Available online at www.sciencedirect.com
SCIENCE DIRECT®

C. R. Palevol 4 (2005) 327–340

COMPTES RENDUS PALEVOL

http://france.elsevier.com/direct/PALEVO/

Vertebrate Paleontology

A new species of the Late Triassic aetosaur *Desmatosuchus* (Archosauria: Pseudosuchia)

William G. Parker

Department of Geology, Northern Arizona University, Box 4099, Flagstaff, AZ 86011 USA †

Received 15 February 2005; accepted after revision 29 March 2005

Available online 13 May 2005

Presented by Philippe Taquet

Abstract

Reanalysis of known armor of the stagonolepidid (aetosaur) *Desmatosuchus* has shown distinct differences in the lateral armor among individuals known from Carnian and Norian age rocks in the southwestern United States. Combined with previously reported cranial differences it is apparent that Norian specimens of *Desmatosuchus* represent a species distinct from the type species *Desmatosuchus haplocerus* and are described herein as *Desmatosuchus smalli* n. sp. *D. smalli* is known solely from Norian age rocks, whereas *D. haplocerus* is known only from Carnian age rocks. The separation of *Desmatosuchus* into distinct Carnian and Norian species suggests some biostratigraphic utility for these taxa. ***To cite this article: W.G. Parker, C. R. Palevol 4 (2005)***.

Résumé

Le réexamen de la cuirasse du stagonolépidide (aétosaure) *Desmatosuchus* a révélé des différences au niveau de la cuirasse latérale parmi les individus connus des sédiments d'âge Carnien et Norien du Sud-Ouest des États-Unis. En les combinant avec les différences crâniennes, il apparaît que les spécimens noriens de *Desmatosuchus* représentent une espèce distincte de l'espèce type *Desmatosuchus haplocerus* ; ils sont décrits ici comme *Desmatosuchus smalli* n. sp. *D. smalli* est connu uniquement dans les sédiments d'âge Carnien. La séparation de *Desmatosuchus* en espèces distinctes du Carnien et du Norien suggère une utilité stratigraphique de ces taxa. ***Pour citer cet article : W.G. Parker, C. R. Palevol 4 (2005)***.

Keywords: Late Triassic; Aetosaur; *Desmatosuchus*; Bull Canyon Formation; Chinle Formation; Texas; Arizona; USA

Mots clés : Trias récent ; Aétosaure ; *Desmatosuchus* ; Formation du Bull Canyon ; Formation Chinle ; Texas ; Arizona ; États-Unis

E-mail address: William_Parker@nps.gov (W.G. Parker).

† *Current address*: Division of Resource Management, Petrified Forest National Park, P.O. Box 2217, Petrified Forest, Arizona 86028, USA

1631-0683/$ - see front matter © 2005 Académie des sciences. Published by Elsevier SAS. All rights reserved.
doi:10.1016/j.crpv.2005.03.002

Version française abrégée

Introduction

En 1892, Cope [10] attribua une cuirasse dermique de la formation de Tecovas du groupe Dockum, dans le comté de Crosby, au Texas, au genre *Episcoposaurus* (dont le type de l'espèce, *E. horridus*, est attribué à *Typothorax*) et à une nouvelle espèce, *E. haplocerus*. Case [2,3] décrivit une partie de squelette comme appartenant à *Desmatosuchus spurensis*, également de la formation de Tecovas, dans le comté de Crosby, au Texas. Les localités de Cope et de Case sont distantes de quelques kilomètres [16]. La révision par Gregory [16] de ces taxa a fait tomber en synonymie *E. haplocerus* et *D. spurensis*, créant la nouvelle association *Desmatosuchu haplocerus*, qui devint l'espèce type du genre.

En 1977, le musée d'Histoire naturelle de Dallas récolta des vertébrés fossiles du Miller Ranch, au sud-est de Post, au Texas. Parmi les spécimens récoltés se trouvaient les restes de deux aétosaures, une partie de squelette de *Paratypothorax* , et des éléments post-crâniens et des plaques de la cuirasse attribuables à *Desmatosuchus* [27,39,40]. À partir de 1980, des équipes de l'université de technologie du Texas rouvrirent la carrière de Post et récoltèrent plusieurs portions de squelettes, en connexion avec l'aétosaure *Desmatosuchus* [4, 5, 27, 38–40].

Bryan Small décrivit l'essentiel de ce matériel dans une thèse non publiée et une série d'articles [38–41], dans lesquels il attribua le matériel à *D. haplocerus*, une attribution qui fut suivie par tous les auteurs suivants (par exemple, [19,27,33,34]). Cependant, la cuirasse n'a jamais été décrite en détail, bien que Small 38,40] eût discuté les différences entre le matériel de la carrière de Post et l'holotype de *Desmatosuchus spurensis* (UMMP 7476) et attribué ces différences au dimorphisme sexuel.

La découverte d'une carapace presque complète de *D. haplocerus* (MNA V9300) dans le membre de la Blue Mesa de la formation Chinle dans l'Arizona [43] a fourni de nombreuses nouvelles informations sur la cuirasse [36]. Les comparaisons entre MNA V9300, qui est identique à UMMP 7476, et le matériel de la carrière de Post révèlent des différences en plus de celles notées par Small 38]. De plus, Small [41] a noté des variations entre le matériel crânien de *Desmatosuchus* de la carrière de Post et celui de la formation du groupe Dockum et du membre Blue Mesa de la formation Chinle.

La position stratigraphique de ces spécimens est importante. En dehors de la carrière de Post et d'une seule découverte en Arizona (MNA V697), tous les spécimens de *Desmatosuchus* sont issus de la formation de Tecovas du groupe Dockum du membre de la Blue Mesa de la formation Chinle, qui est considérée comme étant d'âge Carnien [11, 24, 25]. La carrière de Post est dans la formation de Bull Canyon du groupe de Dockum, qui est considérée comme d'âge Norien [4, 24, 39]. MNA V697 est dans le membre « supérieur » de la forêt pétrifiée de la formation Chinle, qui est aussi d'âge Norien [14,25].

Paléontologie systématique

Archosauria Cope, 1869 [8]
Pseudosuchia Zittel, 1887–1890 [46]
Stagonolepididae Lydekker, 1887 [30]
Desmatosuchinae Huene, 1942
Desamatosuchus Case, 1920

Espèce type. *Desmatosuchus haplocerus* (Cope, 1892).

Diagnose révisée (pour le genre). *Desmatosuchus* peut être différencié des autres aétosaures : par la présence d'épines allongées et recourbées sur les ostéodermes cervicaux latéraux, la 6^{e} série étant plus fortement développée ; par des plaques paramédianes et latérales, avec des bords élargis et avec une surface articulaire en languette–gouttière ; par les plaques paramédianes et latérales, qui possèdent des lames antérieures fines et déprimées, plutôt qu'épaisses, et portent des barres antérieures ; par l'ornementation de la plaque paramédiane, qui consiste en une combinaison de fosses et de crêtes et une éminence située dorsalement, qui ne migre jamais médialement.

Distribution. Trias supérieur, Sud-Ouest des États-Unis.

Desmatosuchus smalli n. sp.

1985 *Desmatosuchus haplocerus* : Small, p. 1, figs. 3–11.

1985 *Desmatosuchus haplocerus* : Long and Ballew, p. 45, figs. 7a, b.

1986 *Desmatosuchus haplocerus* : Murry, p. 122.

1986 *Desmatosuchus* : Chatterjee, p.145.

1989 *Desmatosuchus haplocerus* : Small, p.301, fig. 1B, pl. 5A–F, I.

1995 *Desmatosuchus haplocerus* : Small, p. 97, figs. 1–9.

Étymologie. Nommé en l'honneur de Bryan Small, pour son travail détaillé sur les aétosaures.

Holotype. TTUP 9024, crâne presque complet et mandibule droite, partie de pelvis, fémurs, cuirasse cervicale presque complète et nombreuses plaques de la carapace.

Localité type et âge. Carrière Post, neuf miles au sud-est de Post, comté de Garza, Texas, USA ; formation de Bull Canyon, groupe de Dockum, Trias supérieur (Norien).

Distribution. Formation de Bull Canyon, groupe de Dockum, Texas, USA ; membre Forêt pétrifiée, formation Chinle, Arizona, USA.

Paratypes. TTUP 9025, fragment de crâne incluant les dents ; TTUP 9170, humérus droit et ulna ; TTUP 9023, crâne bien préservé incluant la boîte crânienne et les mandibules, le supra-coracoïde, l'humérus, une seule vertèbre dorsale, des épines cervicales latérales, une armure dorsale en connexion ; TTUP 9027, pelvis.

Matériel associé. DMNH 8655, épine cervicale latérale ; DMNH 8656, plaque latérale : DMNH 8657, portion d'épine cervicale latérale ; DMNH 9893 fragment de plaque paramédiane ; DMNH 9906, vertèbre caudale antérieure ; DMNH 9909, plaque cervicale latérale ; DMNH 9910, corne cervicale distale droite ; DMNH 9913, vertèbre caudale moyenne ; DMNH 9939, vertèbres sacrées soudées et côtes ; DMNH 9940, plaques paramédianes ; DMNH 9941, plaque caudale latérale ; MNA V697, portion de plaque latérale dorsale droite.

Diagnose. *D. smalli* diffère de *D. haplocerus* : par la possession de pariétaux qui ne présentent pas de faible concavité ou de sulcus s'étirant transversalement entre les fenêtres supra-temporales ; par une fosse antéorbitaire grandement réduite comparée à *D. haplocerus*, repli pharyngé médial du basiptérygoïde extrêmement à modérément faible, contrastant avec celui de *D. haplocerus*, qui est profond ; par un vide marqué entre les tubercules basaux et le processus basiptérygoïde ; par des exoccipitaux ne se rejoignant pas sur la ligne médiane du foramen magnum ; par un nombre de dents maxillaires de 10–12 contre 12–13 chez *D. haplocerus* ; par la cuirasse cervicale antérieure latérale et postéro-dorsale à épines graciles allongées, qui sont beaucoup plus développées que chez *D. haplocerus* ; par les épines de la cuirasse postérieure dorsale latérale, légèrement recourbées.

Description

Terminologie de l'armure des aétosaures

Les aétosaures ont une large carapace d'ostéodermes dermiques (plaques), qui couvrent tout leur dos, depuis l'arrière des pariétaux jusqu'au bout de la queue (Fig. 1) L'armure est disposée en quatre « colonnes » antéro-postérieures, consistant en plaques quadrangulaires qui forment des bandes transversales (ou rangées) autour du corps [18]. Deux colonnes paramédianes qui chevauchent la ligne médiane sont flanquées chacune d'une colonne de plaques latérales. Les rangées sont divisées, selon leur position, en régions cervicale, dorsale, caudale en fonction du type de vertèbre que les ostéodermes recouvrent.

L'armure latérale de *Desmatosuchus* est grossièrement rectangulaire et s'infléchit médio-latéralement d'environ 90°. Ce point de flexion est généralement au centre de l'ossification de la plaque [31] et est marqué par une éminence prononcée qui se projette au-dessus de la surface dorsale de la plaque et qui divise effectivement celle-ci en deux ailes. L'aile dorsale s'allonge horizontalement le long du dos de l'animal, s'articulant avec l'armure paramédiane à son angle médial, tandis que l'aile latérale se projette ventralement, couvrant le flanc de l'animal. Le coin ventro-latéral de l'aile latérale ne s'articule pas avec les autres éléments.

Comparaison du matériel de D. haplocerus et D. smalli

Plaques paramédianes et antérieures dorsales latérales. Il n'y a pas de différences entre l'armure paramédiane et les plaques antéro-dorsales latérales de *D. haplocerus* et *D. smalli*. Cet article s'intéresse à l'armure cervicale, postérieure dorsale et antérieure caudale latérale, où existent des différences entre *D. haplocerus* et *D. smalli*.

Armure cervicale latérale. L'armure cervicale latérale de l'holotype (UMMP 7476) de *D. spurensis* (= *D. haplocerus*) possède des épines fortement développées de chaque côté de la carapace ; cependant, seules les épines de la dernière série sont très développées [3 (pl. 8)]. Au contraire, *D. smalli* possède des cornes très développées sur plusieurs des séries cervicales latérales. En fait, plusieurs épines prélevées dans l'holotype (TTUP 9024) sont si similaires en taille, qu'il est extrêmement

difficile de déterminer exactement quelle épine pourrait être l'analogue de la corne cervicale la plus postérieure de UMMP 7476 (Fig. 2A et B). De plus, les épines de la carrière Post sont beaucoup plus graciles et moins recourbées que la grosse corne de UMMP 7476. Small [38-40] attribuait ces différences entre l'amure cervicale latérale de UMMP 7476 et les spécimens TTUP au dimorphisme sexuel.

Plaques postérieures dorsales latérales. Derrière les plaques les plus antéro-dorsales latérales, l'aile dorsale de la plaque s'élargit de manière significative médio-latéralement et devient plus courte antéro-postérieurement au fur et à mesure que les éminences s'allongent progressivement et en forme d'épine (Fig. 3A–D). Le développement des épines derrière celles des séries cervicales atteint un maximum dans les régions pelvienne et antéro-caudale des deux espèces de *Desmatosuchus* (contra Long et Ballew [26]). Cependant, les épines dorsales et caudales latérales de *D. smalli* sont spécialement bien développées, et tendent à être plus longues et légèrement recourbées ventralement comparées à celles de *D. haplocerus* (Fig. 3E–F). Une grande partie de l'armure postérieure dorsale latérale est présente chez *D. smalli*. Cependant, parce que la carapace représentée par TTUP 9024 est incomplète et non articulée, il est difficile de placer chaque plaque dans sa position exacte. Ce qui est immédiatement clair cependant, c'est que les éminences dorsales dans la région dorsale latérale sont plus larges et plus développées que les plaques correspondantes chez *D. haplocerus* (comparer la Fig. 3A–D à Case [4 (pl. 8)]). La longueur des épines sur les plaques postérieures dorsales latérales de *D. smalli* atteint 68 mm, comparée aux 42 mm de *D. haplocerus* pour un animal de même taille. En plus, chez *D. smalli*, l'éminence (épine) semble entrer en contact avec le bord postérieur de la plaque (Fig. 3C), tandis que chez *D. haplocerus*, l'éminence est plus centrale (Fig. 3E). En vue latérale, les éminences de *D. smalli* sont légèrement incurvées ventralement (Figs. 3B et D), tandis que, chez *D. haplocerus*, elles sont droites (Fig. 3F).

MNA V697 est une portion de plaque dorsale latérale du côté droit, du membre de la Forêt pétrifiée du de la formation Chinle (sensu Woody [44]), juste à l'ouest du parc national de la Forêt pétrifiée, dans le Nord-Est de l'Arizona. Cette plaque a été identifiée par Long et Ballew [26] comme une épine cervicale latérale gauche. L'aile dorsale de cette plaque est en grande partie manquante, mais la présence d'une fine lame antérieure bien développée permet d'attribuer cet élément à la région cervicale, parce que, chez *Desmatosuchus*, cette lame tend à être très épaissie dans la région cervicale. Cette plaque peut être attribuée à *D. smalli*, parce que l'épine est recourbée ventralement (Fig. 4A et B). La localité où a été récoltée cette plaque contient aussi *Typothorax coccinarium*. C'est la seule indication d'une coexistence entre *T. coccinarium* et *Desmatosuchus* en dehors de la carrière Post.

Armure caudale. Chez TTUP 9024, n'est conservée qu'une simple plaque antérieure caudale latérale du côté droit (Fig. 5A et B). Les dimensions et la morphologie générale des ailes de cette plaque sont similaires à celles de la région caudale antérieure de *D. haplocerus* par la possession des plus larges épines postérieures des séries cervicales. Cependant, l'épine sur TTUP 9024 diffère de celle de *D. haplocerus* en étant moins robuste et allongée et en possédant une extrémité qui est légèrement incurvée ventralement (Fig. 5C et D). L'épine de TTUP 9024 mesure plus de 100 mm de longueur, tandis que l'épine post-cervicale la plus longue chez MNA V9300 (*D. haplocerus*) atteint à peine 80 mm.

Crâne. Small [38–41] a donné une description détaillée du crâne de *Desmatosuchus*, notant des différences significatives parmi les spécimens TTUP 9023, TTUP 9024, TTUP 9025 (*D. smalli*) et les spécimens UMMP 7476 et UCMP 27408 (cf. *D. haplocerus*). Celles-ci et d'autres différences sont les suivantes : (1) la surface supérieure des pariétaux est généralement plate chez *D. smalli* , tandis que chez *D. haplocerus* une faible concavité ou sulcus est située sur la moitié postérieure des pariétaux entre les fenêtres supra-temporales (Fig. 6A) ; (2) en accord avec Small [41], les exoccipitaux de *D. smalli* ne se joignent pas sur la ligne médiane du foramen magnum, tandis que Small [38] estimait qu'ils se rencontraient sur la ligne médiane chez *D. haplocerus*, excluant le supraoccipital de la participation au condyle occipital. Cependant, Small [41] notait aussi que cette disposition était peu claire chez UMMP 7476 et UCMP 27408 ; (3) *D. smalli* possède un récessus pharingé du basisphénoïde peu profond (voir 43]), tandis que, chez *D. haplocerus*, ce recessus est profond (Fig. 6B et D). Chez *D. smalli*, il y a un large

espace entre le tubercule basal et le processus basiptérygoïde, tandis que, chez *D. haplocerus* cet espace n'existe pas (Fig. 6B et D) [41] ; (4) la fosse antéorbitaire chez *D. smalli* est très réduite et presque absente, mais encore proéminente chez *D. haplocerus* (Fig. 6A et C) ; (5) le nombre de dents maxillaires chez *D. smalli* atteint 10–12, tandis que chez *D. haplocerus*, il est de [12–13 41].

Discussion

Des différences significatives existent entre le matériel de *Desmatosuchus* de la carrière de Post et celui du comté de Crosby, au Texas (UMMP 7476 et matériel type), et du Nord-Est de l'Arizona, incluant MNA V9300 et le matériel de la carrière de *Placerias*. Celles-ci comprennent des différences notables entre l'armure dorsale cervicale et postérieure dorsale latérale, le toit crânien, la boîte crânienne et le nombre de dents maxillaires. Toutefois, la création d'une nouvelle espèce pour le matériel de la carrière Post est souhaitable. Bien que une ou plus des différences puissent être dues à un dimorphisme sexuel, il n'y a actuellement pas suffisamment de matériel pou tester cette hypothèse. En revanche, comme toutes les différences notées ci-dessus séparent effectivement toutes les découvertes de *D. smalli* et de *D. haplocerus* selon leur horizon stratigraphique, l'explication la plus parcimonieuse aujourd'hui est de penser que ces différences sont taxonomiques. *Desmatosuchus haplocerus* est restreint à la partie inférieure de la formation Chinle du groupe Dockum, tandis que *D. smalli* est actuellement connu seulement dans les parties supérieures des mêmes unités. La séparation de *Desmatosuchus* en deux espèces distinctes, du Carnien et du Norien, suggère une utilisation biostratigraphique de ces taxa, mais seulement avec du matériel adéquat du crâne ou de l'armure latérale.

1. Introduction

Stagonolepidid (aetosaur) taxonomy has been in constant flux since these animals were first discovered in the late 19th century. Originally considered parasuchians [1,2,9,23], it was not until Sawin's [37] description of *Longosuchus* (*Typothorax) meadei* that the aetosaurs were recognized as forming a distinct pseudosuchian clade. Still, aetosaur taxa were underrepresented; in the southwestern United States only two genera were recognized (*Desmatosuchus* and *Typothorax*). Elder [12] considered *Desmatosuchus* to be a sexual dimorph and therefore a synonym of *Typothorax*, thus reducing the number of recognized taxa to a single genus; however, Small [40] and Long and Ballew [26] provided evidence to the contrary and this hypothesis has been rejected. Even more confusing for aetosaur taxonomy was that for decades, rectangular osteoderms (plates) identical to those of aetosaurs were thought to belong to phytosaurians [17].

Long and Ballew [26] produced a seminal paper based particularly upon work within Petrified Forest National Park in northeastern Arizona, and demonstrated that the dermal armor of aetosaurs possess unique characters that can diagnose taxa. Long and Ballew convincingly showed that the material assigned to one or two aetosaur taxa and a phytosaur represented at least four valid aetosaur taxa present in the southwest United States; *Desmatosuchus*, *Typothorax*, '*Calyptosuchus*' (=*Stagonolepis*), and *Paratypothorax*. In addition, they proved conclusively that phytosaurs do not possess aetosaur-like dermal armor and that the armor in question belonged to a European species of *Paratypothorax*. Since this work a flurry of aetosaur discoveries and research has indicated that in addition to the four taxa recognized by Long and Ballew [26], many more are present in the southwestern United States. These include *Coahomasuchus kahleorum* [18], '*Redondasuchus*' *reseri* [20,31], *Acaenasuchus geoffreyi* [27,34], '*Desmatosuchus*' *chamaensis* [21,36,45], and several undescribed forms [32,35]. In addition to these new discoveries, research has shown much variation in material previously assigned to *Paratypothorax*. Martz et al. [32] argue that based on characteristics of the armor at least two valid taxa are included in this material, a conclusion also reached by Parker [36].

Interestingly, while '*Redondasuchus*' *reseri*, *Acaenasuchus geoffreyi*, and '*Desmatosuchus*' *chamaensis* all represent valid species, their generic placement has been questioned. Martz [31] considered '*R.*' *reseri* to represent a species of *Typothorax*, while Parker [36] demonstrated that '*D.*' *chamaensis* does not represent a valid species of *Desmatosuchus* and instead is assignable to a new genus. Heckert and Lucas [18,19] consider *Acaenasuchus geoffreyi* to represent the juvenile form of *Desmatosuchus haplocerus*; however, this cannot be substantiated, given our currently poor knowledge of aetosaur ontogeny.

The history of aetosaur taxonomy began in America in the late 1800s. E. D. Cope [10] assigned dermal armor from the Tecovas Formation of the Dockum Group in Crosby County, Texas, to the genus *Episcoposaurus* (the type species of which, *E. horridus*, is referable to *Typothorax*) as a new species, *E. haplocerus*. Case [2,3] described a partial skeleton as *Desmatosuchus spurensis*, noting that this material also came from the Tecovas Formation in Crosby County, Texas. These two localities of Cope and Case are just a few kilometers apart [16]. Gregory's [16] revision of these taxa synonymized *E. haplocerus* and *D. spurensis*, creating the new combination *Desmatosuchus haplocerus*, which became the type species for the genus.

In 1977, the Dallas Museum of Natural History collected vertebrate fossils from the Miller Ranch, southeast of Post, Texas. Among the specimens collected were the remains of two aetosaurs, a partial skeleton of *Paratypothorax*, and postcranial elements and armor plates attributable to *Desmatosuchus* [27,39,40]. Beginning in 1980, crews from Texas Tech University reopened the Post Quarry (also called the Miller Quarry), collecting a wealth of vertebrate material including the type specimens of the rauisuchid *Postosuchus kirkpatricki*, the poposaur *Chatterjeea elegans*, and the controversial archosaurs *Shuvosaurus inexpectatus* and *Protoavis texensis* [4,6,7]. In addition, a large amount of aetosaur material was recovered including several associated partial skeletons of the aetosaur *Desmatosuchus* [4,27,38–40].

Bryan Small initially described much of this aetosaur material in an unpublished thesis and a series of preliminary articles [38–40], and provided a more thorough description of the cranial material in 2002 [41]. In all of these studies, he assigned the *Desmatosuchus* material from the Post Quarry to *D. haplocerus*, an assignment that was followed by all subsequent authors [e. g., 19, 27, 33, 34]. Unfortunately, the Post Quarry armor has never been thoroughly described, although Small [38,40] discussed some slight differences between the TTUP material and the holotype of *Desmatosuchus spurensis* (UMMP 7476) and figured some of the material [40:pl. 5a-b]. Small [40:303] also noted that "one specimen (TTUP 9024) exhibits unusually large lateral cervical spines immediately anterior to the usually large shoulder horn [that] differ from Case's [2] description of *Desmatosuchus* (UMMP 7476)" and attributed these differences to sexual dimorphism.

The discovery of an almost complete carapace (MNA V9300) from the Blue Mesa Member (*sensu* Woody [43]) of the Chinle Formation of Northern Arizona [43] has provided much new information about the armor of *Desmatosuchus haplocerus* [36]. Comparison between MNA V9300, which closely resembles UMMP 7476, and the Post Quarry material reveals additional differences in the lateral armor besides those noted by Small [38]. Furthermore, Small [38,41] noted variation between *Desmatosuchus* skull material from the Post Quarry and the Tecovas Formation of the Dockum Group and the Blue Mesa Member of the Chinle Formation, listing several character states to support these distinctions.

The stratigraphic occurrence of these specimens is of significance. The Post Quarry is located in the Bull Canyon (= Cooper Canyon) Formation of the Dockum Group [4,5]. The Bull Canyon Formation is generally agreed to be Norian in age [4,24,27–29,33,39,41] based on index taxa that include pseudopalatine-grade phytosaurs and the aetosaur *Typothorax coccinarum*. All other documented occurrences of *Desmatosuchus* (see [27] and [36] for listings) are from the Tecovas Formation of the Dockum Group and the Blue Mesa Member of the Chinle Formation [43], which have both been determined to be Late Carnian in age based on pollen content and their vertebrate faunas [11,14,25,28].

Until recently, *Desmatosuchus* was thought not to occur in upper Chinle Formation sediments in New Mexico or Arizona. However, recent investigations of the Delaney Tank area, immediately west of Petrified Forest National Park in northeastern Arizona, have provided the first co-occurrence of *Desmatosuchus* and *Typothorax* armor outside Texas [36].

Institutional abbreviations: **DMNH**, Dallas Museum of Natural History, Texas; **MNA**, Museum of Northern Arizona, Flagstaff; **TTUP**, The Museum at Texas Tech University, Lubbock; **UCMP**, University of California Museum of Paleontology, Berkeley; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor.

2. Systematic paleontology

Archosauria Cope, 1869 *sensu* Gauthier, 1986 [15]

Pseudosuchia Zittel, 1887–1890 *sensu* Gauthier, 1986 [15]

Stagonolepididae Lydekker, 1887 *sensu* Walker, 1961 [42]

Desmatosuchinae Huene, 1942 *sensu* Heckert and Lucas, 2000 [22]

Desmatosuchus Case, 1920

Type species. *Desmatosuchus haplocerus* (Cope, 1892)

Revised Diagnosis (for genus). *Desmatosuchus* can be differentiated from other aetosaurs by the possession of the combination of the following characters; large aetosaur, adult length of at least four meters; premaxilla edentulous; infratemporal fenestra reduced and oval in outline; external mandibular fenestra relatively small; humerus with epicondylar foramen instead of groove; presence of elongate and recurved spikes on cervical lateral osteoderms (plates) with the 6th series being most strongly developed; cervical paramedian and lateral plates with thickened margins and a tongue-and–groove articular surface; paramedian and lateral plates possess depressed thin, anterior laminae rather than thickened, raised anterior bars; paramedian plate ornamentation consists of a combination of random pits and ridges and a dorsal eminence which consists of a low rounded boss that is generally situated slightly posterior to the center of the plate and never migrates medially.

Distribution. Upper Triassic, Southwestern United States

Desmatosuchus smalli n. sp.

1985 *Desmatosuchus haplocerus*: Small, p. 1, figs. 3–11.

1985 *Desmatosuchus haplocerus*: Long and Ballew, p. 45, figs. 7a, b.

1986 *Desmatosuchus haplocerus*: Murry, p. 122.

1986 *Desmatosuchus*: Chatterjee, p. 145.

1989 *Desmatosuchus haplocerus*: Small, p. 301, fig. 1B, pl. 5A–F, I.

1995 *Desmatosuchus haplocerus*: Long and Murry, p. 89, fig. 86A.

2002 *Desmatosuchus haplocerus*: Small, p. 97, figs. 1–9.

Etymology. Named in honor of Bryan Small for his detailed work on aetosaurs, especially the Post Quarry *Desmatosuchus* specimens.

Holotype. TTUP 9024, almost complete skull and right mandible, partial pelvis, femora, nearly complete cervical armor and numerous plates from the rest of the carapace.

Type locality and age. Post (Miller) Quarry, TTUP and DMNH locality, nine miles southeast of Post, Garza County, Texas, USA; Bull Canyon Formation, Dockum Group, Late Triassic (Norian).

Distribution. Bull Canyon Formation, Dockum Group, Texas, USA; Petrified Forest Member, Chinle Formation, Arizona, USA.

Paratypes. TTUP 9023, well-preserved skull including braincase and mandibles, scapulocoracoid, humerus, a single dorsal vertebra, lateral cervical spine, assorted dorsal armor; TTUP 9025, partial skull including teeth; TTUP 9170, right humerus and ulna; TTUP 9027, pelvis.

Referred material. DMNH 8655, cervical lateral spine; DMNH 8656, lateral plate; DMNH 8657, partial cervical lateral spine; DMNH 9893, paramedian plate fragment; DMNH 9906, anterior caudal vertebra; DMNH 9909, cervical lateral plate; DMNH 9910, distal right cervical horn; DMNH 9913, mid-caudal vertebra; DMNH 9939, fused sacral vertebrae and ribs; DMNH 9940, paramedian plates; DMNH 9941, caudal lateral plate; MNA V697, partial right dorsal lateral plate.

Diagnosis. *D. smalli* differs from *D. haplocerus* in possessing parietals that do not possess a shallow concavity or sulcus running transversely between the supratemporal fenestrae; antorbital fossa highly reduced compared to *D. haplocerus*; medial pharyngeal recess of the basipterygoid extremely to moderately shallow in contrast to that of *D. haplocerus* which is deep; sizeable gap occurs between the basal tubera and the basipterygoid process; exoccipitals do not meet at the midline of the foramen magnum; maxillary tooth count of 10–12 compared to 12–13 in *D. haplocerus*; anterior cervical lateral armor and posterior dorsal lateral armor possess elongate gracile spines that are much more developed than those in *D. haplocerus*; spines of the posterior dorsal lateral armor are slightly recurved. The average length of the posterior dorsal lateral spines in similar size specimens of *D. smalli* is 68 mm compared to 42 mm in *D. haplocerus*.

3. Description

3.1. Aetosaur armor terminology

Aetosaurs have an extensive carapace of dermal osteoderms (plates) that cover the entire back from

behind the parietals to the tip of the tail, as well as the belly and appendages (Fig. 1). The armor that covers the back is arranged in four antero-posterior 'columns', and the carapace is segmented into quadrangular plates that form transverse bands (or 'rows') around the body [18]. Four columns of plates include two paramedian columns that straddle the midline of the animal and are each flanked laterally by a column of lateral plates. Thus, each transverse row consists of two paramedian and two lateral plates. These rows can be divided by their position on the carapace into cervical, dorsal, and caudal regions. This nomenclature is based upon the type of vertebrae that the osteoderms cover. In addition, some aetosaurs had a ventral carapace that consisted mainly of square overlapping plates that covered the underbelly, whereas the fore- and hindlimbs were at least partially covered by small round to subround scutes that did not articulate.

The ornamentation of aetosaur dermal armor is diagnostic to at least the genus level [26]. Aetosaur dermal

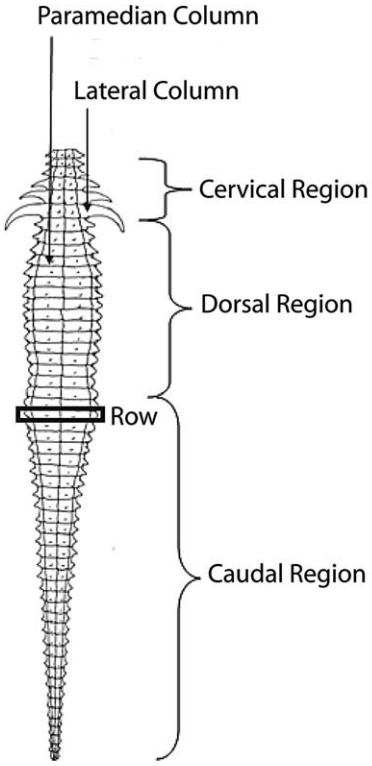

Fig. 1. Diagram demonstrating the division of the aetosaur carapace into distinct rows and regions. Modified from Long and Murry [27].
Fig. 1. Diagramme montrant la division de la carapace de l'aétosaure en deux rangées et deux régions distinctes. Modifié d'après Long et Murry [27].

plates possess suites of characters and although individual characters may be shared by several genera, the combinations of particular characteristics are what are diagnostic [32].

The lateral armor of *Desmatosuchus* is roughly rectangular and flexed mediolaterally approximately 90 degrees, so that the lateral plate forms dorsolateral corners on the body of the animal. This point of flexion is generally at the center of ossification of the plate [31] and is marked by a pronounced eminence that projects from the dorsal surface of the plate. This flexure and eminence effectively divides the plate into two 'flanges'. The dorsal flange runs horizontally along the back of the animal, articulating with the paramedian armor at its medial edge, whereas the lateral flange projects ventrally, covering the flank of the animal. The ventrolateral edge of the lateral flange does not articulate with any other element.

3.2. Comparison of material of D. haplocerus and D. smalli

3.2.1. Paramedian and anterior dorsal lateral plates

There are no distinct differences between the paramedian armor and the anterior dorsal lateral plates of *D. haplocerus* and *D. smalli*. Full descriptions of these elements for *D. haplocerus* were given by Parker [36] and will be formally presented in a future paper. This paper will focus on the lateral armor of the cervical, posterior dorsal, and anterior caudal lateral armor, where distinctions between *D. haplocerus* and *D. smalli* exist.

3.2.2. Cervical lateral armor

The cervical lateral armor of *Desmatosuchus* is highly distinctive and is one of the most commonly recovered elements of this genus. Of particular note are the huge, posteriorly recurved horns (spines) of the last cervical series [3 (fig. 17)]. The holotype (UMMP 7476) of *D. spurensis* (= *D. haplocerus*) has been restored with a total of five cervical lateral plates (see discussion below) that possess strongly developed spines on each side of the carapace; however, only the spines of the last series are strongly developed [3: pl. 8]. In contrast, *D. smalli* possesses very large, strongly developed horns on several of the other cervical lateral series. In fact, several spines preserved in the holotype (TTUP 9024) are so similar in size that it is extremely difficult

to determine exactly which spine would be analogous to the posterior-most cervical horn of UMMP 7476 (Fig. 2A and B). In addition, the Post Quarry spines are much more gracile and less recurved than the large horn of UMMP 7476 (Fig. 2C). The cervical lateral armor of MNA V9300 (Fig. 2D) is identical to that of UMMP 7476. Small [38,40] attributed these differences between the cervical lateral armor of UMMP 7476 and the TTUP specimens to sexual dimorphism.

Interestingly, TTUP 9024 appears to possess at least six rows of plates in the cervical series, placing the large recurved spine in the 6th series, not the 5th as reconstructed by Case [4 (pl. 8)] for *D. haplocerus*. Thus *D. haplocerus* also possessed at least six rows of cervical plates and UMMP 7476 is missing the anteriormost series. Indeed, this increased number of plates had been inferred by Elder [12] based on similarities between the cervical armor of *Desmatosuchus* and *Longosuchus*, which possesses seven rows of cervical plates as restored by Sawin [37]. Furthermore, MNA V9300

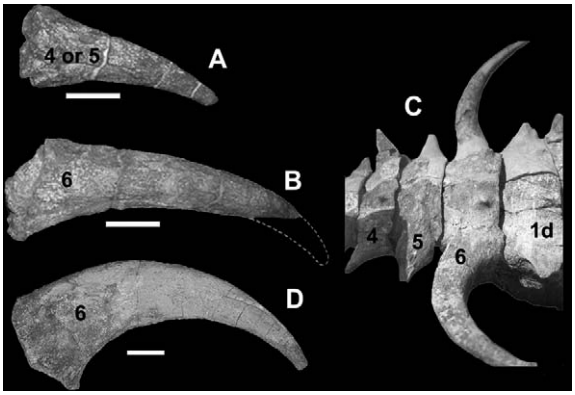

Fig. 2. Cervical armor of *Desmatosuchus*. Numbers depict position in the cervical series. **1d**, first dorsal lateral series. (**A**) TTUP 9024, *D. smalli*, right cervical lateral spine of the ?4th series in dorsal view. (**B**) TTUP 9024, *D. smalli*, right cervical lateral spine 6th series in dorsal view. (**C**) MNA V9300, *D. haplocerus*, right posterior-most cervical spine in dorsal view. (**D**) UMMP 7476, *D. haplocerus*, armor from the 4th cervical series through the first dorsal series showing differences in the lateral spines between the 4th and 6th cervical series. Scale bars are 5 cm.

Fig. 2. Armure cervicale de *Desmatosuchus*. Les nombres donnent la position dans la série des cervicales. **1d**, première série dorsale latérale (**A**) TTUP 9024, *D. smalli*, épine cervicale latérale droite de la ?4^{e} série en vue dorsale. (**B**) TTUP 9024, *D. smalli*, épine cervicale latérale droite 6^{e} série en vue dorsale. (**C**) MNA V9300, *D. haplocerus*, épine cervicale droite la plus postérieure en vue dorsale. (**D**) UMMP 7476 *D. haplocerus*, armure de la série des 4^{e} cervicales jusqu'à la première série dorsale montrant les différences des épines latérales entre la série des 4^{e} et 6^{e} cervicales. Échelle : 5 cm.

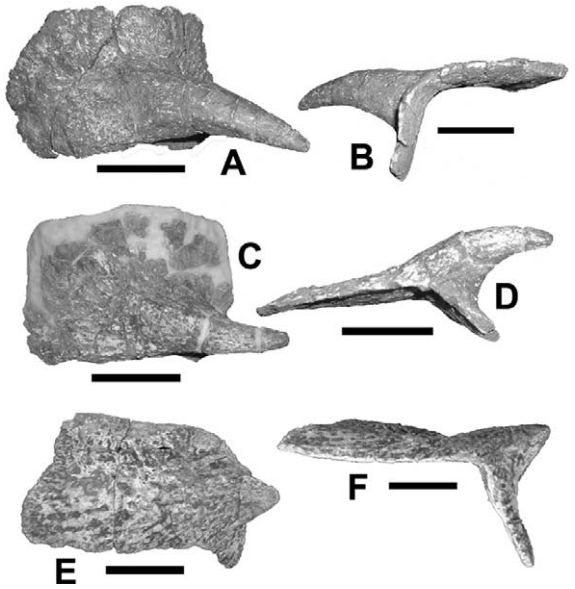

Fig. 3. Dorsal region armor of *Desmatosuchus*. (**A, B**) TTUP 9024, *D. smalli*, right posterior dorsal lateral plate in dorsal (**A**) and anterior (**B**) views; (**C, D**) TTUP 9024, *D. smalli*, right posterior dorsal lateral plate in dorsal (**C**) and posterior (**D**) views; (**E, F**) MNA V9300, *D. haplocerus*, right dorsal lateral plate in dorsal (**E**) and posterior (**F**) views. Scale bars are 5 cm.

Fig. 3 Armure de la région dorsale de *Desmatosuchus*. (**A, B**) TTUP 9024, *D. smalli,* , plaque dorsale latérale droite en vue dorsale (**A**) et antérieure (**B**) ; (**C, D**) TTUP 9024, *D. smalli*, plaque postérieure dorsale latérale droite en vue dorsale (**C**) et postérieure (**D**) ; (**E, F**) MNA V9300, *D. haplocerus*, plaque dorsale latérale droite en vue dorsale (**E**) et postérieure (**F**). Échelle : 5 cm.

(*D. haplocerus*) possesses a cervical lateral plate of the right side in which the eminence (spine) is barely developed. This plate was interpreted by Parker [36] as belonging to the first lateral series. None of the cervical spines in UMMP 7476 are as weakly developed, further suggesting that the anteriormost series is missing in that specimen and that both species of *Desmatosuchus* did possess six rows of cervical armor.

3.2.3. Posterior dorsal lateral plates

Behind the anteriormost dorsal lateral plates the dorsal flange of the plate widens significantly mediolaterally, and becomes shorter antero-posteriorly as the eminences become increasingly elongate and spine-like (Fig. 3A–D). The development of the spines behind those of the cervical series reaches a maximum in the pelvic and anterior caudal regions of both species of *Desmatosuchus* (contra Long and Ballew [26]). However, the dorsal and caudal lateral spines of *D. smalli*

are especially well-developed, and tend to be much longer and slightly recurved ventrally compared to those of *D. haplocerus* (Fig. 3E and F). It should be noted that in the reconstructions of *D. haplocerus* by Case [4] and Long and Murry [27], the dorsal and lateral flanges of the lateral dorsal armor were misidentified, so the lateral flanges were incorrectly depicted articulating with the paramedian plates. As a result the elements of the left side in these reconstructions are actually elements of the right side and vice versa. This indicates that both species of *Desmatosuchus* possess a much wider carapace than previously reconstructed and are more similar in overall body plan to *Longosuchus*, which also possesses rectangular lateral plates with wide dorsal flanges and well-developed spines. Parker [36] provides a new reconstruction for *Desmatosuchus haplocerus* based on this information.

A large amount of posterior dorsal lateral armor is present for *D. smalli*. However, because the carapace represented by TTUP 9024 is incomplete and not articulated, it is difficult to place each plate in its exact position. What is immediately obvious, however, is that the dorsal eminences in the dorsal lateral region are larger and much more developed than the respective plates in *D. haplocerus* (compare Fig. 3A–D to Case [4]:pl. 8). The length of the spines on the posterior dorsal lateral plates of *D. smalli* average 1 about 68 mm, compared to 42 mm in *D. haplocerus* for a similar-sized animal. In addition, in *D. smalli*, the eminence (spine) appears to contact the posterior margin of the plate (Fig. 3C), whereas in *D. haplocerus* the eminence is more centralized (Fig. 3E). In lateral view, the eminences of *D. smalli* are slightly recurved ventrally (Fig. 3B and D), whereas in *D. haplocerus* they are straight (Fig. 3F).

MNA V697 is a partial dorsal lateral plate of the right side from the Petrified Forest Member of the Chinle Formation (sensu Woody [44]), just west of Petrified Forest National Park in northeastern Arizona. This plate was identified by Long and Ballew [26] as a left cervical lateral spine. The dorsal flange of this plate is mostly missing, but the presence of a thin, well-developed anterior lamina precludes assignment of this element to the cervical region, because in *Desmatosuchus* these laminae tend to be extremely thickened in the cervical region. This plate can be assigned to *D. smalli*, because the spine is ventrally recurved (Fig. 4A and B). The locality from which this plate was collected also contains *Typothorax coccinarum*. This is the only documented co-occurrence of *T. coccinarum* and *Desmatosuchus* outside the Post Quarry. '*Desmatosuchus*' *chamaensis* from the Snyder Quarry of the Petrified Forest Member of New Mexico also co-occurs with *T. coccinarum* [21], however, this species is not referable to *Desmatosuchus* and represents a distinct genus [36].

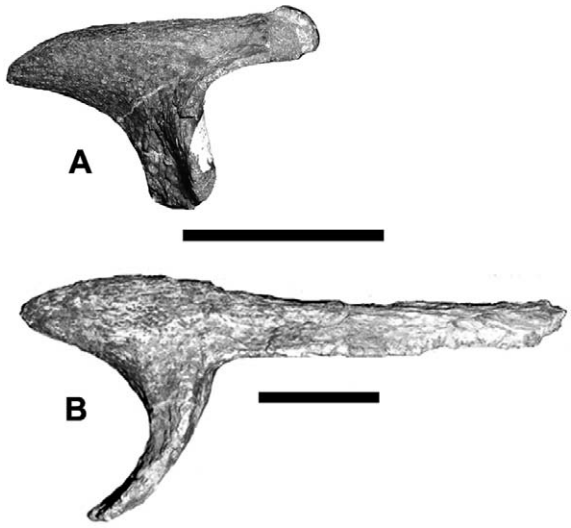

Fig. 4. (**A**) MNA V697, *D. smalli* referred specimen, right dorsal mid-lateral plate in anterior view. (**B**) TTUP 9024, *D. smalli* holotype, left dorsal mid-lateral plate (reversed for comparison) in anterior view. Scale bars are 5 cm.
Fig. 4. (**A**) MNA V697, spécimen attribué à *D. smalli*, plaque dorsale mi-latérale en vue antérieure. (**B**) TTUP 9024, holotype de *D. smalli*, plaque dorsale mi-latérale (inversée pour la comparaison) en vue antérieure. Échelle : 5 cm.

As noted in § 3.1, the posterior dorsal lateral plates of *Desmatosuchus smalli* are strongly flexed; the angle of flexion approaches 90 degrees in some plates. Medial edges are sigmoidal in more anterior plates of the dorsal region and straight in more posterior dorsal and pelvic plates. The plates are thinner than those of the anterior dorsal and cervical areas but still possess the complex tongue-and-groove articular surfaces that are diagnostic of *Desmatosuchus*.

3.2.4. Caudal armor

TTUP 9024 preserves a single anterior caudal lateral plate of the right side (Fig. 5A and B). The dimensions and overall morphology of the flanges of this plate are similar to those from the anterior caudal region of *D. haplocerus* in possessing the largest spines posterior to the cervical series. However, the spine on TTUP 9024 differs from that of *D. haplocerus* in being less

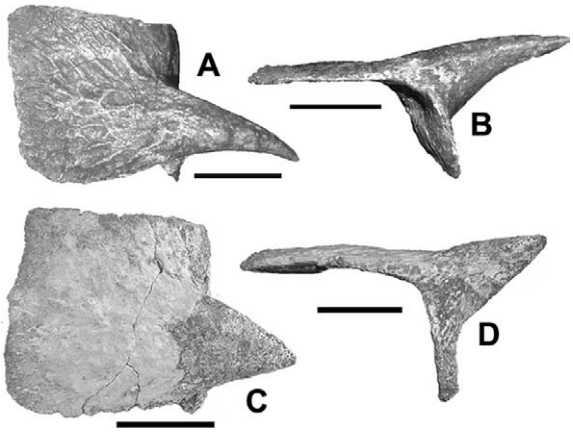

Fig. 5. Anterior caudal lateral plates of *Desmatosuchus*. (**A, B**) TTUP 9024, *D. smalli*, right plate in dorsal (**A**) and posterior (**B**) views; (**C, D**) MNA V9300, *D. haplocerus*, right plate in dorsal (**C**) and posterior (**D**) views. Scale bars are 5 cm.
Fig. 5. Plaques antérieures caudales de *Desmatosuchus*. (**A, B**) TTUP 9024, *D. smalli*, plaque droite en vue dorsale (**A**) et postérieure (**B**) ; (**C, D**) MNA V9300, *D. haplocerus*, plaque droite en vue dorsale (**C**) et postérieure (**D**). Échelle : 5 cm.

robust and elongate and possessing a tip that is only slightly ventrally recurved (Fig. 5C and D). The TTUP spine measures over 100 mm in length, whereas the longest post-cervical spine in MNA V9300 (*D. haplocerus*) is little more than 80 mm.

3.2.5. Skull

Small [38,41] provided a detailed description of the skull of *Desmatosuchus*, noting significant differences among specimens TTUP 9023, TTUP 9024, TTUP 9025 (*D. smalli*) and specimens UMMP 7476 and UCMP 27408 (*D. haplocerus*). These and other differences are as follows:

1) *parietals:* the upper surface of the parietals is generally flat in *D. smalli*, whereas in *D. haplocerus* a shallow, transverse concavity or sulcus is located on the posterior half of the parietals between the supratemporal fenestrae (Fig. 6A) (B.J. Small, pers. comm., 2002);
2) *exoccipitals:* according to Small [41], the exoccipitals of *D. smalli* do not meet at the midline of the foramen magnum, whereas Small [38] stated that they do meet at the midline in *D. haplocerus*, excluding the supraoccipital from participation in the occipital condyle. However, Small [41] also notes that this condition is generally unclear in UMMP 7476 and UCMP 27408;
3) *basisphenoid: D. smalli* possesses a very to moderately shallow median pharyngeal recess (see [43]), while in *D. haplocerus* this recess is deep (Fig. 6B and D). In *D. smalli* there is a wide gap between the basal tuber and basipterygoid process, while in *D. haplocerus* this gap is almost non-existent (Fig. 6B and D) [41];
4) *antorbital fossa:* the antorbital fossa in *D. smalli* is greatly reduced and almost absent, but is more prominent in *D. haplocerus* (Fig. 6A and C) (J.W. Martz, pers. comm., 2004).
5) *maxilla:* the maxillary tooth count in *D. smalli* ranges from 10–12, whereas in *D. haplocerus* it is 12–13 [41].

3.2.6. Pelvis

Several pelves that have been assigned to *Desmatosuchus*, including TTUP 9027 and part of TTUP 9024, were recovered from the Post Quarry. Unfortunately, they are not well preserved and have not been completely prepared. It is important to note that the pelvis described by Small [38] is not from the Post Quarry, but rather from the Tecovas Formation and therefore most likely referable to *D. haplocerus*, and not *D. smalli*.

4. Discussion

The Post Quarry has provided a wealth of *Desmatosuchus* material. But much of it has not yet been completely prepared and the associations are unclear. What is clear, however, is that significant distinctions exist between the Post Quarry *Desmatosuchus* material and that from Crosby County, Texas (UMMP 7476 and the type materials) and northeastern Arizona, including MNA V9300 and the *Placerias* Quarry material. These include notable differences in the cervical and posterior dorsal lateral armor, the skull roof, braincase, and maxillary tooth counts. Therefore, erection of a new species for the Post Quarry material is warranted. In addition, a single lateral plate from northeastern Arizona (MNA V697) can be referred to the new species. Whereas one or more of these differences may be attributable to sexual dimorphism, there is not currently a large enough sample size to test this hypothesis. Instead, because all of the differences noted above effectively divide all occurrences of *D. smalli* from *D. haplocerus*

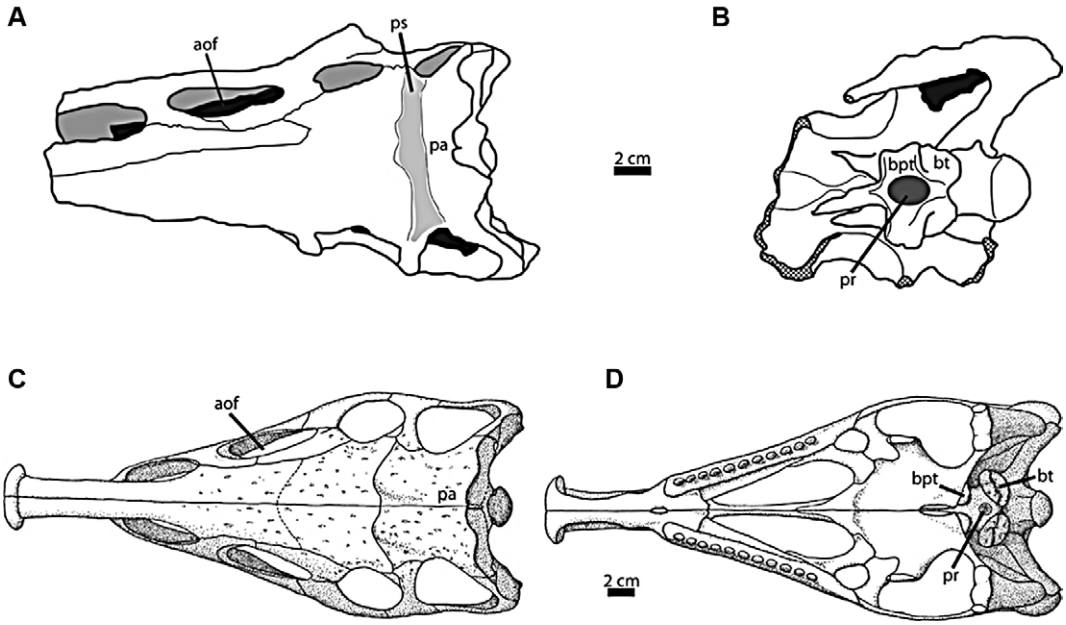

Fig. 6. Comparison of the skulls of *Desmatosuchus*. (**A**) UMMP 7476, *D. haplocerus*, skull in dorsal view (redrawn from Case [3]); (**B**) UMMP 7476, *D. haplocerus*, rear portion of skull in ventral view (redrawn from Case [3]); (**C**) *D. smalli*, composite drawing of skull in dorsal view based mainly on TTUP 9024 (modified from Small [41]); (**D**) *D. smalli*, composite drawing of skull in ventral view based mainly on TTUP 9024 (modified from Small [41]). aof, antorbital fenestra; bpt, basipterygoid; bt, basal tuber; pa, parietal; pr, medial pharyngeal recess; ps, parietal sulcus. Cross-hatching indicates broken surfaces. Scale bars are 2 cm.

Fig. 6. Comparaison des crânes de *Desmatosuchus*. (**A**) UMMP 7476, *D. haplocerus*, crâne en vue dorsale (redessiné d'après Case [31]) ; (**B**) UMMP 7476, *D. haplocerus*, portion arrière de crâne en vue ventrale (redessiné de Case [31]) ; (**C**) *D. smalli*, dessin composite du crâne en vue dorsale, basé surtout sur TTUP 9024 (modifié d'après Small [41]) ; (**D**) *D. smalli*, dessin composite du crâne en vue ventrale, basé surtout d'après TTUP 9024 (modifié d'après Small [41]). **Aof**, fenêtre antéorbitaire ; **bpt** : basiptérygoïde ; **bt** : tuberosité basale ; **pa** : pariétal ; **pr** : recessus pharyngé médial ; **ps**, sulcus pariétal. Les hachures indiquent les surfaces brisées. Échelle : 2 cm.

by stratigraphic horizon as well, the most parsimonious explanation at this time is that these differences are taxonomic.

Because limb, pectoral girdle and anterior lower jaw material of *Desmatosuchus* from the Post Quarry are now assigned to a different species, these elements are now unknown for *D. haplocerus*. Long and Murry [27] assigned much postcranial material from the *Placerias* Quarry from the lower Chinle Formation of northeastern Arizona to *Desmatosuchus haplocerus*. However, because almost all of the material from this quarry shows almost no association [13] and the quarry contains at least three taxa of aetosaurs including *Stagonolepis*, *Desmatosuchus*, and an undescribed *Paratypothorax*-like form (pers. obs.), assignment of non-armor elements to specific taxa such as those proposed by Long and Murry [27] should be considered tenuous. Consequently, comparisons between the anterior lower jaw, pectoral girdle, limbs, vertebrae, and caudal armor of *D. haplocerus* and *D. smalli* cannot currently be made.

Desmatosuchus haplocerus is currently restricted to the lower portions of the Chinle Formation and Dockum Group, whereas *D. smalli* is currently known only from the upper portions of the same units. The separation of *Desmatosuchus* into distinct Carnian and Norian species suggests at least some biostratigraphic utility for these taxa, but only when adequate cranial or lateral armor material is available [8,30,46].

Acknowledgements

I thank Bryan Small, Daniel Woody, and Randall Irmis for profitable discussion of many of the ideas presented in the paper; comments by Jeff Martz, Kevin Padian, Lori Browne, Randall Irmis, and an anonymous reviewer greatly improved the manuscript. Ran-

dall Irmis also created Fig. 6. Thanks to Sankar Chatterjee and the crew from the Museum at Texas Tech for allowing access to the Post Quarry specimens, Tony Fiorillo for the Post Quarry specimens at the Dallas Museum of Natural History, and Janet Whitmore Gillette for specimens at the Museum of Northern Arizona. Bill Mueller provided photographs of the holotype material. This manuscript represents a portion of a MS thesis from Northern Arizona University.

References

[1] C.L. Camp, A study of the phytosaurs, with description of new material from western North America, Mem. Univ. Calif. 10 (1930) 1–161.

[2] E.C. Case, Preliminary description of a new suborder of phytosaurian reptiles with a description of a new species of *Phytosaurus*, J. Geol. 28 (1920) 524–535.

[3] E.C. Case, New reptiles and stegocephalians from the Upper Triassic of western Texas, Carnegie Inst. Publ. 321 (1922) 1–84.

[4] S. Chatterjee, *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs, Phil. Trans. R. Soc. Lond., Ser. B 309 (1985) 395–460.

[5] S. Chatterjee, The Late Triassic Dockum vertebrates: their stratigraphic and paleobiogeographic significance, in: K. Padian (Ed.), The beginning of the age of dinosaurs: Faunal change across the Triassic-Jurassic boundary, Cambridge University Press, Cambridge, 1986, pp. 139–150.

[6] S. Chatterjee, Cranial anatomy and relationships of a new Triassic bird from Texas, Phil. Trans. R. Soc. Lond., Ser. B 332 (1991) 277–342.

[7] S. Chatterjee, *Shuvosaurus*, a new theropod, Nat. Geog. Res. Expl. 9 (1993) 274–285.

[8] E.D. Cope, Synopsis of the extinct Batrachia, Reptilia, and Aves of North America, Trans. Am. Phil. Soc. 14 (1869) viii + 1–252.

[9] E. D. Cope, Report upon the extinct Vertebrata obtained in New Mexico by paries of the expedition of 1874: US Geographical Surveys west of the 100th Meridian [Wheeler], part 2, 1877, pp. 1–370.

[10] E.D. Cope, A contribution to the vertebrate paleontology of Texas, Proc. Am. Philos. Soc. 30 (1892) 123–131.

[11] R.E. Dunay, M.J. Fisher, Palynology of the Dockum Group, (Upper Triassic), Texas, USA, Rev. Palaeobot. Palynol. 28 (1979) 61–92.

[12] R.L. Elder, Paleontology and paleoecology of the Dockum Group, Upper Triassic, Howard County, Texas, M. Sci. thesis, University of Texas, Austin, USA, 1978, p. 205.

[13] A.R. Fiorillo, K. Padian, C. Musikasinthorn, Taphonomy and depositional setting of the *Placerias* Quarry (Chinle Formation:Late Triassic, Arizona), Palaios 15 (2000) 373–386.

[14] M.J. Fischer, R.E. Dunay, Palynology of the Petrified Forest Member of the Chinle Formation (Upper Triassic), Arizona, USA, Pollen Spores 26 (1984) 241–284.

[15] J.A. Gauthier, Saurischian monophyly and the origin of birds, Mem. Calif. Acad. Sci. 8 (1986) 1–55.

[16] J.T. Gregory, *Typothorax* and *Desmatosuchus*, Postilla 16 (1953) 1–27.

[17] J.T. Gregory, F. Westphal, Remarks on the phytosaur genera of the European Trias, J. Paleontol. 43 (1969) 1296–1298.

[18] A.B. Heckert, S.G. Lucas, A new aetosaur from the Upper Triassic of Texas and the phylogeny of aetosaurs, J. Vertebr. Paleontol. 19 (1999) 50–68.

[19] A.B. Heckert, S.G. Lucas, Taxonomy, phylogeny, biostratigraphy, biochronology, paleobiogeography, and evolution of the Late Triassic Aetosauria (Archosauria:Crurotarsi), Zbl. Geol. Paläont., Teil I, Heft 11–12 (2000) 1539–1587.

[20] A.B. Heckert, A.P. Hunt, S.G. Lucas, Redescription of *Redondasuchus reseri*, a Late Triassic aetosaur (Reptilia: Archosauria) from New Mexico (USA) and the biochronology and phylogeny of aetosaurs, Geobios 29 (1996) 619–632.

[21] A.B. Heckert, K.E. Zeigler, S.G. Lucas, Aetosaurs (Archosauria: Stagonolepididae) from the Upper Triassic (Revueltian) Snyder Quarry, New Mexico, Bull. New Mex. Mus. Nat. Hist. Sci 24 (2003) 115–126.

[22] F.-V. Huene, Die fossilen Reptilien des südamerikanischen Gondwanalnades, Ergebnisse dur Sauriergrabung in Sübbrasilien 1928/1929, C.H. Beck'sche Verlagsbuchhandlung, Munich, Germany, 1942, pp. 161–332.

[23] T.H. Huxley, The crocodilian remains found in the Elgin Sandstones with remarks on the ichnites of Cummingstone, Mem. Geol. Surv. UK, Monogr. 3 (1877) 1–58.

[24] T.M. Lehman, S. Chatterjee, J. Schnable, The Cooper Canyon Formation, (Late Triassic) of western Texas, Tex. J. Sci. 44 (1992) 349–355.

[25] R.J. Litwin, A. Traverse, S.R. Ash, Preliminary palynological zonation of the Chinle Formation, southwestern USA, and its correlation to the Newark Supergroup (eastern USA), Rev. Palaeobot. Palynol. 68 (1991) 269–287.

[26] R.A. Long, K.L. Ballew, Aetosaur dermal armor from the Late Triassic of southwest North America with special reference to material from the Chinle Formation of Petrified Forest National Park, Mus. N. Ariz. Bull. 54 (1985) 45–68.

[27] R.A. Long, P.A. Murry, Late Triassic (Carnian and Norian) tetrapods from the southwestern United States, New Mex. Mus. Nat. Hist. Sci. Bull. 4 (1995) 1–254.

[28] S.G. Lucas, Global Triassic tetrapod biostratigraphy and biochronology, Palaeogeogr. Palaeoclimatol. Palaeoecol. 143 (1998) 347–384.

[29] S.G. Lucas, A.P. Hunt, Revised Triassic stratigraphy in the Tucumcari Basin, east-central New Mexico, in: S.G. Lucas, A.P. Hunt (Eds.), The dawn of the age of dinosaurs in the American Southwest, University of New Mexico Press, Albuquerque, 1989, pp. 150–170.

[30] R. Lydekker, The fossil Vertebrata of India, Rec. Geol. Survey India 20 (1887) 51–80.

[31] J.W. Martz, The morphology and ontogeny of *Typothorax coccinarum* (Archosauria, Stagonolepididae) from the Upper Triassic of the American Southwest, M. Sci. thesis, Texas Technical University, Lubbock, 2002, p. 279.

[32] J.W. Martz, B. Mueller, B.J. Small, Two new aetosaurs (Archosauria, Stagonolepididae) from the Upper Triassic of Texas and Colorado, and problems in aetosaur identification and taxonomy, J. Vertebr. Paleontol. 23 (2003) 76A.

[33] P.A. Murry, Vertebrate paleontology of the Dockum Group, western Texas and eastern New Mexico, in: K. Padian (Ed.), The beginning of the age of dinosaurs: Faunal change across the Triassic–Jurassic boundary, Cambridge University Press, Cambridge, 1986, pp. 109–137.

[34] P.A. Murry, R.A. Long, Geology and paleontology of the Chinle Formation, Petrified Forest National Park and vicinity, Arizona and a discussion of vertebrate fossils of the southwestern Upper Triassic, in: S.G. Lucas, A.P. Hunt (Eds.), Dawn of the age of dinosaurs in the American southwest, University of New Mexico Press, Albuquerque, 1989, pp. 29–64.

[35] P.A. Murry, R.A. Long, A diminuative carnivorous aetosaur from the Upper Triassic of Howard County, Texas, J. Vertebr. Paleontol. 16 (1996) 55A.

[36] W.G. Parker, Description of a new specimen of *Desmatosuchus haplocerus* from the Late Triassic of Northern Arizona, M. Sci. Thesis, Northern Arizona University, Flagstaff, USA, 2003, p. 315.

[37] H.J. Sawin, The Pseudosuchian reptile *Typothorax meadei*, J. Paleontol. 21 (1947) 201–238.

[38] B.J. Small, The Triassic thecodontian reptile *Desmatosuchus*: osteology and relationships, M. Sci. thesis, Texas Tech University, Lubbock, USA, 1985, p. 83.

[39] B.J. Small, Post Quarry, in: S.G. Lucas, A.P. Hunt (Eds.), Dawn of the age of dinosaurs in the American Southwest, University of New Mexico Press, Albuquerque, 1989, pp. 145–148.

[40] B.J. Small, Aetosaurs from the Upper Triassic Dockum Formation, Post Quarry, West Texas, in: S.G. Lucas, A.P. Hunt (Eds.), Dawn of the age of dinosaurs in the American Southwest, University of New Mexico Press, Albuquerque, 1989, pp. 301–308.

[41] B.J. Small, Cranial anatomy of *Desmatosuchus haplocerus* (Reptilia: Archosauria: Stagonolepididae), Zool. J. Linn. Soc. 136 (2002) 97–111.

[42] A.D. Walker, Triassic reptiles from the Elgin area: *Stagonolepis, Dasygnathus*, and their allies, Phil. Trans. R. Soc. Lond., Ser. B 244 (1961) 103–209.

[43] L.M. Witmer, Craniofacial air sinus systems, in: P.J. Currie, K. Padian (Eds.), Encyclopedia of Dinosaurs, Academic Press, San Diego, 1997, pp. 151–159.

[44] D.T. Woody, Revised geological assessment of the Sonsela Member, Chinle Formation, Petrified Forest National Park, Arizona, M. Sci. thesis, Northern Arizona University, Flagstaff, USA, 2003, p. 205.

[45] K.E. Zeigler, A.B. Heckert, S.G. Lucas, A new species of *Desmatosuchus* (Archosauria: Aetosauria) from the Upper Triassic of the Chama Basin, Bull. New Mex. Mus. Nat. Hist. Sci. 21 (2002) 215–219.

[46] K.A. Zittel, Handbuch der Palaeontologie. 1. Abteilung: Palaeozoologie, 3. – XII + 900 S., 719 Abb.; München & Leipzig, 1887–1990.