

# Jaw biomechanics in the South American aetosaur *Neoaetosauroides engaeus*

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**Abstract** The function of the jaw apparatus and the possible dietary habits of the aetosaur *Neoaetosauroides engaeus* from the Triassic of South America were analyzed in comparison with Northern Hemisphere aetosaurs *Desmotosuchus haplocerus* and *Stagonolepis robertsoni* and the living short-snouted crocodile *Alligator mississippiensis*. The adductor and depressor jaw musculature of these was reconstructed on the basis of dental and skeletal comparisons with living closest relatives' extant phylogenetic bracket (EPB), followed by the analysis of the moment arms of these muscles to infer feeding habits. The aetosaurian skull design indicates that the total leverage of the inferred jaw musculature provides force rather than speed. However, within aetosaurs, the high ratios of muscle moment arms to bite moments indicate stronger bites in the northern Hemisphere forms, and faster ones in *Neoaetosauroides*. These differences indicate more developed crushing, chopping, and slicing capacities, especially at the back of the tooth series for *D. haplocerus* and *S. robertsoni*; whereas it opens a window to consider different abilities in which speed is involved for *N. engaeus*. There

are differences among aetosaurs in dental characteristics, position of the supratemporal fenestra, location of the jaw joint relative to the tooth row, and shape of the lower jaw. *Neoaetosauroides* does not show evidence of dental serrations and wear facets, probably consistent with a relatively soft and non-abrasive diet, for example soft leaves and/or larvae and insects without hard structures. It might be possible that *Neoaetosauroides* represents a tendency towards insectivorous feeding habits, exploiting a food source that was widespread in continental environments throughout the Triassic.

**Keywords** Archosauria · Aetosauria · *Neoaetosauroides* · Skull · Functional morphology · Jaw biomechanics

**Kurzfassung** Die Funktion der Kiefer und die möglichen Ernährungsgewohnheiten des Aetosauriers *Neoaetosauroides engaeus* aus der Trias von Südamerika wurden mit den Aetosauriern *Desmotosuchus haplocerus* und *Stagonolepis robertsoni* aus der nördlichen Halbkugel und dem lebenden kurzschnäuzigen *Alligator mississippiensis* verglichen. Die Adduktoren und Depressoren der Kiefermuskulatur wurden auf der Grundlage eines Vergleiches der Kiefer und Zähne mit den nächsten lebenden Verwandten rekonstruiert, und die Hebelarme dieser Muskeln wurde analysiert, um Rückschlüsse auf die Ernährungsweise zu gewinnen. Die Struktur des Schädels der Aetosaurier deutet darauf hin, dass die Hebelarme der rekonstruierten Kiefermuskeln eher auf Kraft denn auf ein schnelles Schließen der Schnauze angelegt sind. Allerdings deuten innerhalb der Aetosaurier das hohe Verhältnis der Hebelarme der Kiefermuskeln zu ihren Drehmomenten auf einen kräftigeren Biß bei den Formen aus der nördlichen Halbkugel hin, gegenüber einem schnelleren Biß bei *Neoaetosauroides*. Diese Unterschiede deuten darauf hin, dass die Kiefer von *D. haplocerus* und

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*S. robertsoni* besser zum zermahlen, schneiden und abbeißen geeignet waren, insbesondere im hinteren Bereich der Zahnreihe, während sie für *N. engaeus* andere Möglichkeiten eröffnen, bei denen die Schließgeschwindigkeit der Kiefer eine Rolle spielt. Unterschiede zwischen verschiedenen Taxa der Aetosaurier finden sich in der Struktur der Zähne, der Position des Supratemporalfensters, der Lage des Kiefergelenkes in Relation zur Zahnreihe und der Form des Unterkiefers. *Neoetosauroides* zeigt keine Anzeichen von Serrationen oder Abnutzungsspuren an den Zähnen, was wahrscheinlich auf eine relativ weiche und nicht-abschleifende Nahrung hindeutet, wie zum Beispiel weiche Blätter und/oder Larven und Insekten ohne harte Panzer. Somit erscheint es möglich, dass *Neoetosauroides* eine Tendenz zur insektenfressenden Ernährungsgewohnheiten aufweist, und somit eine Nahrungsquelle ausnutzte, die in kontinentalen Ökosystemen während der Trias überall weit verbreitet war.

**Schlüsselwörter** Archosauria · Aetosaurus · *Neoetosauroides* · Schädel · funktionelle Anatomie · Kiefermechanik

## Introduction

The Aetosauria is a clade of armoured quadrupedal crurotarsan archosaurs. This group was a characteristic component of continental ecosystems during much of the Late Triassic in North America, Europe, North Africa, India, and South America (Heckert and Lucas 1999, 2000). Aetosaurs were characterized by dorsal, ventral and appendicular armour, and a small head with an external naris longer than antorbital fenestra and an edentulous anterior dentary. They were 0.80–5 m long, the largest being the North American *Desmatosuchus*. The South American forms, *Aetosauroides* Casamiquela, 1960 from Brazil and Argentina, and *Neoetosauroides* Bonaparte, 1967 from Argentina, were small to medium-sized (1.5–3 m of body length).

Postcranial remains and osteoderms usually outnumber cranial elements among aetosaurian fossils. To date, reasonably complete, well-described skull materials are known for the aetosaurs *Desmatosuchus haplocerus* (Cope 1892; Small 1985, 2002), *D. smalli* (Parker 2005), *Stagonolepis robertsoni* (Agassiz 1844; Huxley 1859, 1875; Walker 1961; Gower and Walker 2002), *Aetosaurus ferratus* (Fraas 1877; Walker 1961; Schoch 2007), *Longosuchus meadei* (Sawin 1947; Parrish 1994), all from the Northern Hemisphere, and *Neoetosauroides engaeus* (Bonaparte 1969, 1971; Desojo and Báez 2007) from South America. Nonetheless, 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 difficult to interpret the interrelationships among aetosaurs and some aspects of their mode of life (Heckert and Lucas 1999, 2000; Parker 2007). Although there are no specific studies on the functional morphology and paleobiology of this group, several authors have discussed the feeding habits and cranial function of these animals, mostly on the basis of morphological evidence. For instance, Walker (1961) and Parrish (1994) proposed herbivory for this group, Sawin (1947) suggested scavenging habits, Bonaparte (1978), Small (2002), and Desojo (2003) suggested omnivory, and Murry and Long (1996) suggested carnivory for some taxa.

Feeding behaviour is related to most aspects of animal biology, from obvious energetic requirements to reproductive biology, life-history strategies, behavioural ecology, habitat preferences, and populational ecology. Sound hypotheses on aetosaur feeding behaviour would not only inform us on the palaeobiology of individual taxa, but might also provide a model system for investigating broader ecological and evolutionary concepts (Barrett and Rayfield 2006). Moreover, feeding mechanisms offer opportunities for assessing large-scale macroevolutionary patterns and processes (such as the coevolution of herbivorous aetosaurs and some plants) (Barrett and Rayfield 2006).

The way to avoid making speculations about the biological role of fossils is by study of form and elaboration of mechanical functional models, and to make hypotheses about capabilities. Witmer and Rose's (1991) work on the gigantic Eocene bird *Diatryma* is regarded as a model for such work (Plotnick and Baumiller 2000). A more updated example is the work by Barrett and Rayfield (2006) on dinosaurs.

*Neoetosauroides engaeus*, the single known species of the genus and youngest aetosaur occurrence from South America, has recently been the subject of detailed anatomical studies (Desojo and Báez 2005, 2007), providing an appropriate background to initiate a line of studies on its biological role. Herein, we reconstructed the adductor and depressor jaw musculature of this species, on the basis of its cranial anatomy and comparisons with living closest relatives, following the detailed analysis of Holliday and Witmer (2007), and analysed the moment arms of these muscles to infer feeding habits. Modern functional morphology studies give us much information about the feeding mechanisms in many amniote taxa. However, there is limited literature on functional aspects and electromyographic studies of feeding in extant short-snouted (Iordansky 1964; Schumacher 1973; Drongelen and Dullemeijer 1982; Busbey 1989; Cleuren and De Vree 1992, 2000) and long-snouted (Endo et al. 2002) crocodiles.

## Institutional abbreviations

PULR, Paleontología Museo de Ciencias Naturales de la Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina.

## Dental morphology

The anterior end of the *Neoaetosauroides engaeus* premaxilla bears a mediolateral expansion that forms, with that of the contralateral bone, the edentulous shovel-like structure of the snout. The dentition is confined to the premaxillary, maxillary, and dentary margins and tooth implantation is thecodont. The upper dentition is composed of four premaxillary and eight maxillary teeth, and the lower consists of seven alveoli. The teeth are large and have a conical overall shape, although a slight constriction separates the low cylindrical basal portion 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. The dentary bears the lower dentition, with an edentulous narrow anterior portion. The lower teeth, similar to the upper teeth, lack denticles and wear facets (Desojo and Báez 2007).

## Materials and methods

This work was based mainly on specimens PVL 4363 (incomplete articulated skull with lower jaw exposed in right lateral aspect and associated paramedian and lateral osteoderms), PVL 5698 (incomplete articulated skull which associated cervical vertebrae and paramedial osteoderms), and PULR 108 (incomplete articulated skull with lower jaw, articulated left femur, tibia, fibula, impression of left pes, and inner cast of appendicular osteoderms). All these specimens are from the upper part of the Los Colorados Formation (Upper Triassic), Ischigualasto-Villa Unión Basin, Western Argentina.

*Neoaetosauroides* was compared with other complete and well-described aetosaur cranial material, such as that of *Stagonolepis robertsoni* (Walker 1961), and *Desmatosuchus haplocerus* (Small 2002), both from the Northern Hemisphere. In addition, we analysed the skull of a representative of the only extant crurotarsan archosaur clade, the Crocodyliformes. The crocodylian jaw muscles are difficult to study, owing to their variability in some details, which results in different interpretation of the homology of some crocodylian muscles (e.g. Schumacher (1973) interpreted the origin and insertion sites of the *Muscle*

*pseudotemporalis* differently from Poglayen-Neuwall (1953) and Iordansky (1964)). A short-snouted crocodile, the living American alligator, *Alligator mississippiensis* was used for these comparisons (Kardong 2002; Erickson et al. 2003).

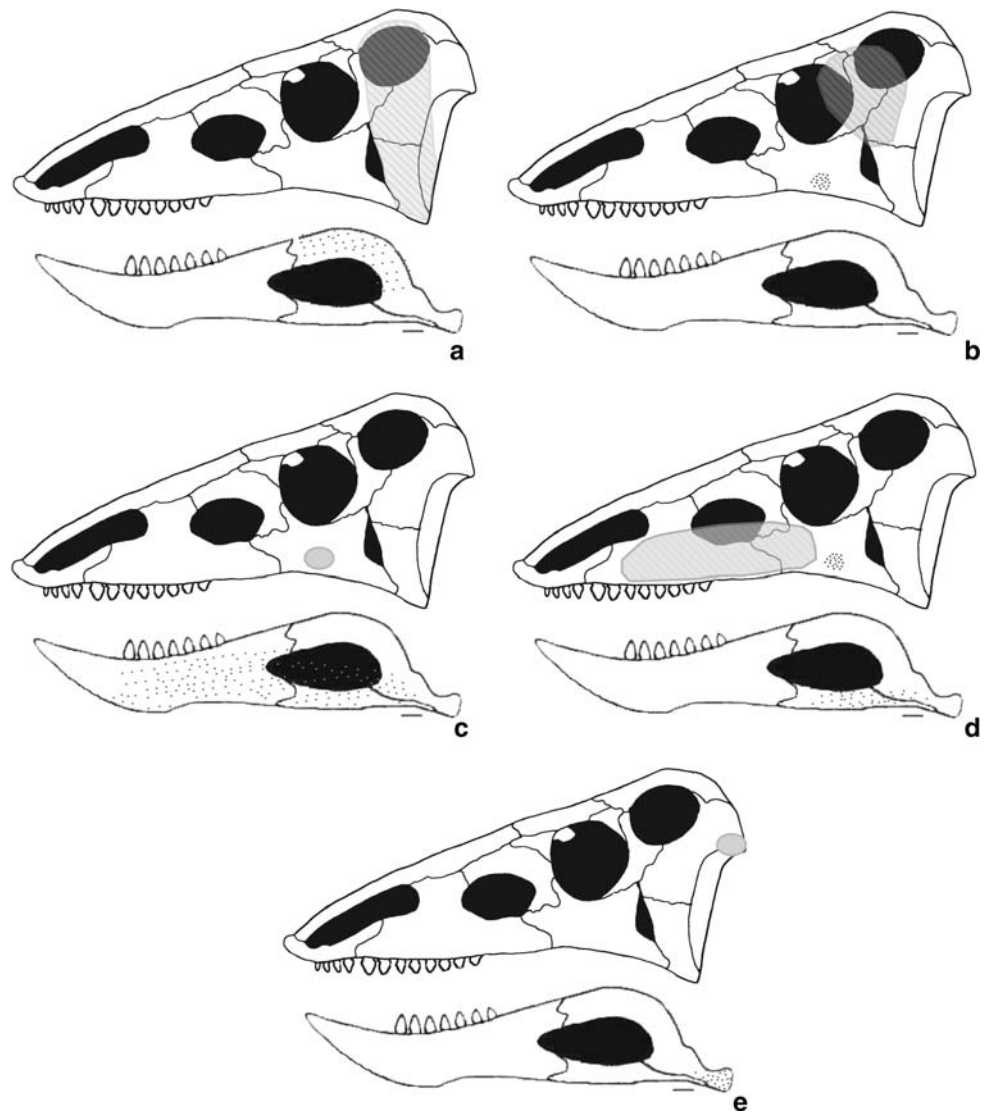
## Reconstruction of musculature

The jaw musculature of *Neoaetosauroides* was reconstructed (Fig. 1) from the scars on the bones and by comparison with extant archosaurs and lizards, following Holliday and Witmer (2007), crocodiles, following Busbey (1989) (which includes both anatomical and mechanical studies), modern birds (Cleuren and de Vree 1992), Paleognathae and Galloanseres (Elzanowski 1987), Charadriiformes (Burton 1974), and lizards (Haas 1973; Abdala and Moro 1996). The reconstruction of the jaw adductor musculature of sauropterygians discussed below is guided by an attempt to keep structures as simple as possible.

There are some uncertainties with regard to the position of some structures that lack a bony insertion; this led us to make some methodological decisions. In crocodiles, the cartilago transiliens (CT), to which various aponeuroses are attached (Drongelen and Dullemeijer 1982; Busbey 1989), lies embedded in a bag of connective tissue between the mandibular adductor tendon and the surangular bone. For aetosaurs (Fig. 2), we positioned the CT on the surangular process described for *Stagonolepis robertsoni* by Walker (1961) and estimated its position for the rest of the aetosaurian taxa where this process is unknown. Recently, Holliday and Witmer (2007) suggest that *M. intramandibularis* is merely the distal portion of *M. pseudotemporalis*, separated by the CT (Holliday and Witmer: hypothesis of homology II). However, other authors (Iordansky 1964; Busbey 1989; Rieppel 1990) consider the *M. intramandibularis* as an independent unit that arises on the ventromedial surface of the CT and inserts into the Meckelian canal (Holliday and Witmer: hypothesis I). Based on the topological patterns of muscle structures observed during the dissection of three skulls of the short-snouted crocodile *Caiman latirostris* (Lecuona et al. 2006), the hypothesis of homology I is further supported; thus, in the present contribution we consider the *M. intramandibularis* to be a different muscle from the *M. pseudotemporalis*.

For the aponeurosis V, related to the insertion of the *M. adductor mandibulae internus pseudotemporalis* and *M. adductor mandibulae internus pterygoideus*, we estimated its position at the lower edge of the jaw by projecting a vertical axis, from a midpoint of the horizontal line between the posterior border of the external mandibular fenestra and the midpoint of the articular facet of the articular bone. In this way, it represents the relative position in crocodiles (Fig. 2).

**Fig. 1** Reconstruction of areas of origin and insertion of the main jaw muscles of *Neoaetosauroides engaeus* (Modified from Desojo and Báez 2007) **a** *Musculus adductor mandibulae externus* (MAME) + *Musculus adductor mandibulae posterior* (MAMP) **b** *Musculus adductor mandibulae internus pseudotemporalis* (MAMIP) **c** *Musculus intramandibularis* (MI) **d** *Musculus adductor mandibulae internus pterygoideus* (MAMIPT) **e** *Musculus depressor mandibulae* (MDM). Angle lines represent origin areas and dotted regions represent insertion areas. Scale 1 cm

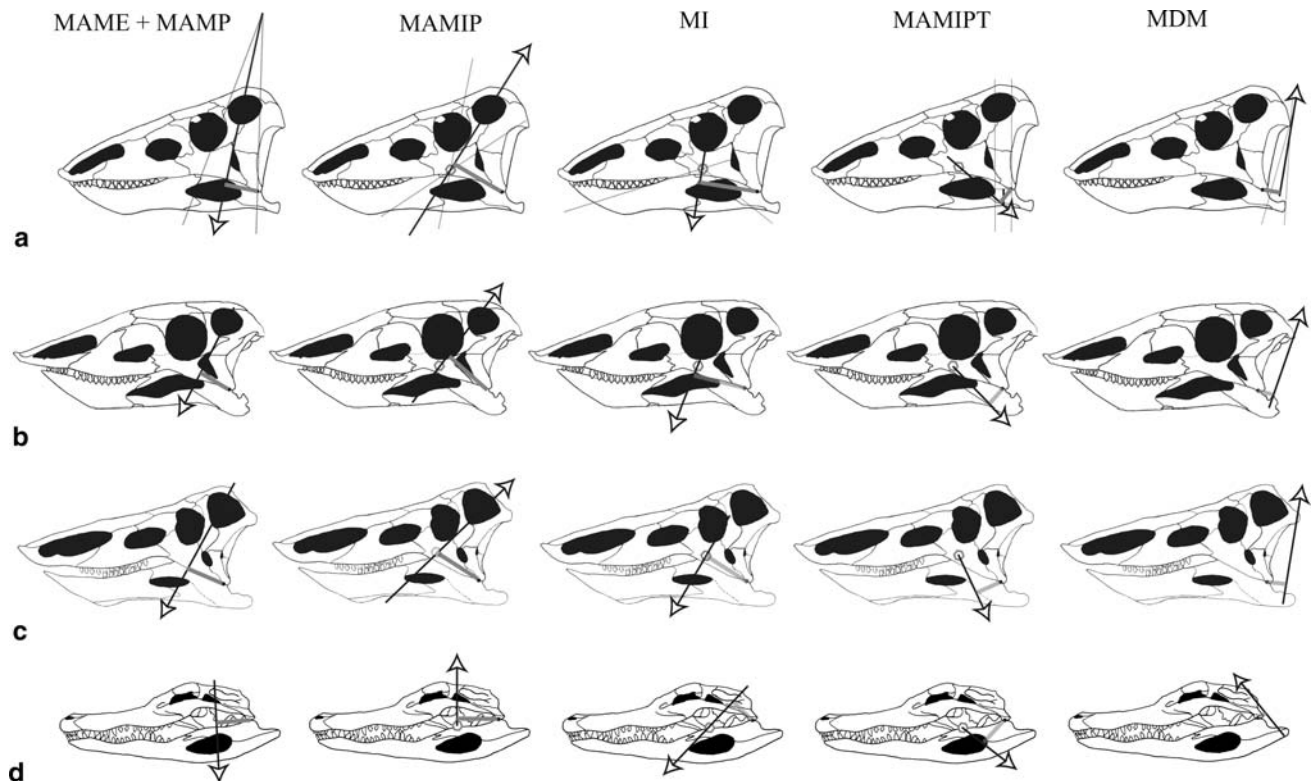


The EPB method used by different authors (Carrano and Hutchinson 2002; Rieppel 2002; Perry and Sander 2004; Holliday and Witmer 2007) utilizes information from soft tissues and osteological correlates based on the phylogenetic position of an organism to infer function by treating it as homology. We use extant taxa to establish primary homology for the muscles of the jaw apparatus in archosaurs. The soft tissue and osteological data from extant and extinct taxa were interpreted via the EPB (Witmer 1995, 1997). A useful method to estimate the level of speculation inherent in a soft tissue reconstruction, termed “levels of inference”, was provided by this author. If soft tissue data from extant bracket taxa (for archosaurs, Crocodylia, and Neornithes) unequivocally support the reconstruction of an unpreserved feature on an extinct taxon (e.g. both outgroups possess the feature), the reconstruction is a Level I inference. Ambiguous support from extant taxa (e.g. one outgroup lacks the feature) is a Level II inference, and the

unequivocal absence of support from extant taxa (both outgroup lack the feature) is a Level III inference. If inferences lack conclusive data from the osteological correlates of soft tissues, they are called Levels I', II', and III' inferences (Witmer 1995). Such inferences have less support than the matching Levels I, II, and III inferences, but more than one at the next overall level.

#### Mechanical analysis

Our mechanical analysis was based mostly on comparison of the moment arms of the jaw musculature among different aetosaurs (e.g. *N. engaeus*, *D. haplocerus* and *S. robertsoni*). The jaw was considered to represent a lever, with its fulcrum or pivot at the quadratoarticular joint. The jaw musculature provides the input force whereas the output force is that exerted by teeth on food. The moment arms of the reconstructed musculature were estimated by



**Fig. 2** Moment arms and action lines of the *Musculus adductor mandibulae externus* (MAME) + *Musculus adductor mandibulae posterior* (MAMP), *Musculus adductor mandibulae pseudotemporalis* (MAMIP), *Musculus intramandibularis* (MI), *Musculus adductor mandibulae internus pterygoideus* (MAMIPT), and *Musculus depressor mandibulae* (MDM) **a** *Neoaetosauroides* (Modified

from Desojo and Báez 2007) **b** *Stagonolepis* (Modified from Walker 1961) **c** *Desmatosuchus* (Modified from Small 2002) **d** *Alligator* (modified from Kardong 2002). Basis of calculations depicted for *Neoaetosauroides* only. Arrows represent action lines, grey lines represent moment arms, and grey circles symbolize the cartilago transiliens. Not to the same scale

adaptation of a geometric method developed in 1998 by Vizcaíno et al. for mammals. This method provides an average moment arm value for muscles for which the line of action is not evident because of their massive nature or when internal architecture cannot be determined, for example the *M. massetericus* in fossil mammals. The basis of the method consists of calculating the average of the potentially most posterior and anterior lines of action, considering the areas of origin and insertion of each individual muscle or muscle complex. These averages are combined as the input force of the lever system and used to calculate a ratio between them and the output forces represented by the moment arms of the bite at different mandible lengths. Total lengths of the skulls were standardised to allow comparisons between forms of different sizes. Consequently, distances measured directly on the drawings, and the units, are used only in comparative terms independent of size. For a complete description of the method see Vizcaíno et al. (1998). However, the different anatomy of the bones and muscles of aetosaurs made some adjustments necessary. For instance, archosaurs lack a zygomatic arch; the adductors do not form a *M. massetericus* as in mammals, and some muscles are simple and

elongated virtually reflecting their line of action, which is not the case for most of the mammalian masticatory muscles.

In crocodiles the *M. adductor mandibulae internus pterygoideus* has dorsal and ventral portions, which are not antagonists but result in a strong adduction working in the horizontal plane (Schumacher 1973, p 148) or have distinct functions, for example the dorsal section, which provides the major portion of the adductor force and prevent, together with the *Musculus adductor mandibulae posterior* (MAMP), dislocation of the jaws (Iordansky 1964). Regardless of the activity patterns, the *M. pterygoideus ventralis* has quite different geometries (Busbey 1989), such as the relatively small size in the long-snouted as opposed to short-snouted crocodiles (Endo et al. 2002). Thus, for practical purposes, we simplified the analysis estimating the line of action of this muscle, considering only its ventral branch as a line from its attachment on the jugal below the orbit to the aponeurosis V. Also, the *M. adductor mandibulae externus*, the most functionally and anatomically variable group of the jaw musculature, and *M. adductor mandibulae posterior* were considered a functional unit, based on Schumacher's (1985) suggestion

that they are fused; this provides a single line of action for estimating the level arm.

## Results

### Muscles (Fig. 1)

We could not find physical evidence on the aetosaur specimen for division of the *M. adductor mandibulae externus* into three parts (pars superficialis, pars medialis, and pars profundus) (Schumacher 1973) or two parts (Iordansky 2000) as described for crocodiles (Holliday and Witmer (2007): an amalgam of variably constructed “temporal” muscles”); we therefore regarded this muscle as a single unit. Other muscles of the constrictor system, for example the *M. constrictor internus dorsalis* and *M. intermandibularis*, because of their origins and insertions in soft tissues, and other functions, like depressor palpebrae inferiolis (Schumacher 1973) are irrelevant for the biomechanical approach performed here.

### Adductor chambers

In sauropsids, using musculoskeletal criteria, three generalized regions were identified: the palatal, temporal, and orbitotemporal regions. According to their relationship to the nerves (*nervus trigeminus*) and vessels, there are four separate groups of muscles: *M. constrictor internus dorsalis*, *M. adductor mandibulae internus*, *M. adductor mandibulae externus*, and *M. adductor mandibulae posterior*, but we concentrate mainly on the adductor musculature (Holliday and Witmer 2007). The latter is an important complex of muscles that also includes the *M. pseudotemporalis*, *M. pterygoideus*, and *M. intramandibularis* (the latter sensu Iordansky 1964, 2000). In crocodylians the dorsal and ventral parts of the *M. pterygoideus* form the bulk of the jaw adductors.

### *Musculus adductor mandibulae externus*

In crocodiles, the three typical partitions (superficial, medial, and deep) arise on the dorsal region of the temporal fossa, medial surfaces of the postorbital and squamosal, and ventral surface of the descending process formed by quadratojugal and quadrate, respectively. The vertically orientated fibres insert primarily on the dorsal and lateral surfaces of the surangular (Holliday and Witmer 2007). Among birds, there are two partitions, *Musculus adductor mandibulae externus* (MAME) rostralis and MAME profundus, and the MAME medialis is not sufficiently distinct to be reliably identified in birds. The MAME arise on the lateral surface of the parietal, laterosphenoid, squamosal,

and dorsolateral surfaces of quadrate otic process and insets on the dorsolateral surface of the coronoid process of the lower jaw, the lateral surface of the latter, and the lateral mandibular process (Holliday and Witmer 2007). This muscle is very complex, including numerous aponeuroses and branches in excess of that observed in crocodiles, making it difficult to establish homologies. In lizards, this muscle is differentiated into superficial, medial, and profundus layers; but in some forms such as *Gekko*, all are more or less confluent. It occupies all the temporal fossa that arise on the rostralateral, rostromedial, and ventromedial surfaces of the squamosal, the caudolateral surface of the parietal, and the ventromedial site of the postorbital. It inserts on the dorsolateral surface of the surangular and the coronoid process. In aetosaurs, the attachment area is undivided (Level I inference) (Fig. 1a).

### *Musculus adductor mandibulae posterior*

In crocodiles, this muscle attaches to most of the quadrate, often by tubercles and a specific crest (Iordansky 1964: crest A and B), and inserts on the medial aspect of the lower jaw, to the medial side of the surangular, dorsal surface of the angular, the Meckelian fossa, and the anterior surface of the articular. In Neornithes this muscle arises in the quadrate body, but in some neoavians this muscle attaches in the proximal region of the orbital process (Elzanowski 1987). It inserts on the caudodorsomedial and caudodorsal surface of the mandible, just posterior to the aponeurosis C (sensu Drongelen and Dullemeijer 1982) from the MAME or mandibular attachments of the MAME profundus. The attachment of this muscle varies greatly among neoavians, from positions in the caudal medial mandibular fossa to large lateral mandibular attachments (Holliday and Witmer 2007). In lizards, this muscle is rather constant, because it arises from the quadrate and inserts well posterior on the medial surface of the lower jaw. In *Neoaetosauroides*, the anterior surface of the articular and the Meckelian fossa bear several striations and bulges that presumably represent the site of attachment for this muscle (Level II inference) (Fig. 1a).

### *Musculus adductor mandibulae internus*

*Muscle pseudotemporalis* (MAMIP) In crocodiles, this is a short muscle that runs from the caudodorsal surface (*M. pseudotemporalis superficialis* sensu Holliday and Witmer 2007) of the laterosphenoid to the dorsomedial surface of the CT, ventrally. On the ventrolateral surface of the laterosphenoid lateral bridge arises the MAMIP profundus (sensu Holliday and Witmer 2007) and attaches on the dorsal crest of the angular, specifically to the lateral surface of aponeurosis V (sensu Drongelen and Dullemeijer

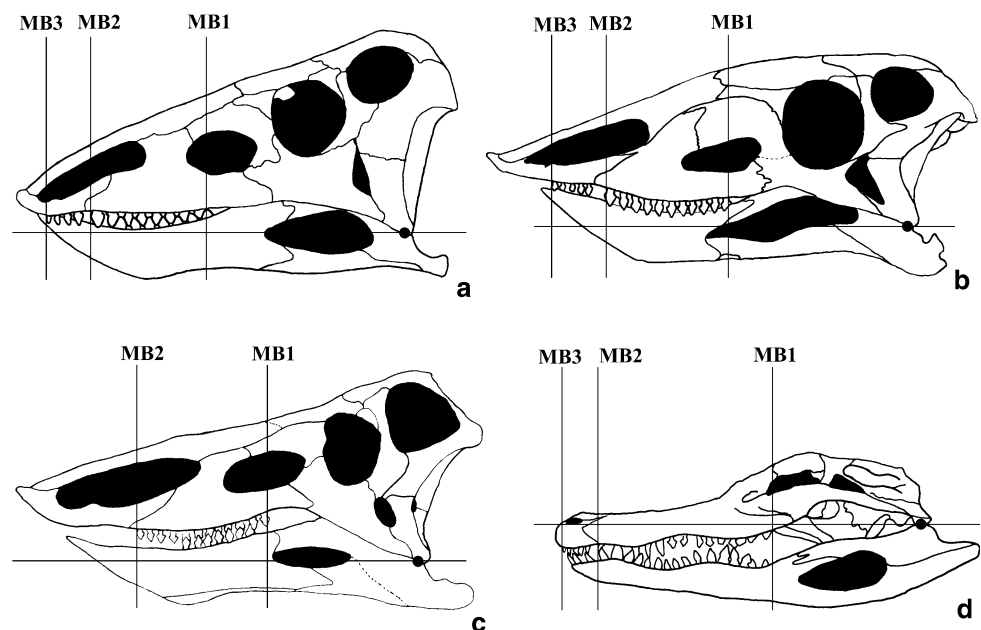
1982), that forms the ventral border of the fenestra. In Neornithes the *M. pseudotemporalis* is divided into the *M. p. superficialis* and *M. p. profundus*. As in crocodiles, the former muscle is an adductor of the lower jaw and originates on the posterior wall of the orbit (rostradorsolateral surface of laterosphenoid) and inserts on the medial surface of the coronoid process by means of a strong tendon. The *M. p. profundus* originates on the rostral surface and the anterior ventral edge of the quadrate orbital process, and attaches to the ventromedial surface of the coronoid process and dorsal to the medial mandibular fossa. In lizards, the MAMIP is bipartite, arising on the lateral surface of the prootic, rostrolateral surface of the parietal, and the dorsal extremity of the epipterygoid, and inserting on the coronoid process. As discussed above, the insertions of the MAMIP in crocodiles and birds are different; thus in aetosaurs (Fig. 1b) we inferred the insertion of this muscle on the CT, as in crocodiles, and without a coronoid process as in Lepidosauria and Neornithes (Level II inference).

***Musculus intramandibularis*** This robust muscle lies for the greater part in the cavity of the lower jaw and fixes the position of widely opened jaws in crocodiles. The fibres run from the ventral surface of the CT to the medial surface of the dentary, angular, coronoid, splenial, and the dorsal surface of Meckel's cartilage. In birds (e.g. Ratites) a thin intertendon connects *M. pseudotemporalis* and *M. intramandibularis*. In lizards, as in turtles, the *M. pseudotemporalis* forms the intramandibular muscle (Haas 1973). The posterior adductor generally originates from the anterior aspect of the quadrate, and inserts directly into the adductor fossa. Its anterior extension into Meckel's canal may result in the formation of an intramandibular muscle (Rieppel

2002). In aetosaurs, the place of origin was estimated on the CT (Fig. 1c), whereas the insertion on the lower jaw is evidenced by scars (Level II inference).

***M. pterygoideus (MAMIPT)*** The dorsal and ventral pterygoid muscles form the bulk of the jaw adductors in crocodiles. The former runs from a vast area of attachment between the orbit and the jugal, immediately caudal to the nasal cavity and dorsomedial surface of the maxilla, palatine, pterygoid, ectopterygoid, and ventral surface of interorbital septum, to the caudomedial and ventromedial surface of angular and articular of the lower jaw (aponeurosis V). The ventral part runs from the caudomedial and caudolateral edge of the pterygoid to the medial surface of the caudoventral area (caudoventral edge of the angular, caudolateral surface of the angular and the surangular) of the lower jaw. In Neornithes, despite slight taxonomic differences in muscle morphology, the *M. pterygoideus dorsalis* consistently runs from the dorsal and lateral surfaces of the palate (palatine and pterygoids) to the medial surface of the lower jaw either immediately rostral or ventral to the medial cotyla of the jaw joint (Holliday and Witmer 2007, p 466); whereas, the *M. pterygoideus ventralis* arises in the ventral surface of the palatine and pterygoid and attaches to the lateral surface of the lower jaw, as in crocodylians. In lizards, the dorsal part of this muscle arises by means of a short and thick tendon located on a depression on the external lateral border of the pterygoid; it reaches the contact region with the ectopterygoid and caudal surface of the interorbital septum, and inserts on the caudomedial surface of the articular and the angular. The ventral part arises on the ventral edge of pterygoid and quadrate by different

**Fig. 3** Moment arms of the bite points in **a** *Neoaetosauroides* (modified from Desojo and Báez 2007) **b** *Stagonolepis* (modified from Walker 1961) **c** *Desmatosuchus* (Modified from Small 2002) **d** *Alligator* (modified from Kardong 2002). Abbreviations: *MB1*, *MB2*, and *MB3*, moment arms at the distal, middle, and proximal teeth; black circle pivot



**Table 1** Moment arms (MA) of the *Musculus adductor mandibulae externus* (MAME), *Musculus adductor mandibulae posterior* (MAMP), *Musculus adductor mandibulae internus pseudotemporalis*(MAMIP), *Musculus intramandibularis* (MI), *Musculus adductor mandibulae internus pterygoideus* (MAMIPT), sum of adductor muscles (MA), and *Musculus depressor mandibulae* (MDM)

Taxon	MAME + MAMP	MAMIP	MI	MAMIPT	MA	MDM
<i>N. engaeus</i>	20 (19.3%)	36 (34.6%)	36 (34.6%)	12 (11.5%)	104	11
<i>S. robertsoni</i>	23 (19.3%)	38 (31.9%)	39 (32.7%)	19 (15.9%)	119	9
<i>D. haplocerus</i>	26 (24.05%)	30 (28.3%)	34 (32%)	16 (15.09%)	106	13
<i>A. mississippiensis</i>	20 (24.09%)	28 (33.7%)	19 (22.8%)	20 (24.09%)	83	8

The data are in millimetres and the numbers in the parentheses are their contribution to the total MA as a percentage

**Table 2** Comparison of the moment arms of the jaw muscles and bite points in aetosaurs and crocodylians

Taxon	MB1	MB2	MB3	R1	R2	R3	ΣR	X
<i>N. engaeus</i>	68	107	123	1.53	0.97	0.85	3.35	1.12
<i>S. robertsoni</i>	62	105	123	1.92	1.13	0.97	4.02	1.34
<i>D. haplocerus</i>	50	96	N/C	2.12	1.10	N/C	3.22	1.61
<i>A. mississippiensis</i>	52	112	124	1.60	0.74	0.67	3.01	1

MB1, MB2, and MB3, moment arms of the bite points at the distal, middle, and proximal teeth, respectively. R, ratio of muscle/bite, that is, the sum of moment arm of the adductor muscles (MA) divided by MB1, MB2, and MB3. ΣR, sum of the ratio. X, average; N/C, not compared (teeth are not present). The data are in millimetres

aponeuroses and inserts in the caudoventrolateral surface of the articular and angular, the lateral surface of jugal, and the postorbital. It was very difficult to determine the origin and insertion places for this muscle in aetosaurs (Fig. 2), so the place of the aponeurosis V was arbitrarily estimated (Level III' of inference).

#### Depressor group

##### *Musculus depressor mandibulae* (MDM)

Crocodylians jaws are opened by this strong abductor muscle. Its parallel fibres originate on the occipital surface of the skull on the squamosal, quadrate, and lateral tip of the paroccipital process, and it attaches to a concave antero-medial surface of the dorsomedially curved articular. In Tinamous birds this muscle consist of three parts: *Pars profunda*, *P. medialis*, and *P. superficialis*. They arise on the cranium (squamosal section of the braincase between *Fossa temporalis* and *Cripta nuchalis*) and insert on the *Fossa caudalis* of the lower jaw. In lizards, this muscle shows two morphologies: undivided and divided. In those taxa with an undivided muscle, the anterior fibres originate at the supraoccipital and the posterior fibres on the *spinalis capitis*; this muscle inserts on the retroarticular process of the mandible. In *Neoaetosauroides*, the supraoccipital, squamosal, and the well-developed retroarticular process show several muscle scars (Fig. 1e), so we inferred the presence of this muscle (Level I inference).

#### Jaw mechanics

Results of the analysis of moment arms are shown in Figs. 2, 3 and Tables 1, 2. The sum of the moment arms (MA) of the aetosaurian adductor musculature shows similar values, with *Neoaetosauroides* and *D. haplocerus* nearly equal, and approximately 10% lower than *S. robertsoni*. The widest difference is between aetosaurs and the short-snouted crocodile *A. mississippiensis*, the value for which is nearly 20% lower than the lowest value for aetosaurs (Table 1).

Another important feature analysed is the proportion by which different muscles contribute to the MA (Table 1). In aetosaurs the MAMIP and *Musculus intramandibularis* (MI) (Fig. 1b, c) are the muscles that contribute in the largest proportion (both around 34%), while MAMIPT (Fig. 1d) is the one with the lowest value, with MAME + MAMP somewhere in the middle (Fig. 1a). Compared with aetosaurs, the contribution of MAMIPT to MA in crocodylians is greatly increased (approximately 24%), whereas the MI is about 30% lower (Fig. 2d). Within aetosaurs, *N. engaeus* has the highest proportion of MI and MAMIP, and the lowest for the MAMIPT, whereas the lowest in *D. haplocerus* and *S. robertsoni* is similar (Table 1). However, *D. haplocerus* has the highest proportion of the MAME + MAMP and the lowest of MAMIP for the aetosaurs.

Considering the ratios of muscle moments to bite moments (i.e. the combined moment arms of the adductor muscles divided by the moment arms around the anterior, middle, or posterior tooth position) (Fig. 3), the ratio of the most anterior maxillary tooth (R2) in the short-snout crocodile is the lowest, and the posterior values (R1) in aetosaurs are higher than in *A. mississippiensis*, except in *Neoaetosauroides* (Table 2).

Within aetosaurs, *D. haplocerus* has the highest posterior value (R1), whereas *Neoaetosauroides* has the lowest. With regard to the most anterior value (R2), *D. haplocerus* and *S. robertsoni* have similar values, higher than that for *Neoaetosauroides*. The anterior value (R3) was not calculated for *D. haplocerus* because this taxon lacks premaxillary teeth (Fig. 3c). In the remaining taxa R3



is highest in *A. mississippiensis*, and lower in *N. engaeus* than in *S. robertsoni* (Table 2).

## Discussion

Although aetosaurs were among the most common members of the Late Triassic continental fauna, until now palaeobiological interpretations were based only on qualitative data, probably because of to the scarcity of well-preserved cranial remains. However, there are several complete skulls of species of different ages from the northern and southern continents. This enabled us to perform the first comparative biomechanical analysis of the jaw apparatus in extinct crurotarsan archosaurs based on *Neoaetosauroides*, *D. haplocerus*, and *S. robertsoni* (Fig. 2).

The skull of *Neoaetosauroides* does not depart significantly from the standard model for aetosaurs. However, there are some differences in the dentition, for example shape, number, size, presence of serrations and wear facets, and position and shape of the mandibular articular facet, which might enable significant speculation on their biological role, as will be discussed below. Although some features (e.g. shape of the glenoid cavity) suggest some lateral component in mandibular movements, this cannot be measured with the approach applied here. The subject certainly requires more detailed analysis in the future. The biomechanical analysis performed herein was partially based on the comparison with the short-snout, 3–4.5 m long crocodile *A. mississippiensis*, one of their closest living relatives, although with a quite different design. The akinetic crocodilian skull is flatter and longer than in aetosaurs, and the snout is longer, more than half of the skull length (Fig. 2d). It also lacks the shovel-shaped premaxilla that is present in many aetosaurs (except in *Aetosaurus*). The symphyseal area is shorter and broader than that of aetosaurs, and the mandibular articular facet is dorsal to the dentary tooth row in *A. mississippiensis*, whereas it is ventral in aetosaurs. In addition, the homology of some of the muscles considered herein is not clear, such as the *M. adductor mandibulae internus pseudotemporalis* (MAMIP), the homology of which in crocodiles and birds is very difficult to establish. Moreover, in the former the position of the line action is vertical, whereas in aetosaurs it is oblique (Fig. 2a–c).

The analysis of the aetosaurian skull indicates a design in which the total leverage of the inferred jaw musculature provides force rather than speed (Table 1). This result for the supposedly herbivorous aetosaurs may appear incongruent when compared with the adult *A. mississippiensis*, an animal that feeds on large turtles and mammals, for example deer and hogs, and in which the bite-force

performance was measured as the highest for any living animal (Erickson et al. 2003). The clue for understanding this apparent contradiction, based on the different cranial structure, might come from analysis of behaviour and the evidence provided here. It seems obvious that the jaw of *A. mississippiensis* has to be at the same time fast, to catch the animals, that are being chased at the border of the water, and strong, to retain them until they die. The high leverage of the *M. adductor mandibulae internus pterigoideus* in this species (Table 1), in contrast with the low values in aetosaurs, suggests a great contribution of this muscle to keeping the mandibles closed, in addition to the remaining musculature (Fig. 2d). Moreover, the long-snouted species have a relatively smaller *M. adductor mandibulae internus pterigoideus* than the short-snout crocodiles, related to lower masticatory power for fish-eating in the former species (Endo et al. 2002).

Some authors (e.g. Iordansky 1964) have suggested that the MAMP prevents dislocation of the mandible joint in crocodiles with MAMIP *profundus*, because its line of action passes very close to the pivot. However, Busbey (1989) reported that the MAMP must perform both roles simultaneously, adduction and maintaining the integrity of the jaw joint during capture and crushing. Although some aspects of the alligator bite have been studied in detail by the latter author, there are some differences from the electromyographic analysis conducted by Drongelen and Dullemeijer (1982) and Cleuren and De Vree (1992) in other taxa of crocodiles, and much remains to be done on the form, function and performance, ecology, and even evolution of crocodilian feeding (Erickson et al. 2003). Furthermore, the diet of the alligator depends upon the availability of the prey, the geographic location and salinity of the habitat, and the size and age of the specimen (Busbey 1989). For example, the long-snouted crocodiles have a relatively smaller *M. adductor mandibulae internus pterigoideus* than the short-snout species, related to a lower masticatory power for fish-eating in the former (Endo et al. 2002).

Within aetosaurs, the high ratios of muscle moment arms to bite moments indicate stronger bites in the northern Hemisphere *D. haplocerus* and *S. robertsoni*, and faster ones in the South American *N. engaeus* (Table 1). These differences, coupled with the presence of wear facets and serrations, and lower skulls, indicate more developed crushing, chopping, and slicing capacities, especially at the back of the tooth series for the first two taxa, and it opens a window to consider different abilities in which speed is involved for *N. engaeus*. These capacities have been already suggested for *S. robertsoni* by Walker (1961) and for *D. haplocerus* by Small (2002) in relation to herbivorous habits, grubbing for soft vegetation and roots, although possibly including some invertebrates in the diet.

Moreover, the higher value for the MAME + MAMP in *D. haplocerus*, the dorsolateral position of supratemporal fenestra, and the absence of premaxillary teeth support different dietary habits.

Unfortunately, there are no appropriate analogues among extant archosaurs, even considering the vast diversity of birds, the latter being completely edentulous. However, the dietary habits mentioned above were considered likely in view of the morphologic parallelisms with living armadillos (Dasypodidae) among mammals, both being armoured forms with edentulous snouts, peg-like teeth, and digging limbs, as suggested by Bonaparte (1978), despite the fact that living armadillos are smaller than aetosaurs (the largest being the ca. 1.5 m long giant armadillos *Priodontes maximus* Kerr). Recently, a revision of *D. haplocerus* by Small (2002) emphasizes the importance of considering parallelism between aetosaurs and armadillos, a subject that will be further developed below. The mandibles of *Neoaetosauroides* are faster than the other aetosaurs (Table 1), and require additional analysis. In herbivorous mammals, fast mandibles are broadly correlated with cropping abilities. This is essentially true for the front of the jaws, which usually bear incisors, and not for the back, where the molars are placed primarily for crushing. As for the aforementioned fast mandibles and feeding behaviour of crocodiles, fast mandibles also suggest carnivory, because they improve the capacity to catch moving prey, although with the help of some sort of fangs. In this context, the edentulous snout in *Neoaetosauroides* indicates that specialised carnivory should be excluded as a working hypothesis. However, this would not be the case if we consider carnivory *sensu lato*, i.e. not in a top predatory sense but feeding on any sort of animal source, better defined as animalivory (see below), as a possible feeding style for this aetosaur. Actually, there are many tetrapods that feed mainly on animals and do not have specialised fangs (e.g. some living amphibians, turtles, birds, etc.). Traditionally, aetosaurs have been interpreted as herbivores based on several cranial features (Figs. 1–3), such as simple conical teeth, mandibular articulation below the tooth row, and edentulous anterior regions of the lower and upper jaws, indicating the possible presence of a keratinous beak in life (Walker 1961; Parrish 1994). Also the relatively massive limbs of all aetosaurs and, especially, the hypertrophy of muscular trochanters were suggested as indications of increased muscle power related to probably predominantly burrowing herbivore habits. However, there are significant differences among aetosaur taxa, such as in dental characters (e.g. number, shape, and size of teeth, presence and position of the premaxillary teeth, presence of serrations and wear facets), position of the supratemporal fenestra (e.g. dorsolateral in *Desmatosuchus* and completely lateral in *Neoaetosauroides*), location of the jaw

joint in relation with the tooth row (e.g. closely below it in *Neoaetosauroides* and well below it in *Desmatosuchus*), and shape of the lower jaw (e.g. lower and longer in *Desmatosuchus* and *Stagonolepis* than in *Neoaetosauroides* and *Longosuchus*) (Fig. 2). The tooth morphology of *Neoaetosauroides* differs from the slightly laterally compressed leaf-like teeth of *D. haplocerus* and *S. robertsoni*. Moreover, unlike the latter taxa, *Neoaetosauroides* does not show evidence of dental serrations or wear facets. These structures appear in various combinations and both occur in herbivorous and carnivorous animals (Small 2002). In contrast, the absence of serrations and wear facets would be consistent with a relatively soft and non-abrasive diet, for example soft leaves and/or larvae and insects (e.g. bees, ants, wasps, termites) without hard skeletal structures (Mancuso et al. 2007). Another important difference with *D. haplocerus* is that this species lacks premaxillary teeth (Fig. 2), whereas *Neoaetosauroides* has four anteriorly placed premaxillary teeth on each upper jaw (Desojo and Báez 2007).

The presence of a keratinous beak has been suggested for aetosaurs by several authors (Walker 1961; Parrish 1994; Gower and Walker 2002), but there is no direct evidence for it, such as thickened anterior ends of the premaxilla and dentary, openings for the vessels and nerves aligned vertically at the anterior portion of the snout, especially on the premaxilla and dentary bones, and sharp margins of the premaxilla, maxilla, and dentary. In *Neoaetosauroides* the presence of anterior premaxillary teeth rules out the presence of a beak, as there is no record of the coexistence of these features in any tetrapod. Although a horny beak was probably present in the putatively herbivorous dicynodonts, rhynchosaurs, and ornithischian dinosaurs (e.g. Ankylosauridae, Hypsilophodontidae, Hadrosauridae), the presence of this structure alone is not indicative of a herbivorous habit.

The mentioned analogy of aetosaurs with living armadillos (Bonaparte 1978) deserves attention. Recently, there has been some progress in the understanding of armadillo morphology and biomechanics, and their correlation with diet, enabling inferences for extinct forms (Vizcaíno et al. 2004). Redford (1985) noted that all living armadillos consume a substantial amount of animal material, stating that they “show a range of trophic specialization from the generalised carnivore-omnivore through the generalist insectivore to the specialist insectivore” (Redford 1985, p 429). Even living euphractines (ca. 6 kg) that constitute Redford’s (1985) carnivore-omnivore group are characterised by a diet that includes many types of plant material (e.g., roots and tubers, nuts of a low palm) mixed with a variety of animal matter that ranges from ants and carrion to birds and mice. Here we follow Vizcaíno et al. (2004) in the use of animalivory instead of carnivory to point out the

tendency to prefer food from an animal source for these armoured mammals, within a generalised omnivory. The animalivores, including fossil taxa, range from ant or termite-feeding specialists (usually referred as mymercophagous) to forms that could have easily preyed on hare-sized animals (for an overview on the matter see Vizcaíno et al. 2004; Vizcaíno et al. 2006; McDonald et al. 2008).

This work is a contribution to understanding the paleobiology and evolution of this intriguing group of crurotarsan archosaurs, though their position within the Crurotarsi is still debated (Serenó and Arcucci 1990; Parrish 1993; Juul 1994; Gower and Wilkinson 1996; Brochu 2001; Gower and Walker 2002). However, many questions remain to be answered. The skull of *A. mississippiensis* is designed to experience discontinuous extremely high peaks of strain, whereas the skull of other amniotes, for example primates, might have been designed to resist more continuous, but lower, strain (Ross and Metzger 2004). In this context, are the aetosaurs designed to resist constant low strain better than sporadic high strain in relation to omnivore rather than specialised carnivore habits? Do the different aetosaur taxa show differences in strain resistance? In relation to the latter, it might be possible that some aetosaur taxa, for example *Neoaetosauroides* and *Longosuchus*, were insectivorous, exploiting a food source that was widespread in continental environments throughout the Triassic (Marsicano et al. 2001; Small 2002; Hasiotis 2003). Moreover, it also enables consideration of the structure and function of ancient ecosystems and the ways in which they compare with those from the Recent.

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