Reassessment of the Aetosaur 'Desmatosuchus' chamaensis with a reanalysis of the phylogeny of the Aetosauria (Archosauria: Pseudosuchia)

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SYNOPSIS Study of aetosaurian archosaur material demonstrates that the dermal armour of *Desmatosuchus chamaensis* shares almost no characters with that of *Desmatosuchus haplocerus*. Instead, the ornamentation and overall morphology of the lateral and paramedian armour of '*D.*' *chamaensis* most closely resembles that of typothoracisine aetosaurs such as *Paratypothorax*. Autapomorphies of '*D.*' *chamaensis*, for example the extension of the dorsal eminences of the paramedian plates into elongate, recurved spikes, warrant generic distinction for this taxon. This placement is also supported by a new phylogenetic hypothesis for the Aetosauria in which '*D.*' *chamaensis* is a sister taxon of *Paratypothorax* and distinct from *Desmatosuchus*. Therefore, a new genus, *Heliocanthus* is erected for '*D.*' *chamaensis*. Past phylogenetic hypotheses of the Aetosauria have been plagued by poorly supported topologies, coding errors and poor character construction. A new hypothesis places emphasis on characters of the lateral dermal armour, a character set previously under-utilised. Detailed examination of aetosaur material suggests that the aetosaurs can be divided into three groups based on the morphology of the lateral armour. Whereas it appears that the characters relating to the ornamentation of the paramedian armour are homoplastic, those relating to the overall morphology of the lateral armour may possess a stronger phylogenetic signal.

KEYWORDS *Heliocanthus*, Aetosauria, Chinle Formation, phylogeny, vertebrate palaeontology, Late Triassic, New Mexico

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Introduction

Aetosaurs are quadrupedal, heavily armoured, possibly omnivorous, pseudosuchian archosaurs common in Late Triassic terrestrial deposits worldwide. They are characterised by an extensive bony carapace, consisting of four dorsal rows of quadrangular osteoderms (plates) that extend from just behind the skull to the tip of the tail. The four rows include two paramedian rows, which span the midline of the body, and two outside or lateral rows (e.g. Walker 1961: fig. 23a). These paramedian and lateral plates are further divided into regions based upon the type of vertebrae that they cover (e.g. dorsal paramedian plates cover the dorsal vertebrae). Some aetosaur taxa also possess ventral armour. Aetosaur armour from all body regions is ornamented and, in some taxa, spines are present.

Long & Ballew (1985) were the first to document the taxonomic utility of aetosaur plate ornamentation and they argued that aetosaurs were much more diverse than had been previously recognised, especially in the southwestern United States. As a result of this recognition, most aetosaur taxa are now diagnosed mainly by using characters of the armour (Heckert & Lucas 2000). Taxa originally based almost solely on recovered armour plates include *Stagonolepis* Agassiz, 1844, *Typothorax* Cope, 1875 and *Paratypothorax* Long & Ballew, 1985.

Cope (1892) described *Episcoposaurus haplocerus* on the basis of a partial skeleton from the Tecovas Formation, in Crosby County Texas. In 1920, E. C. Case described another aetosaur, *Desmatosuchus spurensis*, from the same general horizon and area. Gregory (1953) re-examined these type specimens and argued that *E. haplocerus* and *D. spurensis* were synonymous. Furthermore, Gregory proposed that the type species of *Episcoposaurus*, *E. horridus*, was synonymous with *Typothorax coccinarum*, thus invalidating the genus *Episcoposaurus*. Therefore, *E. haplocerus* was assigned to the next available genus, *Desmatosuchus* Case, 1920.

Paratypothorax andressi was described from a series of aetosaur plates from the Stubensandstein of Germany that were previously attributed to the phytosaur '*Phytosaurus*' (Meyer 1861; Gregory & Westphal 1969; Long & Ballew 1985). Because the species name honours the 'Andress family', Heckert (1997) emended the binomen for this taxon to *Paratypothorax andressorum*. A partial carapace from the Petrified Forest National Park of Arizona, USA, as well as many isolated armour plates from the southwestern United States with paramedian armour that is nearly identical to the German material, have been referred to *Paratypothorax* sp. by Long & Murry (1995) and Hunt & Lucas (1992).

Zeigler *et al.* (2003a) described a purported new species of *Desmatosuchus*, *D. chamaensis*, from the Snyder Quarry of northern New Mexico. The Snyder Quarry occurs in the Petrified Forest Member of the Chinle Formation (= Painted Desert Member of the Petrified Forest Formation of Lucas 1993), which is generally considered to be Norian in age, based upon the occurrences of *Typothorax coccinarum* and the phytosaur *Pseudopalatus buceros* (Lucas 1998). Based on the recovery of new topotype material from the Snyder Quarry, Heckert *et al.* (2003) reinterpreted the type materials of '*Desmatosuchus*' *chamaensis*. Both Zeigler *et al.* (2003a) and Heckert *et al.* (2003) assigned these materials to *Desmatosuchus*, based upon ostensible similarities between their new form and *D. haplocerus*. Similarities include the hypothetical presence of spikes on the lateral cervical armour, random pitting on the dorsal paramedian armour and the perceived occurrence of a thin anterior lamina on the anterior regions of the paramedian and lateral armour. They provided no phylogenetic analysis to support their assignment of '*D.*' *chamaensis* to *Desmatosuchus*.

Previously published phylogenies of the Aetosauria (Parrish 1994; Heckert *et al.* 1996; Heckert & Lucas 1999) have been plagued by coding inconsistencies, published typographic errors and overall poor character support in published trees (Harris *et al.* 2003a). Thus, relationships among aetosaurian taxa remain ambiguous.

Institutional abbreviations

ANSP, Academy of Natural Sciences, Philadelphia, USA; **DMNH**, Dallas Museum of Natural History, Texas, USA; **MNA**, Museum of Northern Arizona, Flagstaff, USA; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, USA; **PEFO**, Petrified Forest National Park, Arizona, USA; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TTUP**, The Museum at Texas Tech University, Lubbock, Texas, USA; **UCM**, University of Colorado Museum, Boulder, Colorado, USA; **UMMP**, University of Michigan Museum of Palaeontology, Ann Arbor, Michigan, USA.

Systematic palaeontology

ARCHOSAURIA Cope, 1869 *sensu* Gauthier, 1986

PSEUDOSUCHIA Zittel, 1887–1890 *sensu* Gauthier, 1986

AETOSAURIA Marsh, 1884

STAGONOLEPIDIDAE Lydekker, 1887 *sensu* Heckert & Lucas, 2000

TYPOTHORACISINAE nov.

Diagnosis. See Taxonomic definitions, below.

PARATYPOTHORACISINI nov.

Diagnosis. See Taxonomic definitions, below.

Genus ***HELIOCANTHUS*** gen. nov.

Type species. *Heliocanthus chamaensis* (Zeigler *et al.* 2003a). Note: Although the publication by Zeigler *et al.* is imprinted 2002, it was actually not published until the Spring of 2003. Therefore, following the ICZN recommendation

22A.2.2, this reference is cited as Zeigler *et al.* (2003*a*) throughout this paper (ICZN 1999).

DIAGNOSIS. As for the only species, see Revised diagnosis, below.

DISTRIBUTION. Petrified Forest Member, Chinle Formation, New Mexico and Arizona, USA; Bull Canyon Formation, Dockum Group, New Mexico, USA. The Petrified Forest Member was restricted by Woody (2003) to contain only the informal lithological unit previously named the upper Petrified Forest Member by Akers *et al.* (1958).

ETYMOLOGY. From '*helios*,' Greek for sun, and '*acanthus*,' Greek for spike. Refers to spikes rising from the posterior paramedian armour and also honours the state of New Mexico, from which the holotype was collected, whose state emblem is a 'spiky' sun (Zia Pueblo symbol).

Heliocanthus chamaensis (Zeigler *et al.*, 2003*a*)
(Figs 1–8)

  1985 *Desmatosuchus* sp.; Carpenter & Parrish: 197–198.
  1986 *Desmatosuchus* sp.; Parrish & Carpenter: 152, fig. 11.3.
  2000 *Desmatosuchus* n. sp.; Zeigler *et al.*: 46.
  2001 *Desmatosuchus* n. sp.; Hunt: 139.
2003*a* *Desmatosuchus chamaensis*; Zeigler *et al.*: 215–219, fig. 2.
  2003 *Desmatosuchus chamaensis*; Heckert *et al.*: 115, figs 2–8.
  2003 *Desmatosuchus chamaensis*; Zeigler: 49–62, figs 6e, 11.
2003*b* *Desmatosuchus chamaensis*; Zeigler *et al.*: 2–3.
2003*c* *Desmatosuchus chamaensis*; Zeigler *et al.*: 71–79.
  2005 *Desmatosuchus chamaensis*; Heckert & Jenkins: 319.
2005*a* *Desmatosuchus chamaensis*; Heckert *et al.*: 27, 36, 37.
2005*b* *Desmatosuchus chamaensis*; Heckert *et al.*: 305, 311, 313–314.
  2005 *Desmatosuchus chamaensis*; Lucas *et al.*: 170, 177.
  2005 '*Desmatosuchus*' *chamaensis*; Parker & Irmis: 49, figs 4f–h.
  2005 *Desmatosuchus chamaensis*; Zeigler *et al.*: 344, 349, figs 3c, 7.

HOLOTYPE. NMMNH P-32793, right anterior caudal paramedian plate (Zeigler *et al.* 2003*a*: fig. 2d).

TYPE HORIZON AND LOCALITY. Snyder Quarry, NMMNH locality 3845, northwest of Abiquiu, Rio Arriba County, New Mexico, USA, Petrified Forest Member, Chinle Formation, Late Triassic (Norian).

PARATYPES. NMMNH P-29045, partial anterior caudal paramedian plate; P-31295, right pelvic lateral plate; P-32795, right anterior mid-caudal paramedian plate; P-32796, left anterior caudal lateral plate; P-32797, partial right mid-dorsal paramedian plate; P-33099, right anterior mid-caudal paramedian plate; P-33100, partial anterior mid-caudal paramedian plate, all from the Snyder quarry (Zeigler *et al.* 2003*a*).

TOPOTYPES. NMMNH P-32794, partial left anterior lateral plate; P-33101, left anterior mid-caudal paramedian plate; P-33820, left mid-dorsal paramedian plate; P-34887, right

mid-dorsal paramedian plate; P-34891, left pelvic lateral plate; P-34892, left anterior caudal lateral plate; P-35201, left anterior caudal lateral plate; P-35349, partial dorsal lateral plate; P-35436, right posterior dorsal paramedian plate; P-35459, left anterior caudal paramedian plate; P-35806, partial right mid-dorsal paramedian plate; P-35807, left mid-dorsal paramedian plate; P-35991, left posterior mid-caudal paramedian plate; P-35993, partial anterior right lateral plate; P-36052, left anterior caudal paramedian plate; P-37300, partial left pelvic lateral plate; P-37348, partial mid-dorsal paramedian plate; P-37349, partial left pre-pelvic paramedian plate; P-39184, partial left (?) caudal lateral plate; P-39520, left anterior caudal lateral plate; P-40395, left dorsal pre-pelvic lateral plate, all from the Snyder quarry (Heckert *et al.* 2003).

REFERRED MATERIAL. NMMNH P-4894, partial posterior dorsal or pelvic paramedian plate (Zeigler *et al.* 2003*a*: fig. 2c); UCM 47725, right mid-caudal paramedian plate (Parrish & Carpenter 1986: fig. 11.3; Zeigler *et al.* 2003*a*: figs 2h,i), both from the Bull Canyon Formation of New Mexico. NMMNH P-35206, left cervical or anterior dorsal paramedian plate (Heckert *et al.* 2003: fig. 7d); NMMNH P-35991, left mid-caudal paramedian plate (Heckert *et al.* 2003: fig. 7c); and NMMNH P-35357, left mid-caudal paramedian plate all from the Snyder Quarry, Petrified Forest Member of New Mexico. PEFO 31162, anterior caudal paramedian plate; PEFO 34040, right (?) pelvic lateral plate fragment; PEFO 34263, plate fragment; and UCMP 129829, right dorsal paramedian plate, all from the Karen's Point Locality (PFV 075), Petrified Forest National Park, Petrified Forest Member, of Arizona.

AGE AND DISTRIBUTION. Petrified Forest Member, Chinle Formation, New Mexico and Arizona, USA; Bull Canyon Formation, Dockum Group, New Mexico, USA. Upper Triassic (Norian).

REVISED DIAGNOSIS. Aetosaur that differs from all other aetosaurs by the presence of posterior dorsal and anterior caudal paramedian plates with a distinct dorsal eminence, which takes the form of an elongate, gracile, recurved, antero-medially directed spike. In addition, *H. chamaensis* has a unique combination of the following character states: (1) anterior dorsal paramedian plates with a reduced eminence, occurring either as a very short, anteriorly recurved spike or a very low, rounded knob; (2) dorsal eminence of cervical and paramedian plates situated just lateral to the medial edge of the plate, being strongly offset as in *Paratypothorax* and *Tecovasuchus*; (3) ornamentation of the paramedian plates consists of elongate grooves, ridges and pits, radiating from the dorsal eminence as in all aetosaurs except *Desmatosuchus* and *Typothorax*; (4) anterior dorsal and posterior cervical armour crescentic in dorsal view as in *Typothorax*, *Stagonolepis* and, probably, *Paratypothorax*; (5) lateral plates possess incised grooves radiating from the eminence as in *Paratypothorax*; (6) mid-caudal paramedian plates equant in shape with a strong anterior bar and robust, short, hook-like eminence, which contacts the posterior margin of the plate; (7) anteromedial corner of paramedian plates possesses a small, sharp process that projects anteriorly as in *Stagonolepis*, *Typothorax* and *Paratypothorax*; (8) median edges of paramedian plates are straight whereas the lateral edges are sinuous in the dorsal and anterior caudal regions; (9) ventral surfaces of paramedian plates are flat and smooth except for a

slight emargination beneath the dorsal eminence; (10) dorsal lateral plates possess two distinct flanges at an acute angle that meet to form an elongate, slightly recurved spine that projects laterally as in *Paratypothorax* and *Tecovasuchus* (11) spine on the dorsal lateral plates is compressed dorsoventrally with a sharp anterior edge and a rounded posterior edge; (12) pelvic and anterior caudal lateral plates are roughly triangular in dorsal view; (13) pelvic and anterior caudal lateral plates possess a sinuous medial margin and a semi-circular posterolateral edge, as in *Typothorax* and *Paratypothorax*; (14) the anterior edge of the pelvic and anterior caudal lateral plates are straight with a raised anterior bar; (15) pelvic and anterior caudal lateral plates possess a radial pattern of incised grooves from a sharp, hook-like eminence, with the plate being slightly flexed ventrally along this eminence. In the anterior caudal lateral plates the hook-like eminence projects posteriorly, overhanging the plate margin.

DESCRIPTION. Zeigler *et al.* (2003*a*) and Heckert *et al.* (2003) provided the initial descriptions of all known *Heliocanthus* material from New Mexico, USA. However, those papers contain many discrepancies regarding plate measurements and positioning, even within the same paper. For example, Heckert *et al.* (2003: fig. 6d) figured the holotype plate NMMNH P-32793 as a right presacral paramedian plate, described it on pp. 122 as a 'postero-dorsal or even anterior caudal paramedian' and then redescribed it on pp. 123 as a 'caudal paramedian scute'. In addition, the width and length given for this plate on pp. 121 are 83 mm and 184 mm, respectively, while in table 2 (Heckert *et al.* 2003: 122), the measurements for this plate are listed as 91 mm and 199 mm; on pp. 123 the measurements for the same plate are given as 99 mm and 199 mm. As a result, it is difficult to determine which data can be accepted with confidence.

According to Zeigler *et al.* (2003*a*) and Heckert *et al.* (2003) much of the *Heliocanthus* armour recovered from the Snyder Quarry was found scattered throughout the quarry with little or no association. Conversely, Zeigler *et al.* (2003*a*: 218) noted that the holotype and paratype material was uncovered within an 'area approximately one square meter in size', thus strongly suggesting that these materials do belong to a single individual. Nevertheless, because the recovered plates of *Heliocanthus* were found disarticulated it is difficult to place individual plates in specific regions of the carapace. Still, enough is known from other associated aetosaur specimens to determine overall trends in armour morphology to provide a fairly reliable reconstruction of armour placement. These general trends are as follows: (1) paramedian plates in all aetosaurs, with the exception of cervical paramedians in *Desmatosuchus*, *Lucasuchus* and *Longosuchus*, are always rectangular (wider than long), except in the mid-caudal region where they are equant in dimensions and in the distal caudal region where they are longer than wide. *Desmatosuchus*, *Lucasuchus* and *Longosuchus* possess cervical paramedians that are more equant in dimensions; but they are greatly thickened in this region effectively distinguishing them from mid-caudal plates; (2) paramedian and lateral plate ornamentation becomes more pronounced posteriorly along the carapace, being most pronounced in the pelvic and anterior caudal regions. This includes pattern incision as well as development of the dorsal eminence (e.g. *Stagonolepis*); (3) dorsal eminences on paramedian and lateral plates are always situated more posteriorly than anteriorly on the plate,

even when the eminence does not contact the posterior plate margin (e.g. *Desmatosuchus*); (4) dorsal eminences of the paramedian plates, when not centred, are situated closer to the medial edge than the lateral edge of the plate (e.g. *Paratypothorax*); (5) the smooth anterior bar or lamina is always situated on the anterior dorsal surface of the plate; (6) in many taxa the anterior bar possesses a sharp anteromedial projection that is directed anteriorly; (7) in most taxa the anterior caudal paramedians are slightly transversely arched (Long & Murry 1995) where the armour molds around the base of the tail; (8) the medial edges of the dorsal paramedian plates are always straight while their lateral edges are often sigmoidal; and (9) on many plates the posterior margin of the ventral plate surface has a thin band of longitudinal striations where the plate overlaps the anterior bar of the subsequent plate.

These criteria allow for a hypothetical placement of isolated osteoderms into the carapace when the animal is incompletely known. This methodology forms the basis for the following description. Table 1 reflects the various interpretations of the holotype and referred plates, as determined by various studies.

1. **PARAMEDIAN PLATES**

The recovered paramedian plates of *Heliocanthus chamaensis* can be divided into five distinct morphologies: cervical and anterior dorsal paramedians (Type A), mid-dorsal paramedians (Type B), posterior dorsal paramedians (Type C), pelvic and anterior caudal paramedians (Type D), and mid-caudal paramedians (Type E). Figure 1 shows the regions where these morphologies occur. Assignments of all known osteoderms of *H. chamaensis* to specific morphologies are listed in the table provided as "Supplementary data" to this paper available from Cambridge Journals Online at: http://www.journals.cup.org/abstract_S1477201906001994

• *Cervical and anterior dorsal paramedian plates (Type A)*: Only a single plate from this region is known from the type specimens, NMMNH P-35206. This plate was figured by Heckert *et al.* (2003: fig. 7D), but not described. The plate is rectangular and strongly crescentic in dorsal view, possessing concave and convex anterior and posterior margins, respectively, which is similar to the anterior paramedian plates of *Typothorax* (Martz 2002) and *Stagonolepis* (pers. obs.). This plate is smaller than more posteriorly positioned paramedian plates, measuring about 117 mm wide and 58 mm long. The plate shows a faint series of oblong, slightly radial pits with no dorsal eminence. The reduced size, faint ornamentation, lack of a dorsal eminence and crescentic shape indicate that this plate is from the cervical or anterior dorsal region. The anterior bar is robust and the medial edge is straight with the anteromedial corner of the bar projecting anteriorly. This projection closely resembles that found in *Typothorax*, *Stagonolepis* and *Paratypothorax*. In fact, this plate is so similar to those of *Typothorax* that it may actually belong to that taxon, which is found in the same quarry. Therefore, at this time this plate is only tentatively referred to *Heliocanthus*. Nevertheless, because the rest of the armour closely resembles that of *Paratypthorax* and as undescribed specimens of *Paratypothorax* all possess cervical paramedian plates that are wider than long (pers. obs.), the cervical paramedian plates of *Heliocanthus* were most probably also of these

Table 1 Osteoderm interpretations of *Heliocanthus* from various studies.

Specimen Number	Zeigler *et al.* 2003*a*	Heckert *et al.* 2003	This study
NMMNH P-4894	Cervical paramedian	Paramedian	Posterior dorsal or pelvic paramedian
NMMNH P-29045	Right (?) cervical lateral	Right (?) 4th (?)cervical lateral	Anterior caudal paramedian
NMMNM P-31295	Right lateral	Right anterior caudal lateral	Right pelvic lateral
NMMNH P-32793	Right presacral paramedian	Right pelvic or anterior caudal paramedian	Right anterior caudal paramedian
NMMNH P-32794	Not described	Lateral	Left anterior lateral
NMMNH P-32795	Right presacral paramedian	Left (?)/Right cervical paramedian	Right anterior mid-caudal paramedian
NMMNH P-32796	Left lateral	Left caudal lateral	Left anterior caudal lateral
NMMNH P-32797	Right presacral paramedian	Right/left cervical?/presacral/posterior dorsal paramedian	Right mid-dorsal paramedian
NMMNH P-33099	Left cervical or presacral paramedian	Left cervical or presacral paramedian	Right anterior mid-caudal paramedian
NMMNH P-33100	3rd cervical lateral	3rd cervical lateral	Anterior mid-caudal paramedian
NMMNH P-33101	Not described	Right (?) cervical lateral	Left anterior mid-caudal paramedian
NMMNH P-33820	Not described	Left mid-dorsal paramedian	Left mid-dorsal paramedian
NMMNH P-34887	Not described	Right posterior dorsal paramedian	Right mid-dorsal paramedian
NMMNH P-34891	Not described	Left lateral	Left pelvic lateral
NMMNH P-34892	Not described	Not described	Left anterior caudal lateral
NMMNH P-35201	Not described	Not described	Left anterior caudal lateral
NMMNH P-35206	Not described	Left paramedian	Left cervical or anterior dorsal paramedian
NMMNH P-35349	Not described	Caudal lateral	Dorsal lateral
NMMNH P-35357	Not described	Not described	Left mid-caudal paramedian
NMMNH P-35436	Not described	Right dorsal or anterior caudal paramedian	Right posterior dorsal paramedian
NMMNH P-35459	Not described	Right paramedian	Left anterior caudal paramedian
NMMNH P-35806	Not described	Not described	Right mid-dorsal paramedian
NMMNH P-35807	Not described	Left mid-dorsal paramedian	Left mid-dorsal paramedian
NMMNH P-35991	Not described	Left caudal paramedian	Left posterior mid-caudal paramedian
NMMNH P-35993	Not described	Right (?) lateral	Right anterior lateral
NMMNH P-36052	Not described	Left/Right (?) lateral	Left anterior caudal paramedian
NMMNH P-36502	Not described	Caudal lateral	Same element as NMMNH P-36052
NMMNH P-37300	Not described	Caudal lateral	Left pre-pelvic or pelvic lateral
NMMNH P-37305	Not described	Lateral	Anterior lateral
NMMNH P-37348	Not described	Mid-dorsal paramedian	Mid-dorsal paramedian
NMMNH P-37349	Not described	Left dorsal or anterior caudal paramedian	Left posterior dorsal paramedian
NMMNH P-39184	Not described	Caudal lateral or paramedian	Left (?) caudal lateral
NMMNH P-39250	Not described	Right lateral	Same element as NMMNH P-39520
NMMNH P-39520	Not described	Right caudal lateral	Left anterior caudal lateral
NMMNH P-40395	Not described	Not described	Left dorsal pre-pelvic lateral
PEFO 31162	Not described	Not described	Left anterior caudal paramedian
PEFO 34040	Not described	Not described	Right (?) pelvic lateral
PEFO 34263	Not described	Not described	Plate fragment
UCM 47725†	Right paramedian	Right paramedian	Right anterior mid-caudal paramedian
UCMP 129829	Not described	Not described	Right dorsal paramedian

Contradictory descriptions from text and figures are reflected with interpretations split by a forward slash (/).
† Parrish & Carpenter (1986) considered UCM 47725 to be a left cervical lateral.

dimensions, regardless of the taxonomic assignment of NMMNH P-35206.

- *Mid-dorsal paramedian plates (Type B)*: The mid-dorsal paramedian plates of *Heliocanthus* (Fig. 2) are the largest in the carapace and possess the highest width–length ratios (minimum of 3.5:1). Similar ratios are found in *Paratypothorax* and other typothoracisine aetosaurs. The ornamentation is deeply incised and strongly radial, consisting of elongate grooves and pits radiating from the dorsal eminence. The eminence consists of a distinctly circular area strongly offset medially from the centre of the plate (Figs 2A & 3A) as in *Paratypothorax* (Fig. 3B), whereas the eminence in *Desmatosuchus* is always more centralised (Fig. 3C) (Parker 2003). The medial edge of the plate is straight; the lateral edge is sigmoidal for articulation

with the corresponding lateral plate (Fig. 2A). These plates are very thin, as are those of *Paratypothorax*, and without the thickened tongue-and groove articular surfaces found in *Desmatosuchus*. Noteworthy is the area of the posterior plate surface directly behind the eminence. Here the edge of the posterior plate swells slightly creating a small posteriorly directed tongue (Figs 2B & C). This is very similar to the condition in the paramedian plates of *Paratypothorax* and is not found in any other aetosaur.

The anterior dorsal surface of these plates possesses a transverse, smooth area that rises slightly above the level of the rest of the plate. Both Zeigler *et al.* (2003*a*) and Heckert *et al.* (2003) described this feature as an anterior lamina (*sensu* Long & Ballew 1985) for *Desmatosuchus*, although Zeigler *et al.* (2003*c*: 76) described it as a 'moderately
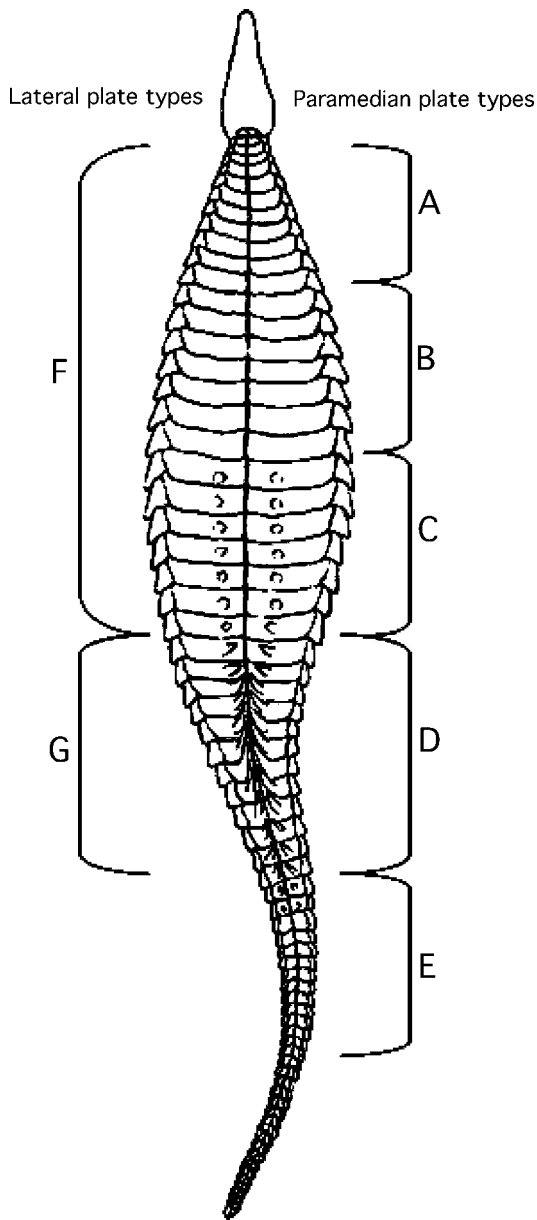
Figure 1 Reconstruction of *Heliocanthus chamaensis* nov. comb. in dorsal view showing plate types associated with their hypothetical position in the carapace.

Figure 2 *Heliocanthus chamaensis* nov. comb., mid-dorsal paramedian plates. **A,** NMMNH P-34887, right paramedian plate in dorsal view; **B,** NMMNH P-33820, left paramedian plate in dorsal view; **C,** NMMNH P-35807, left paramedian plate in dorsal view; **D,** NMMNH P-32797, partial right paramedian plate in dorsal view; **E,** UCMP 129829, right paramedian plate in dorsal view. ab, anterior bar; al.p, anterolateral process; br.e, broken edge; de, dorsal eminence; le, lateral edge; me, medial edge; p.de.p, posterior process related to the dorsal eminence. Scale bars = 5 cm.

developed anterior bar'. True anterior laminae, such as those seen in *Desmatosuchus* (Fig. 3C), are depressed relative to the rest of the plate, whereas anterior bars are raised. The structure present on this plate is raised and therefore represents an anterior bar similar to that of *Paratypothorax* (Fig. 3B), which is generally more moderately developed than those found in other taxa such as *Typothorax* and *Stagonolepis* (Martz & Small 2006).

In summary, Type B plates share numerous characters with *Paratypothorax* (e.g. moderately developed anterior bar, high width–length ratio, radial ornamentation and a medially offset dorsal eminence). In fact, the only character shared with *Desmatosuchus* is the absence of contact of the dorsal eminence with the posterior margin of the plate. However, this character is also present in the anterior and
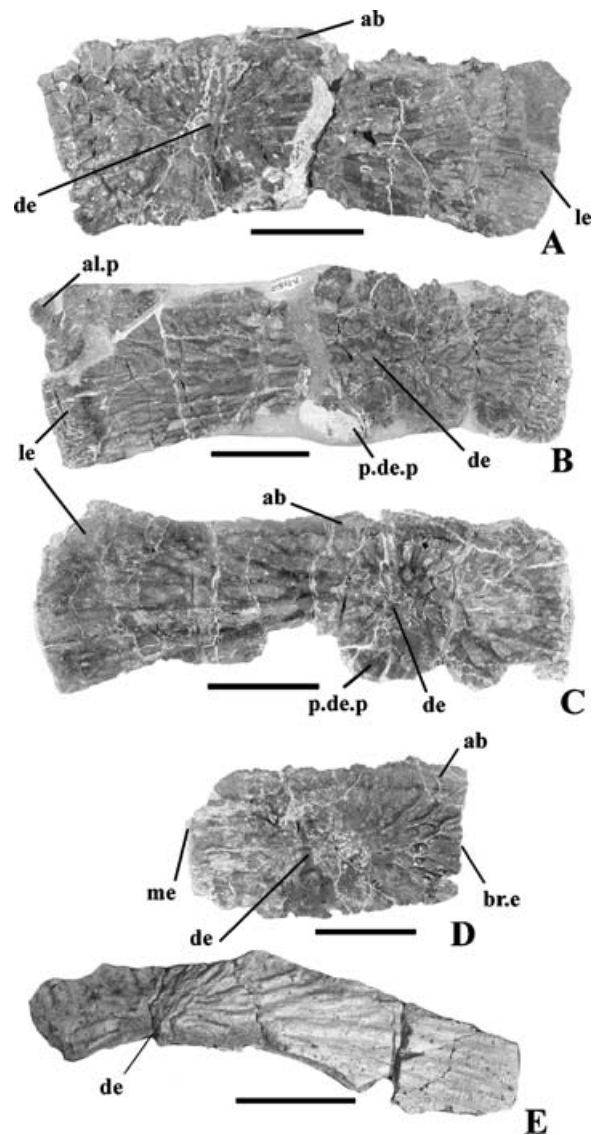
mid-dorsal paramedian plates of *Paratypothorax* (*contra* Long & Ballew 1985 and Heckert & Lucas 2000).

Zeigler *et al.* (2003*a*) and Heckert *et al.* (2003) both described NMMNH P-32797 (Fig. 2D) as complete; but examination of the right edge of the plate suggests otherwise. The ornamentation in aetosaur plates never directly contacts the lateral or median margins and instead terminates just lateral or medial to the plate edge resulting in a smooth dorsal margin. In NMMNH P-32797 this smooth edge is absent, indicating that the plate is incomplete. Comparison with other Type B plates, especially in the medial placement of the dorsal eminence, suggests that
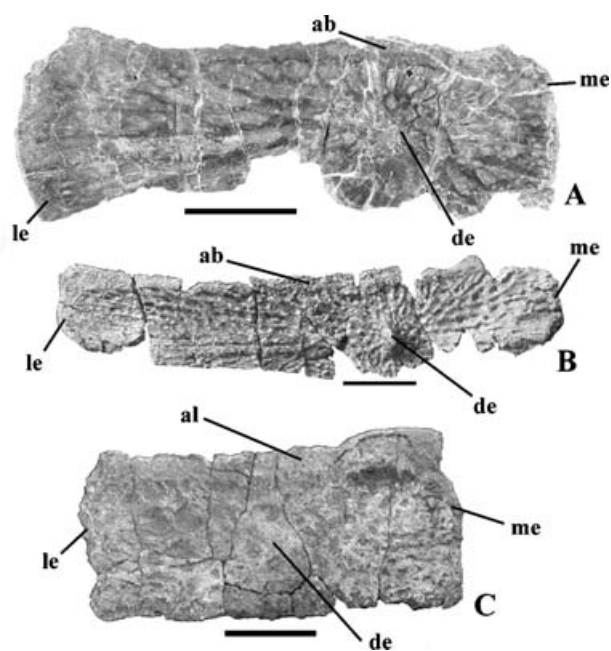
Figure 3 Comparison of mid-dorsal paramedian plates in several aetosaur taxa. **A**, NMMNH P-35807 *Heliocanthus chamaensis*, left paramedian plate in dorsal view; **B**, PEFO 26690 *Paratypothorax* sp., left paramedian plate in dorsal view; **C**, MNA V9300 *Desmatosuchus haplocerus*, right (reversed) paramedian plate in dorsal view. ab, anterior bar; al, anterior lamina; de, dorsal eminence; le, lateral edge; me, medial edge. Scale bars = 5 cm.

Figure 4 *Heliocanthus chamaensis* nov. comb., posterior dorsal paramedian plates. **A**, NMMNH P-35436, right posterior dorsal paramedian plate in dorsal view; **B**, NMMNH P-35436, in anterior view; **C**, NMMNH P-37349, left posterior dorsal paramedian plate in dorsal view; **D**, NMMNH P-37349 in posterior view. ab, anterior bar; al.p, anterolateral process; de, dorsal eminence; le, lateral edge; me, medial edge. Scale bars = 5 cm.

almost a third of the plate width is missing. Therefore, the eminence is not centrally positioned on the plate as described by Zeigler *et al.* (2003*a*) and Heckert *et al.* (2003). Furthermore, Heckert *et al.* (2003) consider it to be from the right side on p. 122 and from the left side on p. 123. It is interpreted here to be from the right side.

- *Posterior dorsal paramedian plates (Type C)*: These plates are similar to Type B paramedian plates except that the dorsal eminence is a short, anteriorly recurved spike (Fig. 4). The orientation of this spike is important, because it demonstrates that spikes of the more posterior paramedian plates of *Heliocanthus* are directed anteriorly. Although this is the case for all of the specimens with spikes, some have been crushed, making interpretation difficult. Another notable difference between these plates and more anterior paramedians (plate types A + B) is that they are slightly arched dorsoventrally (Figs 4B & D). This arching, as well as the development of the dorsal eminence, supports placement of these plates in the posterior dorsal and pelvic regions.

- *Pelvic and anterior caudal paramedian plates (Type D)*: The majority of the plates of *Heliocanthus* recovered from the Snyder Quarry are pelvic and anterior caudal paramedians (Figs 5 & 6). These plates are distinguished by the development of the dorsal eminence into the elongate, anteromedially recurved spike that is diagnostic for the species. The position of the anterior bar supports the anteromedial interpretation for the trend of the spike. These plates are dorsoventrally arched with anterior bars and they have an ornamentation of grooves and ridges
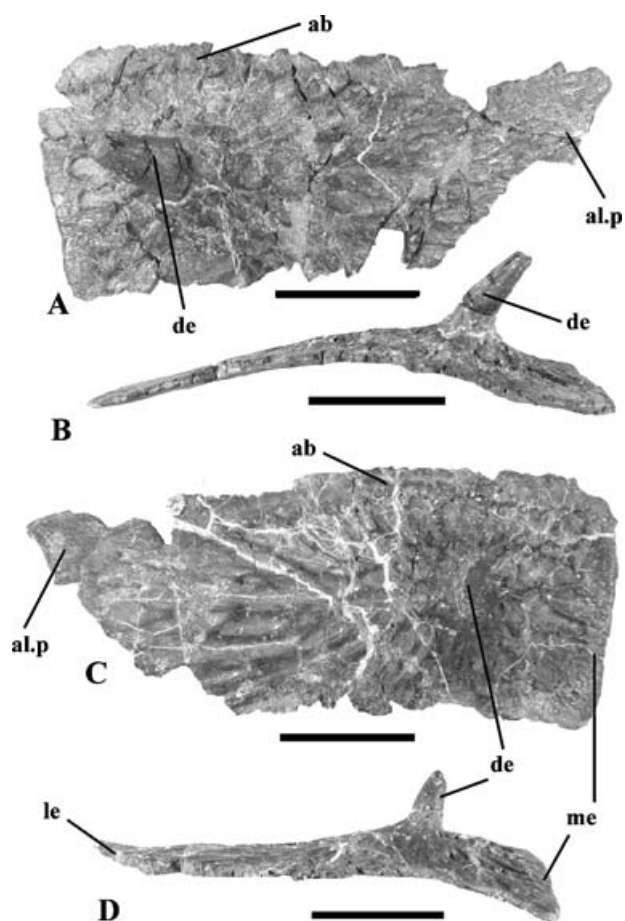
strongly radiating from the dorsal eminence. Immediately posterior to the anterior bar, the grooves and ridges are coarser and trend anteroposteriorly, whereas the ornamentation on the rest of the plate trends transversely. Medial margins are straight and lateral margins, where preserved, are slightly sigmoidal. Plate widths decrease posteriorly through this series, while plate lengths and eminence lengths increase. All of these plates taper posteromedially showing that they are situated in the posterior portion of the carapace.

The holotype plate, NMMNH P-32793 (Figs 5A–C), was considered by Zeigler *et al.* (2003*a*) to represent a right presacral plate, whereas Heckert *et al.* (2003) reinterpreted it as a posterior dorsal or anterior caudal paramedian. The plate is not complete, missing much of the posterior edge. The missing portion results in a much more crescentic shape in dorsal view than is probably genuine. The posterior cervical and anterior dorsal paramedians of *Typothorax* are strongly crescentic in dorsal view (Martz 2002). However, the lateral edge slopes posterolaterally in that taxon, while the lateral edge of NMMNH P-32793
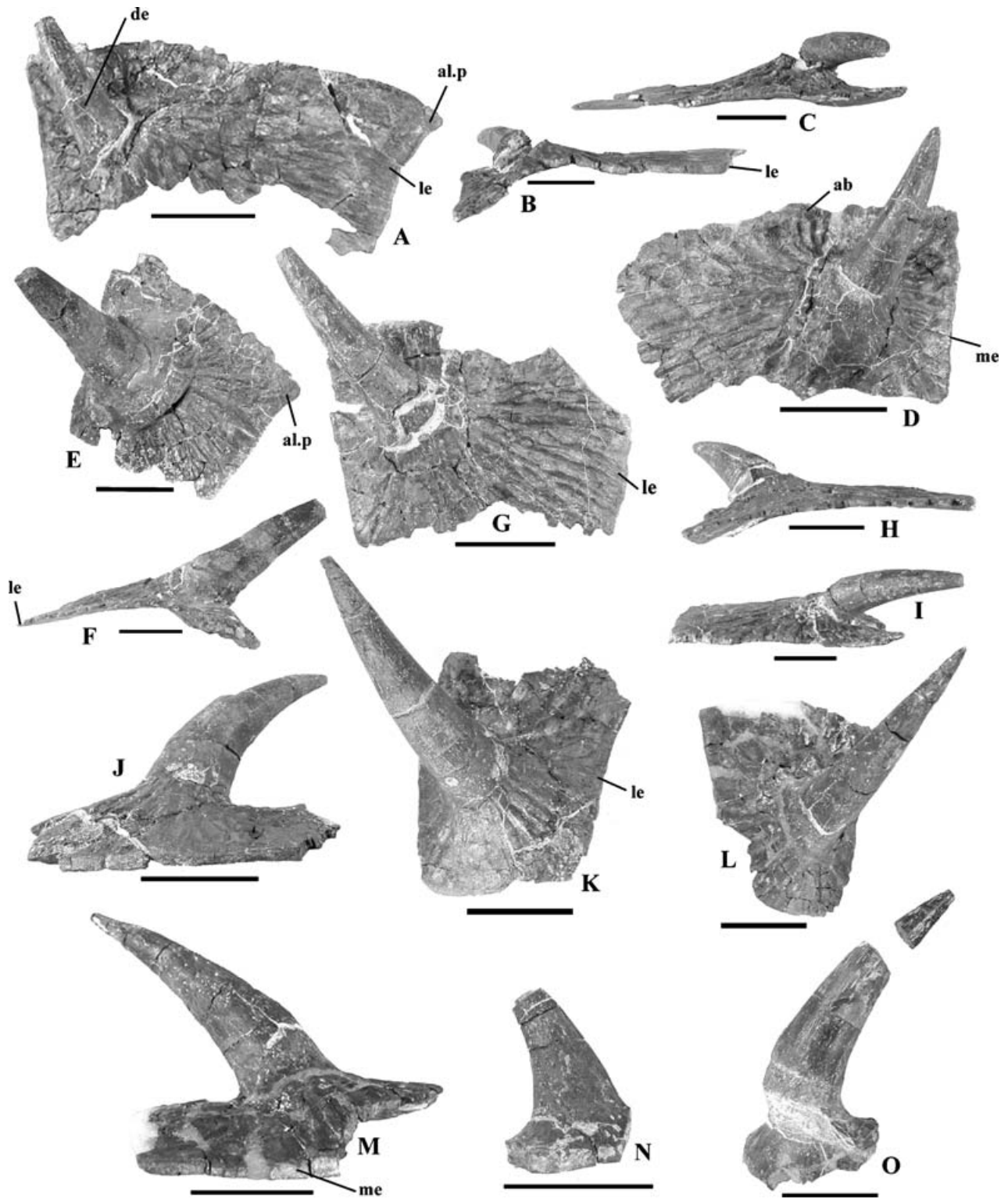
Figure 5 *Heliocanthus chamaensis* nov. comb., anterior caudal paramedian plates. **A,** NMMNH P-32793, right anterior caudal paramedian plate in dorsal view; **B,** NMMNH P-32793 in posterior view; **C,** NMMNH P-32793 in anterior view; **D,** NMMNH P-35459, left anterior caudal paramedian plate in dorsal view; **E,** NMMNH P-36052, left anterior caudal paramedian plate in dorsal view; **F,** NMMNH P-36052 in anterior view; **G,** NMMNH P-33099, right anterior mid-caudal paramedian in dorsal view; **H,** NMMNH P-33099 in posterior view; **I,** NMMNH P-33099 in anterior view; **J,** NMMNH P-32795 right anterior mid-caudal paramedian plate in lateral view; **K,** NMMNH P-32795 in dorsal view; **L,** NMMNH P-33101, left anterior mid-caudal paramedian plate in dorsal view; **M,** NMMNH P-33101 in medial view; **N,** NMMNH P-29045, partial anterior caudal paramedian plate in medial view; **O,** NMMNH P- 33100, partial anterior mid-caudal paramedian plate in lateral view. ab, anterior bar; al.p, anterolateral process; le, lateral edge; me, medial edge. Scale bars = 5 cm.

slopes posteromedially. Therefore, Heckert *et al.* (2003) were correct in their assessment that NMMNH P-32793 does not represent a cervical plate.

The dorsal eminence is situated strongly medially and consists of a gracile, elongate, recurved spike that is directed anteromedially. The medial edge is straight while the lateral edge is sigmoidal for articulation with a lateral plate. The width–length ratio of NMMNH P-32793 is approximately 2:1 and the plate is slightly arched dorsally, thus indicating that it represents an anterior caudal paramedian plate very similar to NMMNH P-33099 and P-35459.

Heckert *et al.* (2003) identified NMMNH P-36052 (Figs 5E & F) as a left lateral plate, but this would give this plate an anterolaterally directed spike rather than the anteromedially directed spike possessed by all other spiked plates. The key to interpreting this plate is to compare it in anterior view (Fig. 5F) with similar plates such as NMMNH P-35436 (Fig. 4B). NMMNH P-36052 has a more pronounced eminence and is narrower than NMMNH P-35436 indicating its more posterior position. Therefore NMMNH P-36052 represents a left anterior caudal paramedian plate.

NMMNH P-32795 (Figs 5J & K) was interpreted as a right presacral paramedian plate by Zeigler *et al.* (2003*a*) and as a third or fourth cervical paramedian plate by Heckert *et al.* (2003) on the basis of it being longer than wide, as in cervical plates of *Desmatosuchus haplocerus*. This interpretation would require that *Heliocanthus* possessed two distinct morphologies of cervical plates, provided the assignment of NMMNH P-35206 by Heckert *et al.* (2003) to this taxon is correct. Furthermore, these authors do not describe the direction of recurvature for the spine although based on their discussion they would consider it homologous with the spines of *Desmatosuchus* and thus recurved posteriorly. This would make the plate from the left side according to their interpretation. Orientating the plate so that the spine recurves anteromedially and considering the nearly equant dimensions and the posterior taper, all place it in the caudal series as a right anterior mid-caudal paramedian plate.

Similar corrections to other plates of these series result in a more probable placement in the carapace. NMMNH P-33099 (Figs 5G–I) was interpreted as a left cervical or presacral paramedian plate by Zeigler *et al.* (2003*a*) and Heckert *et al.* (2003). Heckert *et al.* also interpreted the spike as being directed posteriorly, in contrast to the noted anterior recurvature of other plates. Again, based on the same criteria mentioned above for NMMNH P-32795, this plate represents a right anterior mid-caudal plate.

NMMNH P-33101 (Figs 5L & M) was described as a right (?) lateral plate with a posteriorly recurved spike by Heckert *et al.* (2003). Those authors noted that there was no preserved anterior bar, thus making interpretation of this plate difficult. However, the morphology of NMMNH P-33101 is identical to NMMNH P-32795 and UCM 47725, which they considered to be paramedian plates. In addition, in lateral view (Fig. 5M) the articular surface with the adjacent lateral plate is visible. Thus, NMMNH 33101 is not a lateral plate. Even though the anterior bar is not preserved, the characteristic patterning (anteroposteriorly orientated deep grooves) that always

occurs just posterior to the bar is present. Orientating the plate according to this criterion gives an anteromedial curvature to the spike and also gives this plate the posterior taper that is typical of aetosaur caudal plates. Therefore, NMMNH P-33101 is reinterpreted here as a left anterior mid-caudal plate.

Two other Type D plates, NMMNH P-29045 and P-33100, described by Zeigler *et al.* (2003*a*) and Heckert *et al.* (2003) are the purported 'cervical horns'. According to Heckert *et al.* (2003: 123), P-29045 (Fig. 5N) was one of the original fossils discovered from the quarry and the 'basis for identifying *Desmatosuchus* at the quarry'. Zeigler *et al.* (2003*a*) did not mention this specimen, but Heckert *et al.* (2003) identified it as a right (?) cervical lateral plate that 'most closely resembles a fourth lateral scute of *D. haplocerus*'. It also strongly resembles a broken spike from a more anteriorly placed Type D paramedian plate of *Heliocanthus*. Broken plate margins at the base of the spike support this interpretation. Comparison with known cervical spikes of *D. haplocerus* show that these so-called 'cervical horns' do not match the morphology of *Desmatosuchus* because they lack the following features: the dorso-ventral flattening, providing an ovate cross-section; the presence of an anterior lamina just anterior to the base of the spike; and distinct lateral and dorsal flanges, with a deep emargination ventral to the spike.

NMMNH P-33100 (Fig. 5O) was identified by Zeigler *et al.* (2003*a*) and Heckert *et al.* (2003) as a spike from a third cervical lateral plate. This 'horn' was considered by those authors to be homologous with the cervical lateral horns of *Desmatosuchus*. However, examination of this specimen and comparison with other Type D plates shows that NMMNH P-33100 represents a spike broken off an anterior mid-caudal paramedian plate of *Heliocanthus*.

Since NMMNH P-36052, P-29045 and P-33100 can conclusively be shown to represent typical Type D paramedian plates of *Heliocanthus* and not lateral plates, there is no strong resemblance between true lateral plates of *Heliocanthus* and those of *Desmatosuchus* (*contra* Zeigler *et al.* 2003*a* and Heckert *et al.* 2003).

PEFO 31162 (Figs 6A & B) was collected from Petrified Forest National Park vertebrate locality 075 (Karen's Point), situated just above Flattops Two sandstone of the Petrified Forest Member (Woody 2003). Although the anterior bar is not preserved, orientating the spike anteromedially indicates that it is a left paramedian plate. The elongate spike and width of the plate places it in the anterior caudal region. This plate represents the first occurrence of *Heliocanthus* outside New Mexico.

UCM 47725 (Figs 6C–E) was interpreted as a cervical lateral plate by Parrish & Carpenter (1986) and a right paramedian plate by both Zeigler *et al.* (2003*a*) and Heckert *et al.* (2003). It is unclear how the latter two authors' interpretations would orientate the plate, but Parrish & Carpenter's interpretation would again cause the eminence to be recurved posteriorly. The figure of this plate by Zeigler *et al.* (2003*a*: fig. 2i) clearly shows an anterior bar. This interpretation allows for the anteromedial curvature of the spike and places UCM 47725 in the anterior mid-caudal region, similar to plate NMMNH P-32795. Furthermore, correctly positioning the anterior
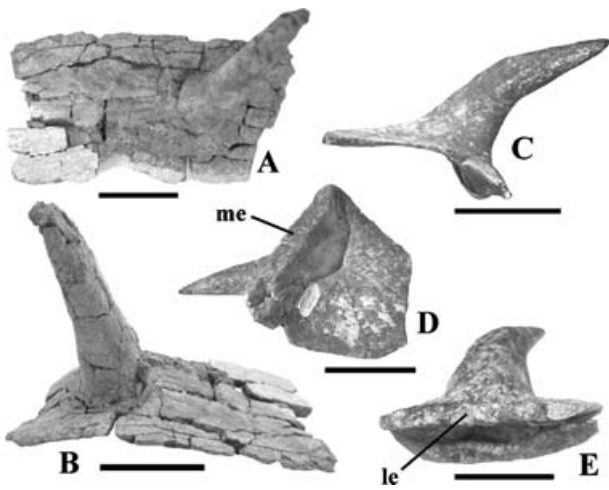
Figure 6   *Heliocanthus chamaensis* nov. comb., referred anterior caudal paramedian plates. **A**, PEFO 31162, left anterior caudal paramedian plate in dorsal view; **B**, PEFO 31162 in anterior view; **C**, UCM 47725, right anterior mid-caudal paramedian in anterior view; **D**, UCM 47725 in ventromedial view; **E**, UCM 47725 in lateral view. le, lateral edge; me, medial edge. Scale bars = 5 cm.
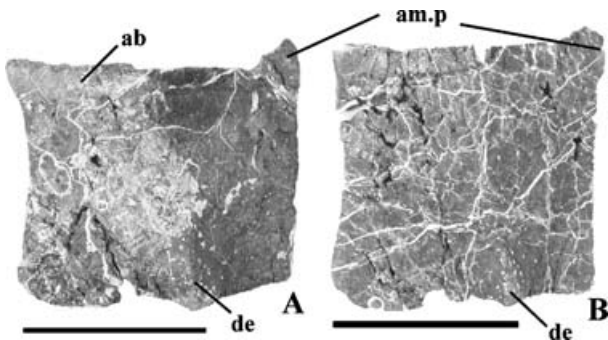

Figure 7   *Heliocanthus chamaensis* nov. comb., mid-caudal paramedian plates. **A**, NMMNH P-35357, left mid-caudal paramedian plate in dorsal view; **B**, NMMNH P-35991, left mid-caudal paramedian plate in dorsal view. ab, anterior bar; am.p, anteromedial process; de, dorsal eminence. Scale bars = 5 cm.

bar and allowing for the anteromedial curvature of the spike places UCM 47725 on the right side of the carapace. This plate also shows sutural contacts on the lateral and medial edges (Figs 6D & E) further demonstrating its proper placement as a paramedian plate rather than a lateral plate.

- *Mid-caudal paramedian plates (Type E)*: Two notable plates in the NMMNH collections from the Snyder Quarry are NMMNH P-35991 and P-35357. Heckert *et al.* (2003: fig. 7c) figured NMMNH P-35991 as a left mid-caudal paramedian plate but they did not describe the plate. Both of these plates (Figs 7A & B) are left paramedian plates from the mid-caudal region, with NMMNH P-35357 being situated more anteriorly due to its greater relative width. These plates are more equant in shape than the other paramedian plates previously described. The anterior bars are apparent and possess a sharp anteromedial tab. The eminences differ from the rest of the series in being pyramidal and contacting the posterior margin of the plate. Indeed,

they are quite similar to those of *Stagonolepis* in this aspect (Walker 1961: fig. 20c; Long & Murry 1995: fig. 71a). Martz (2002: fig. 4.32c) figures a similar type of plate from *Typothorax*. This poses a problem similar to that of the cervical paramedian plate NMMNH P-35206 (Type A), because it is possible that these plates belong to *Typothorax* rather than *Heliocanthus*. If these plates do belong to *Heliocanthus* then there is an abrupt shift between caudal plates with pronounced spikes and those with a low pyramidal eminence. The anterior margin of NMMNH P-35357 measures 8 cm; in NMMNH P-32795 it measures approximately 10 cm. In the rapidly tapering tail of aetosaurs a 2 cm difference in width would probably afford no more than four or five plate positions for the switch from elongate spike to low pyramidal eminence. This condition has not been noted in any other aetosaur; therefore these two plates are only tentatively referred to *Heliocanthus* at this time.

2. **LATERAL PLATES**
Lateral plates of *Heliocanthus* can be divided into two distinct morphologies, Type F have reduced, triangular dorsal flanges and elongate flattened recurved 'spines', and Type G are sub-triangular plates with a sharp, hooked eminence. Figure 1 shows the general regions of the carapace where these plate morphologies are considered to occur. Assignment of all known osteoderms of *H. chamaensis* to specific morphologies is listed in the table provided as supplemental information to this paper.

These plates are important to the phylogenetic placement of *Heliocanthus* within Aetosauria because of their strong resemblance to the lateral plates of *Paratypothorax*. This resemblance has been noted by other authors. For example, Zeigler *et al.* (2003b: 3) state 'some specimens we tentatively assign to *D. chamaensis* resemble lateral scutes of *Paratypothorax*, but we have not found any paramedian scutes of *Paratypothorax* at the Snyder Quarry so we refrain from identifying them as *Paratypothorax*.' Heckert & Zeigler (2002: 9) note 'still we began to encounter more aetosaur material, principally scutes of *Desmatosuchus*. I (ABH) originally thought one of these was referable to *Paratypothorax*, but I was mistaken'. Finally, Heckert *et al.* (2003: 124) state 'overall these three scutes (NMMNH P-35993, P-32794, P-37305, all Type F plates) ... most closely resemble UMMP 8869, a left lateral cervical (?) scute that Lucas *et al.* (1995) tentatively assigned to *Paratypothorax*... there are some strong similarities between these specimens corresponding to the shape of the minimal dorsal flange. However, given the absolute lack of *Paratypothorax* dorsal paramedian scutes from the Snyder Quarry, we are hesitant to assign these scutes to that taxon.'

Nevertheless, as demonstrated above, the paramedian and lateral plates of *Heliocanthus* resemble those of *Paratypothorax* much more than they do *Desmatosuchus*. Rather than considering these plates to belong to a new species of *Desmatosuchus*, a more plausible explanation would be that *Heliocanthus* represents a distinct form that is more closely related to *Paratypothorax*.

- *Dorsal lateral plates (Type F)*: These plates are characterised by an eminence that is triangular in ventral and dorsal views and forms a slightly posteriorly recurved horn that
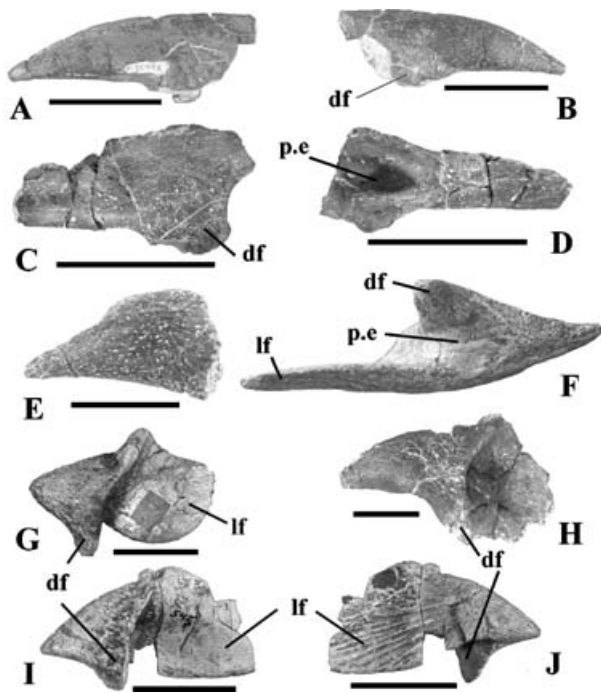
Figure 8 Anterior lateral plates of paratypothoracisine aetosaurs. **A**, NMMNH P-35993, *Heliocanthus* right lateral plate in ventral view; **B**, NMMNH P-35993 in dorsal view; **C**, NMMNH P-32794, *Heliocanthus* left lateral plate in dorsal view; **D**, NMMNH P-32794 in posterior view; **E**, PEFO 3004, *Paratypothorax* sp., ?right lateral plate in ventral view; **F**, SMNS (unnumbered) holotype of *Paratypothorax andressorum*, right lateral plate in posterior view; **G**, SMNS (unnumbered) holotype of *Paratypothorax andressorum*, left lateral plate in dorsomedial view; **H**, UMMP V8869, *Paratypothorax* sp., left lateral plate in dorsal view; **I**, *Tecovasuchus*, left lateral plate in dorsomedial view; **J**, *Tecovasuchus*, left lateral plate in ventral view. df, dorsal flange; p.e, posterior emargination; lf, lateral flange. Scale bars = 5 cm.

Figure 9 Comparison of pelvic and anterior caudal lateral plates of *Heliocanthus, Paratypothorax* and *Desmatosuchus*. **A**, NMMNH P-31295, *Heliocanthus*, right lateral plate in dorsolateral view; **B**, SMNS (unnumbered), holotype of *Paratypothorax andressorum*, right lateral plate in dorsolateral view; **C**, PEFO 3004, *Paratypothorax* sp., right lateral plate in dorsolateral view; **D**, MNA V9300, *Desmatosuchus haplocerus*, right lateral plate in dorsolateral view. de, dorsal eminence; me, medial edge. Scale bars = 5 cm.

is dorsoventrally flattened. The anterior edge is sharp and the posterior edge rounded. The horn projects from near the proximal portion of the plate where it is formed by the union of two plate flanges. The dorsal flange is extremely short, having a sigmoidal edge for articulation with the accompanying paramedian plate. The posteromedial corner of the dorsal flange is extended into an elongate rounded process. The ventral flange is more plate-like; however it is only partially preserved in NMMNH P-35993 (Fig. 8A) and not preserved at all in NMMNH P-32794. In P-35993 the preserved portion is ornamented by radiating grooves. The two flanges meet in a tight acute angle and the underside of the horn where the flanges meet is emarginated in P-32794 (Fig. 8D).

These plates closely resemble lateral plates assigned to *Paratypothorax* including PEFO 3004 (Fig. 8E), DMNH 9942 (Long & Murry 1995: figs 133b–e), the holotype of *P. andressorum* (Figs 8F & G) and UMMP 8869 (Lucas *et al*. 1995; Heckert *et al*. 2003; Fig. 8H). They are also very similar to *Tecovasuchus* (Figs 8I & J) and to lateral plates of *Typothorax* (Martz 2002: figs 4.36a–f), except that the 'horn' in *Typothorax* is not as robust as in *Heliocanthus*, *Paratypothorax* and *Tecovasuchus*. The acute angle of flexion between the flanges suggests that these plates represent dorsal lateral plates as found in *Typo-*
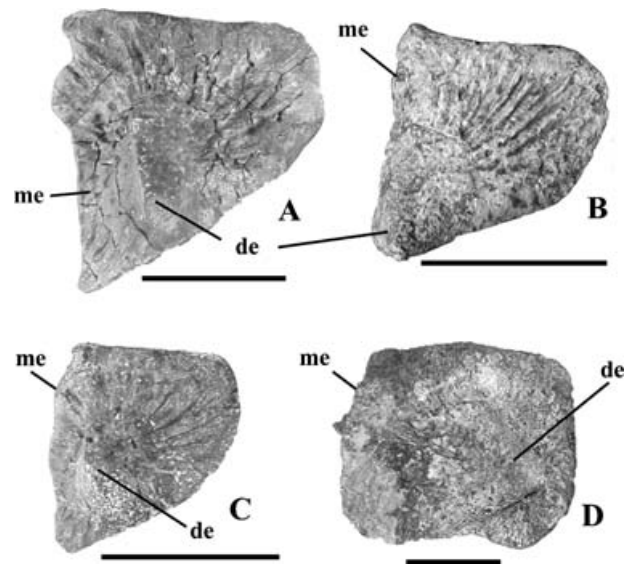
thorax (Martz 2002). The sigmoidal edge of the dorsal flange also supports assignment to the dorsal region where the lateral margins of the dorsal paramedian plates are sigmoidal. These plates differ substantially from those of *Desmatosuchus* in being dorsoventrally flattened, in having flanges that meet at an acute angle and in having a dorsal flange that is shorter than the lateral flange.

- *Pelvic and anterior caudal lateral plates (Type G)*: As with the anterior caudal paramedian (Type D) plates, the plates most likely to be assignable to the pelvic and anterior caudal lateral regions are the most recovered plate type of *Heliocanthus* from Snyder Quarry. These plates are distinguished by their sub-triangular shape, being roughly equant in length and width (Fig. 9A). The medial edge is sigmoidal for articulation with the adjacent dorsal paramedian plate. The anterior edge is straight, while the lateral and posterior edges are confluent and form a semi-circular posterolateral edge. The anterior edge has a weakly developed anterior bar. The ornamentation consists of a series of grooves and ridges radiating from the dorsal eminence as in the paramedian plates. The dorsal eminence is a sharp, slightly posteriorly recurved hook. In dorsal view, the eminence trends posterolaterally, similar to the eminences on similar plates of *Stagonolepis* and *Paratypothorax*. In more posterior plates (anterior caudals) the eminence is larger and overhangs the posterior portion of the plate (Figs 10A–G). Overall, these plates are like those of *Paratypothorax* (Figs 9B & C) and roughly similar to those of *Typothorax* (Martz 2002: figs 4.35a & c). They are very different from the pelvic and anterior caudal lateral plates of *Desmatosuchus* (Fig. 9D). In *Desmatosuchus*, the lateral plates are rectangular and flexed at 90° around the eminence forming distinct dorsal and lateral flanges. In
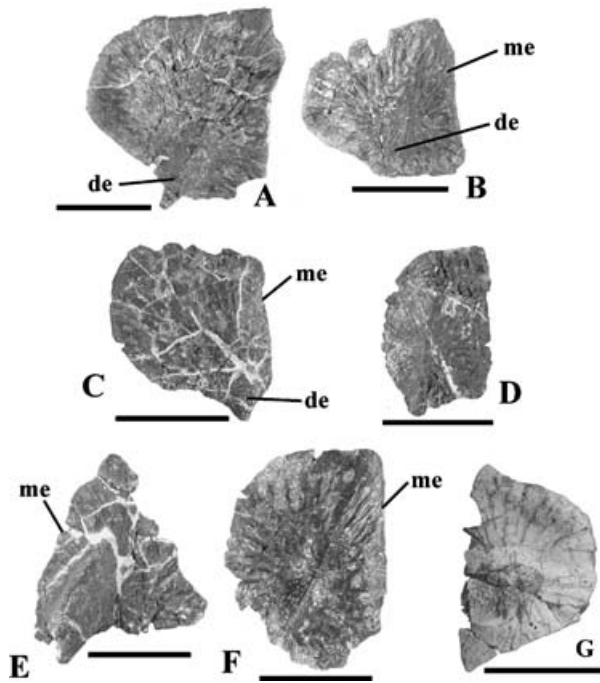
Figure 10 *Heliocanthus chamaensis* nov. comb., pelvic and anterior caudal lateral plates. **A**, NMMNH P-32796, left lateral plate in dorsolateral view; **B**, NMMNH P-34891, left lateral plate in dorsolateral view; **C**, NMMNH P-34892, left lateral plate in dorsolateral view; **D**, NMMNH P-35201, left lateral plate in dorsolateral view; **E**, NMMNH P-39520, left lateral plate in dorsolateral view; **F**, NMMNH P-37300, left lateral plate in dorsolateral view; **G**, PEFO 34034, partial ?right lateral plate in dorsal lateral view. de, dorsal eminence; me, medial edge. Scale bars = 5 cm.

the dorsal lateral series, the lateral flanges in *Desmatosuchus* are much longer (2:1) than the ventral flanges. In addition, the dorsal eminence is in the form of a spike that projects laterally and slightly dorsally (Parker 2003).

3. APPENDICULAR ELEMENTS

Heckert *et al.* (2003) referred several tarsal elements from the quarry to '*Desmatosuchus*' *chamaensis* based on differences from the tarsals of *Typothorax* (the only other aetosaur recognised from the quarry) and resemblances to tarsals referred to *Desmatosuchus* by Long & Murry (1995). At the present time the validity of these referrals cannot be confirmed because tarsal elements are unknown for *Desmatosuchus*. Tarsals are not present in ANSP 14688 (lectotype), UMMP 7476, TTUP 9024, or MNA V9300, the four most complete *Desmatosuchus* specimens known to date. Long & Murry (1995) referred many isolated elements, including tarsals, from the *Placerias* quarry to *Desmatosuchus*. However, because at least three taxa of aetosaurs occur in the *Placerias* quarry, including another form that is very similar to *Paratypothorax* and was unrecognised by Long and Murry, all assignments of isolated elements to lower level taxa should be regarded as tenuous at best. Unfortunately, tarsal elements of *Paratypothorax* are also unknown, although it is possible that some of the *Placerias* quarry and Snyder quarry material is referable to a closely related taxon. For these reasons these elements are only referred to Aetosauria indet.

RECONSTRUCTIONS. The description given above was used to develop life reconstructions of *Heliocanthus*. Figure 11A shows the reconstructed animal in dorsal view, whereas Fig. 11B shows the reconstructed animal in right lateral view. *Heliocanthus* lacks the strong discoidal shape of aetosaurs such as *Typothorax* and *Paratypothorax*. The anteromedially projecting spines of the pelvic and anterior caudal region are interpreted as non-overlapping. A function for these spines is conjectural, but their distribution and direction of recurvature would seem to preclude a defensive use. Instead it is hypothesised that these spines were used for species recognition as advocated by Padian *et al.* (2004) for similar structures in dinosaurs.

DISCUSSION. *Heliocanthus chamaensis* was originally described by Zeigler *et al.* (2003*a*) and then redescribed by
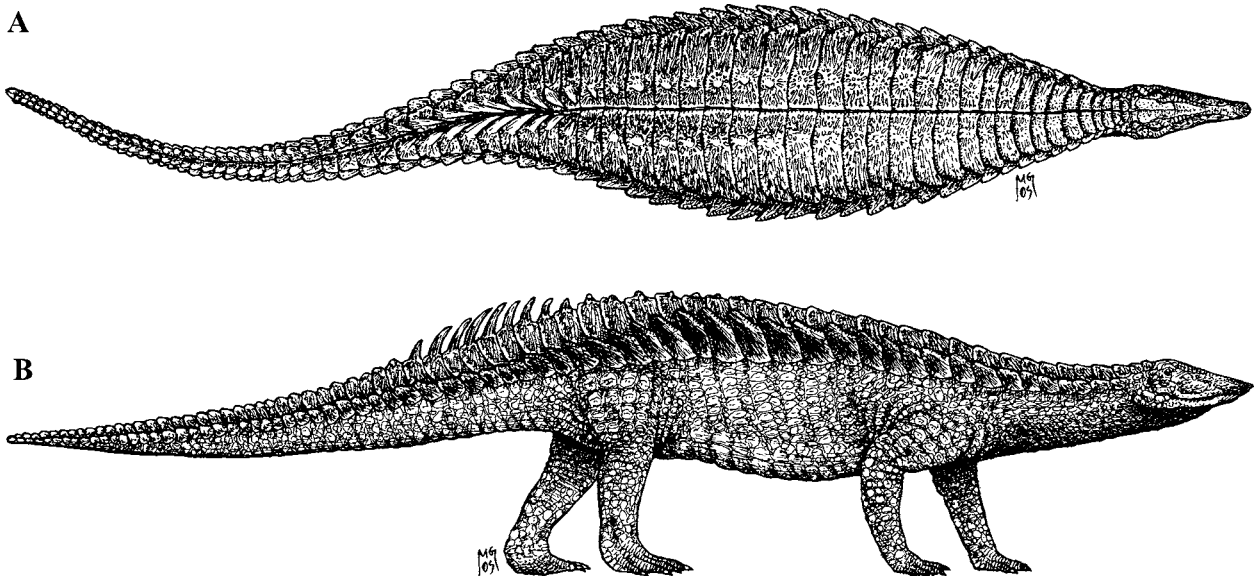

Figure 11 Life reconstructions of *Heliocanthus chamaensis* nov. comb. **A**, dorsal view; **B**, right lateral view.

Heckert *et al.* (2003) as a new species of *Desmatosuchus* based on several supposed synapomorphies. However, inspection of the type and referred material does not reveal any shared synapomorphies with *Desmatosuchus* except that the dorsal eminence of the paramedian plates does not contact the posterior edge of the plate. The plates of *Heliocanthus* possess a radial ornamentation and a dorsal eminence that is strongly offset medially, highly reminiscent of *Paratypothorax* (Figs 3A & B). In fact, *Heliocanthus* shares numerous characters with *Paratypothorax,* especially the morphology of the dorsal lateral plates. These plates are similar in both taxa with the exception of somewhat larger size in *Heliocanthus* (Figs 9A–C).

The type specimen of *H. chamaensis* includes armour from the posterior cervical, dorsal and caudal paramedian areas, as well as representative lateral plates from several regions of the carapace. Unfortunately, many of the plate edges are incomplete, making orientation and placement in the body difficult. However, aetosaur armour in general possesses many characters that allow reconstruction including anterior bars, sigmoidal lateral edges and medially placed dorsal eminences. In addition, where anterior bars are present on the spiked paramedian plates, they show that the spiked dorsal eminences were recurved anteromedially. It is doubtful that some of the spiked eminences would be recurved anteriorly whereas others would be recurved posteriorly as suggested by Heckert *et al.* (2003). In addition, all spiked paramedians are very similar in their overall morphology, differing only in the length of the dorsal eminence and in the width of the plates. These differences are best explained by increase in the size of dorsal eminences and the gradual narrowing of the carapace through the pelvic and anterior caudal regions, as in all aetosaurs. Therefore, it does not seem likely that *Heliocanthus* possessed spiked cervical paramedian plates. In addition, the supposed cervical horns of *Heliocanthus,* purported to be homologous with the lateral cervical plates of *Desmatosuchus*, are actually broken spikes from incomplete plates of the pelvic and anterior caudal regions. Thus, *Heliocanthus* possesses only two distinct lateral plate morphologies, spike-like lateral plates and sub-triangular lateral plates with a sharp hook-like eminence. Both of these morphologies are found in aetosaurs such as *Paratypothorax* and *Tecovasuchus* (Parker 2003; Martz & Small 2006). In addition, these morphologies are very similar to those of *Typothorax* and notably different from those of desmatosuchine aetosaurs such as *Longosuchus* and *Desmatosuchus*.

Based on the above, in addition to a lack of shared characters with *Desmatosuchus*, 'D' *chamaensis* is referred to a new genus allied more closely with *Paratypothorax*. The morphology of the lateral plates, ornamentation of the paramedian plates and the strongly medial offset of the dorsal eminence suggest a strong relationship with *Paratypothorax*. Similarities of the lateral plates of *Heliocanthus chamaensis* and *Paratypothorax andressorum* may suggest that the two belong in the same genus; however the presence of elongate recurved spikes on the paramedian plates is unique to *H. chamaensis* and therefore I maintain the generic distinction.

Heckert *et al.* (2003: 124) explicitly addressed the question of generic distinction for this material, concluding that 'key features of *D. chamaensis*' were also synapomorphies of *D. haplocerus*, including the presence of anterior laminae versus an anterior bar, large recurved spikes on the lateral

plates, irregular pitting on dorsal paramedian plates and the low boss (eminence) just medial to the centre of the plate. Interestingly, Zeigler *et al.* (2003*b*: 76) in the same volume (correctly) differentiated *H. chamaensis* and *D. haplocerus* by 'the presence of long, recurved spikes on the dorsal scutes, a pattern of ridges and grooves radiating from the boss . . . and the presence of a moderately developed anterior bar'. Thus, the same authors in separate papers refute their own supposed synapomorphies for assigning the Snyder Quarry material to *Desmatosuchus*.

PHYLOGENETIC ANALYSIS OF THE AETOSAURIA

The purpose of this study was to test the hypothesis that *Typothorax* and *Paratypothorax* are more closely related to each other than either is to *Longosuchus* and *Desmatosuchus* and that *Heliocanthus chamaensis* and *Tecovasuchus* form a clade with *Paratypothorax* (Parker 2003). Another hypothesis to be tested is that *Aetosaurus* is not the sister taxon to all other aetosaurs but instead is more closely related to *Stagonolepis*, as argued by Walker (1961).

The systematics of the Aetosauria has a long, confusing history. Agassiz (1844) first described *Stagonolepis* as a Devonian non-tetrapod. Huxley (1859) was the first to recognise the reptilian affinities of this taxon, placing it with 'Belodon' in his Parasuchia. Along with the later discoveries of *Typothorax* (Cope 1875), 'Episcoposaurus' (Cope 1887, 1892), 'Stegomus' (Marsh 1896) and *Desmatosuchus* (Case 1920), *Stagonolepis* was believed to represent a distinct form of phytosaur. This confusion was mostly caused by the mixture of phytosaur and aetosaur bones in type materials of these taxa and of the genus 'Phytosaurus,' as well as the fragmentary nature of the material. Aetosauria was considered a valid taxon as early as 1884 (Marsh 1884), consisting of the two species of *Aetosaurus*, which are known mainly from 22 relatively complete specimens of *A. ferratus*, including excellent skull material from the Stubensandstein of Germany (Fraas 1877; Walker 1961). Unfortunately, according to Walker (1961) the earliest cranial reconstructions of *Aetosaurus* (e.g. Fraas 1877; Huene 1920) are incorrect; thus even with the discovery of good skull material of *Desmatosuchus* in Texas (Case 1920, 1922), the close affinities between the European and North American material were not recognised. By the time of the description of 'Typothorax' *meadei* (Sawin 1947) and a revision of many of the known aetosaurs by Gregory (1953), aetosaurs were finally considered to be separate from the phytosaurs. However, they were still lumped into the 'Thecodontia,' a polyphyletic taxon containing most of the Triassic non-dinosaurian archosaurs. Walker's (1961) redescriptions of *Stagonolepis* and *Aetosaurus* initiated the current understanding of what constitutes the taxon Aetosauria.

In most of the recent analyses of archosaurian systematics (e.g. Gauthier 1986; Sereno 1991; Parrish 1993; Gower & Wilkinson 1996; Benton 1999) Aetosauria is considered to be the sister group of a clade consisting of the rauisuchians and crocodylomorphs (Rauisuchia of Parrish 1993). Alternatively, in a recent paper describing the braincase of *Stagonolepis*, Gower & Walker (2002) argue that aetosaurs may be closer to crocodylomorphs than rauisuchians are. It is hoped that future studies will shed more light on these

relationships, although all of these recent analyses do not dispute that the aetosaurs are a monophyletic group of suchian archosaurs.

Previous work

Although their position as suchian archosaurs is considered secure, the phylogenetics of the Aetosauria is replete with problems (see Harris *et al*. 2003*a*, *b*). Parrish (1994) was the first worker to attempt a parsimony analysis of the Aetosauria. Unfortunately, discrepancies between the coding and character descriptions, as well as a lack of informative characters have restricted the utility of this study. Harris *et al*. (2003*a*) addressed many of these problems and reconstructed new matrices using Parrish's (1994) data (Fig. 12*a*). However, Harris *et al*. (2003*a*: 248) concluded that the matrix included too few characters to 'provide a well-supported hypothesis'.

Heckert *et al*. (1996) published the next parsimony analysis of the Aetosauria in order to place the genus *Redondasuchus* into a phylogenetic framework. They composed a matrix of nine taxa and 23 characters, but did not provide an outgroup and instead rooted the tree with *Aetosaurus*. An initial run of a restricted matrix provided five Most Parsimonious Trees (MPTs), while inclusion of a 23rd character provided a single MPT (Heckert *et al*. 1996). Again, errors exist in the coding and published matrix, with the corrected matrices and trees being provided by Harris *et al*. (2003*a*; see Fig. 12B). However, low support for the trees and the impact of the corrections on topologies led Harris *et al*. (2003*a*) to conclude that the relationships inferred from this study could not be considered robust.

The most recently published study of aetosaurian systematics as a whole was conducted by Heckert & Lucas (1999) as part of their discussion of a new taxon, *Coahomasuchus*. They used an expanded matrix of 60 characters for 14 taxa (with Rauisuchia as the outgroup), resulting in a single MPT (Fig. 12C). These results were used to discuss relationships within the Aetosauria and to name three new clades. Unfortunately, this matrix also contains several typographic errors, with a corrected matrix and resulting tree (Fig. 12D) being provided by Harris *et al*. (2003*a*). It is especially important to note that the revised tree generated by Harris *et al*. (2003*a*) for Heckert & Lucas' (1999) corrected dataset is very different from the one originally published (Fig. 12C), especially regarding the relationships between *Longosuchus* and *Desmatosuchus* and between *Typothorax* and '*Redondasuchus*' (Harris *et al*. 2003*a*, *b*; *contra* Heckert & Lucas 2003). The lack of support for many of the recovered nodes in these studies, however, reflects problems with a large number of uninformative characters present in the matrix (Harris *et al*. 2003*a*).

Kischlat (2000) provided another proposed phylogeny (Fig. 12E) for the Aetosauria in his review of the Late Triassic fauna of South America. This topology is of interest because the results are broadly similar to those from Heckert & Lucas (1999) (Fig. 12D) as corrected by Harris *et al*. (2003*a*). One major difference is the polytomy of *Stagonolepis*, '*Calyptosuchus*' and *Aetosauroides*, all of which have been proposed to be synonymous (Long & Murry 1995; Heckert & Lucas 1999, 2000, 2002*a*). Unfortunately Kischlat (2000) did not discuss this topology nor provide the data from which it was generated.

Finally, in addition to providing corrected matrices and the resulting cladograms of past studies, Harris *et al*. (2003*a*) combined data from these studies to determine a new consensus phylogeny (Fig. 12F). While support for this tree is generally weak, it does support relationships between *Typothorax* and *Redondasuchus* and between *Desmatosuchus* and *Acaenasuchus*. The paraphyletic status of *Stagonolepis* is not substantiated by morphological comparisons and probably is a result of the lateral armour of *Paratypothorax*-like forms being mistakenly assigned to the cervical lateral region of *S. wellesi* by Long & Murry (1995).

Harris *et al*. (2003*a*) provided strong criticisms regarding the character constructions used for these past studies, in particular those of Heckert & Lucas (1999). Harris *et al*. (2003*a*) argued that osteoderms represent intraorganismal homologues and that the reductive type of coding used by Heckert & Lucas (1999) provides perhaps too much weight to certain non-independent characters, distorting true relationships. For example, *Typothorax* and *Desmatosuchus* are purported to be united by three synapomorphies (Heckert & Lucas 1999: 64): (1) random pitting of the cervical, (2) dorsal and (3) caudal paramedian plates. The evidence conferred by these synapomorphies counterbalances synapomorphies between *Longosuchus* and *Desmatosuchus* (Heckert & Lucas 1999: 64) such as (1) spikes on cervical lateral plates, (2) spikes on dorsal lateral plates and (3) the high degree of angulation of the lateral spikes. Indeed, when a more composite coding is used (Harris *et al*. 2003*a*: fig. 2) a relationship between *Longosuchus* and *Desmatosuchus* becomes apparent. The overlying problem is not necessarily a poor fossil record of aetosaurs (as implicated by Heckert & Lucas 2003) but, instead, the need to critically evaluate character constructions and determine what morphological features unite groups (clades) within the Aetosauria (Harris *et al*. 2003*a*, *b*). Surprisingly, relatively complete skeletons including skull material are known from all eight taxa used in Heckert & Lucas' (1999) analysis, although the lack of preparation and study of some of this material has hindered its usage in developing characters.

One of the major assumptions of conducting phylogenetic analysis of aetosaurs based mainly on the characters from dermal osteoderms is that these osteoderms are truly phylogenetically informative. While no detailed study of postcrania, especially limbs, has been undertaken to provide a test, recent work including that by Martz (2002), Gower & Walker (2002) and Desojo & Heckert (2004) on braincase characters will, hopefully, allow a future assessment regarding the phylogenetic usefulness of osteoderms. Several challenges facing aetosaur workers wishing to provide robust postcranial characters relate to the fact that much of the existing material is divided between three continents and has not been adequately prepared or figured. Confusing the issue even more is that although Long & Murry (1995) assign much postcranial material from the *Placerias* Quarry to individual taxa, explicitly *Desmatosuchus* and *Stagonolepis*, these assignments are extremely tentative and should be viewed with great caution. There is little association between elements recovered from this quarry (Camp & Welles 1956; Fiorillo *et al*. 2000) and Long & Murry (1995) essentially divided all of the aetosaur material from this quarry between these two aetosaur taxa using unknown criteria. Furthermore, there is a previously unrecognised *Paratypothorax*-like aetosaur also present in the quarry and some of the historical material may
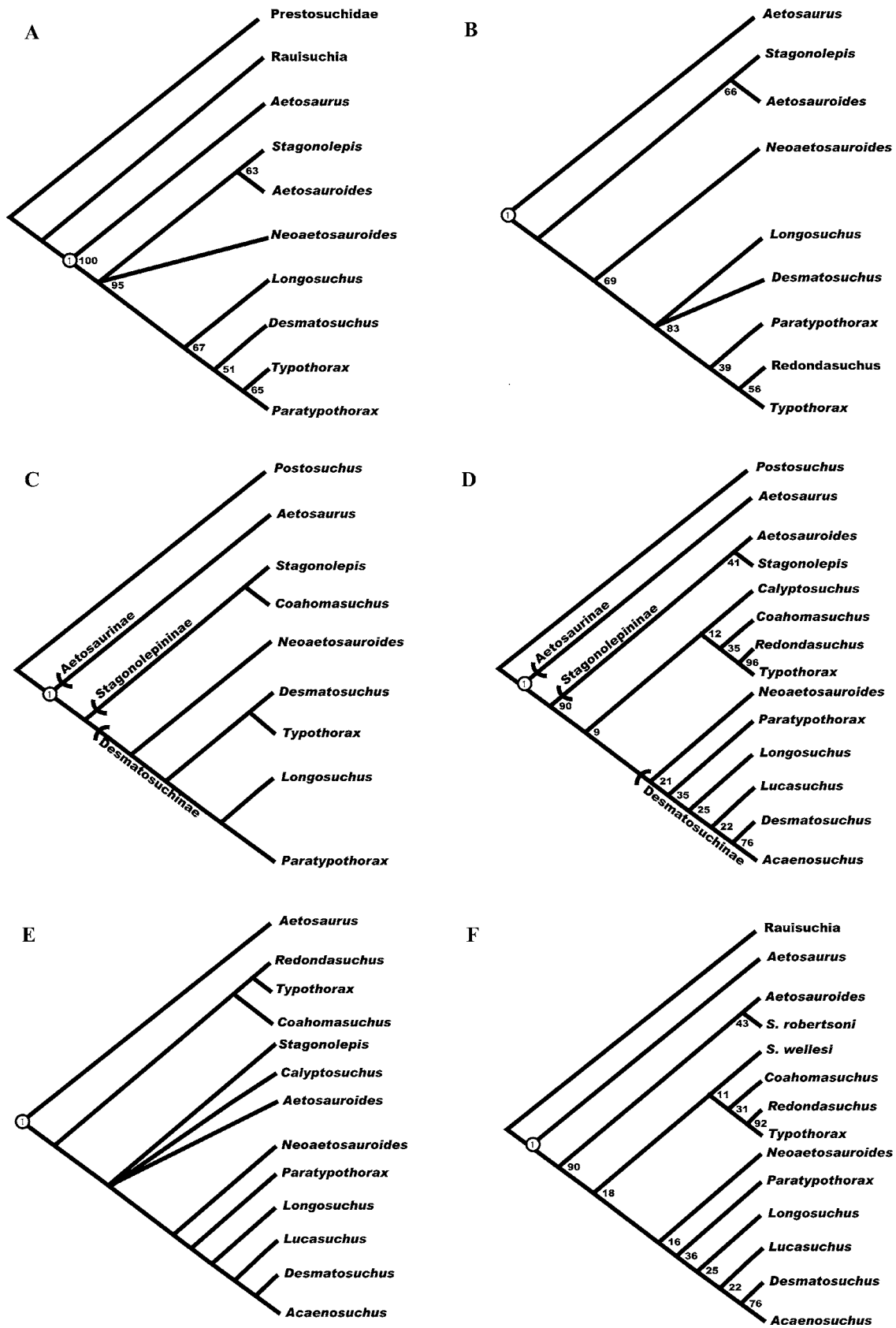
Figure 12 Previously published cladograms of the Aetosauria. **A**, corrected topology of Parrish (1994) from Harris *et al.* (2003*a*); **B**, corrected topology of Heckert *et al.* (1996) from Harris *et al.* (2003*a*); **C**, from Heckert & Lucas (1999); **D**, corrected topology of Heckert & Lucas (1999) from Harris *et al.* (2003*a*); **E**, from Kischlat 2000; **F**, from Harris *et al.* (2003*a*). Nodes marked with a 1 refer to Aetosauria. Other numerals refer to bootstrap proportions listed for these studies by Harris *et al.* (2003*a*) and are placed at their respective nodes.

belong to this taxon (Parker 2006). Unfortunately, much of this material has already been used to make comparisons between *Desmatosuchus haplocerus*, *Stagonolepis wellesi* and other aetosaurs (e.g. Parrish 1993; Small 2002; Heckert *et al*. 2003).

Despite this, I argue that lateral plate morphologies may provide a strong phylogenetic signal. All aetosaurs can be divided into three groups based on the morphology of the lateral armour: symmetrical, asymmetrical with the dorsal flange longer than the lateral flange and asymmetrical with the lateral flange longer than the dorsal flange. The utility of lateral plate morphology was demonstrated above as being key to determining the relationships of *Heliocanthus* throughout this study.

Appendix 2 presents a critical analysis of characters used by past workers that were rejected for the current study.

A new hypothesis for aetosaurian phylogeny

As seen from the above discussion and the character analyses in Appendices 1 and 2, there are numerous problems with past phylogenetic studies, extending beyond those already presented by Harris *et al*. (2003*a*). In all fairness to these workers, the past 5 years have seen several important new aetosaur specimens come to light, including the *Typothorax* specimen described by Martz (2002), the *Desmatosuchus* specimen described by Parker (2003) as well as *Heliocanthus*. With the knowledge gained from this new material it is possible to clarify and improve much of the data presented in the past in order to develop a new phylogenetic hypothesis. Still, without additional specimens and new anatomical research to provide better character construction and to remove much of the missing data this work should be best considered 'a work in progress.'

The new matrix consists of 18 taxa and 37 characters (see Appendices 1 and 3). *Postosuchus* ('Rauisuchidae') and *Revueltosaurus callenderi* (Pseudosuchia *incertae sedis*) (Parker *et al*. 2005) are used as outgroups. *Revueltosaurus* is included because it possesses aetosaur-like paramedian armour. Aetosaurian taxa analysed were *Acaenasuchus geoffreyi, Aetosaurus ferratus, Coahomasuchus kahleorum, Aetosauroides scagliai, Stagonolepis robertsoni, Stagonolepis wellesi, Desmatosuchus haplocerus, Desmatosuchus smalli, Heliocanthus chamaensis, Longosuchus meadei, Lucasuchus hunti, Neoaetosauroides engaeus, Typothorax coccinarum, Redondasuchus reseri, Paratypothorax andressorum* and *Tecovasuchus chatterjeei*. For this study *Acaenasuchus, Aetosauroides* and *Lucasuchus* are considered valid taxa (*contra* Heckert & Lucas 1999, 2000, 2002*a*, *b*). The holotype specimen of *Typothorax antiquum* Lucas *et al*. 2002 cannot be differentiated from material of *T. coccinarum* and therefore was not considered in this analysis. Moreover, despite the argument by Desojo (2003) that *Chilenosuchus* represents an aetosaur, the discovery of aetosaur-like plates in the pseudosuchian *Revueltosaurus callenderi* (Parker *et al*. 2005) demonstrates that non-aetosaurs possessed similar plates and, therefore, *Chilenosuchus* was also not included in this analysis pending further examination.

Twenty-six of the characters are taken and/or modified from the three previous studies (Parrish 1994; Heckert *et al*. 1996; Heckert & Lucas 1999). In addition there are 11 new characters. All analyses were performed using PAUP* ver-
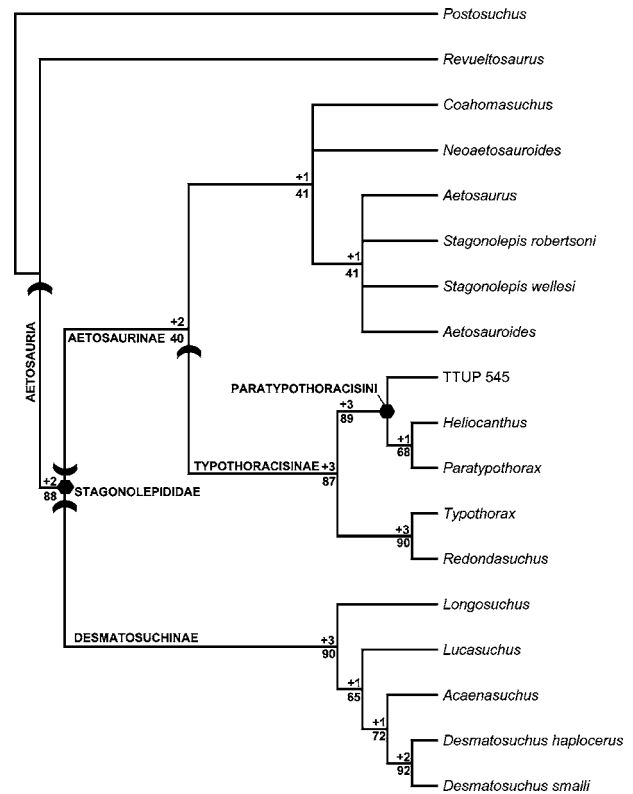

Figure 13 Strict consensus tree resulting from the 10 Most Parsimonious Trees (MPTs) for the Aetosauria from the current study. Decay indices and bootstrap values are listed above and below branches, respectively. Under Adams consensus, *Stagonolepis wellesi* and *Aetosauroides* form a sister group (Decay Index = 0; bootstrap value = 25).

sion 4.0b10 for 32-bit Microsoft Windows (Swofford 2003). Characters were weighted equally, nine were treated as additive (ordered: characters 4, 6, 9, 10, 11, 12, 14, 25, 28 and 31) with two characters being parsimony-uninformative. The heuristic search was run using a tree-bisection-reconnection (TBR) algorithm. This resulted in 10 MPTs, the strict consensus of which (Fig. 13) has a length of 63, a consistency index (CI) of 0.73, a retention index (RI) of 0.85 and a rescaled consistency index (RC) of 0.62. The homoplasy index (HI) is 0.28. Bootstrap proportions (1000 replicates) are listed for nodes. Bremer support (= Decay Index) was calculated using PAUP* by running successive heuristic searches, keeping all trees one step longer than the MPT and then computing a strict consensus for all resulting trees in each search. This was continued until all in-group branches collapsed. An Adams-consensus tree (not shown) provides slightly more resolution in one portion of the tree where support for clades is very weak.

The resulting consensus tree (Fig. 13) is quite different from those published by Heckert & Lucas (2000) and more like the one obtained from their earlier study (Heckert *et al*. 1996). The Aetosauria consist of two major clades, the Aetosaurinae and the Desmatosuchinae. Heckert & Lucas (2000: 1546) defined Aetosaurinae as a stem-based taxon containing all taxa more closely related to *Aetosaurus* than to the last common ancestor of *Aetosaurus* and *Desmatosuchus*. These same authors (p. 1551) defined Stagonolepininae as

all aetosaurs more closely related to *Stagonolepis* than to the last common ancestor of *Stagonolepis* and *Desmatosuchus*. These definitions were constructed under the hypothesis that *Aetosaurus* was the sister taxon of all other aetosaurs, a hypothesis not supported by the current analysis. As a result Aetosaurinae and Stagonolepininae contain the same taxa and the former is used here due to page priority of that name.

For this study Aetosaurinae consists of two clades. The first is an unnamed, poorly resolved clade, containing *Coahomasuchus*, *Neoaetosauroides*, *Aetosaurus*, *Stagonolepis*, and *Aetosauroides*. This clade is also poorly supported (Decay Index = +1). The second clade is more robust (Decay Index = +3) with a bootstrap value of 87. It contains *Typothorax*, *Redondasuchus* and the *Paratypothorax*-like aetosaurs.

Desmatosuchinae (Heckert & Lucas, 2000) consists of *Longosuchus*, *Lucasuchus*, *Acaenasuchus* and *Desmatosuchus*. This analysis does not support the proposed synonymy of *Lucasuchus* and *Longosuchus* as advocated by Heckert & Lucas (1999, 2000; also see Harris *et al*. 2003*a*), although they are only removed from each other by a single step.

A significant difference from past studies is that *Aetosaurus* is not the sister taxon to all other aetosaurs, although its exact relationship with *Aetosauroides*, *Stagonolepis*, *Coahomasuchus* and *Neoaetosauroides* has not been resolved. However, in all trees considered in this study, these taxa consistently group together, presumably based on the strong similarities between their lateral armour. The proposed synonymy of *Aetosauroides*, *Stagonolepis wellesi* and *S. robertsoni* (Heckert & Lucas, 1999, 2000, 2002*a*) is not supported by this study as these taxa form a clade in only 41 of 1000 bootstrap replicates (Fig. 13). *Redondasuchus* and *Typothorax* form a robust clade (bootstrap value = 90; Decay Index = +3) consistent with the proposed synonymy of these taxa by Martz (2002). *Heliocanthus* groups within the Typothoracisinae (bootstrap value = 89; Decay Index = +3) and specifically with *Paratypothorax* (bootstrap value = 68) rather than *Desmatosuchus*, not forming a clade with the later taxon until the tree collapses into an unresolved polytomy with an additional three steps.

Discussion

Harris *et al*. (2003*a*: 243) argued that only three hypotheses of aetosaur relationships were consistent in the past three analyses of aetosaur phylogeny; '(1) *Aetosaurus* is the sister group of all other aetosaurians, (2) *Aetosauroides* is the sister group of *Stagonolepis* (*robertsoni*) and (3) *Longosuchus* and *Desmatosuchus* are more closely related to each other than either is to *Neoaetosauroides*.' However, support for these relationships is eroded given that: (1) *Aetosaurus* was mis-scored in all three of the past analyses; (2) *Neoaetosauroides* had been poorly understood because, until the work of Desojo & Báez (2005), it had never been adequately compared to other aetosaurs and (3) *Stagonolepis* (= *Calyptosuchus*) *wellesi* has similar plate ornamentation to both *S. robertsoni* and *Aetosauroides*. Harris *et al*. (2003*a*) also point out scoring errors in the studies by Parrish (1994), Heckert *et al*. (1996) and Heckert & Lucas (1999). If the trees resulting from the corrected matrices for these studies are analysed (Harris *et al*. 2003*a* figs. 6 & 9) and compared to the hypothesis presented in this paper, another robust hypothesis can be made: that '*Redondasuchus*' and *Typothorax*

consistently group together and, thus, may be congeneric (Martz 2002) if not synonymous. This synonymy is supported by the fact that there are no morphological features that differentiate *Typothorax* and *Redondasuchus* (Martz 2002). It should also be emphasised that the present study indicates that if *Aetosaurus* is scored according to its description by Walker (1961), it can no longer be considered the sister group of the rest of the aetosaurs, as had been proposed by previous studies.

Unfortunately, even with the matrix errors corrected (Harris *et al*. 2003*a*: figs 8–9; Fig. 12D), the phylogeny presented by Heckert *et al*. (1999) is still very poorly supported (over half of the characters are uninformative) and the revised topology is vastly different from the published one. Therefore, most of the relationships presented in their paper (Heckert & Lucas 2000) are uncorroborated. The dataset from Heckert *et al*. (1996) is better supported (Harris *et al*. 2003*a*: fig. 6; Fig. 12B) and more closely resembles the tree obtained from the current study; however, their study did not include all currently known taxa.

The following hypotheses are supported by the topology constructed by the current study: (1) *Typothorax* and *Paratypothorax* are more closely related to each other than either are to *Longosuchus* or *Desmatosuchus*; (2) *Aetosaurus* is not the most basal aetosaur and could possibly be more closely related to *Stagonolepis* as postulated by Walker (1961) and (3) *Heliocanthus chamaensis* is not closely related to *Desmatosuchus*, but rather to *Paratypothorax* and therefore its removal from *Desmatosuchus* is supported.

A problem with the current study is that there is no resolution within the non-typothoracisine aetosaurines, especially regarding the relationships between *Aetosauroides* and the two species of *Stagonolepis*. Hopefully, with updated information regarding *Aetosaurus*, *Paratypothorax*, *Neoaetosauroides* and *Stagonolepis wellesi* (all have new specimens currently under study or are being re-examined), additional phylogenetically informative characters will improve the resolution of aetosaur phylogentic relationships. Still, the Desmatosuchinae and two new clades proposed in the next section have moderate support. If the hypothesis that lateral armour is phylogenetically informative stands, I am confident that future expanded matrices, incorporating more non-armour characters, will support the validity of these clades.

TAXONOMIC DEFINITIONS

Aetosauria Marsh, 1884

Heckert & Lucas (2000: 1544) defined Aetosauria 'as a stem-based taxon consisting of all crurotarsans more closely related to *Desmatosuchus* than the immediate sister group, recognising that the sister group may be rauisuchians, prestosuchians, or another suchian taxa' and used *Postosuchus* as the outgroup. They also noted that this definition was tentative. Given the unresolved relationships of archosaurs (Gower & Wilkinson 1996) this definition is ambiguous and is not valid because it does not actually define any relationships. Aetosauria is defined here as a stem-based taxon that consists of all taxa closer to *Aetosaurus* and *Desmatosuchus* than to *Leptosuchus*, *Postosuchus*, *Prestosuchus*, *Poposaurus*, *Sphenosuchus*, *Alligator*, *Gracilisuchus* and *Revueltosaurus callenderi*. Aetosaurs are united by several

synapomorphies including external nares that are more elongate than the antorbital fenestra, laterally exposed supratemporal fenestrae, a 'downturned' jugal, an edentulous anterior portion of the dentary and a 'slipper-shaped' mandible.

Stagonolepididae Lydekker, 1887 *sensu* Heckert & Lucas 2000

Heckert & Lucas (2000) defined Stagonolepididae as a node-based taxon consisting of the last common ancestor of *Aetosaurus* and *Desmatosuchus*. In the current study Stagonolepididae consists of the stem-based taxa Desmatosuchinae and Aetosaurinae. An important caveat regarding this definition is that if in future studies *Aetosaurus* is found to represent a more derived aetosaurine, then it is possible that more basal taxa will fall outside this clade as non-stagonolepidid aetosaurs.

Benton (2004: 11) defined Stagonolepididae as 'those taxa stemming from the last common ancestor of *Stagonolepis robertsoni* and *Aetosaurus ferratus* and sharing a more recent common ancestor with those species than with *Mystriosuchus planirostris*, *Ornithosuchus longidens*, or Crocodylia'; however, this definition does not imply whether it is stem- or node-based. Furthermore, according to the current study, both *Stagonolepis robertsoni* and *Aetosaurus ferratus* are part of an unresolved clade that excludes the majority of known aetosaur taxa. Following rules for phylogenetic taxonomy proposed by de Queiroz & Gauthier (1992), the first valid definition for a clade should have priority. Therefore, I consider the definition by Heckert & Lucas (2000) to define the clade Stagonolepididae.

Aetosaurinae Marsh, 1884 *sensu* Heckert & Lucas 2000

Heckert & Lucas (2000) defined Aetosaurinae as a stem-based taxon containing all taxa more closely related to *Aetosaurus* than to the last common ancestor of *Aetosaurus* and *Desmatosuchus*. In this study Aetosaurinae contains Typothoracisinae and an unnamed clade containing ([*Coahomasuchus* + *Neoaetosauroides*] + [*Aetosaurus* + *Stagonolepis robertsoni* + *Stagonolepis wellesi* + *Aetosauroides*]). With the phylogenetic hypothesis presented here, Aetosaurinae contains the same taxa as Stagonolepininae Heckert & Lucas, 2000. This clade is weakly supported and diagnosed by only a single synapomorphy: dorsal eminence of paramedian plates is offset medially.

Unnamed clade ([*Coahomasuchus* + *Neoaetosauroides*] + [*Aetosaurus* + *Stagonolepis wellesi* + *Stagonolepis robertsoni* + *Aetosauroides*])

This clade is very weakly supported by parsimony analysis with no synapomorphies.

Unnamed Clade (*Stagonolepis robertsoni* + *Stagonolepis wellesi* + *Aetosauroides* + *Aetosaurus*)

This clade is unresolved and currently diagnosed by a single synapomorphy: mid-dorsal paramedian plates strongly flexed ventrally (also present in *Typothorax* and *Redondasuchus*).

Typothoracisinae (new taxon)

Typothoracisinae is a stem-based taxon defined here as all aetosaurs closer to *Typothorax* than to *Stagonolepis* or *Desmatosuchus*. In the context of the phylogenetic hypothesis presented here, Typothoracisinae contains *Typothorax*, *Re-*

dondasuchus and Paratypothoracisini. Typothoracisinae is diagnosed by six synapomorphies: (1) transverse processes of dorsal vertebrae elongate and buttressed ventrally (unknown in *Redondasuchus*, *Tecovasuchus* and *Heliocanthus*); (2) width to length ratio of widest dorsal paramedian plates more than 3.5:1; (3) minimum angle of flexion between the dorsal and lateral flanges of the dorsal lateral plates strongly acute (unknown in *Redondasuchus*); (4) dorsal and lateral flanges of dorsal lateral scutes asymmetrical with lateral flange being longest (unknown in *Redondasuchus*); (5) pelvic and anterior caudal dorsal lateral plates are roughly triangular in lateral view and possess a semicircular ventrolateral border and a hook-like eminence (unknown in *Redondasuchus*); and (6) dorsal lateral plates with triangular or tongue-like dorsal flange of the lateral plate (unknown in *Redondasuchus*).

Unnamed clade (*Typothorax* + *Redondasuchus*)

Hunt & Lucas (1991) followed by Heckert *et al.* (1996) considered *Redondasuchus* to represent a distinct taxon based on the lack of lateral plates, although these authors did note similarities in the armour ornamentation to *Typothorax*. Martz (2002) demonstrated that these authors had interpreted the holotype dorsal paramedian plate backwards and that when orientated correctly, it closely resembled that of *Typothorax*. Due to this similarity, Martz concluded that *Redondasuchus* did possess lateral plates. Long & Murry (1995) argued that *R. reseri* is a junior synonym of *Typothorax coccinarum*. Martz concurred that *Redondasuchus* is a synonym of *Typothorax* but kept *T. reseri* as a valid species. This analysis is consistent with both of these interpretations.

Paratypothoracisini (new taxon)

Paratypothoracisini is a node-based taxon that includes *Tecovasuchus*, *Heliocanthus* and *Paratypothorax* as well as all descendents of their most recent common ancestor. Paratypothoracisini is currently diagnosed by five synapomorphies: (1) dorsal eminence of the paramedian plates never or almost never contacts the posterior margin of the plate (convergent in *Desmatosuchus* and *Lucasuchus*); (2) paramedian plates flat lying with little or no ventral flexure at the centre of ossification (convergent with *Longosuchus*, *Lucasuchus* and *Desmatosuchus*); (3) dorsal flange of the dorsal lateral plates is tongue-shaped (Martz & Small, 2006); (4) lateral spikes in the cervical and anterior dorsal region form a dorsoventrally flattened 'horn'; and (5) dorsal eminence of the dorsal paramedian plates is strongly offset medially.

Unnamed clade (*Paratypothorax* and *Heliocanthus*)

These taxa are united by a single synapomorphy: presence of an anterior bar that is weakly or moderately raised (Zeigler *et al.* 2003; Martz & Small 2006).

Desmatosuchinae Huene, 1942 *sensu* Heckert & Lucas, 2000

Heckert & Lucas (2000: 1555) redefined Huene's Desmatosuchinae as a stem-based taxon that includes all aetosaurs more closely related to *Desmatosuchus* than the last common ancestor of *Desmatosuchus* and *Stagonolepis*. In this study Desmatosuchinae consists of *Longosuchus* + *Lucasuchus* + *Acaenasuchus* + (*Desmatosuchus haplocerus* + *Desmatosuchus smalli*). *Lucasuchus* is considered here to be a valid taxon (*contra* Heckert & Lucas 1999, 2000) as

was argued by Harris *et al.* (2003*a*). *Acaenasuchus* (Long & Murry 1995) is also considered to be valid (*contra* Heckert & Lucas 2002*b*). Desmatosuchinae is diagnosed by six synapomorphies: (1) tongue-and-groove articulations for lateral plates present in dorsal presacral paramedian plates; (2) well-developed, elongate spikes in the lateral cervical, dorsal and caudal armour; (3) presence of spikes on the dorsal and caudal lateral plates; (4) dorsal and lateral flanges of dorsal lateral plates asymmetrical with the dorsal flange being longest; (5) raised dorsal eminences present on the cervical and anterior dorsal paramedian plates; and (6) cervical paramedian plates that are longer than wide.

Unnamed clade (*Lucasuchus* + *Acaenasuchus* + [*Desmatosuchus haplocerus* + *Desmatosuchus smalli*])

These taxa are united by one synapomorphy: dorsal eminences that never contact the posterior margin of the paramedian plates (convergent with Paratypothoracisini).

Unnamed clade (*Acaenasuchus* + [*Desmatosuchus haplocerus* + *Desmatosuchus smalli*])

This clade is united by the following synapomorphy: random patterning of paramedian plates (convergent with *Typothorax* and *Redondasaurus*).

Unnamed clade (*Desmatosuchus haplocerus* + *Desmatosuchus smalli*)

These taxa are united by three synapomorphies: 1) the presence of an anterior lamina (Long & Ballew 1985) rather than a raised bar on the paramedian and lateral armour; 2) the cervical lateral plates of the 6th series possess spines that are extremely elongate and recurved posteriorly; and 3) the dorsal eminences of the anterior dorsal lateral plates have the form of a low, broad "mound".

CONCLUSIONS

Morphological data subjected to parsimony analysis demonstrate that '*D.*' *chamaensis* is not a species of *Desmatosuchus*; instead it represents a new taxon more closely related to *Paratypothorax*. This new taxon, *Heliocanthus*, can be distinguished from *Desmatosuchus* by the presence of paramedian plates with a high (<3.5:1) width: length ratio, radial instead of random patterning and a distinct anterior bar. Furthermore, the dorsal lateral plates of *Heliocanthus* possess ventral flanges that are larger than the dorsal flanges, unlike the condition in *Desmatosuchus* where the dorsal flange is larger. *Heliocanthus* can be distinguished from *Paratypothorax* on the basis of the elongation of the dorsal eminence of the posterior paramedian plates into an anteromedially recurved spike.

According to this study, *Heliocanthus* is a member of the clade Paratypothoracisini, which represents derived typothoracisines. Paratypothoracisins represent a previously unrecognised, diverse group of aetosaurs that includes several undescribed taxa (Parker 2003; Martz *et al.* 2003). This analysis also suggests that *Aetosaurus* is not the sister taxon to all other aetosaurians and instead is more closely related to *Stagonolepis*, as postulated by Walker (1961).

Past analyses of the Aetosauria have been plagued by erroneous scorings, published typographic errors and poor character construction (Harris *et al.* 2003*a*). Furthermore, some of the characters derived from paramedian plate morphology (e.g. dorsal eminence contacting posterior plate margin) are polymorphic, while others (e.g. pyramidal-shaped eminence) are homoplastic. Whereas current phylogenetic analyses of the Aetosauria have been based on the assumption that dorsal osteoderms are the most phylogenetically informative elements, parsimony analysis of the Aetosauria focusing on lateral plate morphology, while not entirely resolved, suggests that aetosaurs can be divided into three clades: the Desmatosuchinae, Typothoracisinae and a group of *Stagonolepis*-like aetosaurs. Thus, the lateral plates of aetosaurs are less homoplastic and provide a stronger phylogenetic signal than the paramedian plates. A phylogeny based on these criteria can form a solid foundation for future analyses that must include expanded datasets of characters from the skull and non-armour postcrania. Recent work on braincase material (e.g. Gower & Walker 2002; Martz 2002; Desojo & Heckert 2004) and postcranial comparisons (Desojo 2004; Desojo & Báez 2005) may help test proposed aetosaurian relationships that are currently based mainly on osteoderm morphology.

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APPENDIX 1: LIST OF CHARACTERS USED IN THIS STUDY

Characters 1–22 taken from Heckert & Lucas (1999) with minor moderation. Characters 1–4 and 14 are originally from

Parrish (1994). Characters 23–27 taken from Heckert *et al.* (1996) with minor modification. Number in brackets corresponds to character number in original papers. Characters 27–37 are new.

1. [1] *Premaxilla edentulous anteriorly, with an anteroventrally inclined, mediolaterally expanded 'shovel' at the anterior end: absent (0) or present (1).* Heckert & Lucas (1999) considered the presence of the 'shovel-like' terminus of the premaxilla to be an aetosaur synapomorphy. Re-examination of the type specimens of *Aetosaurus* shows that this character is not present in that taxon. Nor is it present in another undescribed taxon from Germany.

2. [3] *Teeth mediolaterally compressed and recurved (0), teeth bulbous and conical with recurved tips (1), teeth bulbous and conical lacking recurved tips (2).* Parrish (1994), Heckert *et al.* (1996) and Heckert & Lucas (1999) all scored the teeth of *Aetosaurus* as being mediolaterally compressed and recurved as in 'rauisuchians'. However, as noted by Walker (1961) only the apices are recurved and the teeth are conical with a bulbous base, as in other aetosaurs. A single tooth preserved in the holotype dentary of *Aetosauroides* appears to be mediolaterally compressed and recurved, but Casimiquela (1967) noted that the teeth were more like those of *Aetosaurus*.

3. [4] *Anterior part of the dentary with teeth (0) or edentulous (1).* State 1 is most probably a synapomorphy of the Aetosauria and thus provides no in-group resolution. Based on reconstructions of the skull of *Aetosaurus* by Fraas (1877) and Huene (1920), Parrish (1994), Heckert *et al.* (1996) and Heckert & Lucas (1999) all scored the anterior part of the dentary in *Aetosaurus* as possessing teeth. However, Walker (1961: 166–167) redescribed the holotype of *Aetosaurus* and noted that the anterior portion of the dentary is edentulous, thus this character is rescored for *Aetosaurus*.

4. [6] *Posterior premaxillary teeth present (0) or absent (1).* This character is scored incorrectly for *Longosuchus* in Heckert *et al.* (1996). Longosuchus does possess premaxillary teeth (Parrish 1994; Small 2002).

5. [8] *External nares shorter than (0) or longer than (1) antorbital fenestra.* This is a synapomorphy of the Aetosauria and does not offer any in-group resolution.

6. [10] *Position of supratemporal fenestra: dorsally exposed (0) or lateral (1).* This is a synapomorphy of the Aetosauria and does not offer any in-group resolution.

7. [14] *Jugal: not downturned (0) or downturned (1).* This is a synapomorphy of the Aetosauria and does not offer any in-group resolution.

8. [15] *'Slipper-shaped' mandible: absent (0) or present (1).* This is a synapomorphy of the Aetosauria and does not offer any in-group resolution.

9. [16] *Dentary tooth count: 9 or more (0) or fewer than 9 (1).* *Aetosaurus* is considered by Heckert & Lucas (1999) to possess State 0, however, according to Walker (1961: 176) the tooth count is actually 7–8.

10. [18] *Transverse processes of dorsal vertebrae short, less than twice as wide as the centrum (0) or elongate, buttressed ventrally (1).* Transverse process lengths vary through the dorsal series, however only *Typothorax coccinarum* and *Paratypothorax* possess elongate processes with a ventral ridge of buttress (pers. obs.). Heckert & Lucas (1999) code *Stagonolepis* as having elongate transverse processes, however, as figured by Walker (1961: 137) they are short. Very elongate processes are considered an autapomorphy of *Stagonolepis wellesi* by Long & Murry (1995) and were scored accordingly by Heckert & Lucas (1999). However, as seen in the holotype of *S. wellesi* (Long & Murry 1995: figs 69b, 75a), these processes belong to the posterior presacral vertebrae, which in *Desmatosuchus* (Parker 2003) and *Typothorax* (Hunt *et al.* 1993) are also extremely elongate and fused to ribs. Thus, these vertebrae do not present a clear representation of transverse process lengths throughout the dorsal series because the posterior-most vertebrae and ribs appear to be particularly modified. This modification occurred to some degree in several other taxa as well. Walker (1961: 137–139) commented on the uniqueness of the posterior dorsals in *S. robertsoni*. A better representative figure of a *S. wellesi* dorsal vertebra was provided by Case (1932: fig. 2) showing that the processes are less than twice the width of the centrum. This is probably also true for *Aetosauroides scagliai*. The series of 'dorsal' vertebrae figured in Heckert & Lucas (2002a: figs 2.7, 2.8) are grooved ventrally, possess chevron facets and the centra are clearly increasing in length while decreasing in overall size, indicating that they are caudals and not dorsals. Indeed, the transverse processes on these vertebrae are more consistent with caudals than dorsals in being very flat and broad and seemingly possessing no rib articulations. The other vertebrae figured by Heckert & Lucas (2002: figs 2.9 – 2.11) are dorsals and even though the transverse processes are incomplete, they do not appear to have been particularly elongate. It should be noted that in their text Heckert & Lucas (2002: 855) consider three of these vertebrae to be dorsals, even though they list them as caudals in the caption for their figure.

11. [19] *Presacral neural spine height high (0) or generally low, less than height of centrum (1).* Heckert & Lucas (1999) consider a low neural spine to be plesiomorphic and score it so for their outgroup. However, 'rauisuchians' have high neural spines and so this character is rescored.

12. [20] *Cervical centra keeled ventrally (0) or unkeeled (1).* According to Desojo & Báez (2005) elongate keels are present on the ventral surface of the cervical centra in *Neoaetosauroides* (*contra* Heckert & Lucas 1999).

13. [29] *Anterior bars on dorsal and lateral plates: absent (0), weakly raised bar (1), strongly raised bar (2). Desmatosuchus* has a depressed lamina rather than a raised anterior bar (Long & Ballew 1985). Zeigler *et al.* (2000) and Martz (2002) describe the anterior bar as being moderately or weakly developed in *Heliocanthus* and *Paratypothorax*, respectively. A raised anterior bar is present in pseudosuchian *Revueltosaurus* (Parker *et al.* 2005).

14. [30] *Width to length ratio of widest dorsal paramedian plates: maximum of less than 3.5/1 (0), 3.5/1 or more (1)*. This character is widely used in aetosaur systematics (Heckert & Lucas 2000), even for taxa in which the whole carapace is not known. While it can be a useful character, it should be used only for taxa that are relatively complete, because in a widening and tapering carapace there is much variation in the width to length ratios of the paramedian plates. Parrish (1994) mis-scores this character for *Paratypothorax* (Harris *et al.* 2003*a*). Furthermore, since only *Paratypothorax* has ratios of more than 4/1, the value was reduced to 3.5/1 to be more inclusive.

15. [31] *Shape of cervical dorsal paramedian plates: wider than long (0) or longer than wide (1)*. The cervical paramedians are scored for *Redondasuchus* as being 'as long as wide' in Heckert *et al.* (1996) and as 'wider than long' in Heckert & Lucas (1999). However, the state is ambiguous in *Redondasuchus* because of the isolated nature of the material and should be scored as unknown. This character is also unknown for *Acaenasuchus* (*contra* Heckert & Lucas 1999).

16. [33] *Patterning of paramedian plates: radiate (0) or random (1)*. This character is mis-scored for *Desmatosuchus* by Heckert *et al.* (1996) and needs to be rescored as being random. All aetosaur taxa do not vary in this character throughout the paramedian series, therefore it is not necessary to distinguish regions for this character (Harris *et al.* 2003*a*; *contra* Heckert & Lucas 1999).

17. [34] *Ornamentation of paramedian plates consists of mixture of pits, elongate pits, grooves and ridges (0) or small subcircular pits only (1)*. Within the Aetosauria only *Typothorax* and *Redondasuchus* have an ornamentation that consists of small subcircular pits. Desojo (2003) also notes this type of ornamentation in the purported aetosaur *Chilenosuchus*, however no other aetosaurian characters are present in the holotype specimen. The discovery of aetosaur-like plates in the pseudosuchian *Revueltosaurus* demonstrates that this plate type is not unique to aetosaurs. *Revueltosaurus* also possesses an ornamentation of small, circular pits (Parker *et al.* 2005), therefore this state could represent the plesiomorphic condition.

18. [35] *Dorsal eminence contacts posterior margin of the paramedian plates majority of the time (0) or almost never (1)*. This character can be ambiguous because of the variability of ornamentation in aetosaur armour. For example, *Paratypothorax* is listed in Heckert *et al.* (1996) and Heckert & Lucas (1999) as possessing a boss that contacts the posterior margin of the plate. Only in a few specimens where the boss is particularly large and hook-like (Long & Murry 1995: fig. 114e) does it contact the margin in *Paratypothorax*, however, this is not the case in most plates (e.g. Case 1932: pl. 4, figs 5–6; Lucas & Hunt 1993: figs 44b,c,f; Jenkins *et al.* 1994: fig. 10; pers. obs.). In *Typothorax*, when bosses do occur on the dorsal paramedian plates they can either be in contact with or just anterior to the posterior margin. Martz (2002) attributes this to position in the carapace, with the margin contacting bosses being on the more posterior plates in *Typothorax* and this condition is most probably the same for *Paratypothorax*. Therefore this character is not valid as originally constructed and the state definitions have been modified for this study.

19. [36] *Raised dorsal eminence on cervical and anteriormost paramedian plates: absent (0), present (1)*. Heckert & Lucas (1999) divided this character among three body regions (characters 36–38). Harris *et al.* (2003*a*) argued that these characters co-vary and that such a reductive coding might give too much weight to this 'group' of characters. However, in the majority of aetosaur taxa, raised dorsal eminences do not occur in the cervical or anterior dorsal paramedian plates. Harris *et al.* (2003a) combined characters 37 and 38 into a single character, but the resultant character offers no in-group resolution since dorsal eminences do occur in the posterior dorsal and caudal regions of all aetosaurs. Therefore, the three characters constructed by Heckert & Lucas (1999) are combined and the resulting single character is redefined for this study. Note that Heckert *et al.* (1996) score dorsal eminences as present in *Neoaetosauroides* whereas Heckert & Lucas (1999) score them as absent. According to Desojo & Báez (2005) they are present in that taxon.

20. [43] *Ventral keel or strut never present (0) or present (1) on some or all paramedian plates*. Heckert *et al.* (1996) and Heckert & Lucas (1999) restricted this character to *Redondasuchus* and *Typothorax* but it is also found in some plates of *Paratypothorax* (pers. obs.), *Stagonolepis wellesi* and *Tecovasuchus* (Martz 2002). Also variable is whether or not this ventral keel (or strut) is continuous across the width of the plate. Heckert & Lucas (1999) list a discontinuous keel as an autapomorphy for '*Redondasuchus*'; however, according to Martz (2002) a discontinuous keel also occurs in *Typothorax, Stagonolepis wellesi, Paratypothorax* and *Tecovasuchus*.

21. [45,46] *Cervical paramedian plates dorsoventrally thickened with tongue-and-groove articulations: no (0) or yes (1)*. Heckert & Lucas (1999) scored two separate characters for this condition; however in taxa where the cervical plates are greatly

thickened, the tongue-and-groove articulation (sensu Long & Ballew 1985) is present.

22. [49] *Lateral cervical armour lacks (0) or possesses (1) spikes or horns, that may be extremely elongate (2). Paratypothorax, Heliocanthus* and *Tecovasuchus* possess cervical lateral plates where the dorsal eminence is in the form of a spine or horn. *Desmatosuchus, Acaenasuchus, Lucasuchus* and *Longosuchus* possess cervical lateral spines that are greatly elongated. The cervical spikes attributed to *Stagonolepis wellesi* by Long & Ballew (1985) actually belong to a *Paratypothorax*-like animal instead.

23. [10] *Flexure of paramedian plates: none or minimal (0), strongly flexed ventrally (1).* Heckert *et al.* (1996) use this character as an autapomorphy for *Redondasuchus*, however it also occurs in *Typothorax*. Paramedian plates of *Typothorax* from a single carapace (PEFO 23388) occur in two forms: transversely flattened and strongly flexed. This flexion also occurs in material from the Canjilon Quarry (Martz 2002). In addition, a partial skeleton of *Stagonolepis wellesi* from Petrified Forest National Park (PEFO 31217) possesses numerous paramedian plates that are strongly flexed ventrally. This character has also been noted for *S. robertsoni* (the 'angulated plates' of Huxley (1859)) and, to some extent, in *A. ferratus* by Walker (1961: 157, 170).

24. [14] *Minimum angle of flexion between the dorsal and lateral flanges of the lateral plates: obtuse (0), approximately 90° (1), or strongly acute (2).* Heckert *et al.* (1996) constructed this character with only two states; obtuse and approximately 90° or less. However, this does not adequately describe the variation seen between aetosaur taxa. The challenge here is to properly acknowledge variation in morphology within a single carapace while reflecting synapomorphies between taxa, yet not giving this data too much weight by providing more reductive character construction (i.e. providing characters for each region or sub-region). Problems arise because most taxa have several distinct lateral plate morphologies, e.g. *Typothorax* has plates that are flattened in the pelvic region of the carapace and sharply angled in the more anterior region (Martz 2002). Nevertheless, acutely folded plates only occur in a few taxa, whereas all of the plates in *Desmatosuchus* and *Longosuchus* are flexed at approximately right angles. Therefore, it is more appropriate to consider minimum angles throughout the entire carapace.

25. [15] *Symmetry of dorsal and lateral flanges of mid-dorsal lateral plates: symmetrical (0), asymmetrical with dorsal flange longest (1), asymmetrical with lateral flange longest (2).* As with the previous character there is much variability in the lateral plates within a single carapace, however groups of taxa possess similar patterns of variability, which are considered here to be homologous. Therefore, a single character can be used to determine synapomorphy within the in-

group rather than heavily weighting the data by using numerous characters.

26. [17] *Presence of a narrow region ('waist') in the carapace anterior to the sacrum: present (0) or absent (1).* This character is discernable only for taxa in which whole carapaces or representative plates from throughout the body are known. A presacral constriction is present in *Stagonolepis* (Case 1932; Walker 1961), *Aetosaurus* (Wild 1989), *Aetosauroides* (Casimiquela 1961), *Neoaetosauroides* (Bonaparte 1971) and *Coahomasuchus* (Heckert & Lucas 1999). It is not present in *Longosuchus* (Sawin 1947), *Typothorax* (Hunt *et al.* 1993) and other wide-bodied forms (e. g. *Paratypothorax*). There is no evidence for this constriction in *Desmatosuchus* (Parker 2003; *contra* Long & Murry 1995) or in *Heliocanthus* or *Tecovasuchus*.

27. *Fusion of last presacral vertebra into sacrum does not occur (0) or occurs (1).* All known pelves that are assignable to *Desmatosuchus, Longosuchus* and *Lucasuchus* possess character state 1 (Elder 1978; Parker 2003). This fusion is not seen in pelves assigned to any other taxa regardless of size and therefore represents a taxonomic rather than ontogenetic character (Parker 2003). Sexual dimorphism cannot be ruled out at present due to a small sample size, but it cannot currently be supported either.

28. *Pelvic and anterior caudal lateral plates: roughly equant in width and length and possessing a sharp medially situated keel (0), or roughly triangular in lateral view with a semicircular ventrolateral border and a hook-like eminence (1) or rectangular and ventral to a well-developed spine (2).* A roughly triangular plate with a semicircular ventrolateral border and a hook-like eminence is shared by several taxa including *Typothorax, Paratypothorax, Heliocanthus* and *Tecovasuchus* and differs strikingly from the spiked plate found in *Desmatosuchus, Longosuchus, Lucasuchus* and *Acaenasuchus* (see Fig. 9). A somewhat similar form occurs in *Aetosaurus, Stagonolepis, Aetosauroides* and *Neoaetosauroides*, but these plates are more squarish rather than triangular.

29. *Dorsal eminence on paramedian plates: centralised (0), moderately offset medially (1) or strongly offset medially (2).* In *Desmatosuchus* the dorsal eminence is always centralised on the paramedian plate. In other taxa the eminence is located medial to centre. The extreme occurs in taxa such as *Paratypothorax* and *Heliocanthus* where the eminence is very close to the medial edge of the plate.

30. *Lateral spikes in anterior and mid-dorsal regions: not present (0), form a dorsoventrally flattened 'horn' (1) or form a conical spine (2).* The dorsoventrally flattened 'horn' is typified by what is seen in *Paratypothorax* and *Tecovasuchus* (Fig. 8), while the morphology seen in *Desmatosuchus* (Parker 2005: fig. 3) typifies the more conical spine.

31. *Number of ventral plate rows: 10 or more (0), less than 10 (1).* Few aetosaur specimens have the complete ventral carapace preserved. While *Desmatosuchus* is known from several fairly complete carapaces, no ventral armour has been recovered with these specimens. It is possible that ventral armour is restricted to a specific clade of aetosaurs.

32. *Dorsal eminences on posterior paramedian plates are in the form of a low pyramid or knob (0) or an elongate spine (1).* The dorsal eminence in *Lucasuchus* is a straight conical spine, whereas the eminence in *Heliocanthus* is an anteromedially recurved spine. Some paramedian plates of *Paratypothorax* possess short, thick, hooked eminences. Not all of the plates in a single carapace possess these elongate eminences and they appear to be restricted to the pelvic region.

33. *Cervical vertebrae extremely shortened antero-posteriorly: no (0) or yes (1).* Extremely shortened cervical centra are currently an autopomorphy of *Typothorax* (Long & Murry 1995); however they may occur in other taxa such as *Heliocanthus* or *Paratypothorax* for which the cervical vertebrae are unknown.

34. *Posterior margin of paramedian plates strongly bevelled: no (0) or yes (1).* Paramedian plates of *Paratypothorax* and *Tecovasuchus* have strongly bevelled posterior margins (Martz *et al.* 2003; Martz & Small 2006) .

35. *Cervical lateral plates of the sixth row extremely enlarged: no (0) or yes (1).* While *Longosuchus* and *Lucasuchus* have elongate spines on the cervical lateral plates, the spines tend to be close in size throughout the series. This differs from what is seen in *Desmatosuchus,* where the posterior-most set of cervical spines is much larger than the rest of the series (Long & Ballew 1985).

36. *Dorsal flange of dorsal lateral plates: rectangular (0), broadly triangular (1) or tongue-shaped (2).* Martz (2002) described the shortened dorsal flange of the dorsal lateral plates as triangular. This contrasts with the tongue-shaped flange in taxa such as *Paratypothorax* and *Tecovasuchus* (Martz *et al.* 2003) and the rectangular dorsal flange of *Desmatosuchus* (Parker 2003).

37. *Mound-like dorsal eminences on anterior dorsal lateral plates absent (0) or present (1).* In *Desmatosuchus*, the dorsal eminence of the anterior-most dorsal lateral plates has the form of a large, broad 'mound' (Long & Ballew 1985: figs 5c, 6a). This appears to be an autapomorphy of that taxon.

APPENDIX 2: PREVIOUSLY USED CHARACTERS NOT INCLUDED IN THIS ANALYSIS

The number before the hyphen represents the character number, while the code behind the hyphen refers to the analysis.

Thus, P94, Parrish (1994); H96, Heckert *et al.* (1996) and H99, Heckert & Lucas (1999).

(1) 5-P94: *Complete carapace, with dorsal and ventral armour: absent (0) or present (1).* State 1 is probably a synapomorphy of the Aetosauria and currently provides no in-group resolution. The proposed lack of lateral and ventral armour in *Redondasuchus* (Hunt & Lucas 1991; Heckert *et al.* 1996) cannot be substantiated due to the fragmentary and incomplete nature of the type and referred specimens. Furthermore, Martz (2002) has demonstrated that the holotype plate of *Redondasuchus* has been misinterpreted and when reversed is identical to the dorsal paramedians of *Typothorax*. Despite the presence of several relatively complete carapaces of *Desmatosuchus*, no ventral armour has been found for this taxon, thus this may represent a less inclusive character within Aetosauria.

(2) 10-P94: *Paramedian osteoderms without (0) or with (1) median excrescences.* According to Walker (1961) and Wild (1989), *Aetosaurus* does possess dorsal eminences (excrescences) on the posterior dorsal and pelvic plates, so this character needs to be re-evaluated and rescored for *Aetosaurus*. This is a probable synapomorphy of the Aetosauria (with the possible exception of *Coahomasuchus* Heckert & Lucas, 1999) and, as constructed, provides no in-group resolution. It should also be noted that the archosaurs *Doswellia* (Weems 1980), *Euscolosuchus* (Sues 1992) and *Revueltosaurus* (Parker *et al.* 2005) all possess rectangular paramedian osteoderms, although those of non-aetosaurians do not have dorsal eminences.

(3) 11-P94; 20-H96; 5-H99: *Maxillary tooth row does (0) or does not (1) extend anterior to the posterior end of the external naris.* Parrish (1994) lists the tooth row as not extending underneath the external naris in *Stagonolepis*, *Longosuchus* and *Aetosauroides*. However, figures of the skull of *Longosuchus* in the same paper show this not to be the case. Heckert *et al.* (1996) correct this error for *Longosuchus* but repeat it again in Heckert & Lucas (1999). The usefulness of this character is disputed by Small (2002) who states that the tooth row is extended in *Stagonolepis* as well.

(4) 13-P94; 13-H96; 49, 50, 51-H99: *Lateral osteoderms without (0) or with (1) spikes or bumps.* This is a highly ambiguous character, because the term 'bump' could include almost the entire range of ornamentation found on aetosaur lateral plates. Parrish (1994) incorrectly scores *Longosuchus* as not possessing spikes. Heckert *et al.* (1996) changed the character construction to include only spikes and this was later expanded into three separate characters by Heckert & Lucas (1999). Harris *et al.* (2003*a*) correctly point out that the character construction used by Heckert & Lucas (1999) upweights what can reasonably be considered to be a single character. Future character constructions regarding lateral 'spikes' need to take into account the variability not only in morphology, but also in position within the lateral row. Unfortunately, the disarticulated and incomplete nature of many aetosaur fossils makes it very difficult to determine direct homologues in lateral armour between taxa.

(5) 14-P94; 22-H96; 7-H99: *Absence (0) or presence (1) of a deep, hemispherical fontanelle in the bottom of the basisphenoid between the basal tubera and basipterygoid processes.* Parrish (1994) lists this character as being absent for *Longosuchus* although he describes it as being present earlier in the text. Heckert & Lucas (1999) code it as being present for *Lucasuchus* although no skull material is known for that taxon. Small (2002) comments that the presence of this character is variable in *Desmatosuchus* and in dispute for *Typothorax* and *Stagonolepis* (*contra* Heckert & Lucas 1999) and that the character needs to be re-evaluated. Gower & Walker (2002) and Desojo & Heckert (2004) also question the usefulness of this character.

(6) 9-H96; 41-H99: *Transverse arching of anterior caudal paramedian scutes: transversely arched (0) or flattened (1).* This character is ambiguous because it is scored by these authors for taxa in which the carapace is incompletely known (e.g. *Paratypothorax*). I agree with Heckert *et al.* (1996) that the plate assigned to *Redondasuchus* in their fig. 4g is a caudal paramedian, as is the plate in fig. 4a (labelled as dorsal paramedian) since this plate looks more like the anterior caudal plates in other taxa such as *Desmatosuchus* (Parker 2003) and *Typothorax* (Martz 2002). Martz (2002: figs 4.32, 4.33) figures several anterior caudal plates and describes them as being transversely arched, but this is to be expected for the caudal armour, which has to conform to the tapering width of the tail.

(7) 12-H96; 57-H99: *Presence of lateral scutes: present (0) or absent (1).* The lack of lateral plates is a proposed autapomorphy for *Redondasuchus* (Hunt & Lucas 1991; Heckert *et al.* 1996; Heckert & Lucas 1999, 2000). *Redondasuchus* is known from a few isolated plates, which do not provide enough data to discount the existence of lateral armour. In addition, as stated earlier, Martz (2002) has demonstrated that the holotype dorsal paramedian plate of *Redondasuchus* has been interpreted backwards and when reversed corresponds precisely to the same plate in *Typothorax*, which does possess lateral armour. As currently constructed, the presence of lateral plates is possibly plesiomorphic for Aetosauria, being shared with non-aetosaurs such as *Doswellia* (Weems 1980) and *Euscolosuchus* (Sues 1992) and offers no in-group resolution.

(8) 13-H96; 49, 50, 51-H99: *Lateral spikes on lateral scutes: absent (0) or present (1).* This character is a variation of Parrish's (1994) character 13 and has been briefly discussed above. Although Heckert & Lucas (1999) improved on the character description, it is still oversimplified because of the amount of variation that occurs in the lateral plates of aetosaurs. Heckert & Lucas (1999) tried to address this variation by expanding Parrish's original single character into three, based on position in the carapace. However, as argued by Harris *et al.* (2003*a*) this coding unfairly weights what should perhaps be a single multi-state character. The lateral plates are highly variable, with most aetosaur taxa possessing at least two distinct morphologies. For example, *Paratypothorax* possesses plates with small, recurved horns in addition to flatter plates with hooked bosses. It is important to note that the two lateral plate morphologies present in *Paratypothorax* are identical to those of *Heliocanthus* and *Tecovasuchus*, while differing vastly from those of *Desmatosuchus* and *Longosuchus*. Overall spike morphology provides much more important characters than the mere presence or absence of spikes and should be emphasised in phylogenetic analyses. As previously mentioned, the cervical spikes attributed to *Stagonolepis wellesi* (Long & Ballew 1985; Long & Murry 1995) almost certainly belong to a *Paratypothorax*-like taxon instead (Heckert & Lucas 2000; Martz 2002; Parker 2003).

(9) 9-H99: *Infratemporal fenestra anteroposteriorly short, dorsoventrally elongate (0) or more equant to square (1).* According to the matrix of Heckert & Lucas (1999), only *Neoaetosauroides* possesses state 1, with *Aetosaurus*, *Stagonolepis*, *Longosuchus* and *Desmatosuchus* possessing state 2. However, according to the text (p. 64), an equant infratemporal fenestra is a potential synapomorphy of *Neoaetosauroides*, *Typothorax*, *Desmatosuchus*, *Longosuchus* and *Paratypothorax*. Nevertheless, this character is unknown in *Neoaetosauroides*, *Paratypothorax*, *Typothorax* and *Longosuchus*. In addition, Small (2002) demonstrates that *Desmatosuchus* possesses the state 1. Therefore no aetosaur actually possesses an equant or square fenestra. Fortunately, new skull material of *Neoaetosauroides* exists (Desojo 2002) and, although it is currently undescribed, promises to shed light on many of these cranium characters.

(10) 22-H99: Apex of scapula: un- or modestly expanded (0) or broadly expanded (1). As constructed, this character is uninformative and offers no in-group resolution. It is listed as an aetosaur synapomorphy by Long & Murry (1995). However, the upper margins of the scapular blade in *Typothorax* and *Neoaetosauroides* are strongly directed posteriorly in comparison to the scapulae of other aetosaurs (Bonaparte 1971; Long & Murry 1995) although it is unclear whether these expansions are homologous.

(11) 23-H99: *Manus gracile and elongate (longer than wide) (0) or short, broad and small (wider than long) (1).* As constructed, this character is uninformative and offers no in-group resolution. It is listed as a synapomorphy of the Aetosauria by Long & Murry (1995). In addition, the manus is unknown for *Desmatosuchus* and should have been scored as unknown for both species.

(12) 24-H99: *Well-developed, robust, short anterior iliac blad: absent (0) or present (1).* This is a synapomorphy of the Aetosauria, is therefore uninformative and offers no in-group resolution (Long & Murry 1995). It is present in *Stagonolepis wellesi* (*contra* Heckert & Lucas 1999).

(13) 25-H99: *Openings in pubis: none or one (0) or two (1).* The presence of two pubic foramina is a possible autapomorphy of *Stagonolepis robertsoni* (Walker 1961); however, more data are needed to confirm this. Two pubic openings are listed as a synapomorphy of the Aetosauria by Long & Murry (1995), but this character is unknown in almost all taxa and when known usually consists of a single opening.

(14) 26-H99: *Coracoid: shallow (0) or robust (1).* Heckert & Lucas (1999) list this as a possible autapomorphy for *Desmatosuchus* based on a scapulocoracoid figured

in Long & Murry (1995: fig. 89a). However, this is an isolated element and cannot be directly associated with any *Desmatosuchus* material with certainty. In addition, the scapulocoracoid figure by Small (1985: fig. 7) from an associated *Desmatosuchus* specimen does not appear to differ from other known aetosaurs.

(15) 27-H99: *Pubes broadened transversely and fused, forming a 'pubic apron' in anterior view: absent (0), or present (1).* A 'pubic apron' occurs in many archosaurs (e.g. *Euparkeria*, *Ornithosuchus* and *Postosuchus* (Krebs 1976: fig. 13; Long & Murry 1995: 128)), although it is possibly more broadened transversely in aetosaurs. Still, all aetosaurs possess this character, including *Neoaetosauroides* and *Longosuchus* (listed as unknown in Heckert & Lucas 1999), consequently it is uninformative in this study.

(16) 39-H99: *Shapes of dorsal bosses: anterior–posterior elongate keel (0) or knob (1).* This character is ambiguous. The boss in *Aetosaurus crassicauda* is a mixture of both states (Wild 1989). *Longosuchus* has a low, pyramidal boss that is neither an elongate keel nor a rounded knob (Sawin 1947). *Typothorax* appears to have a keel anteriorly and a pyramidal boss posteriorly (Martz 2002). The dorsal boss in *Paratypothorax* can occur in several different forms depending on position in the carapace (unpublished data). This character needs to be scored as unknown in *Redondasuchus* because the entire carapace is unknown.

(17) 47-H99. *Patterning of lateral scutes: radiate (0) or random (1).* This is probably a useful character (*contra* Harris *et al.* 2003*a*), because *Typothorax* possesses random ornamentation on the dorsal paramedian plates and radial patterning on the dorsal lateral plates (Martz 2002). However, this character suite is presently uninformative given that this combination appears to be an autapomorphy of *Typothorax*. Harris *et al.* (2003*a*: 242) argued that the characters presented by Heckert & Lucas (1999) to describe variations in the patterning of the paramedian, lateral and ventral plates co-vary and preferred to combine these characters in their own matrix. However, given the condition in *Typothorax* and its potential in other undescribed taxa, these characters may be useful in future analyses if properly constructed and scored. It was not used in the current study pending further examination of material to ensure proper scoring.

(18) 48-H99: *Posterior emargination of lateral scute, revealing hollow on the posterior side of the lateral spike: absent/not applicable (0) or present (1).* Rauisuchians do not have lateral plates, so this character cannot be scored for the outgroup. Character state 0 should be changed to 'absent.' This is also true for characters 49–53 in Heckert & Lucas (1999).

(19) 49-H99: *Lateral spikes on cervical lateral scutes: absent (0) or present (1).* 50-H99: *Lateral spikes on dorsal lateral scutes: absent (0) or present (1).* 51-H99: *Lateral spikes on caudal lateral scutes: absent (0) or present (1).* These three characters do co-vary as argued by Harris *et al.* (2003*a*) because taxa with lateral spikes tend to have them throughout the carapace. What does tend to vary is whether the cervical spikes are strongly developed as in *Desmatosuchus* and *Longosuchus*, as well as whether the lateral plates have spikes at all. This is described by two new characters (see characters 22 and 35 of this study).

(20) 56-H99: *Incision of ornamentation: shallow or faint (0) or deeply incised (1).* This character is highly variable based mainly on the position of the plate in the carapace. Anterior (cervical) plates tend to have weak ornamentation while the ornamentation on plates over the pelvis is generally much more pronounced (Heckert & Lucas 1999: 59). This variability is present in all aetosaur taxa and therefore this character should not be used.

(21) 58-H99: *Patterning of ventral scutes: radiate (0) or random (1).* All aetosaurs preserved with ventral armour have state 0 so, at present, this character is uninformative.

Appendix 3: Character–taxon matrix

Taxon/character	10	20	30	37
Postosuchus	0 0 0 0 0 0 0 0 0 0	0 0 0 0 X 0 0 X X 0	X X 0 X X 0 1 X 0 X	X 0 0 X X X X
Revueltosaurus	0 X 0 0 0 0 0 0 ? 0	0 0 2 0 0 1 1 X 0 0	0 X 0 X X 1 0 X X 0	X x 0 0 x x x
Aetosaurus	0 1 1 0 1 1 1 1 0 0	0 ? 2 0 0 0 0 0 0 ?	0 0 1 0 0 0 0 0 1 0	1 0 0 0 0 0 0
Stagonolepis robertsoni	1 2 1 0 1 1 1 1 0 0	0 0 2 0 0 0 0 0 0 ?	0 0 1 0 0 0 0 0 1 0	0 0 0 0 0 0 0
Stagonolepis wellesi	? ? ? ? ? ? ? ? ? 0	0 0 2 0 0 0 0 0 0 1	0 0 1 0 0 0 0 0 1 0	? 0 0 0 0 0 0
Aetosauroides	1 1 1 0 1 1 1 1 0 0	0 0 2 0 0 0 0 0 0 ?	0 0 1 0 0 0 0 0 1 0	? 0 0 0 0 0 0
Coahomasuchus	? ? 1 ? ? ? ? 1 ? ?	? 0 2 0 0 0 0 0 0 ?	0 0 0 0 0 0 0 0 1 0	1 0 0 0 0 0 0
Desmatosuchus haplocerus	1 2 1 ? 1 1 1 1 ? 0	1 1 0 0 1 1 0 1 1 0	1 2 0 1 1 1 1 2 0 2	? 0 0 0 1 0 1
Desmatosuchus smalli	1 2 1 1 1 1 1 1 1 0	1 1 0 0 1 1 0 1 1 0	1 2 0 1 1 1 1 2 0 2	? 0 0 0 1 0 1
Heliocanthus	? ? ? ? ? ? ? ? ? ?	? ? 1 1 0 0 0 1 0 0	? 1 0 2 2 1 ? 1 2 1	? 1 ? 0 1 2 0
Longosuchus	1 2 1 0 1 1 1 1 1 0	0 1 2 0 1 0 0 0 1 0	1 2 0 1 1 1 1 2 0 2	? 0 0 0 0 0 0
Lucasuchus	? ? ? ? ? ? ? ? ? ?	? ? 2 0 1 0 0 1 ? 0	1 2 0 1 1 1 1 2 0 2	? 1 ? 0 0 0 0
Neoaetosauroides	1 2 1 0 1 1 1 1 1 ?	? 0 2 0 0 0 0 0 0 ?	0 0 0 0 0 0 ? 0 1 0	? 0 ? 0 0 0 0
Typothorax	1 2 1 1 1 1 1 1 0 1	1 1 2 1 0 1 1 0 0 1	0 0 1 2 2 1 0 1 1 0	? 0 1 0 0 1 0
Paratypothorax	? ? ? ? ? ? ? ? ? 1	1 ? 1 1 0 0 0 1 0 1	? 1 0 2 2 1 ? 1 2 1	? 1 ? 1 0 2 0
Redondasuchus	? ? ? ? ? ? ? ? ? ?	? ? 2 1 ? 1 1 0 0 1	? ? 1 ? ? ? ? ? ? ?	? 0 ? 0 ? ? ?
Tecovasuchus	? ? ? ? ? ? ? ? ? ?	? ? 2 1 0 0 0 1 0 1	? 1 0 2 2 1 ? 1 2 1	? 0 0 1 0 2 0
Acaenasuchus	? ? ? ? ? ? ? ? ? ?	? ? 2 0 ? 1 0 1 ? 0	1 2 0 1 1 ? ? 2 0 2	? 0 ? 0 0 0 ?

?, unknown; x, not applicable.