

The postcranial skeleton of *Neoaetosauroides* (Archosauria: Aetosauria) from the Upper Triassic of west-central Argentina

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Abstract. The postcranial skeleton of *Neoaetosauroides* (Archosauria: Aetosauria) from the Upper Triassic of west-central Argentina. The postcranial skeleton of the aetosaur *Neoaetosauroides* Bonaparte, based on previously studied specimens and additional material, is described herein. The new material consists of proatlases, cervical vertebrae, and appendicular dermal scutes collected in the Los Colorados Formation, Ischigualasto-Villa Unión Basin. All these materials are compared with those of other aetosaur taxa and functionally significant characters of the pelvic girdle and hindlimbs are in particular discussed. This study reveals a great anatomical diversity (*e.g.*, differences in degree of pelvic expansion, femoral flexure, and crural and tarsal morphology) and suggests that Aetosauria might have included semi-erect and erect forms. This possible spectrum of locomotor postures, together with their wide size range, support previous propositions of more varied lifestyles among aetosaurs than traditionally recognized.

Resumen. Se describe el esqueleto postcraniano del aetosaurio *Neoaetosauroides* Bonaparte en base a material edito y adicional. El nuevo material consiste en proatlases, vértebras cervicales y placas dérmicas apendiculares colectados de la Formación Los Colorados, Cuenca de Ischigualasto-Villa Unión. Todos estos materiales se comparan con los de otros taxones de aetosaurios, y se discuten particularmente caracteres de la cintura pélvica y miembros posteriores considerados de importancia funcional. Este estudio revela una gran diversidad anatómica (*e.g.*, diferencias en el grado de expansión pélvica, curvatura del fémur, morfología del *crus* y tarso) y sugiere la existencia en Aetosauria de formas semierectas y erectas. Este posible espectro de posturas locomotoras, junto a la amplitud de su rango de tamaño, sustenta propuestas previas de una mayor diversidad de modos de vida entre los Aetosaurios que la reconocida tradicionalmente.

Key words. Archosauria. Aetosauria. *Neoaetosauroides*. Triassic. Ischigualasto-Villa Union Basin. Los Colorados Formation. Argentina.

Palabras clave. Archosauria. Aetosauria. *Neoaetosauroides*. Triásico. Cuenca Ischigualasto-Villa Unión. Formación Los Colorados. Argentina.

Introduction

The aetosaurs are quadrupedal armored archosaurs from the Upper Triassic and their Northern Hemisphere record is particularly abundant, as much in terms of represented taxa and in numbers of specimens. However, recent findings in South America have been extending our knowledge of this group in this continent, initially based only on records from Argentina (Casamiquela, 1980; Bonaparte, 1969, 1971a). To these have been added material from Chile (Casamiquela, 1980; Desojo, 2001, 2003), Brazil (Lucas and Heckert, 2001; Da Rosa y Leal, 2002), and additional specimens from Argentina (Desojo, 2002). Consequently, the diversity of forms known from the continent has been increased.

The first mention of this group in South America is based on original materials from continental sequences of the Ischigualasto- Villa Union Basin, in the western margin of Argentina. These remains, from the Ischigualasto Formation, were considered to represent the new genera *Aetosauroides* and *Argentinosuchus* (Casamiquela, 1960). Later, these materials were described in greater detail (Casamiquela, 1961, 1967). Other aetosaurs were later discovered in the Los Colorados Formation, which lies unconformably on the Ischigualasto Formation (Bossi and Stipanovic, 2002). The first records from the Los Colorados Formation date from the 1960s, during which Bonaparte and collaborators conducted much fieldwork in the Sierra Morada Mountains, La Rioja Province. These specimens were assigned to another new taxon, *Neoaetosauroides engaeus* (Bonaparte, 1969, 1971b, 1978). From this record, combined with those of basal dinosaurs, archosaurs, and therapsids, Bonaparte (1966, 1971a, 1997) recognized a faunal association different from the well-known one in the underlying Ischigualasto Formation. Due to the abundance of prosauropods and to the presence of presumably derived characteristics in *Neoaetosauroides*, Bonaparte initially proposed the age of the Los Colorados Formation as “Norian-Rhaetian”. In 1973 he considered that the upper portion of the Los Colorado Formation, which contains among other faunal elements the aetosaur *Neoaetosauroides*, represents the upper “Coloradense Reptile Age” attributed to the Norian-Rhaetian (Bonaparte, 1973:125). Later new materials of aetosaurs were collected from the Los Colorados and deposited in the Museo de Ciencias Naturales de la Universidad Nacional de La Rioja (Caselli *et al.*, 2001).

In the present work the postcranial remains of the holotype of *Neoaetosauroides engaeus* Bonaparte is redescribed as well as new postcranial material and appendicular dermal plates that are assignable to the same species. Also discussed in particular are characters of the pelvic girdle and the hind limbs which are of functional importance in the literature.

Geologic context and origin of the materials

The Ischigualasto-Villa Union Basin constitutes an elongate extensional depression with a noticeable halfgraben geometry (Milana and Alcober, 1995) that was developed between the provinces of San Juan and La Rioja. The sedimentary filling consists of continental sediments of Triassic age, those that have been reunited in several stratigraphic units: the Talampaya and Tarjados Formations (Romer and Jensen, 1966), and the Grupo Agua de la Peña (Bossi, 1971). This last unit is integrated, from bottom to top, by the Chañares, Ischichuca, Los Rastros, Ischigualasto and the Los Colorados Formations (Groeber and Stipanovic, 1953).

The Los Colorados Formation includes a succession of reddish sandstone beds with tabular and parallel lamination, with reddish limestone interleaves, and whose depositional environment has been interpreted as a meandering fluvial type with fine floodplain facies (Kokogian *et al.* , 2001; Caselli *et al.*, 2001) or fluvial-like ephemeral

one (Lopez Gamundi *et al.*, 1989). The sequence demonstrates a progressive aridization of the land (Limarino *et al.*, 1990).

| The outcrops of this unit are all on the flanks of the Sierra Morada ~~mountain range~~, Rajado hill, Bola hill and in one narrow strip to the west of the Mogote del Gualo in the Campo de Talampaya ([figure 1](#)). The thickness in this last zone is only 100 m, whereas it varies between 900 and 1,000 m in the Ischigualasto-Ischichuca zone (Stipanovic and Bonaparte, 1979; Casselli *et al.*, 2001; Kokogian *et al.*, 2001).

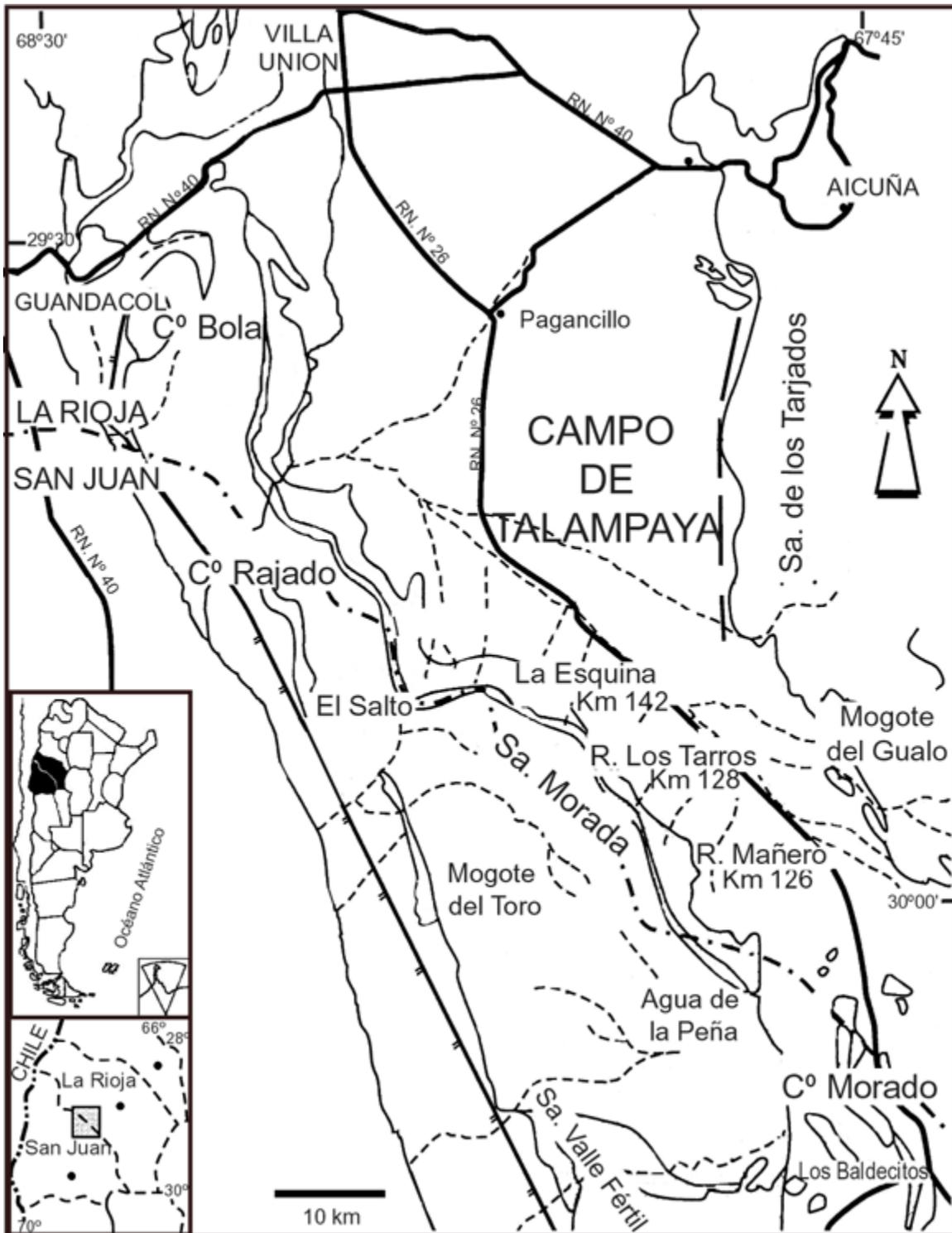


Figure 1. Map of the Ischigualasto- Villa Union region showing the location of the aetosaur-bearing sites. Modified from Kokogian et al. , 2001.

The materials assigned to *Neoaetosauroides* come from several localities throughout the outcrops of the sierra Morada, from the source of the Mañero River to La Esquina, La Rioja province ([figure 1](#)). The first three specimens of *Neoaetosauroides* described by Bonaparte (1969) come from the upper layers of the La Rioja Formation. Specimens PVL 3525 (holotype) and PVL 3528 were collected from the same layer in the Cabecera del río Mañero locality, kilometer 126 of Provincial Route 26, unlike PVL 3842 which comes from the same locality but “about 60 meters above... in the top of the La Rioja Formation” (the Bonaparte, 1971b: 87). Other materials collected in the same area but at different localities ([figure 1](#)) are original specimens PVL 3665 from the source of the Los Tarros river, kilometer 128 of Provincial Route 26, and PVL 5698 from the layers between La Esquina and the head of the Los Tarros river, kilometer 140 of Provincial Route 26 (Caselli *et al.*, 2001).

Abbreviations. CPE, Coleção Municipal, São Pedro do Sul, Brasil; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, USA; PVL, Instituto Miguel Lillo, Tucumán; TTUP, Texas Tech University Paleontology, Lubbock, USA.; TMM, Memorial Texas Museum, Austin, USA.; UCMP, University of Californian Museum of Paleontology, Berkeley, USA.; PULR, Paleontología Museo de Ciencias Naturales, Universidad Nacional de La Rioja, La Rioja.

Systematic Paleontology

Archosauria Cope, 1869

Crocodylotarsi Benton and Clark, 1988

Aetosauria Marsh, 1884

Genus *Neoaetosauroides* Bonaparte, 1969

Type Species. *Neoaetosauroides engaeus* Bonaparte, 1969.

Emended Diagnosis. The same for *Neoaetosauroides engaeus*, the only well-known species.

Neoaetosauroides engaeus Bonaparte, 1969

[Figure 2](#)

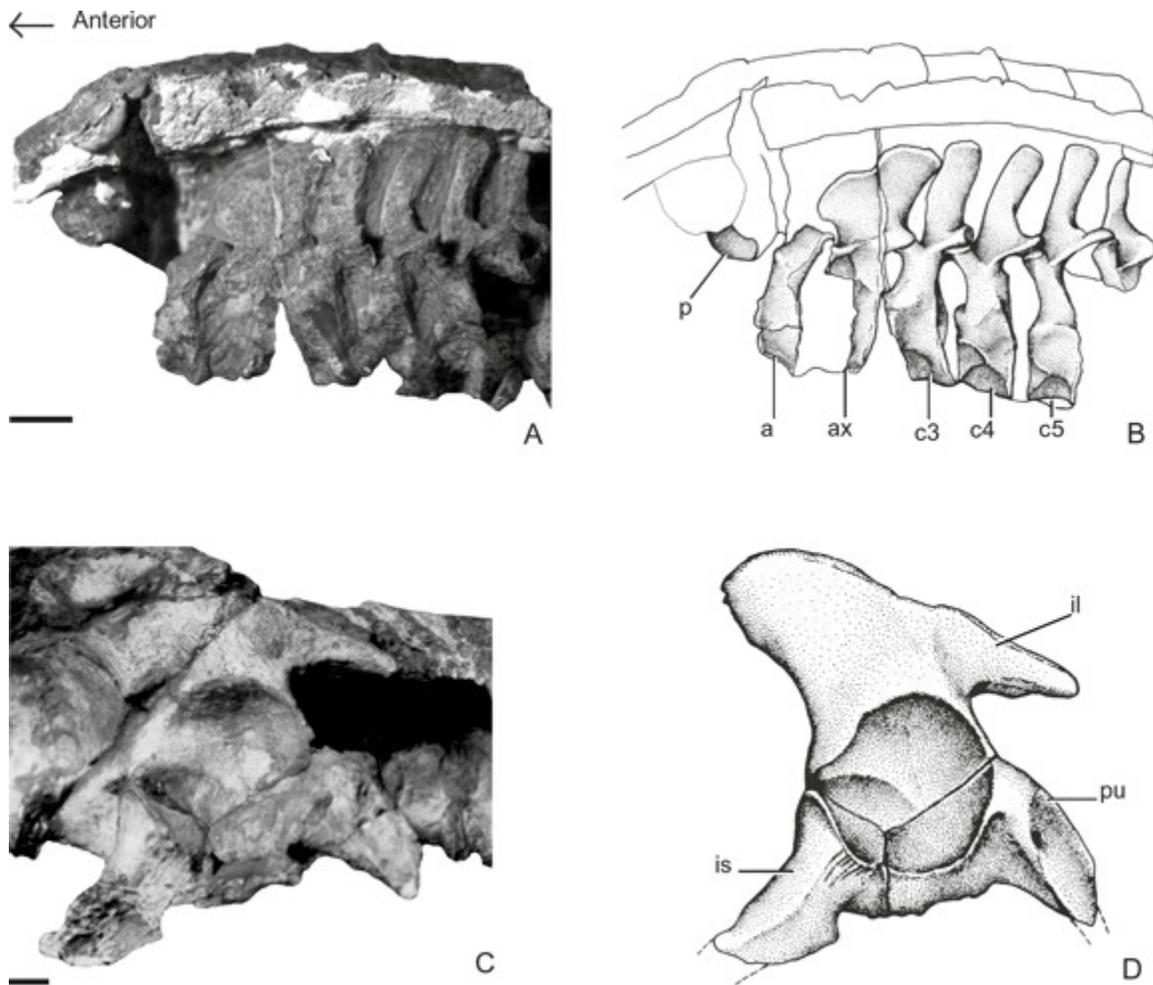


Figure 2. *Neoaetosauroides engaeus* Bonaparte. **A**, PVL 5669, cervical region in lateral view; **B**, interpretive drawing of cervical region in lateral view; **C**, PVL 3525, right half of pelvic girdle in lateral view; **D**, interpretive drawing of right half of pelvic girdle in lateral view. Scale: 1,5 cm. Abbreviations: **a** atlas; **ax**, axis; **c3-c5**, cervical centra 3 to 5; **il**, ilium; **is**, ischium; **p**, proatlas; **pu**, pubis.

Holotype. PVL 3525, mandible, much of the articulated postcranial skeleton, dorsal armor and ventral osteoderms.

Paratypes. PVL 3528: fragments of premaxilla and maxilla with teeth, vertebrae and dermal plates; indeterminate bones; PVL 3842: fragments of dorsal and ventral armor, impression of 8 rows of dermal paramedial plates and the corresponding vertebrae.

Referred material. PVL 4363: skull exposed in lateral view and right mandible, impressions of 4 paramedian and 1 ventral dermal plates; PVL 5698: skull, proatlas, 6 articulated cervical vertebrae, 6 articulated left cervical plates; PVL 3665: proximal end of femur and left humerus, left scapulocoracoid fragment and of 1st caudal vertebra; PULR 108: skull in palatal view and mandibles, impression of femur, distal portion of the left tibia and fibula, internal mold of the appendicular plates; PULR 109: impression of the articulated dorsal armor.

Horizon and type locality. Los Colorados Formation, uppermost section; kilometer 126 of Provincial Route 26, Patquia a Villa Unión, Provincia de La Rioja, Argentina.

Emended Diagnosis. Aetosaur that differs from the others by the presence of coracoids with an acute posteromedially directed process, cervical vertebrae with shorter centra and neural spines lower than the height of the vertebral centrum, cavity of the calcaneus for astragular condyle with poorly delimited edges, digit V of the foot with two phalanges and a short caudal section made up of 26 rows of plates. In addition *Neoaetosauroides* differs from other aetosauroids except *Longosuchus* in having a short, high and broad mandible and large, conical teeth in the maxilla and mandible, and differs from *Longosuchus* in having vertebral centra with ventral keels and lacks horns “*tongue and groove*” articular surfaces in the lateral plates.

Description

Vertebral Column. Specimen PVL 3525 (holotype) is the only one available in which part of the articulated vertebral column has been preserved, made up of 11 dorsal vertebrae, 2 sacrals and 4 caudals. The caudal vertebrae posterior to the 4th caudal appear to have been preserved but they cannot be observed because they are not prepared. The same is true for the dorsal vertebrae, which can be observed in ventral view because dorsally they are covered by the armor. It must be emphasized that this material is on exhibition at the Museo del Instituto Miguel Lillo, Tucumán, and the portion of the neck that articulates anteriorly with the skull and posteriorly with the dorsal region in fact belongs to another specimen, PVL 5698. The descriptions of the cervical vertebrae as well as of the proatlases are based on this last specimen (figures 2.A, B). However, the descriptions of the dorsal, sacral, and caudal vertebrae are based on specimen PVL 3525.

Immediately before the first cervical vertebra (atlas), and contained in an anteriorly displaced block (figure 2.A), the presence of a pair of bony pieces can be observed that form a V. These bones are equal in height to the neural arches of the cervical vertebrae (figure 2.B), with a dorsal end that corresponds to the vertex of the V but more anterior than the ventral ends. This vertex contacts a visible depression in the occipital region of the skull, dorsal to the foramen magnum, whereas the posterior ends contact the atlas. This element has been identified as a proatlas, whose presence is recognized for the first time for the clade Aetosauria.

The atlas is half of the anteroposterior length of the axis. The pedicels of the neural arch contacts ventrally with the intercentrum and for that reason the atlas has the form of ring. It can be observed in this specimen that the odontoid process of the axis crosses it. The postzygapophyses are located posterodorsally, articulating with the prezygapophyses of the axis. In ventral view two posteriorolateral projections for articulation with the first pair of cervical ribs are observed that have not been preserved. The neural spine of the axis has an appreciable anteroposterior length, generating an ample surface that in lateral view is 2 times wider than the spines of the following vertebrae (figure 2.A). The upper margin of the spine is inclined posteriorly, increasing its height posteriorly. The pedicels of the neural arch of the axis are more extensive anteroposteriorly than those of the more posterior vertebrae; at the base are the postzygapophysis articulating with the prezygapophysis of the 3rd cervical. In ventral view a bony lamina can be observed

directed towards the atlas that corresponds to left posterior half of the floor of the odontoid process, but the vertebral centrum of the axis has not been preserved.

The neural spine of the third cervical vertebra is the highest in this series; also, from this vertebra the anteroposterior length of the neural arches is reduced. The posterior margin of the spine is straight. The processes that support the prezygapophyses extend anteriorly to the base of the pedicels and are anterior to the anterior margin of the neural spine. Contrarily, the origin of the postzygapophysis is located anterior to the posterior margin of the spine. The vertebral centrum is taller than the neural spine, and in ventral view it can be observed that the right parapophysis articulates with the cervical rib. In ventral view the centra of cervical vertebrae III through V are observed; all of them possess a well-developed ventral keel, perpendicular to the articular faces. The neural spines of cervical vertebrae IV to VI have more posteroventally inclined distal surfaces than the preceding vertebra (III). The size of the zygapophysis increases remarkably from the articulation between vertebrae III and IV. The vertebral centrum of the cervical vertebra VI has not been preserved. Between the cervicals it is noticed that the position of the parapophysis is more dorsal and closer to the diapophysis. Three right double headed cervical ribs have been preserved corresponding to the cervical vertebrae III, IV and V, whose distal processes are united posterolaterally forming a channel between the ribs and the vertebral centra for the passage of the vertebral artery.

In the holotype eleven articulated presacral dorsal vertebrae have been preserved. They only can be observed in ventral view, except the first dorsal vertebra whose long neural spine is directed anteroposteriorly and shorter than the height of the vertebral centrum. Also, the transverse process of this vertebra is wider and longer than the neural spine. The articular apophyses of the dorsal vertebrae are not well preserved, unlike the transverse processes that articulate with double-headed ribs until the ninth presacral vertebra and diminish in length posteriorly. The diapophyses are wider than the parapophyses, but both are in the horizontal plane. The anterior dorsals have spool-like vertebral centra, flattened laterally. From the fourth vertebra the size of the centrum increases posteriorly. The centra of vertebrae IX to XI are cylindrical, anteroposteriorly short and very robust. Unlike the cervical vertebrae, ventral keels are not observed. The dorsal ribs are wide and long, exceeding the lateral edge of the dorsal armor.

The right sacral ribs of the two sacral vertebrae are fused with the right ilium, the first sacral rib, quadrangular in cross-section, is more robust than second. Unlike the first sacral rib, the second originates farther back and projects anteriorly to fuse with the posterior portion of the ilium that forms the margin of acetabulum. The centra of these vertebrae are the most robust of the vertebral column. The four first caudal vertebrae possess anteroposteriorly wide and very long transverse processes. The vertebral centra, whose size diminishes posteriorly, are short and wide. From the second caudal vertebra articular faces for chevrons are observed.

Shoulder girdle (v. Bonaparte, 1971b: figure 36). The scapula and the coracoids are firmly united, and the suture between both is visible (*e.g.*, PVL 3525, 3665). The scapular blade is flat and expanded distally, especially posteriorly, which equals the end of the coracoid lip of the glenoid cavity. On the contrary, its anterior end is not expanded. The scapular blade continues ventrally as the scapular shaft, which is triangular in cross-section at its base, in whose posterior margin and proximal to the scapular lip of the glenoid cavity possesses a small tubercle corresponding to the zone of insertion for the *triceps* muscle. Ventrally, the scapula is expanded, taking in its posterior portion the scapular lip of the glenoid cavity. Its anterior portion possesses a thickening that extends dorsally throughout the anterior margin to the base of the scapular shaft. This thickening has been interpreted to be where the distal portion of clavicle fused to scapula (Bonaparte, 1971b). The coracoid possesses a convex external (ventral) surface and a concave internal (dorsal) one. The anterior margin is not expanded and of little thickness, unlike the posterior margin that is more robust. Ventral to the glenoid cavity a keel is developed in the external surface of the coracoid that delimits anteriorly a flat surface and another depression (concavity) of triangular form that is projected strongly posteriorly. The coracoids possess very small coracoid foramen, barely observable, located anteriorly in the external surface of the glenoid cavity and proximal to the scapulocoracoid suture.

Anterior limb (v. Bonaparte, 1971b: figure 38). In general lines, the humerus is a robust bone and expanded both ends. The proximal expansion (dorsal), greater than the distal (ventral), has a very wide articular surface and a dorsal thickening formed by the humeral head. Posteriorly on the humeral head the internal tubercle does not exceed the level of the lateral edge of ectepicondyle. The anterior margin of the proximal expansion possesses an expansion that projects anteroventrally, originating the deltopectoral crest, which is very well developed compared with those of other crurotarsans. This crest extends parallel to the lateral margin of the humerus until the beginning of the diaphysis, where it disappears. Between the crest and the lateral surface a triangular, concave area is observed. The diaphysis is short, wide and of triangular cross-sectional section. The distal end possesses an ectepicondyle that is more developed than the entepicondyle. The entepicondyle in external view possesses a depression that corresponds to the articulation with the olecranon process of ulna. In internal view, the depression of ectepicondyle is for articulation with the radius, along with the depression of entepicondyle, a concave surface for the olecranon process. In the distal end of the humerus a furrow is observed that ends distally in the ectepicondilar foramen (*e.g.*, PVL 3525), which it corresponds to the passage of the radial nerve and blood vessels (Romer, 1956).

The radius is straight and of smaller size than the ulna. The proximal end is expanded more mediolaterally than anteroposteriorly, and is more developed than the distal end. In the proximal end the articular surface has a flat surface, whereas the medial portion is more robust and it projects more anteromedially. The diaphysis, of circular cross-sectional section, is wide and continues imperceptibly with the distal end. The articular surface is missing in the only specimen in which the radius has been preserved (PVL

3525). The ulna is more robust than the radius, and its proximal end, of greater size than the distal, is anteroposteriorly expanded and compressed laterally. The articular surface for the reception of medial condyle of the humerus is concave. The olecranon is well defined. The diaphysis diminishes in size from the proximal end to the distal; the distal end is small and of oval cross-section. No elements of the manus have been preserved (*contra* Heckert and Lucas, 1999).

Pelvic girdle. The ilium has a flat, high iliac blade, robust, with a sharp anterior projection that extends past the pubic peduncle (*sensu* Long and Murry, 1995). This projection has a ventrally directed end and its end is blunt. The posterior portion of the iliac blade is wide, square shaped in lateral view and directed dorsomedially, with a straight dorsal edge and concave posterior edge ([figure 2.C](#)). The preacetabular portion of the iliac blade is narrower than postacetabular portion and contacts the anterior end of the first sacral rib, whereas the rib of the second sacral vertebra meets with the postacetabular expansion. The acetabulum, of lateroventral position, is not perforated, is deep and of great size in relation to the bones that form it. Dorsally any structure throughout its contact with the iliac blade is not observed; ventrally it possesses a depression bordered by pubis and ischium ([figure 2.D](#)). The pubis is triangular in shape and smooth in cross-section. Its distal end has not been preserved in the available material. The pubis forms a portion of the acetabulum by means of a fine lamina separated by a bony rim of the anterior portion that contacts the ischium ventral to the acetabulum. In the anterior portion of the pubis the obturator foramen can be observed ([figure 2.D](#)). The ischium is of similar size to the pubis; its proximal end contacts posteriorly with the ilium and anteriorly it forms the acetabulum, separated by a bony rim. The ischium projects posteroventrally and ends in an incompletely preserved distal end.

Posterior limb (v. Bonaparte, 1971b: figures 39 and 40). The femur is a very robust bone, of slightly sigmoidal form and whose length is almost twice that of the humerus. Its proximal end is narrower than the distal. The articular surface of the proximal end possesses a well-developed, shallow intertrochanteric fossa. The anterior margin of the femoral head is rounded and wide; it is continued by a bony lamina that ends near the fourth trochanter, site of insertion of the *caudofemoralis longus* muscle. The distance from the proximal end to the fourth trochanter is equivalent to 1/3 of the femoral length. The diaphysis is wide, short and triangular in cross-section. At the distal end is a shallow intercondylar fossa. The internal condyle is larger than the external and well-lateral to the position of the fibula.

The tibia has a proximal end that is wider than the distal. The proximal end possesses a crest that extends past the anterior surface of the diaphysis. The proximal articular surface has two small but deep depressions and one lateral projection with which it contacts fibula. In anterior view the pronounced cnemial crest is observed and extends throughout the entirety of this bone, for the insertion of the *femoral quadriceps* muscle. The diaphysis, robust and straight, is triangular in cross-section. The distal end possesses an

articular surface for the astragalus that is flat and wide in the anterior portion and convex in its posterior continuation. The fibula, less robust than the tibia, is almost straight in lateral view and the diaphysis is triangular in cross-sectional. Its proximal end is expanded more anteroposteriorly than mediolaterally. In anterior view this bone has a prominent iliofibular trochanter for the insertion of the *iliofibularis* muscle, which projects anterolaterally for 1/3 of the length of the bone in respect to the proximal end. The diaphysis narrows proximally and is curved distally. The distal end possesses a flat articular surface for the calcaneum.

The astragalus (Bonaparte, 1971b: figures 40 and 41) possesses proximally a tibial facet that extends for the entire length of the bone. This facet is shorter anteroposteriorly than mediolaterally and it is subdivided by a raised area with two surfaces that face different directions, which confers the characteristic saddle shape. However, the well-defined fibular facet is of small size, rectangular in shape and is oriented almost vertically. The ventral condyle for articulation with the calcaneum is rounded. The calcaneum possesses a rounded cavity and is not very deep for articulation with the astragular condyle. This cavity is continued medially in a perpendicular plane with an oblong and concave area that receives the posteroventrally convex surface of astragalus. In dorsal or ventral view both concavities are contained in planes that form an obtuse angle. This extended concave-convex articulation between the astragalus and the calcaneum characterizes the crocodile-normal articulation (*sensu* Chatterjee, 1978). Medially there projects a process that is known as the *sustentaculum* (Parrish, 1986). In the posterior portion of the calcaneum projects a well-developed tuberosity that constitutes a strongpoint of the *gastrocnemius* muscle, the main flexor plantar between *crus* and the foot. Nevertheless, a well-formed dorsoventral furrow is not noticeable.

Only two distal tarsals have been preserved (v. Bonaparte, 1971b: figure 42). The one of small size is in contact with the base of metatarsal III, whereas the largest contacts proximally with the calcaneum and distally with metatarsals IV and V. These distal tarsals have been interpreted as III and IV respectively (Parrish, 1986). The foot is formed by five digits, of which the first four are superposed partially through the expanded proximal ends of the metatarsals and the fifth is divergent. The metatarsals have a triangular cross-section and proximal ends that are more expanded than the distal ends. Metatarsal I is the shortest and most robust, with III being the longest one. Metatarsal V, with its hook form, is separated of the rest of the metatarsals, and the reason why the foot is expanded mediolaterally. The phalangeal formula is 2-3-4-5-2. All the preserved terminal phalanges are pointed distally, whereas the remaining phalanges have are spool-like. The length of the toes decreases IV>III>II>I>V.

Osteoderms. The osteoderms form a dorsal carapace, arranging itself in two rows of paramedian plates that are related one to one with the underlying vertebrae, and bordered laterally by a row of lateral plates ([figure 3](#)). Additionally, ventral and appendicular osteoderms have been preserved. All these plates have an anterior bar, except for the

appendicular plates. The ornamentation consists of shallow grooves and ridges in a radial pattern. The dorsal armor begins with two small cervical dermal plates, wider than long with a rounded lateral margin. Posterior to these are approximately seven cervical paramedian plates, wider than long, surrounded laterally by a row of quadrangular lateral plates. The dorsal plates articulate posteriorly with the caudal plates. The width/length ratio of the dorsal paramedian plates is 3:1. The lateral plates have an acute angle and accompany the constriction in the sacral region, because in this region the width/length ratio of the paramedian plates is 2:1. Posteriorly the armor continues with twenty-six caudal plates. The ventral dermal plates are square to hexagonal in shape. In the holotype they have been preserved only in the caudal region, forming a caudal sheath although the presence of isolated ventral plates with an anterior bar in the anterior region, suggests the presence of a ventral carapace (figure 3). The appendicular dermal plates, preserved as impressions in specimen PULR 108, have a rhomboid form, are small, and were immersed in the dermis. Their ornamentation cannot be observed as only the internal surface is preserved.

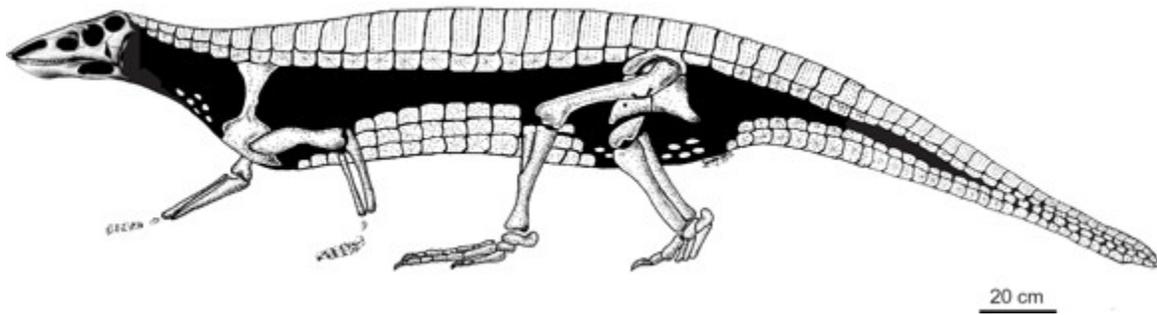


Figure 3. *Neoaetosauroides engaeus* Bonaparte. Restoration of the skeleton and carapace.

Comparative analysis

In the last 10 years numerous phylogenetic analyses have been made to solve the interrelations of the diverse groups of archosaurs, including the aetosaurs (*e.g.*, Sereno and Arcucci, 1990; Sereno, 1991; Parrish, 1993; Juul, 1994; Gower and Wilkinson, 1996; deRicqlès *et al.*, 2003). In those works the clade Aetosauria was included within Crurotarsi, a monophyletic group that also includes Ornithosuchidae, Parasuchia, Rausuchia, and Crocodylomorpha (Sereno and Arcucci, 1990), although there is no consensus with respect to taxa included in these groups and to their interrelationships. Furthermore, the monophyly of Rausuchia is in doubt (Gower and Wilkinson, 1996). The aetosaurs have been considered to be a sister group of the Rausuchia, or more recently of the Crocodylomorpha (Gower and Walker, 2002). Against this general phylogenetic background some postcranial characters of *Neoaetosauroides* and other archosaurs are discussed. Also, the relationships between aetosaur taxa are not completely resolved either, having several proposed alternative hypotheses (Heckert *et al.*, 1996; Heckert and Lucas, 1999, 2000, 2003; Harris *et al.*, 2003a, 2003b).

The comparisons of the postcranial skeleton of *Neoaetosauroides* with other aetosaur taxa are based on the following literature: *Aetosaurus* O. Fraas (Walker, 1961), *Aetosauroides* Casamiquela (Casamiquela, 1960, 1961, 1967), *Coahomasuchus* Heckert and Lucas (Heckert and Lucas, 1999), *Desmatosuchus* Case (Case, 1920; Small, 1985), *Longosuchus* Hunt and Lucas (Sawin, 1947; Hunt and Lucas, 1990), *Lucasuchus* Long and Murry (Long and Murry, 1995), *Stagonolepis* Agassiz (Walker, 1961; Long and Ballew, 1985; Long and Murry, 1995) and *Typothorax* Cope (Cope, 1875; Long and Murry, 1995). That information has been complemented by observations of one of the authors (J.B.D.), identifying in that case the corresponding examples. The proatlas is an even or uneven bone, although always originated from a pair of cartilages, put in between the occipital region and the atlas (Goodrich, 1958). This element has been described in numerous groups of living and fossil tetrapods, although its identification in *Neoaetosauroides* in the present work constitutes the first observed for an aetosaur. It has been observed in most of the other groups of crurotarsans, like phytosaurs (Chatterjee, 1978), ornithosuchids (e. g., Bonaparte 1971b) and crocodylomorphs (e.g., Walker, 1990), and its presence in aetosaurs is presumably plesiomorphic.

The cervical vertebrae of *Neoaetosauroides*, that were previously unknown, possess a ventral keel on their centra, as it appears in the aetosaurs of the Northern Hemisphere *Stagonolepis*, *Aetosaurus*, *Coahomasuchus* (NMMNH P-3004 J.B.D obs. pers.) and *Typothorax*. In *Desmatosuchus*, however, its presence varies individually (TTUP 10008, UCMP 78705, UCMP 78704, UCMP 177315, J.B.D obs. pers.), whereas in *Longosuchus* (TMM 31185, TMM 31185-84b, CP.E2.168, J.B.D obs. pers.) the cervical vertebral centra lack keels (Long and Murry, 1995). It is possible that the presence of cervical vertebrae with keeled centra is a plesiomorphic character for aetosaurs, given its presence in other crurotarsans, like phytosaurs (Camp, 1930; Chatterjee, 1978; Lucas et al., 2002), ornithosuchids (Walker, 1964; Bonaparte, 1971b), rauisuchians (Sill, 1974; Chatterjee, 1985) and crocodylomorphs (Nash, 1975; Walker, 1990; Wu et al., 1997) although it is not constant characteristic in all of those groups. The proportions of the cervical vertebrae vary widely between the different genera of aetosaurs. Thus, the cervical centra in *Neoaetosauroides* are higher than wide, which contrasts with the cervicals of *Typothorax* and *Desmatosuchus* (UCMP 78705, UCMP 78704, UCMP 139912, UCMP 139913, J.B.D obs. pers.) whose centra are clearly wider than high. Also, the neural spines of the cervical vertebrae of *Neoaetosauroides* are equal to or higher than the vertebral centra, like those of *Stagonolepis welllesi* Long and Ballew and *Longosuchus*. In contrast, the cervicals of *Typothorax* and *Desmatosuchus* have short neural spines, which never exceed the height of the vertebral centrum.

In *Neoaetosauroides* the distance between the ends of the transverse processes of the presacral vertebrae is twice the width of the vertebral centrum; that distance is equal or greater than twice the width of the centrum in most aetosaurs, except *Desmatosuchus* and *Lucasuchus*, as indicated in the phylogenetic analysis of the Aetosauria by Heckert and Lucas (1999).

The general form of the pectoral girdle of *Neoaetosauroides* is more similar to those of *Longosuchus* and *Typothorax*, than to those of *Desmotosuchus* and *Stagonolepis*. In these last two genera the scapula is comparatively wider and shorter than in the first two genera. In *Neoaetosauroides*, in contrast to *Stagonolepis robertsoni*, *Aetosauroides*, and possibly *S. wellesi* and *Desmotosuchus*, is no discreet clavicle-like element. Nevertheless, as already mentioned in the original description, it has been interpreted in *Neoaetosauroides* that the clavicle is fused to scapula. The sharpened form of the posterior end of the coracoid, ventral to the coracoid lip, is characteristic of *Neoaetosauroides*. That end is rounded in shape in *Desmotosuchus*, *Stagonolepis*, and *Longosuchus*.

The proximal end of the humerus is relatively unexpanded in *Neoaetosauroides* and *Typothorax*, unlike *Desmotosuchus* and *Stagonolepis*, in which it is highly expanded and the deltopectoral crest extends halfway down the bone. The internal tuberosity does not exceed the lateral margin of ectepicondyle in *Neoaetosauroides* and *Typothorax* unlike *Stagonolepis* and *Desmotosuchus* where the proximal end is strongly expanded in anteroposterior sense. The wide diaphysis, short and triangular in cross-section in *Neoaetosauroides* and *Longosuchus*, contrasts with the long diaphysis of the humerus, which narrows dorsoventrally in *Desmotosuchus*. The presence of a smooth furrow that finishes in the ectepicondilar foramen on the lateral face of the radial condyle of the humerus is a character of *Neoaetosauroides* that shared with *Desmotosuchus* and *Longosuchus*, between the aetosaurs. In other archosaurs the radial nerve and several blood vessels run in an open furrow, without giving rise to a closed ectepicondilar foramen (Romer, 1956).

The presence of a prominent anterior projection of the iliac blade not only is present in *Neoaetosauroides* but also in other aetosaurs like *Stagonolepis wellesi* Long and Ballew, *Typothorax coccinarum* Cope, *Desmotosuchus haplocerus* Cope, and *Aetosauroides scagliai* Casamiquela. The anterior iliac projection is somewhat shorter in *Longosuchus* and *S. robertsoni* Walker. This anterior expansion of the iliac blade has important functional implications, since it makes possible the modification of the insertion of iliotibialis and iliofemoralis muscles that are extensors and protractors of the hindlimb respectively and both important femoral rotators (Parrish, 1986). The anterior and dorsal displacement of the origin of those muscles with respect to the joint of the hip extends the level arm of these, which in conjunction with other anatomical characteristics makes possible different actions.

Between the aetosaurs the position of the acetabulum varies, which must be related to a different morphology and position of the femora. In *Neoaetosauroides* and *Desmotosuchus* (UCMP 25989, TMM 31100-1, TMM 10008, TMM 31100-313, J.B.D obs. pers.) the acetabulum is in an oblique plane with respect to the sagittal plane and possesses a noticeable dorsal rim that overlies the top of femur when it is articulated. However, in *Typothorax*, *Aetosauroides* and *Longosuchus* (TMM 3100-236, TMM 31185 - 40, NMMNH 36075 J.B.D obs. pers.) the ilium has an almost perpendicular position to the sagittal plane, reason why the acetabulum is practically horizontal (Casamiquela, 1961, 1967). According to the reconstruction by Walker (1961), in *Stagonolepis* the

acetabulum would be vertical, a condition similar what is present in some basal archosauromorphs. The femur of *Neoaetosauroides* is distinguishingly robust and, like in *Desmotosuchus*, is different in that the inclination of the articular head forms an acute angle with the longitudinal axis of the diaphysis (figure 4). However, in *Longosuchus* and *Aetosauroides* the angle of inclination of the femoral head with respect to the diaphysis is smaller, which would be correlated with the horizontal position of acetabulum. In this last genus the femur displays torsion around its longitudinal axis, which confers a sigmoidal configuration characteristic of the taxon (Casamiquela, 1961: figure 20).

In general, the tibia of *Neoaetosauroides* is a thin bone, similar to that of *Stagonolepis*, and less robust than in *Longosuchus*, *Desmotosuchus* and *Typothorax*. In these two last taxa the tibia is noticeably shorter in relation to femur and more robust, which could be related to its great size with respect to other aetosaurs (figure 4). The cnemial crest is noticeable, as in *Longosuchus*. The articulation between the astragalus and the calcaneum in *Neoaetosauroides* differs from some of other aetosaurs in which these elements are preserved (e.g., *Typothorax*, *Longosuchus*) because the planes that contain the concavities for the astragalus form an angle greater than 90°. The lateral distal tarsal is of greater size than the medial one, as in *Stagonolepis*, *Aetosauroides* and *Aetosaurus* (Casamiquela, 1967), the only taxa in which those bones have been preserved.

Neoaetosauroides retains a pattern of the foot that is generalized for the Crurotarsi with regard to the smaller size of digits I and V, and metatarsal V with a medially directed proximal process (it forms a “hook”). It differs from other aetosaurs and other groups of crurotarsans in which the foot is known by the presence of a digit IV that is longer than digits II and III. Another peculiar character of the foot of this taxon is the reduction of the number of phalanges in digit V, possessing the smallest number of phalanges known for aetosaurs (3 in *Longosuchus*, 4 in *Stagonolepis*). This tendency for the reduction of phalanges of digit V occurs independently in other crurotarsans. The size of the ungual phalanges of digits I and II is generally greater than those of the most lateral digits, but this difference is noticeably greater in *Neoaetosauroides* than in other aetosaurs (figure 4). The metatarsals of *Neoaetosauroides*, including the recurved digit V, are relatively graceful and similar in their proportions to those of *Stagonolepis* and *Longosuchus*. They contrast with short and wide metatarsals of *Typothorax* (NMMNH 36075) and *Desmotosuchus* (UCMP 34497).

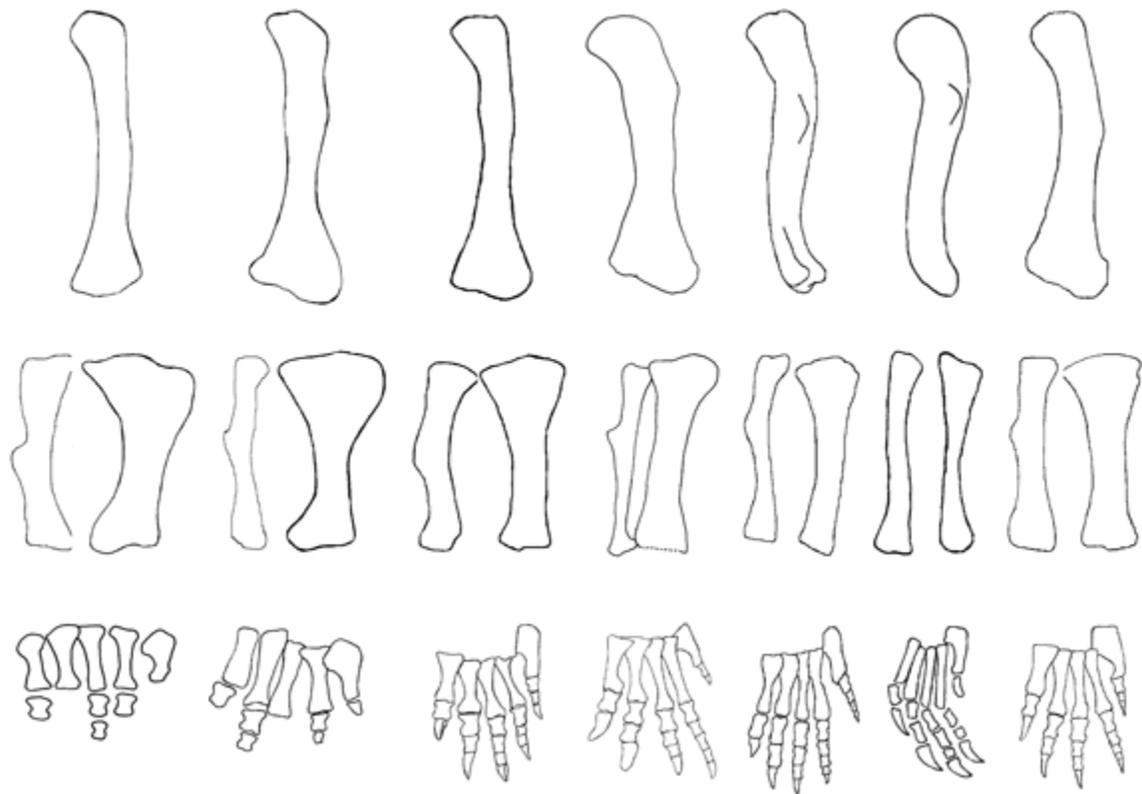


Figura 4. Sketches of femurs, fibulae, tibiae, and pes.; **A**, *Desmatosuchus* ; **B**, *Typothorax* ; **C**, *Longosuchus* ; **D**, *Neoaetosauroides* ; **E**, *Aetosauroides* ; **F**, *Aetosaurus* ; **G**, *Stagonolepis robertsoni*. Not to the same scale.

Discussion

Neoaetosauroides, next to *Aetosauroides*, is one of the better represented taxa of South American aetosaurs, constituting one of the youngest known forms at the world-wide level. On the other hand, this taxon is one of the few represented by specimens with articulated postcranial which allows more in-depth study. Many characteristics of the hindlimbs of the archosauromorphs have been interpreted as parts of character complexes whose significance regarding locomotive capacity has been reiterated by different authors. Nevertheless, an analysis of the pattern of acquisition of postcranial structural modifications and their evolution in the aetosaurs in a historical context requires an explicit and reliable phylogenetic framework. Indeed, a revision of the phylogenetic relations of this group is the reason why this study has only interpreted these characters in light of functional hypotheses postulated by other authors for basal archosaurs.

Different aspects from the pelvic girdle, femur, tibia, the articulation between the zeugopod and autopod and plantigrade or digitigrade was used by Charig (1972) to characterize stages in the evolution of walking “improved” or erect from a primitive condition to a sprawling gait. But, as it indicated Bonaparte (1984), these locomotive innovations occurred independently in different lineages of archosaurs with different

characteristics according to their phylogenetic history. Various models regarding the morphological characteristics in archosaurian with different walking styles, sprawling, intermediate and erect, were presented by Parrish (1986), although recent studies object the use of the modern crocodiles as intermediate models of a semi-erect locomotive position (Reilly and Elias, 1998). In his analysis Parrish (1986) included the aetosaurs, which he considered as a group with plantigrade posture and a crocodile-normal crurotarsal ankle (*sensu* Chatterjee, 1978) to walk improved or erect. It turns out, therefore, interesting to test the approval of the affirmation on the basis of the information provided by the restudy of *Neoaetosauroides*. In other words, does this genus adhere to all the aspects of the corresponding morphofunctional model?

1. The acetabulum is deep, permitting femoral protraction and retraction only in a parasagittal plane. It is possible to indicate that the direction varies between the aetosaurs, being somewhat oblique, as in *Neoaetosauroides*, or horizontal, as in *Aetosauroides*.

2. The iliac blade is expanded anteriorly; the ischia and pubes are not complete distally in the available material but they seem to be moderately extended elements. These characteristics would tend to favor the vertical orientation of the femur.

3. The crural morphology displays expectable characteristics of erect walking forms. The presence of two depressions corresponding to a pair of meniscifor articulation with the femur helps to restrict the movement of this segment of the limb to a simple flexion and extension with respect to this bone. The raised distal end for articulation with the astragalus is moderately curved, but not so marked as in other aetosaurs (e.g., *Desmatosuchus*, *Typothorax*) nor flat as in sprawling forms. In many ways the complementary raising of the astragalus and the distal end of the tibia favors a narrow articulation. This results in a tibio-astragal column that restricts the flexion and extension of the calcaneum with respect to astragalus to a parasagittal plane.

4. The astragalo-calcaneal articulation is well-defined as in the erect forms, although the cavity for the astragalar condyle does not possess delimited edges as in other genera of aetosaurs which reduce the level of fit in-between these bones.

5. The calcaneum possesses a posteriorly directed tuberosity, perpendicular to its axis of rotation.

6. The autopod is characterized by the possession of metatarsals that are superposed in the expanded proximal portions and divergent digits, not consolidated *sensu* Parrish (1986). A consolidation of the metatarsal, including an anteriorly directed digit V, provides a stable base for plantar flexion with respect to the crus. Accordingly, the pedal morphology of *Neoaetosauroides* would represent an intermediate condition.

The study of the postcranial skeleton of *Neoaetosauroides* and its comparison with other aetosaurs has demonstrated a great anatomical diversity in this group. Many differences in the degree of pelvic expansion, curvature of the femur, morphology of crus and tarsals suggest that some members of this group could have walked semi-erect, whereas others would have had erect locomotion. This possible spectrum of locomotor positions, combined with the diverse range of sizes (0.8-5.0 m), supports proposals of a greater range of lifestyles between these armored archosaurs than traditionally supposed (Bonaparte, 1971b, 1978; Small, 2002; Desojo, 2003).

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