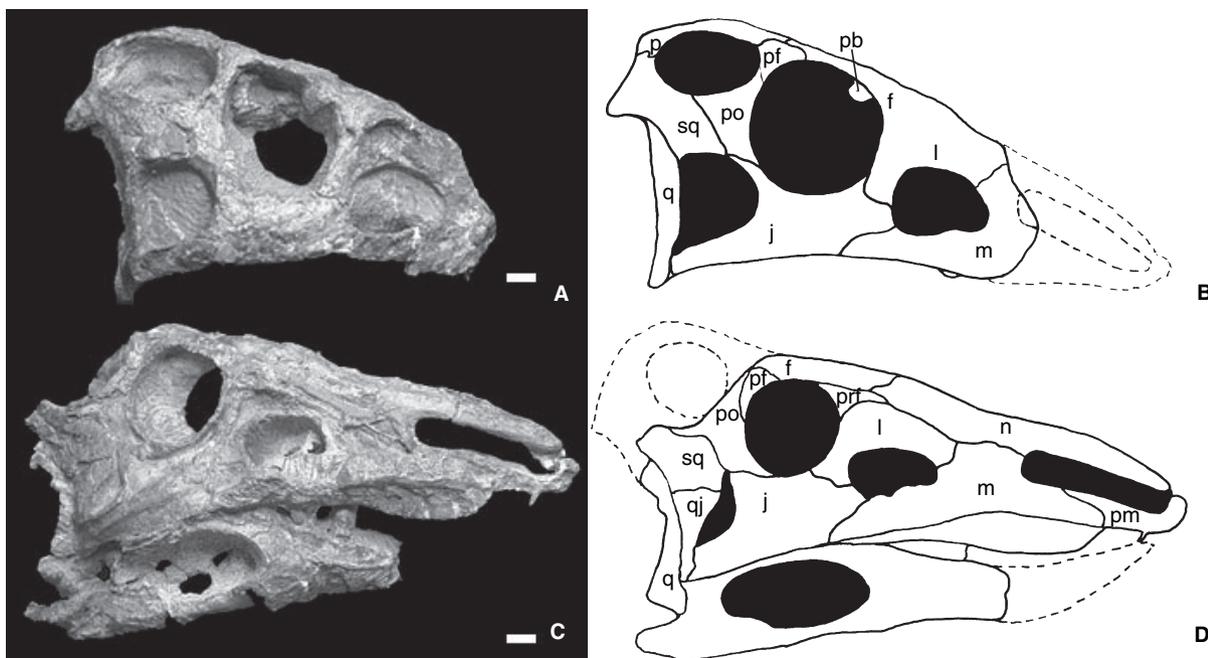
1978 *Neoetosauroides engaeus* Bonaparte, p. 300, fig. 139.

1982 *Neoetosauroides* Bonaparte, p. 108, fig. 4e.

2000 *Neoetosauroides engaeus*: Heckert and Lucas, p. 1555.

2005 *Neoetosauroides engaeus*: Desojo and Báez, p. 115, figs 2–3

Holotype. Partial lower jaw, articulated postcranial skeleton, dorsal armour, and ventral osteoderms of an adult individual (PVL 3525).



TEXT-FIG. 1. Skull of *Neoetosauroides engaeus* Bonaparte. A–B, photograph of PVL 5698 in right lateral view and interpretive line drawing. C–D, photograph of PVL 4363 in right lateral view and interpretive line drawing. Note that the antorbital and infratemporal openings in PVL 5698 have been enlarged by poor preparation. Scale bars represent 1 cm.

Type locality. Cabecera del Río Mañero, km 126, Provincial Route 26, La Rioja Province, Argentina (erroneously cited as Quebrada de los Jachaleros, El Salto, San Juan by Caselli *et al.* 2001; Arcucci *et al.* 2004).

Type horizon. Upper part of the Los Colorados Formation (Upper Triassic).

Paratypes. Fragmentary premaxilla and maxilla with teeth, vertebrae, and osteoderms (PVL 3528); incomplete dorsal and ventral armours, and vertebrae preserved as impressions (PVL 3842). These specimens are from the type locality and stratigraphic unit, although PVL 3842 is from a higher horizon than the holotype and PVL 3528.

Referred cranial material. PVL 4363 (km 142 Provincial Route 26, La Rioja), incomplete articulated skull with lower jaw exposed in right lateral aspect and associated paramedial and lateral osteoderms; PVL 5698 (km 140 Provincial Route 26, La Rioja), incomplete articulated skull and associated cervical vertebrae and paramedial osteoderms; PVL 5732 (km 142 Provincial Route 26, La Rioja), fragmentary left portion of lower jaw, and cervical and dorsal vertebrae; PULR 108 (Quebrada de los Jachaleros, La Rioja), incomplete articulated skull with lower jaw, articulated left femur and epipodials and impression of pes. All these specimens are from the upper part of the Los Colorados Formation.

Revised diagnosis. Medium-sized aetosaur having a premaxillary tooth row that nearly reaches the shovel-like premaxillary anterior end, upper dentition composed of four premaxillary and eight maxillary relatively conical teeth; premaxilla lacking long posterior process that

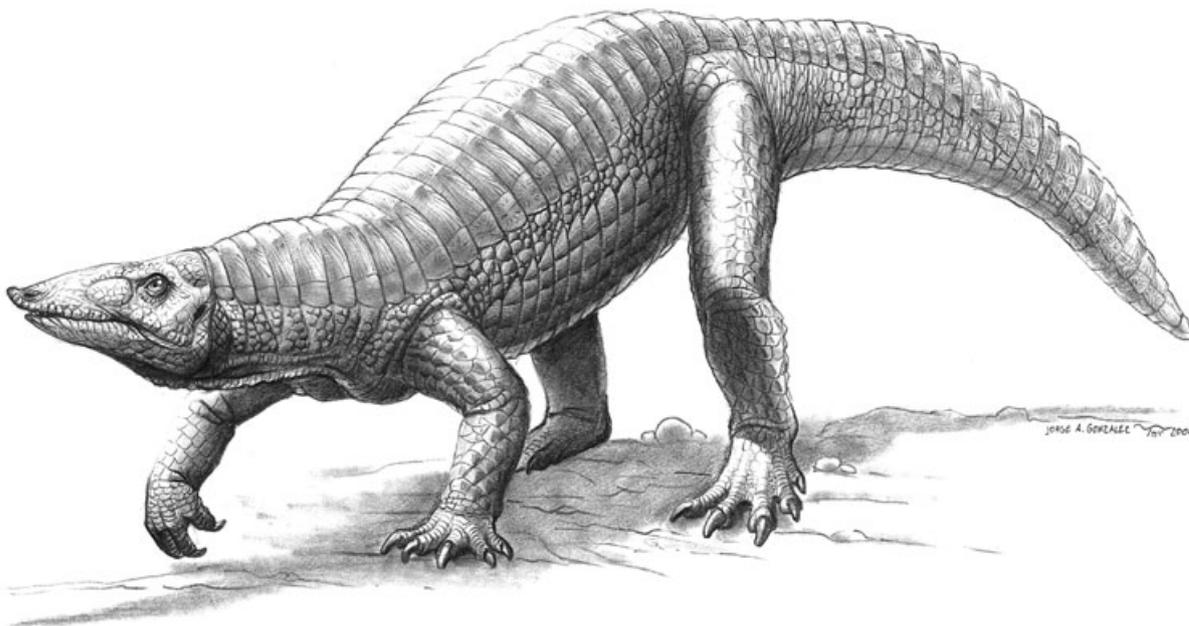
underlies vomer, elongate choana and suborbital fenestra of similar size, coracoid bearing a postglenoid process, cervical vertebrae bearing neural arches lower than height of centra and ventral keels on centra; socket on calcaneum for articulation with astragalus shallow, lacking distinct edge; metatarsal V with two phalanges; osteoderms with weakly incised ornamentation, caudal armour formed by 26 rows of osteoderms.

Description

The description presented herein is composite owing to the lack of a single complete skull; it is based mainly on specimens PVL 4363 and 5698 and PULR 108 (Text-fig. 1). Additional information is supplied by PVL 3525 and 3528. Features of the anterior snout are observable in PVL 4363, which consists of an endocast of the right side of the skull; in this specimen a posterior portion of the lower jaw has been preserved articulated with the rest of the skull (Text-fig. 1C–D). Although the braincase of PVL 5698 is nearly complete, thus providing significant information on this cranial region, further preparation of this specimen might reveal finer details. The palatal complex is well preserved as an endocast in PULR 108.

In dorsal view, the skull is triangular with a relatively narrow base and pointed apex; it is high and small relative to the postcranial skeleton, as the restoration of the animal shows (Text-fig. 2). The estimated length of the skull based on the three most complete specimens is around 20 cm, whereas that of the entire skeleton is 200 cm (Desojo and Báez 2005).

Skull roof. The nasal is the longest bone of the skull roof, accounting for over half of its length (Text-figs 1, 3). Anteriorly, this bone contacts with the premaxilla and forms the dorsal margin of the large opening for the external nares, or fenestra



TEXT-FIG. 2. Life restoration of *Neoaetosauroides engaeus* Bonaparte.

exonarina. Laterally, and from front to back, the nasal is in contact with the maxilla, lacrimal and prefrontal, whereas posteriorly it articulates with the frontal.

The frontal has an overall rectangular shape and, together with the prefrontal and postfrontal, forms most of the dorsal margin of the orbit. The frontal meets the nasal at the level of the posterior quarter of the antorbital fenestra; the suture between these bones at first is inclined forward from the midline; hence, an angle with the anterior apex is determined (Text-fig. 3B). The suture between the frontal and the parietal is irregular, unlike that between the frontal and the nasal; however, both are complex sutures with irregularly rugose textures on their surfaces (e.g. PVL 4363), a type of suture termed lamellae by Kathe (1999).

The parietal is short and quadrangular. It forms most of the dorsal margin of the supratemporal fenestra (Text-fig. 3A–B). The posterior portion of the parietal bears a thick overhanging flange to accommodate the first pair of osteoderms (e.g. PVL 5698), a feature that characterizes aetosaurs. Lateral to this region, the parietal projects lateroventrally to reach the dorsal portion of the squamosal. The dorsal surfaces of parietals and frontals are distinctly sculptured with short ridges and grooves.

Several openings, fenestrae for the external nares, antorbital fenestrae, orbits, supratemporal and infratemporal fenestrae, occur in the dorsal and lateral aspects of the skull (Text-fig. 3A–B). Additionally, the palate is perforated by the openings for the internal nares, palatal vacuities and suborbital fenestrae (Text-fig. 3C), whereas each of the lower jaws bears a mandibular fenestra (Text-fig. 4B–C). The fenestra exonarina is oval and lies almost parallel to the sagittal plane; it is the longest of the skull openings. The antorbital fenestra, located at the midlength of the skull, is slightly smaller than the round orbit. Both temporal fenestrae are exposed laterally at the posterior third of the skull. Unlike the round and relatively large supratemporal fenestra, the infratemporal fenestra has a triangular outline with an anterior apex (PVL 4363, PULR 108 and PVL 5698). It is noteworthy that the shape of this latter fenestra was misinterpreted by Heckert and Lucas (1999) owing to the inadequate preparation of the single specimen available to them (Text-fig. 1A–B). A small hole on the left side of the occipital region of the only specimen in which this region is preserved (PVL 5698) is interpreted as the left posttemporal fenestra.

The skull is high and triangular in lateral view owing to the gently sloping cranial roof. The anterior end of the premaxilla bears a mediolateral expansion that forms, with that of the contralateral bone, the distinctive shovel-like structure of the aetosaur snout. The slender premaxilla surrounds the anterior half of the ventral margin of the nasal opening. The anterior part of this bone is edentulous and contacts the nasal, whereas the posterior part bears four teeth. At the level of the second tooth a small protuberance is visible on its dorsal surface. The suture with the maxilla is posterodorsally orientated.

The maxilla forms the posterior and posteroventral margins of the fenestra exonarina and most of the anteroventral margin of the antorbital fenestra, making up the bony bridge that separates these openings. Dorsally, the maxilla contacts the nasal and lacrimal, whereas posteriorly it meets the jugal and medially the palatine. The maxilla bears eight teeth along the anterior three-

quarters of its length. On PVL 4363 a small cavity on the internal surface of the right maxilla is interpreted as the pneumatic accessory cavity.

The lacrimal is thin and narrow and forms part of the anterior rim of the orbit. Ventrally, it forms the posterodorsal margin of the antorbital opening and posteroventrally it contacts the jugal. The nasolacrimal canal runs dorsomedially over the antorbital cavity and within the lacrimal to open near the contact of this latter bone with the prefrontal. Anteriorly, the nasolacrimal canal extends to reach the fenestra exonarina as Walker (1961) suggested for *Stagonolepis*.

The prefrontal is a small, thick triangular bone. Internally, this bone, together with the jugal, makes up the anterior wall of the orbit. The dorsal margin of each prefrontal extends anteriorly slightly in front of the suture between the nasal and the frontal. Adjacent to this latter bone, a curved palpebral bone, or supra-orbital, is preserved on both sides of the skull (PVL 5698).

The postfrontal and the postorbital form the postorbital bar between the orbit and the supratemporal fenestra. The former bone has an extensive contact with the parietal, unlike the contact between the latter and the postorbital.

The jugal extends from the antorbital fenestra to the infratemporal fenestra to form the posterior part of the ventrolateral margin of the skull. Anteriorly, the jugal contacts the maxilla and, thus, forms the posteroventral edge of the antorbital fenestra. Dorsally, the jugal meets the lacrimal anteriorly and the postorbital posteriorly, whereas between these contacts it forms the ventral rim of the orbit. The posterior margin of the jugal sutures ventrally with the quadratojugal, whereas more dorsally it is emarginated and bounds the triangular infratemporal fenestra.

The squamosal is a laminar bone in contact anteriorly with the postorbital and ventrally with the quadratojugal; posteriorly it meets the large quadrate. Dorsally, the squamosal forms part of the posteroventral border of the supratemporal fenestra and sutures with the parietal. The squamosal laterally invests a horn-like posterior projection, the paroccipital process (Text-fig. 3A).

The quadratojugal forms the posterior border of the infratemporal fenestra. Ventrally this bone sutures with the jugal whereas posteriorly it contacts the quadrate, which is pierced by the quadrate foramen.

Braincase. The braincase is preserved in PVL 5698 only, although it was somewhat altered during preparation prior to the present study. The absence of sutures between exoccipitals and opisthotics indicates that these bones are fused to each other (Text-fig. 4A). The former bones form the lateral borders of the foramen magnum and the dorsal surfaces of the occipital condyles. Ventrally each exoccipital sutures with the basioccipital, and dorsally with the supraoccipital. A distinct foramen, presumably for the hypoglossal nerve (XII), occurs at each side of the foramen magnum.

The opisthotic has a laterally projecting, wing-like structure that unites with the prootic to form the paroccipital process. Dorsally, the opisthotic sutures with the supraoccipital, and ventrally it partially overlaps the pterygoid and the pterygoid wing of the quadrate. The region of the contact between the opisthotic and the parietal is damaged in the single specimen

available for this trait. Ventrally, the opisthotic forms part of the posterior border of the fenestra ovalis and the metotic foramen (IX–X–XI), whereas anteriorly is in contact with the prootic.

The dorsal rim of the foramen magnum is partially formed by the flat and triangular supraoccipital. Two protuberances are visible close to the dorsal rim of the foramen magnum. These structures are associated with the proatlas in PVL 5698; therefore, we interpret them as a modification of the supraoccipital for the reception of the proatlas. In addition, a medial ridge occurs on the supraoccipital, probably for the insertion of the nuchal ligament of the paroccipital process (Text-fig. 4A).

The basioccipital extends ventrally to the foramen magnum and forms the major part of the occipital condyle, the articular facet of which is circular and ventrally sloping. Ventrally, the basioccipital, together with the basisphenoid, forms the basal tubera, a pair of ventrally projecting knobs for the attachment of the subvertebral muscles (Romer 1956). One of these protuberances, incompletely preserved, is visible on the right side of PVL 5698. The suture between the basioccipital and basisphenoid is located in a deep groove that extends through the tubera

(Text-fig. 3C). Dorsally, the basioccipital, together with the opisthotic and basisphenoid, forms the edges of the fenestra ovalis and the metotic foramen. The oval foramen housed the mandibular branch (V3) of the trigeminal nerve, which includes sensory fibres from the skin of the head and mouth as well as somatic motor fibres to muscles of the mandibular arch (Kardong 1998). Nerves IX, X and XI and the jugular vein emerged through the metotic foramen (Romer 1956).

The basisphenoid forms the basiptyergoid processes anteriorly, whereas posteriorly it participates in the formation of the basal tubera. Anterior to the latter structures and posterior to the basiptyergoid processes, a distinct rounded depression is present (Text-fig. 3C). Dorsally, the basisphenoid forms the posterior border of the hypophyseal fenestra on each side of the braincase.

The parasphenoid is a thin dermal bone that invests the floor of the braincase but it is only visible through the small palatal vacuity owing to the extensive contact between both pterygoids. The absence of a suture between the parasphenoid and the basisphenoid suggests that these elements are fused.

The prootic contacts the parietal dorsally, the anterior portion of the opisthotic posteriorly, and the laterosphenoid anteriorly. Near the suture with this latter bone, the prootic bounds part of the foramen for the trigeminal nerve (V).

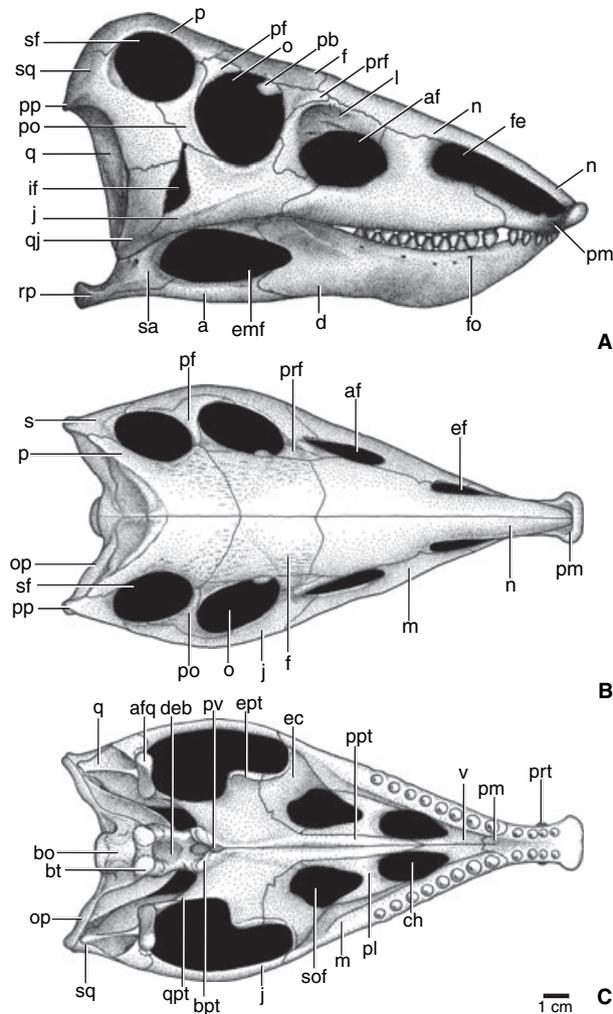
The laterosphenoid meets the parietals near the parietal-frontal suture. Ventrally, the laterosphenoid is in contact with the basisphenoid, and posteriorly with the prootic. The large foramen for the optic nerve (II) is visible on the ventromedial margin of the laterosphenoid.

Palatal complex. The complete palatal region is preserved in PULR 108; also, the anterior portion is present in PVL 4363 and the posterior part in PVL 5698. The palate is perforated by the large choanae anteriorly and the suborbital fenestrae posteriorly (Text-fig. 3C).

The vomers are thin and contact one another along the midline. They extend from the premaxillae, anteriorly, to the anterior ends of the pterygoid palatine processes, posteriorly. The prechoanal portions of these bones are relatively wide and remain mostly exposed in ventral view because only their anterior parts are invested ventrally by the premaxillae. These latter bones reach to the level of the space between the first and second maxillary teeth. The narrow posterior portions of the vomers form a bony bridge that separates the anterior halves of the choanae.

The palatine is an H-like bone that forms the major part of the posterior margin of the choana. The transverse bar separates the choana from the suborbital fenestra, the lateral bar contacts extensively with the maxilla, whereas the medial bar is in contact with the pterygoid and the ectopterygoid (Text-fig. 3C).

The triradiate pterygoids are in contact with each other along the midline. Their narrow anterior, or palatine, process, together with the one from the other side, forms a tongue that separates the right and left palatine bones and reaches the vomers anteriorly. The lateral, wing-shaped, process of each pterygoid projects ventrally and contacts the ectopterygoid anteriorly. The posterior process, termed the quadrate process, consists of a bony lamina that articulates with the inner (medial) side of the quadrate pterygoid process and contacts the anterior margin of the basiptyergoid process (Text-figs 3C, 4A).



TEXT-FIG. 3. Restored skull of *Neoaetosauroides engaeus* in A, right lateral, B, dorsal, and C, ventral views.

The ectopterygoid forms the posterior wall of the suborbital fenestra. Laterally, this bone forms a bar-shaped process that meets the jugal.

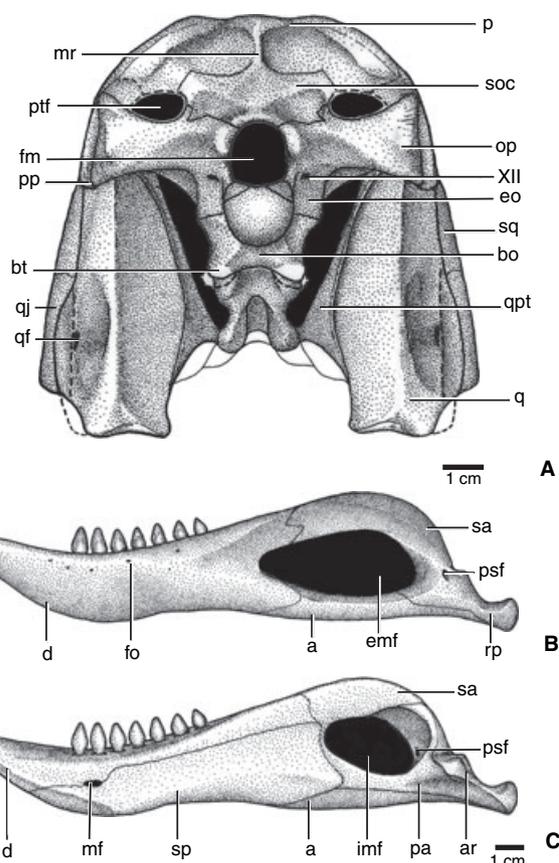
The quadrate is a high, narrow element, which is triangular in cross-section. Dorsally, it articulates with both the paroccipital process, medially, and the squamosal, laterally (Text-fig. 4A). Additionally, the quadrate forms a lamina that dorsally contacts the squamosal and ventrally the quadratojugal. The articular facet of the pars articularis quadrati is medially concave and laterally convex, and is orientated perpendicularly with respect to the sagittal plane of the skull.

The dentition is confined to the premaxillary, maxillary and dentary margins, and the tooth implantation is thecodont, as in other archosaurs. The upper dentition is incomplete in all specimens examined; however, it was possible to estimate the total number of premaxillary and maxillary teeth based on the number of alveoli. The most anterior tooth occurs at level of the nasal-premaxilla suture (Text-fig. 3A–C). Posteriorly, the upper tooth row extends up to the level of the anterior margin of the suborbital fenestra. The upper dentition is composed of four premaxillary and eight maxillary teeth. The teeth are large and have a conical overall shape, although a slight constriction separates the low cylindrical basal portion ('neck') from the distal portion. The premaxillary teeth are smaller than those on the maxilla and dentary, and increase slightly in size posteriorly. The maxillary teeth show size heterodonty, the anterior ones being the largest of the upper row.

In general, the archosaur lower jaw is moderately long, slender, and highly conservative in the presence of the mandibular fenestra, absence of the coronoid process, and number (one endochondral and six dermal elements) and general disposition of the bones (Romer 1956). The aetosaur mandible is no exception to this overall morphological pattern.

In *Neoaetosauroides* the lower jaw is sharp, somewhat short and high in comparison with that of other aetosauroids, but with their characteristic slipper shape (Text-fig. 4B–C). It is laterally compressed; however, at the level of the anterior edge of the mandibular fenestra it becomes broader. In lingual view, the symphyseal area is slender, posteroventrally sloping and long (one-third of the jaw length). The glenoid cavity is located slightly ventral to the dentary tooth row. The external mandibular fenestra is visible posterolaterally; this opening is relatively large with respect to that of other aetosauroids, its length/height ratio being approximately 2:5. The external mandibular fenestra of the holotype (PVL 3525) depicted by Bonaparte (1969, fig. 7) is somewhat larger than the same structure in the present reconstruction, as the size of this fenestra was exaggerated during technical preparation.

The dentary forms more than half of the labial surface of the jaw and bears the lower dentition. The anterior portion of this bone narrows into an edentulous tip (e.g. PULR 108). Lingually, the dentary has an extensive contact with the splenial; a small Meckelian foramen is visible at the anterior quarter of the dentary-splenial suture length. Ventral to the tooth row, there are several small foramina for fibres of the mandibular branch of the trigeminal nerve (V3). Specimen PVL 4363 preserves the inner cast of the channel that housed soft structures, such as the mandibular branch of the trigeminal nerve. In labial view,



TEXT-FIG. 4. Restored skull and lower jaw of *Neoaetosauroides engaeus* Bonaparte in A, in occipital, B, labial and C, lingual views.

the dentary forks posteriorly into two branches of equal length, which form the anterior margin of the external mandibular fenestra. The dorsal branch articulates with the surangular, whereas the ventral one contacts the angular. The angular is a narrow trough-like bone that forms the floor of the external mandibular fenestra. Labially, the angular is posteriorly in contact with the surangular, whereas lingually it meets the splenial anteriorly, and the prearticular dorsally. The surangular forms the dorsal margin of the external and internal mandibular fenestrae. In lingual view, this bone contacts the prearticular anteriorly, and the articular posteriorly. This latter element forms most of the glenoid cavity, as well as a posteromedial projecting shelf for the attachment of the depressor mandibulae muscle. This latter structure, termed retroarticular process, is covered laterally by the surangular. The surangular is perforated by a channel for a branch of the inferior alveolar nerve, which is a derivative of the mandibular nerve. Foramina for the entrance and exit of this branch are visible on the outer and inner sides of the surangular, respectively (Text-fig. 4B–C). The prearticular, only exposed in lingual view of the jaw, forms the ventral margin of the internal mandibular fenestra. This bone sutures with the articular along the retroarticular process.

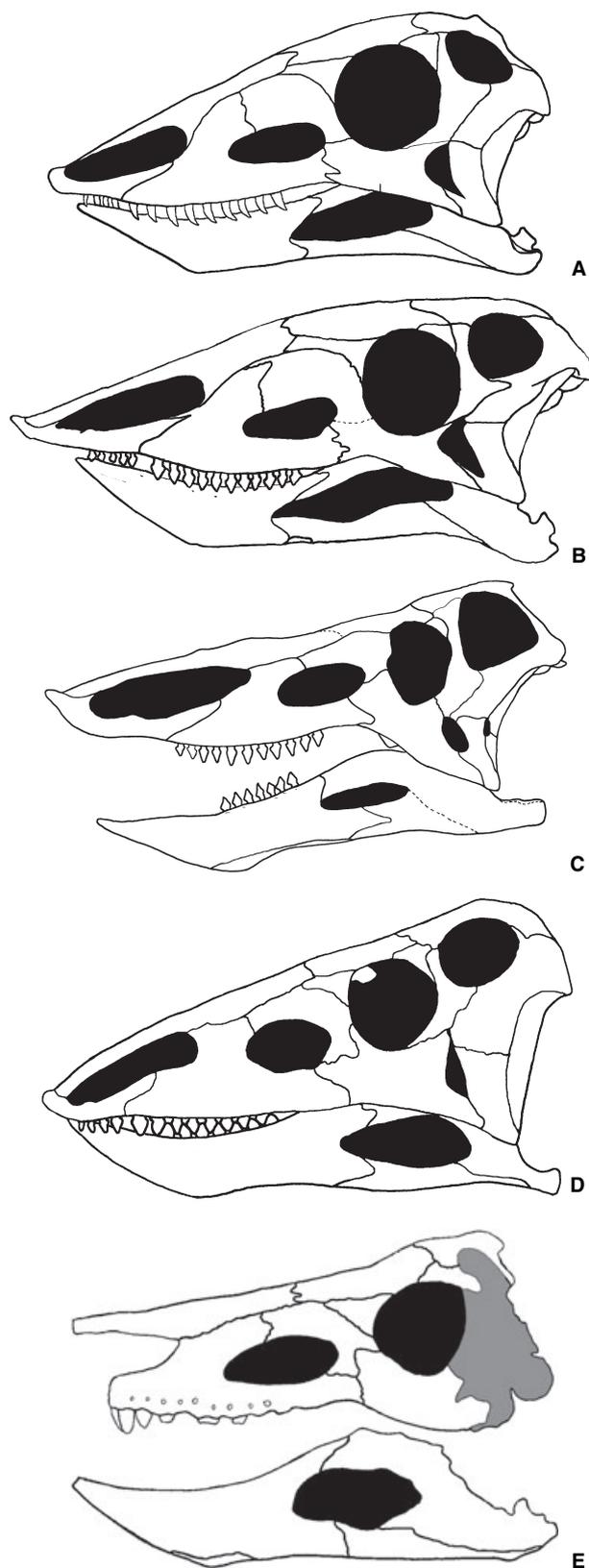
A complete row of seven alveoli is preserved on the right dentary of the holotype (PVL 3525). Specimen PULR 108 preserves a few teeth on the dentaries, the shape of which is similar to that of those of the upper dentition. These teeth gradually decrease in size posteriorly. The lower teeth, as the upper teeth, lack denticles and wear facets.

DISCUSSION

The cranial remains of *Neoaetosauroides* described herein provide relevant information about anatomical diversity among aetosaurs, albeit within their highly characteristic overall skull pattern. The skull of *Neoaetosauroides* is comparatively shorter and higher than in other aetosaurs for which this skeletal part is known (Text-fig. 5). In addition, the lower jaw articulation is located at a level only slightly below that of the dentary tooth row, whereas this joint is usually more ventral in other aetosaurian taxa (Parrish 1994). It is also noteworthy that, in contrast to other aetosaurs, in *Neoaetosauroides* the upper tooth row extends anteriorly to reach near the expanded premaxillary tip. In *Stagonolepis* and *Aetosaurus* (Walker 1961) a large anterior portion of the premaxilla lacks teeth, and in *Desmatosuchus* and *Typothorax* (Small 2002; Parker 2005) premaxillary teeth are absent altogether. The condition in *Aetosauroides* is unknown owing to the lack of preservation of the anterior portion of the skull in all available specimens (Desojo 2005).

The teeth of *Neoaetosauroides* resemble those of *Longosuchus* in their conical shape, although a proximal neck is not evident in the teeth of the latter taxon. This general tooth morphology differs from the slightly compressed teeth of *Desmatosuchus*, *Stagonolepis* and *Typothorax*, and the distinctly recurved teeth of *Aetosaurus* and *Aetosauroides* (Text-fig. 5). Moreover, unlike *Desmatosuchus*, *S. robertsoni* and possibly *Typothorax*, *Neoaetosauroides* does not show evidence of dental wear facets. This diversity of dental morphology suggests a variety of food-item preferences among aetosaurs (Small 2002; Desojo 2003).

The nasals of *Neoaetosauroides* and *Aetosaurus* are relatively longer than those of *Stagonolepis* and *Longosuchus*. In the first two taxa the sutures between these bones and the frontals are located at the level of the posterior quarter of the antorbital fenestrae. These sutures occur further anteriorly in *Stagonolepis* and *Longosuchus* as their position coincides with the midlength of the latter openings. *Neoaetosauroides*, however, resembles *Stagonolepis* and



TEXT-FIG. 5. Diversity in cranial morphology among aetosaurs. A, *Aetosaurus* (modified from Walker 1961). B, *Stagonolepis* (modified from Walker 1961). C, *Desmatosuchus* (modified from Small 2002). D, *Neoaetosauroides*. E, *Longosuchus* (modified from Parrish 1994). Not to scale.

Aetosauroides in having a nasal–frontal suture at first inclined forward from the midline (Walker 1961). As in *Aetosaurus*, palpebral bones occur next to the frontals. However, in *Neoaetosauroides* a single element is present in each orbit whereas in *Aetosaurus* a set of three bones forming an arch occurs on each side (Walker 1961). These dermal protecting bones have been described in many archosauromorphs and may have been common in aetosaurs, although as these elements are not firmly attached to the skull their preservation is unlikely.

The depression on the ventral surface of the basisphenoid between the basal tubera and basiptyergoid processes, medial pharyngeal recess *sensu* Witmer (1997a), is present not only in *Neoaetosauroides* but also in all known aetosaurs and many archosauromorphs (Desojo and Heckert 2004). However, the shape and depth of this recess varies even in closely related species (e.g. *Desmatosuchus haplocerus* and *D. smalli* Parker, 2005). In *Neoaetosauroides* it is hemispherical and relatively large, resembling the depression in *Aetosauroides*. An elongated and smaller cavity was observed in *Stagonolepis* and *Coahomasuchus* (Walker 1961; Heckert and Lucas 1999). As commented on by previous authors (Gower and Walker 2002; Small 2002; Desojo and Heckert 2004), the presence of this depression is a synapomorphy not of an aetosaurian subclade, as suggested by Parrish (1994) and Heckert and Lucas (1999), but rather of a more inclusive clade.

The exceptional preservation of the palatal region has allowed us to discern the extent and relationships of the conforming bones in *Neoaetosauroides*, although comparisons with other aetosaurs are limited owing to the few taxa for which this region is known. The anterior palate differs strikingly from that of both *Desmatosuchus* and *Stagonolepis* in lacking the premaxillary posterior processes that in these latter taxa invest the ventral surface of the vomers extensively. In turn, the vomers extend back to form only the anterior half of the bar that separates the choanae instead of forming most of it, as in *Desmatosuchus* and *Stagonolepis*. In *Neoaetosauroides* the suborbital fenestrae are comparatively large, their anteroposterior length being nearly that of the choanae. By contrast, the suborbital fenestrae are notably smaller than the choanae and more rounded in shape in *Desmatosuchus* and *Stagonolepis*. The ample-sized suborbital fenestrae also characterize the palate of many crurotarsans (Bonaparte 1978; Witmer 1997b; Sulej 2005) and might be a plesiomorphic feature.

The oval external mandibular fenestra of *Neoaetosauroides* recalls that of *Longosuchus*, but it is unlike the narrower opening that pierces the lateral surface of the lower jaw in *Aetosaurus*, *Coahomasuchus*, *Desmatosuchus* and *Stagonolepis*. As in *Desmatosuchus* and *Longosuchus*, the retroarticular process of the lower jaw of *Neoaetosauroides*

is posteromedially orientated. This process, which was the point of attachment for muscles that open the jaw, is rotated in *Stagonolepis* and *Aetosaurus* and, hence, it is more ventrally directed in these taxa. When articulated to the skull, the mandible extends well forward in *Neoaetosauroides* and *Aetosaurus*, the anterior tip extending to the level of the shovel-like process formed by the premaxillae in these taxa (Text-fig. 4B–C). Instead, in *Stagonolepis* and *Desmatosuchus* the anterior end of the lower jaw does not extend so far forward and, thus, an edentulous portion of the snout projects in front of the latter.

Although the functional interpretation of many distinctive features of the cranial architecture of *Neoaetosauroides* is outside the scope of this paper, it is evident that at least some of these features reflect changes in associated musculature with respect to other aetosaurian taxa. Moreover, some features in which other aetosaurs differ from *Neoaetosauroides*, such as the edentulous anterior end of the upper jaw, have been related to a distinctive feeding habit in this group relative to early archosaurs and to the presence of a keratinous beak (Parrish 1994). This South American species does not seem to conform to this stereotype, its morphology suggesting that it probably had differing dietary adaptations. In this regard, the diverse tooth morphology and varied evidence of wear amongst aetosaurian taxa, as noted above, also provides indication of a wider range of dietary preferences in this group than previously suspected. However, an unambiguous interpretation of these features in the context of aetosaurian evolution calls for a well-supported phylogenetic hypothesis. Several hypotheses of interrelationships, mostly based on osteoderm characters, have been proposed in the last 10 years (Parrish 1994; Heckert *et al.* 1996; Heckert and Lucas 1999; Harris *et al.* 2003). *Neoaetosauroides* does not appear as a highly derived member of the group in any of the phylogenetic topologies proposed, despite being one of the youngest representatives, but its relationships as well as those of other aetosaur taxa are far from resolved. Several recent studies (Martz 2002; Parker 2003; Desojo 2005) have focused on the skeletal anatomy, thus providing a promising source of data for future parsimony analyses.

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