Redescription of *Calyptosuchus wellesi* (Archosauria: Pseudosuchia: Aetosauria) from the Late Triassic of the southwestern United States (#21320)

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Redescription of *Calyptosuchus wellesi* (Archosauria: Pseudosuchia: Aetosauria) from the Late Triassic of the southwestern United States

William G Parker Corresp. [1]

[1] Division of Science and Resource Management, Petrified Forest National Park, Petrified Forest, Arizona, United States

Corresponding Author: William G Parker
Email address: William_Parker@nps.gov

Calyptosuchus wellesi is a medium-sized desmatosuchian aetosaur common in Adamanian (early to middle Norian) age rocks from the Chinle Formation and Dockum Group of the western United States. Known chiefly from osteoderms, this taxon has never been fully described and non-osteoderm material assigned to *Calyptosuchus* has been done so based on questionable criteria. Mapping of aetosaurian elements from the *Placerias* Quarry allows for the recognition of associated material providing support for referrals of non-osteoderm material. Furthermore, another previously undescribed specimen from the Chinle Formation of Arizona provides more details about this taxon. Presently *Calyptosuchus* lacks discrete autapomorphies, but can be distinguished from other aetosaurs based on a unique combination of characters.

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William G. Parker

Division of Science and Resource Management, Petrified Forest National Park, Petrified Forest, Arizona 86028

William_Parker@nps.gov

ABSTRACT

Calyptosuchus wellesi is a medium-sized desmatosuchian aetosaur common in Adamanian (early to middle Norian) age rocks from the Chinle Formation and Dockum Group of the western United States. Known chiefly from osteoderms, this taxon has never been fully described and non-osteoderm material assigned to *Calyptosuchus* has been done so based on questionable criteria. Mapping of aetosaurian elements from the *Placerias* Quarry allows for the recognition of associated material providing support for referrals of non-osteoderm material. Furthermore, another previously undescribed specimen from the Chinle Formation of Arizona provides more details about this taxon. Presently *Calyptosuchus* lacks discrete autapomorphies, but can be distinguished from other aetosaurs based on a unique combination of characters.

INTRODUCTION

In 1931 Ermine Cowles Case of the University of Michigan Museum of Paleontology (UMMP) discovered a well-preserved articulated partial carapace with an associated vertebral column and pelvis of an aetosaurian in Upper Triassic strata of the Texas Panhandle. Although described in detail, the taxonomic affinities of the specimen were considered enigmatic and the material was assigned only to Phytosauria (Case, 1932).

That same year Charles Lewis Camp of the University of California Museum of Paleontology (UCMP) began excavating a vast deposit of bones in the Upper Triassic Chinle Formation of Arizona at a site he christened the *Placerias* Quarry because of the large number of bones of the dicynodont *Placerias gigas* (=*Placerias hesternus*) recovered there. In addition, Camp recovered a large number of aetosaurian 'skin plates' (his term for osteoderms) as well as portions of the endocranial skeletons of dozens of individuals (e.g., Long & Murry, 1995). Comparison of this material to that of *Stagonolepis robertsoni* from the Elgin Sandstone (now the Lossiemouth Sandstone Formation) of Scotland led Camp to believe that much of his Arizona material represented a very similar animal, possibly of the same genus (C. L. Camp,

unpublished notes, 1935). Unfortunately Camp never published descriptions or taxonomic notes regarding these specimens, only referring them in passing to "*Typothorax*" (as in *Longosuchus meadei*) and "*Episcoposaurus*" (as in *Desmatosuchus spurensis*) (Camp & Welles, 1956:259).

Both the Texas and Arizona material remained undescribed until it was restudied as part of a field investigation of the Triassic of Arizona by crews from the UCMP in the 1980s (Long & Ballew, 1985). During this time it was named *Calyptosuchus wellesi* and Case's specimen was designated as the holotype of this new taxon (Long & Ballew, 1985). The genus name was only used for a very short time before it was noted again that the material appeared to be very similar to that of *Stagonolepis robertsoni*, and was reassigned to the genus *Stagonolepis*, as *Stagonolepis wellesi* (Murry & Long, 1989). *Stagonolepis wellesi* was differentiated from *Stagonolepis robertsoni* by the presence of short horns on the cervical lateral osteoderms (Long & Ballew, 1985; Long & Murry, 1995); however, these were later demonstrated to belong to a previously unrecognized paratypothoracin aetosaur that was present in the *Placerias* and Downs quarries at St. Johns Arizona, probably *Tecovasuchus* (Parker, 2005a; Heckert et al., 2007). Thus, specific characters to diagnose *Stagonolepis wellesi* sensu Long & Murry (1995), exclusive of other aetosaurians, are lacking. Initial comparisons of the dorsal osteoderms with those of *Stagonolepis robertsoni* for this study revealed strong differences (see discussion below) and the use of *Calyptosuchus wellesi* for the North American material is recommended (e.g., Parker, 2008a; Parker & Martz, 2011; Desojo et al., 2013).

Scoring *Calyptosuchus wellesi* into a phylogenetic analysis has proved challenging because the holotype consists of the articulated carapace from just anterior to the pelvic region back through the middle of the tail and lacks both limb and cranial material. Furthermore, the specimen was set in plaster and mounted upright behind heavy glass in the UMMP. The associated vertebral column and pelvis were separated from the osteoderms during the initial study by Case and are presently in poor condition (W. Parker, pers. obs., 2000).

Besides Case's (1932) description of UMMP 13950 and his descriptions of a referred isolated pelvis and associated vertebrae (UMMP 7470; Case, 1922, 1929), *Calyptosuchus wellesi*

has never been adequately described. The initial study in which the taxon was named only provides a general list of characters of the osteoderms (Long & Ballew, 1985). Superficial descriptions of various referred endoskeletal elements were provided by Long & Murry (1995), who did not redescribe the type or referred osteoderms in more detail.

Institutional Abbreviations

AMNH FR, Frick Collection, American Museum of Natural History, New York, NY, USA; **MNA**, Museum of Northern Arizona, Flagstaff, AZ, USA; **PEFO**, Petrified Forest National Park, Arizona, USA; **PVL**, Paleontología de Vertebrados, Instituto 'Miguel Lillo,' San Miguel de Tucumán, Argentina; **TMM**, Texas Vertebrate Paleontology Collections, University of Texas, Austin, Texas, USA; **TTU**, The Museum at Texas Tech, Lubbock, TX, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, CA, USA; **UKNHM**, The Natural History Museum, London, UK; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, MI, USA;

Geological Setting of the *Placerias* Quarry

The *Placerias* Quarry is situated in a small area of badlands in Apache County, Arizona southwest of the city of St. Johns. These outcrops represent the Upper Triassic Chinle Formation (Akers, 1964) and the quarry itself is developed in an olive gray claystone lens with abundant carbonate nodules (Fiorillo et al., 2000). The quarry has been interpreted as a stagnant waterhole or bog (Camp and Welles, 1956), but a more recent study found the local sedimentology to be consistent with pedogenically modified fluvial sediments in an area with seasonally high water tables and periods of aridity (Fiorillo, Padian & Musikasinthorn, 2000).

The stratigraphic position of the quarry is controversial because of poor exposure of the outcrops (Fiorillo, Padian & Musikasinthorn, 2000), but all authors agree that it occurs in the

lower portion of the Chinle Formation (Camp & Welles, 1956; Jacobs & Murry, 1980; Long & Murry, 1995; Lucas, Heckert & Hunt, 1997; Fiorillo, Padian & Musikasinthorn, 2000; Parker & Martz, 2011). Lithostratigraphic correlation from Petrified Forest NP, approximately 62 km northwest of the quarry, demonstrates that the quarry is located either in the uppermost portion of the Blue Mesa Member or in the lowermost portion of the Sonsela Member (Parker & Martz, 2011; Irmis et al., 2011; WGP unpublished data). Redbeds above the quarry level assigned to the Bluewater Creek Member of the Chinle Formation by Lucas, Heckert & Hunt (1997) are actually deposits of the Miocene-Pliocene Bidahochi Formation separated from the Chinle Formation by angular unconformities (Akers, 1964; WGP unpublished data). The maximum age of the quarry is established by high precision U/Pb geochronology to be 219.39±0.16 Ma (Ramezani et al., 2014). This would make it equivalent in age to the upper part of the Lot's Wife beds of the (lower) Sonsela Member in Petrified Forest National Park (Martz & Parker, 2010; Ramezani et al., 2011; Atchley et al., 2013). The quarry is in the Adamanian Teilzone (Martz & Parker, 2017).

MATERIALS AND METHODS

Calyptosuchus material from the *Placerias* Quarry

The largest collection of material referred to *Calyptosuchus wellesi* is from the *Placerias* Quarry and potentially contains bones from most portions of the skeleton including a few isolated skull bones and basicrania (see below). Long & Murry (1995) referred much of this material to *Calyptosuchus*; however, many of these elements have received unique catalogue numbers and any original association has been lost. Furthermore, Camp & Welles (1956) stated that little of the material in the quarry was associated. Thus, it is not clear on what basis the endocranial material was assigned to *Calyptosuchus* by Long & Murry (1995). However, several

125 disarticulated archosaur specimens from the quarry fit together perfectly demonstrating that they
126 belong to the same individual. The best example from the quarry are five elements (UCMP
127 25962, right ilium, UCMP 25974, left ilium, UCMP 25999, pubis, UCMP 25993, ischium,
128 UCMP 78719, sacral vertebrae), which can be combined to reconstitute a nearly complete pelvis
129 of *Poposaurus gracilis* (Long & Murry, 1995:figs. 151, 153). The quarry also contains
130 associated pelvic and limb material from a single individual of *Calyptosuchus wellesi* (Long &
131 Murry, 1995:fig. 79), which is discussed in more detail below.
132 Fortunately, the collectors at the *Placerias* Quarry excavated utilizing a grid system
133 (Camp & Welles, 1956) and physically marked the grid of collection in permanent ink on many
134 of the bones. These numbers can be matched to the published quarry map (Camp & Welles,
135 1956:fig. 2), and although the exact placements within the grid for each bone have not been
136 preserved, the numerous smaller grids measure about 2.25 square meters and the largest about 9
137 square meters (Camp & Welles, 1956), allowing for some degree of association to be estimated.
138 With the exception of a few endocranial elements discussed in the text, only the osteoderm
139 material can be assigned with any certainty to the genera *Calyptosuchus* and *Desmatosuchus*. For
140 this study a spreadsheet was created listing all of the material (over 1000 specimens) assigned to
141 these taxa by Long & Murry (1995) along with the associated field/grid number. These data were
142 sorted by field/grid to look for potential associated specimens. The element types were then
143 plotted onto the quarry map with the exception of the majority of the numerous caudal centra,
144 which are indeterminate to genus or species (Figure 1). No other aetosaurians were recognized in
145 the plotted osteoderm sample even though rare paratypothoracin lateral osteoderms are
146 recognized from collections from the area made at later dates (Parker, 2005a). Thus, all of the
147 material is considered referable to *Calyptosuchus* or *Desmatosuchus* with the caveat that the
148 slight possibility does exist that some of the endoskeletal bones could represent the extremely
149 rare paratypothoracin that is known from armor in the quarry.
150

Plotting the sorted data shows large accumulations of *Calyptosuchus wellesi* osteoderms in grids C71S and C72S, as well as in C64M and C65M (Figure 1). *Desmatosuchus spurensis* osteoderms are accumulated particularly in C75W, C64, and C62M (Figure 1). Thus there is some distinction between large accumulations of osteoderms of these taxa and it is possible that these associations could represent single individuals. This information is used to make suggestive referrals of material to *Calyptosuchus wellesi* and is discussed in more detail in the following description. Unfortunately there is no way to calculate a genuine minimum number of individuals for each taxon; however there are 14 aetosaurian basicrania in the overall sample (including three that lack field numbers). Numerous endoskeletal elements in CD1, CD2, CE1, CE2, CF1, CF2 are associated with very few osteoderms presenting a potentially interesting taphonomic question of why they are lacking; however, Camp & Welles (1956:259) note that in this portion of the excavation "most of the numerous isolated dermal scutes of *Typothorax*, as well as broken ribs and other fragmentary material, were not collected". Thus the majority of osteoderms in the *Placerias* Quarry sample were collected in 1931 from the west side of the quarry and in 1932, during excavation of the east side, the osteoderms were ignored. This is reflected in the plotted data (Figure 1). Note that by listing "*Typothorax*", Camp & Welles (1956) were actually referring to *Calyptosuchus*, although they are may also be using this name to encompass all of the aetosaurian paramedian osteoderms.

SYSTEMATIC PALEONTOLOGY

Archosauria Cope, 1869 *sensu* Gauthier & Padian, 1985

Pseudosuchia Zittel, 1887-90 *sensu* Gauthier & Padian, 1985

Aetosauria Marsh, 1884 *sensu* Parker, 2007

Desmatosuchia Case, 1920 *sensu* Parker, 2016a

Desmatosuchinae Case, 1920 *sensu* Heckert & Lucas, 2000

Calyptosuchus Long & Ballew, 1985

Calyptosuchus wellesi Long & Ballew, 1985

(Figs. 2 - 18)

1922 Phytosaur: Case, p. 73, fig. 28b.
1929 Phytosaur: Case, p. 49, fig. 21.
1932 *Phytosaurus*?: Case, p. 57, figs. 1-6, pl. 1-3, pl. 4, fig. 1.
1953a *Typothorax*: Gregory, p. 13.
1953a *Desmatosuchus haplocerus*: Gregory, p. 15.
1961 Unnamed aetosaur: Walker, p. 157
1961 *Desmatosuchus haplocerus*: Walker, p. 181.
1961 *Typothorax*: Walker, p. 184.
1962 *Phytosaurus*: Gregory, p. 682.
1985 *Calyptosuchus wellesi*: Long & Ballew, p. 47, figs. 13b, 14b, 15-16, pl. 4-5. [non fig. 13a, 14a (= *Scutarx deltatylus*)].
1986 *Calyptosuchus*: Long & Padian, p. 165.
1986 *Calyptosuchus*: Parrish & Carpenter, p. 158.
1986 *Calyptosuchus wellesi*: Murry, p. 123.
1988 *Calyptosuchus wellesi*: Long & Houk, p. 50.
1989 *Stagonolepis wellesi*: Murry & Long, p. 32.
1995 *Stagonolepis wellesi*: Long & Murry, p. 1, figs. 68-70, 71a, c, d, 72a, c-d, f-g, 73-77, 79-81, 83-84. [non figs. 71b, 72b, e (=*Scutarx deltatylus*), 71e-f (=Paratypothoracini), 78, 82 (=Stagonolepididae)].
1996a *Stagonolepis wellesi*: Lucas & Heckert, p. 70.
1996b *Stagonolepis wellesi*: Lucas & Heckert, p. 60, fig. 4 (in part). [non fig. 4 (in part) (=*Scutarx deltatylus*)].
1997 *Stagonolepis*: Heckert & Lucas, p. 14.
1997 *Stagonolepis wellesi*: Lucas, Heckert & Hunt, p. 40.
1998 *Stagonolepis wellesi*: Lucas, p. 366, fig. 11b (in part). [non fig. 11b (in part) (=*Scutarx deltatylus*).
2000 *Stagonolepis wellesi*, Heckert and Lucas, p. 1543, figs. 4a-b
2002 *Stagonolepis wellesi*, Heckert and Lucas, p. 12.
2005 *Stagonolepis wellesi*: Heckert, Lucas & Hunt, p. 23.
2005 *Stagonolepis wellesi*: Parker, p. 38.
2005 *Stagonolepis wellesi*: Parker & Irmis, p. 50. [non fig. 4a (=*Scutarx deltatylus*)].
2005 *Stagonolepis wellesi*: Irmis, p. 77, fig. 6e.
2006 *Stagonolepis wellesi*: Parker, p. 47.
2007 *Stagonolepis wellesi*: Parker, p. 54.
2008 *Desmatosuchus haplocerus*: Lucas & Connealy, p. 26.
2010 *Stagonolepis*: Lucas, p. 464.

2011 *Calyptosuchus wellesi*, Parker & Martz, p. 240, fig. 3.
2013 *Calyptosuchus wellesi*: Desojo et al., p. 206.
2013 *Calyptosuchus wellesi*: Martz et al., p. 346. [non figs. 7a-d (=*Scutarx deltatylus*)].
2016a *Calyptosuchus wellesi*: Parker, p. 2, fig. 24a.
2016b *Calyptosuchus wellesi*: Parker, p. 13.

Holotype – UMMP 13950, partial articulated skeleton consisting of the osteoderms of the posterior dorsal series through the mid-caudal region, the associated partial vertebral column and the sacrum (Case, 1932).

Referred Specimens – UMMP 7470, mostly complete pelvis with associated posterior trunk vertebrae and paramedian osteoderms; UCMP 27225, dentary fragment, dentigerous bone fragment, cervical centra, paramedian, lateral, and ventral osteoderms. Much material from near St. Johns, Arizona is referable to *Calyptosuchus wellesi* as is some from Petrified Forest National Park (Long & Murry, 1995; Parker & Martz, 2011; see description below).

Locality, Horizon, and Age – upper part of the Blue Mesa Member and lower part of the Sonsela Member (sensu Martz & Parker, 2010), Chinle Formation, Arizona; Tecovas Formation, Dockum Group, Texas. Adamanian Estimated Holochronozone and Estimated Holochron (224-215 Ma; Martz & Parker, 2017, early Norian (e.g., Furin et al., 2006).

Revised Diagnosis –Medium sized (less than four meters length) aetosaur that presently lacks discrete autapomorphies, but differs from other aetosaurs based on a unique combination of characters: large knob-like dorsal eminences that contact the posterior margin of the dorsal and caudal paramedian osteoderms; moderate width/length ratios of the dorsal trunk paramedian osteoderms; strongly radial pattern of ridges and furrows on paramedian osteoderms;

anterolateral and anteromedial projections of the anterior bar of the paramedian osteoderms as in non-desmatosuchins; triangular projection of the anterior bar anterior to the dorsal eminence on the dorsal trunk paramedian osteoderms; dorsal paramedian osteoderms with a 'scalloped' anterior margin of the anterior bar between the medial edge and the anterior triangular projection; dorsal trunk paramedian osteoderms with a weak ventral strut as in typothoracisins; cervical vertebrae are keeled ventrally; trunk vertebrae lack hyposphene -hypantrum articulations; base of the postzygapophyses of the trunk vertebrae bearing a posterior projection that rests upon the ventral bar of the prezygapophyses; neural spines taller than the centra in the mid-trunk vertebrae; dentary with nine tooth positions. Differs from *Scutarx deltatylus* in that the cervical and dorsal trunk paramedian osteoderms lacks a pronounced triangular protuberance in the posterolateral corner. Differs from *Aetosauroides scagliai* in possessing a dentary that bears a sharp inflexion on the ventral margin.

DESCRIPTION

Cranial bones

The only skull bone unambiguously referable to *Calyptosuchus wellesi* is a partial right dentary from UCMP 27225, which was neither mentioned nor described by Long & Ballew (1985) or Long & Murry (1995). This partial dentary is missing all of the anterior portion as well as the posterior articulations with the angular and surangular (Figure 2a). The element is slightly crushed and still covered in part by a hematite crust, but many details can be discerned. Overall the element is dorsoventrally shallow and possesses the sharp inflexion on the ventral margin of the dentary described by Desojo & Ezcurra (2011) as present in *Desmatosuchus smalli*, *Stagonolepis robertsoni*, and *Neoaetosauroides engaeus*, and as lacking in *Aetosauroides*

scagliai. The medial surface is inscribed by an elongate, tapering Meckelian groove, which extends anteriorly to the level of the third alveolus (Figure 2b). The anteroventral corner of the medial surface bears a rugose patch that represents the beginning of the dentary symphysis. The occlusal surface is slightly concave, edentulous anteriorly and preserving nine oval alveoli posteriorly. The alveoli are closely spaced and slightly imbricated (Figure 2c). No complete teeth are preserved although root fragments are present in some of the alveoli. A second dentigerous fragment in UCMP 27225 bears five alveoli and represents a portion of the maxilla.

There are numerous aetosaur frontals and parietals in the UCMP collection from the *Placerias* Quarry, but none can be referred with certainty to *Calyptosuchus*. There are also approximately nine basicrania in the same collections. Two (UCMP 27414, UCMP 27419) possess anteroposteriorly elongate basisphenoids with divergent basipterygoid processes. These differ significantly from those of *Desmatosuchus* (TTU P-9023; UMMP 7476) and may belong to *Calyptosuchus*; however, this cannot be presently ascertained.

There are also two maxillary fragments that also differ in morphology from known specimens of *Desmatosuchus* (e.g., TTU P-9024; UMMP 7476) in possessing a distinct antorbital fossa delineated ventrally and anteriorly by a sharp rim (Figure 3). The first (UCMP 195193) is a fragment of a right maxilla which preserves the main body ventral to the anterior portion of the antorbital fossa including the base of the ascending process of the maxilla (Figure 3a-c). The lateral face is divided into two sections by a sharp horizontal ridge that forms the ventral border of the antorbital fossa. Anteriorly this ridge forms a broad dorsally sweeping curve that extends up onto the ascending process of the maxilla. A similar ridge is present in *Stagonolepis olenkae* (Sulej, 2010), *Aetosauroides scagliai* (PVL 2073), *Stagonolepis robertsoni* (Walker, 1961), and *Revueltosaurus callenderi* (PEFO 34561), but is absent or extremely weak

in *Desmatosuchus* (e.g., TTU P-9024) and *Longosuchus meadei* (TMM 31100-98). In *Stagonolepis olenkae* the ventral portion is not as deep and as a result the ridge does not split the main body of the maxilla in two equal portions. This maxillary fragment is missing the anterior and posterior portions as well as the majority of the ascending process and as preserved has a length of 45.7 mm and a height of 36.8 mm. The height from the ventral margin to the antorbital fenestra is 18.2 mm. The margin of the antorbital fenestra is thin. The fenestra was longer than high, and ovate in outline. The contact with the nasal is preserved as a shallow, concave groove with a sharp, medial ridge (s.na, Figures 3a-b). In lateral view this groove slopes anteroventrally.

In ventral view the anterior portion of the maxillary fragment is mediolaterally crushed. Four complete and part of a fifth alveoli are preserved. The third alveolus (from the front) preserves an unerupted tooth, but no further details can be made out. Interdental plates are present, but unfused (Figure 3c). Medially there is a transverse ridge above the tooth row for articulation with the palate and forms a broad shelf bordering the antorbital fenestra (sh, Figure 2.3b). There is a marked foramen (corresponding to the pneumatic accessory cavity of Small, 2002) at the anteroventral corner of the antorbital fenestra, which is visible medially and dorsally. The anterior portion of the maxillary body is concave and a small ridge marks about where the upper border of the antorbital fenestra would be located. Dorsal to this is another smooth concave area.

The second specimen (UCMP 195194) is also from the right side and therefore from a different individual (Figure 3d-e). The anterolateral surface below the antorbital fossa is slightly rugose. The ‘pneumatic accessory cavity’ (Small, 2002) is visible in medial view and has possibly been enlarged by preparation. Anteriorly the nasal articulation is preserved and similar to the first specimen. Anterior to this is a thin rim of bone that represents the posteroventral

311 margin of the external naris. Thus the maxilla enters the naris, differing from the condition in
312 *Aetosauroides scagliai* (PVL 2073), where a thin contact of the premaxilla and the nasal exclude
313 the maxilla from the margin of the external naris (Casimiquela, 1961; Desojo & Ezcurra, 2011).
314 On the medial surface, a sharp raised ridge is preserved anteriorly that represents the palatal
315 process of the maxilla. Only three alveoli are preserved in this fragment.
316 Despite the strong possibility of these cranial elements belonging to *Calyptosuchus*
317 *wellesi*, they should not be used to score phylogenetic characters until they can be assigned with
318 absolute certainty.

319 **Postcrania**

320 ***Atlas/Axis***
321 There are many axes in the collection from the *Placerias* Quarry. Case (1922) describes the
322 ventral surface of the axis in *Desmatosuchus spurensis* as flat, and most of the specimens in the
323 collection possess flat ventral surfaces. However, UCMP 139803 (from CF1) has a distinct
324 ventral keel (Figure 4a) and therefore mostly likely is referable to *Calyptosuchus wellesi* which
325 has keeled cervical vertebrae (e.g., UCMP 27225) rather than *Desmatosuchus spurensis* which
326 has cervicals with a smooth ventral surface (e.g., UMMP 7476; MNA V9300). The upper portion
327 of the neural arch, including the zygapophyses, is broken (Figures 4b-d). The atlantal neural
328 arches are also broken. The centrum of the axis has distinct concave sides that are overhung by a
329 thickened ridge, which bears the diapophyses (Figure 4d). The parapophyses are situated
330 anteroventrolaterally on the centrum and are connected ventrally by a thickened crescentic ridge
331 that forms the anterior portion of the atlas intercentrum (Figure 4a). The suture between the atlas
332 intercentrum and the axis centrum is visible in ventral view.

The parapophyseal facets are round and directed ventrolaterally and slightly posterior. The odontoid process is attached (Figures 4a-b, d-e); its sutures with the centrum are still visible so the fusion is not complete. The dorsal surface of the odontoid process forms a slightly concave trough that opens posteriorly into the neural canal (Figure 4e). The canal is large, about one half the diameter of the posterior articular face of the centrum. In posterior view, the articular face of the centrum has a flat (horizontal) dorsal margin. The face is concave with well-developed rims. The length of the atlas/axis including the odontoid process is 48.7 mm. The axis centrum has a width of 30.6 mm and a height of 25.4 mm.

Postaxial cervical vertebrae

Numerous vertebrae were recovered in grid square CF1, where the atlas/axis (UCMP 139803) was recovered, including several cervical vertebrae. These centra possess cervical keels and therefore cannot be referred to *Desmatosuchus* (Long & Murry, 1995) and are assigned to *Calyptosuchus*. The presence of ventral keels on the cervical centra of *Calyptosuchus* is verified by specimen UCMP 27225. Long & Murry (1995:fig. 74) figured what presumably they thought to represent a cervical series of *Calyptosuchus*, but unfortunately did not provide explicit specimen numbers to identify the specimen further and it could not be located for the current study.

The cervical vertebrae of *Calyptosuchus* are amphicoelous, the anterior face being anteriorly concave and the posterior face nearly flat. Both faces are oval and taller than wide. On the anterior cervicals (e.g., UCMP 139793, 139794) the small, subrounded parapophysis is situated at the base of the centrum (Figures 4f-i). On more posterior centra (e.g., UCMP 139813) the parapophysis is located closer to the top of the centrum, below the neurocentral suture (Figures 4j-m). Anterior cervicals are also anteroposteriorly shorter than the posterior cervicals

(Figures 4h, k). The ventral keel is well-developed and in some specimens (e.g., UCMP 78714) the keel is expanded posteriorly into a small tab (Figures 4n, o). UCMP 78714 also preserves a portion of the neural arch. Although crushed and distorted it shows that the zygapophyses were elongate (Figure 4p). Prezygadiapophyseal and postzygadiapophyseal laminae (*sensu* Wilson, 1999) are present.

Trunk vertebrae

The trunk vertebrae of *Calyptosuchus* are more difficult to identify than the cervical vertebrae from the mixed collection of material from the *Placerias* Quarry; however, there are vertebrae with more elongate neural spines that also lack typical accessory articulations (hyposphenes-hypantra) on the neural arch. This readily distinguishes them from the trunk vertebrae of *Desmatosuchus spurensis* which possess much shorter (dorsoventrally) neural spines as well as hyposphenes and hypantra (Parker, 2008b; Stefanic, 2017). The trunk centra of *Calyptosuchus* lack the lateral fossae present in *Aetosauroides scagliai* (Desojo & Ezcurra, 2011). There are also posterior trunk vertebrae preserved in the holotype (UMMP 13950; Case, 1932).

UCMP 139694 is most likely the 10th presacral (first trunk) vertebra as it is transitional in the position of the parapophysis between the cervical and trunk series (Figures 5a-b). The parapophysis is situated on the anterodorsal surface of the centrum and confluent with the transverse process, connected by a well-developed anterior centrodiapophyseal lamina (acdl; *sensu* Wilson, 1999). In *Desmatosuchus spurensis* this specific placement of the parapopohysis occurs in the 10th presacral position and in the following vertebra (11th presacral) the parapophysis moves onto the transverse process (Case, 1922; Parker, 2008b). The neural arch of UCMP 139694 also bears a posterior centrodiapophyseal lamina (pcdl) but it is not as well developed as the anterior centrodiapophyseal lamina (acdl). The joining of these two laminae

379 forms a ventrolaterally opening shallow triangular fossa situated ventral to the transverse
380 process. A postzygadiapophyseal lamina (podl; Wilson, 1999) is present as a well-developed thin
381 ridge of bone connecting the transverse process and the postzygapophysis. The centrum is
382 spool-shaped, amphicoelous, ventrally smooth, and measures 37.9 mm in length (Figure 5b). The
383 centrum also has a height of 31.8 mm and a width of 31.6 mm.
384 UCMP 139796 from CF1 (Figures 5c-h) has the typical amphicoelous, spool-shape found
385 in aetosaurs and represents a mid-trunk vertebra. The centrum measures 43.4 mm in length, with
386 a height of 35.4 mm and a width of 32.4 mm; thus the lengths of the centra increase along the
387 trunk portion of the vertebral column similar to *Desmatosuchus spurensis* (Parker, 2008b). The
388 articular faces of the centrum are nearly flat, with expanded rims (Figures 5c-d). The neural arch
389 is taller than the centrum articular faces and the oval neural canal is large (19.4 mm high) (Figure
390 5e). In right lateral view the transverse process is mostly broken away (Figure 5d), but a thick
391 strut originates on the posterolateral corner of the neural arch and terminates on the ventral
392 surface of what is left of the transverse process. This strut represents the posterior
393 centrodiapophseal lamina (pcdl). A postzygadiapophyseal lamina (podl) forms a shelf from the
394 posterior edge of the transverse process to the right postzygapophysis. A shallow
395 postzygapophyseal centrodiapophyseal fossa (*sensu* Wilson et al., 2011) opens posterolaterally,
396 formed by the junction of these two laminae (Figure 5d). Although the posterior portion of the
397 neural arch is broken it is clear that there is no deep hyposphene between the postzygapophyses
398 as in *Desmatosuchus* (MNA V9300). The postzygapophyses are not steeply inclined, instead
399 projecting at about 30 degrees above horizontal. The postzygapophyses project well posterior to
400 the posterior face of the centrum (Figure 5f). Anteriorly on the neural arch there is a deep round
401 fossa between the prezygapophyses and the neural spine, the spinoprezygapophyseal fossa (sprf,

Wilson et al., 2011; Figure 5d). The neural spine is not anteroposteriorly elongate measuring only about 27mm at the base and the spinal laminae are present but weakly developed.

Another trunk vertebra from CF1 (UCMP 139702) preserves a few more details. In front of the anterior fossa (sprf) described for UCMP 139796, the prezygapophyses meet to form a broad shelf or ventral bar (Figure 5g) as in *Stagonolepis robertsoni* (Walker, 1961:fig. 7j). There is no hypantrum. The right transverse process is nearly complete. It is broad, about 26.7 mm in width, compared to the centrum, which has a width of 25.7 mm. The upper surface of the transverse process is flat and the ventral surface thickened with the strut described for UCMP 139796, which continues onto the base of the neural arch. The parapophysis is positioned 29.3 mm laterally from the origin of the transverse process. The distal end of the transverse process, the diapophysis, is not preserved but even incomplete the process has a length of 44.4 mm. The zygapophyses are inclined at close to 45 degrees to the horizontal. The centrum length is 39.9 mm long and 28.3 mm high.

A third trunk vertebra from CF1 (UCMP 139795) preserves the postzygapophyseal region extremely well. As with the other trunk vertebrae there are no accessory processes (hyposphene). Instead at the base of the medial union of the postzygapophyses there is a small posteriorly pointed projection that would rest on top of the ventral bar formed by the joined prezygapophyses of the subsequent vertebra. This pointed projection also occurs in *Scutarx deltatylus* (PEFO 34045). The ventral bar and posterior projection in the trunk vertebrae is also shared with some phytosaurians (e.g., *Smilosuchus*, TMM 43685-206).

Two other well preserved trunk vertebrae (Figure 6a-d) referable to *Calyptosuchus wellesi* are from UMMP 7470, which includes a partial sacrum and the two trunk vertebrae, as well as two paramedian osteoderms. The best preserved vertebra is a nearly complete anterior

mid-trunk vertebra (Case, 1932: figs. 2-4). The centrum is laterally compressed and ventrally concave because of the flaring articular rims. It has a length of 48.7 mm, and width of 42.3 mm, and a height of 42.8 mm. The neural arch and spine are tall, twice the height of the centrum at 78.8 mm, with 55.2 mm for the neural spine height. The neural spine is mediolaterally thin, expanded anteroposteriorly (34.2 mm long) and terminates with a pronounced lateral expansion (spine table). The postzygapophyses extend posteriorly past the posterior articular face of the centrum and are oriented at 45 degrees above horizontal. The prezygapophyses form a flat plate almost indistinguishable from the transverse processes (Figures 6a, c). The transverse processes are broad with a flat dorsal surface, and nearly twice the width of the centrum (82.3 mm). The processes are of the typical aetosaurian arrangement with both rib articulations situated on the transverse processes (Figures 6a, c). Transverse processes and postzygapophyses are connected by a thin sharp postzygapohyseal lamina (podl), which forms the deep spinopostzygapophyseal fossa (spof) just anterior to the postzygapophyses (Figures 6b, d).

Long & Murry (1995:fig. 75a) considered the transverse processes of the dorsal series extremely elongate throughout the entire column. However, they figured posterior trunk vertebrae of UMMP 13950 as an example, which have the ribs fused to the transverse processes, giving the appearance of greatly elongate processes (as noted by Case, 1932). This fusion of transverse process and rib is also found in *Scutarx deltatylus* (PEFO 34045) as well as *Desmatosuchus spurensis* (MNA V9300; Parker, 2008b). However, the processes in *Calyptosuchus wellesi* differ from those two taxa in that they are flat dorsoventrally and anteroposteriorly broad (Case, 1932: pl. 4, fig. 1). The centra of the posterior most trunk vertebrae are anteroposteriorly short in comparison with those of the mid-trunk vertebrae, with large flaring articular rims.

Sacral Vertebrae

The best preserved sacral vertebrae are in the holotype (UMMP 13950) as well as in the partial pelvis (UMMP 7470) and were well-described and figured by Case (1922, 1929, 1932). There are two vertebrae in the series, which differ from those of desmatosuchine aetosaurs in that they are not fused to each other (Parker, 2008b; Griffin et al., 2017) although Case (1932) noted that the zygapophyses between the two sacral vertebrae were reduced in size. The articular faces of the centra are round. The neural arches are robust and bear the heavy, expanded sacral ribs, and the neural spines are also robust and taller than the centra. The neural spines possess expanded apices or 'spine tables.'

An isolated specimen (UCMP 139785) from grid block C78W in the *Placerias* Quarry is most likely referable to *C. wellesi* as it does not show fusion to the other sacral as do others in the collection (e.g., UCMP 139787). The vertebra is very massive with the proximal portions of the sacral ribs firmly sutured to the neural arch (Figures 7a-d). The upper surface of the ribs is swept posteriorly (Figure 7b). The centrum faces are roughly 'heart-shaped' and the ventral surface lacks a keel (Figures 7c, d). The neural spine is broken off, but was obviously robust (thick and elongate) as in UMMP 7470. There is a distinct spinoprezygapophyseal fossa (Figure 7a) under the prezygapophyses.

Caudal Vertebrae

The *Placerias* Quarry collection contains dozens of aetosaur caudal centra with broken neural arches; however, at this time it is not possible the assign these elements to particular taxa. However, the first seventeen vertebrae of the caudal series of *Calyptosuchus wellesi* are well-preserved in articulation in the holotype (UCMP 13950) and were described by Case (1932). The most notable feature of the caudal series of UCMP 13950 is the height of the neural spines, which is greater than the height of the centrum. This differs from aetosaurs such as

Desmatosuchus spurensis (MNA V9300) and *Paratypothorax* (PEFO 3004) where the height of the neural spine is equal to or less than the height of the centrum. It is similar to the condition in *Aetosauroides scagliai* (PVL 2073) and *Stagonolepis robertsoni* (Walker, 1961: fig. 10).

Long & Murry (1995:83) state that the ventral grooves of the caudal centra in *Calyptosuchus wellesi* are narrower than those of *Desmatosuchus spurensis* and "bear faint, longitudinal ridges". However, they provide no basis for their taxonomic referrals nor any specimen numbers, so this claim cannot be verified. The caudal ribs or transverse processes of paratypothoracins originate close to the base of the centrum (e.g., PEFO 3004). No centra with low caudal ribs are currently known from the *Placerias* Quarry, and thus all of the preserved centra presumably belong to *Calyptosuchus wellesi* or *Desmatosuchus spurensis* although they cannot be distinguished between those taxa.

Scapulocoracoid

No bones of the pectoral girdle are preserved in the holotype of *Calyptosuchus wellesi* (UMMP 13950). Long & Murry (1995) assign several scapulocoracoids (UCMP 78698, UCMP 32196, UCMP 27976) from the *Placerias* Quarry to *Calyptosuchus wellesi*; however these elements were recovered from areas CD and CE which provided many osteoderms of *Desmatosuchus spurensis* and none referable to *Calyptosuchus wellesi* (Figure 1). Furthermore, coracoids assigned to *Calyptosuchus wellesi* (UCMP 32196, UCMP 27976; Long & Murry, 1995) from C8 and C75W, also from areas that provided predominantly material of *Desmatosuchus* (Figure 1). Thus, none of the *Placerias* Quarry material can be unambiguously assigned to *Calyptosuchus wellesi*. Differences between the coracoids of *Desmatosuchus smalli* (TTU P-9023) and *Stagonolepis robertsoni* (Walker, 1961) pertain to the development of the subglenoid buttress. Unfortunately this area is not preserved in any of the *Placerias* Quarry specimens.

Forelimb

As with the shoulder girdle, no forelimb elements are present in the holotype of *Calyptosuchus wellesi* (UCMP 13950). Moreover, Long & Murry (1995) did not assign any forelimb material to *Calyptosuchus wellesi*. The UCMP *Placerias* Quarry collection contains numerous aetosaur humeri but none can be clearly referred to *Calyptosuchus wellesi*. All with preserved distal ends have an ectepicondylar foramen rather than a groove, which is a synapomorphy of *Desmatosuchus spurensis* and *Longosuchus meadei* (Small, 1985). Long & Murry (1995) reported a foramen as present in *Typothorax coccinarum* (UCMP 34240) and this was verified by Martz (2002). In *Aetosauroides scagliai* (PVL 2073) and *Stagonolepis robertsoni* (Walker, 1961) there is an ectepicondylar groove rather than a foramen on the lateral side of the radial condyle. Bonaparte (1971), Small (1985), and Martz (2002) stated that *Neoaetosauroides engaeus* possesses a foramen rather than a groove in the holotype (PVL 3525). Thus, the predicted condition in *Calyptosuchus* is equivocal and the distal ends of humeri from the *Placerias* quarry cannot be assigned below the level of Aetosauria with any certainty.

Pelvic Girdle

Several pelvic girdles have been referred to *Calyptosuchus wellesi* including the holotype (UCMP 13950; Figure 8), a specimen from the Dockum Group of Texas (UMMP 7470), and elements from the *Placerias* Quarry (Case 1929, 1932; Long & Murry, 1995). The *Placerias* Quarry elements include a left ilium (UCMP 32422) and a corresponding left ischium (UCMP 32148), both from grid CF1 (Figure 9a-b), and figured by Long & Murry (1995:figs. 79-80). The collection from CF1 also contains a crushed, but complete right ilium (UCMP 25941) and a right ischium (UCMP 32153) (Figure 9c). These elements match the two figured by Long & Murry (1995) perfectly and all four elements probably belong to the same individual (Long & Murry, 1995). The difference in color between these elements in Figure 9 is a photographic lighting

519 artifact. Grid CF1 contains a fair amount of material referable to *Calyptosuchus*, mainly cervical
520 vertebrae, including some paramedian osteoderms, so referral of these pelvic elements to
521 *Calyptosuchus wellesi* is supported.
522 The problem with assigning isolated ilia from the quarry to specific taxa is that the
523 morphology of the ilium of *Desmatosuchus* is poorly understood. The holotype of
524 *Desmatosuchus spurensis* (UMMP 7476) preserves only a fragmentary left ilium that is missing
525 almost the entire posterior portion of the iliac blade. A referred specimen of *Desmatosuchus*
526 *spurensis* (MNA V9300) as well a specimen of *Desmatosuchus smalli* (TTU P-9172) preserve
527 nearly complete sacra; however, the anatomy of the ilia is difficult to interpret on these
528 specimens because they are highly distorted, in part because of the complete fusion of the sacral
529 ribs to the ilia (see Parker, 2008b). Long & Murry (1995:figs. 91-92) assigned an isolated right
530 ilium from Crosby County Texas (UMMP 7322) to *Desmatosuchus spurensis*. This specimen
531 possesses an acute angle between the anterior portion of the iliac blade and the anterior edge of
532 the iliac body as well as a triangular (in lateral view) posterior iliac blade. The holotype ilium
533 (UMMP 7476) as preserved is consistent with this although much of the anterior portion of the
534 iliac blade is damaged. If UMMP 7322 is indeed referable to *Desmatosuchus spurensis* UCMP
535 32422 differs from it mainly in that the posterior iliac blade is squared off and not pointed as in
536 UMMP 7322. This is the character Long & Murry (1995) used to assign ilia to *Calyptosuchus*
537 *wellesi* and this referral is followed here.

538 ***Ilium***
539 The ilia in *Calyptosuchus wellesi* have ventrally directed acetabula; however, to make the
540 following description easier to follow the element is described as if it is oriented vertically, thus
541 the iliac blade is dorsal and the acetabulum ventral and lateral. The preacetabular process of the

iliac blade in UCMP 25941 is short and does not extend far anterior of the pubic peduncle (Figures 9a-b). It is mediolaterally thick and triangular in lateral view with a ventrally curved tip and is 50 mm long. The postacetabular portion of the iliac blade extends well beyond the posterior edge of the pubic peduncle and is thickened very close to its proximal end. The entire iliac blade is 180 mm long, and 52 mm high above the acetabulum. The dorsal surface is highly rugose, marked with scars for the attachment of the *M. iliotibialis* 1-3 (Schachner, Manning & Dodson, 2011). The acetabular area is roughly diamond-shaped in lateral view and delineated dorsally by a well-developed supraacetabular rim (Figure 9a). The main iliac body is slightly concave dorsal to the acetabulum, lacking the deep recess found between the supraacetabular rim and the posterior portion of the iliac blade in *Scutarx deltatylus*.

The pubic and iliac peduncles are thickened anteriorly and posteriorly respectively, and both are comma-shaped in ventral views. The two peduncles meet at a ventrally directed point ventral to the iliac portion of the acetabulum. Medially, there are scars for the two sacral ribs, which cover not only the iliac neck but also a large portion of the ilium ventral to the iliac blade and medial to the acetabulum (Figure 9b). This is a result of the ventrally directed acetabula as in *Aetosauroides scagliai* (PVL 2073) and *Typothorax coccinarum* (PEFO 33967). The iliac blade thins dorsally from the sacral rib scars. Overall the ilium of *Calyptosuchus wellesi* is very similar to that of *Aetosaurides scagliai* (PVL 2073) and *Ebrachosaurus singularis* (Kuhn, 1936). It differs from *Neoaetosauroides engaeus* (PVL 3525) in having a much more robust anterior process of the iliac blade. It differs significantly from the ilium of *Typothorax coccinarum* (UCMP 122683) which has a taller, but anteroposteriorly shorter iliac blade, as well and a more gracile, and 'hooked' anterior process which does not extend anteriorly past the pubic peduncle (Long & Murry, 1995:figs. 106-107). The right ilium is well-preserved in the referred specimen

565 UMMP 7470 (Case, 1922: fig. 28b). It is nearly identical to UCMP 25941 with the thickened,
566 short, recurved anterior iliac blade. Both ilia are present in the holotype (UMMP 13950) but
567 both are incomplete, crushed, and presently badly broken (Figure 4.8; Case, 1932, pl. II). Note
568 that the photo of the pelvic girdle and vertebral column in Plate II in Case (1932) is reversed.

569 ***Ischium***

570 The left ischium (UCMP 32148) associated with the UCMP ilium described above is
571 nearly complete (Figure 9a). It is anteroposteriorly short, not much longer than tall, with a length
572 of 110 mm and a height of 97 mm. This differs from the ischia of *Aetosauroides scagliai* (PVL
573 2073), *Stagonolepis robertsoni* (Walker, 1961); and *Aetosaurus ferratus* (Schoch, 2007), where
574 the posterior process is more elongate. The pubic peduncle is comma-shaped in dorsal view and
575 contacts the corresponding peduncle of the ilium. The oval acetabular surface is deeply concave
576 and bordered posteriorly and ventrally by a strongly raised, curved rim. The main body of the
577 ischium is essentially a thickened 'rod' that curves posteriorly and dorsally. A mediolaterally
578 thin flange of bone extends ventrally for the entire length of the 'rod' (Figure 9a). The ventral
579 margin is straight. The lateral surface of the thin flange is rugose presumably for attachment of
580 the third head of the *M. puboischiofemoralis externus* (Schachner, Manning & Dodson, 2011).
581 Medially there is an elongate suture for the opposing ischium. The anterior margin bears a
582 distinct notch. This notch is also present on the right ischium of UMMP 7470. The posterior
583 process of UMMP 7470 is more elongate than that of UCMP 32148, but still not as elongate as
584 in Walker's (1961) reconstruction of *Stagonolepis robertsoni*. The ischia are also present in
585 UMMP 13950 but are poorly preserved (Figure 8). Case (1932: pl. III) restores the ischium as
586 dorsoventrally deep and anteroposteriorly short, consistent with UCMP 32148.

Pubis

The best preserved pubis from the *Placerias* Quarry material is a left element (UCMP 32150) from grid CF2 (Figures 9d-g). It shares the same preservation, color and size with the ilium and ischium described above, but does not quite articulate. The pubic rod is slender and its distal end is broken away (Figures 9d-e). The concave acetabular surface is reduced compared to the area on the ischium and there is a groove just ventral to this surface. The articular surface for the ilium is comma-shaped in dorsal view (Figure 9f). The obturator flange is broken away (Figure 9g) so the number of in this element cannot be determined. Walker (1961) restored the pubis of *Stagonolepis robertsoni* with pubic foraminae and a pubis of *Scutarx deltatylus* (PEFO 31217) also has two openings. Only a single foramina is present in the pubis of *Desmatosuchus spurensis* (MNA V9300) and the number of foraminae is unknown in *Aetosaurus ferratus* (Schoch, 2007).

The proximal portion of the right pubis is present in UMMP 7470 (Case, 1922: fig. 28b). The posterior margin as preserved shows the anterior border of an obturator foramen but the element is not complete enough to determine if there was a second opening. The proximal head of UMMP 7470 bears a deep lateral groove that originates at the acetabular rim and extends parallel to the anterior margin of the pubis. The distal end of the element is broken away so that the extent of the groove cannot be determined. This groove is only weakly developed in UCMP 32150, which is also missing its distal end. UMMP 13950 preserves the distal end of the pubis, which expands into the broad pubic 'apron' typical for suchians (Case, 1932). Case (1932:pl. III) reconstructs the pubic as dorsoventrally shallow with the distal margin of the pubis at the same horizontal level as the ventral margin of the ischium. This differs greatly from the condition in *Desmatosuchus spurensis* (MNA V9300) where the pubis extends well below the level of the ischium, but is similar to the short pubes of *Typothorax coccinarum* (Long & Murry, 1995).

611 The distal end of the pubic rod extends slightly past the ventral margin of the pubic
612 apron, as is typical for aetosaurs. This end is slightly swollen as in *Stagonolepis robertsoni*
613 (Walker, 1961), but does not form the distinct knobby pubic boot found in *Desmatosuchus*
614 *spurensis* (MNA V9300).

615 ***Femur***
616 The best preserved femur that can be referred to *Calyptosuchus wellesi* is UCMP 25918, which is
617 a left side element from CF1 (Figures 10a-d; Long & Murry, 1995:figs. 81, 83). It is of similar
618 preservation and the right size to match the pelvic elements described above so it is very possible
619 that all of these elements belong to a single individual. Long & Murry (1995) describe it as
620 "more gracile" than femora from the quarry that they assign to *Desmatosuchus spurensis*.
621 Overall it is less sigmoidal than the femur of phytosaurs, as is characteristic of aetosaurs (Figures
622 10a-c). It has a total length of 329 mm. The proximal head is badly eroded (Figures 10a-b). The
623 fourth trochanter is a pronounced crescent-shaped ridge located about 120 mm ventral to the
624 proximal end (Figure 10a). The distal femoral condyles are well-preserved (Figure 10d). The
625 medial condyle has a posteromedial corner with an angle of 90 degrees and a rounded
626 anteromedial corner. The lateral condyle is larger than the lateral and anterolaterally bears a
627 distinct crista tibiofibularis. The angle between the crista tibiofibularis and the lateral condyle is
628 obtuse. The posterolateral corner of the lateral condyle is rounded and expanded posteriorly.

629 ***Tibia***
630 UCMP 25887 from C64M occurs within a cluster of osteoderms of *Calyptosuchus*
631 *wellesi*, but material referable to *Desmatosuchus spurensis* material occurs in that grid as well.
632 Nonetheless, this left tibia is much more gracile than others found in the quarry (e.g., UCMP
633 25877), which probably belong to *Desmatosuchus* (Figure 11; Long & Murry, 1995). UCMP

25887 (Figure 12a-d) has a length of 186 mm, shorter than the femur as is typical for aetosaurs. The proximal head is oval in proximal view with a width of 73 mm, a length of 52 mm and is divided into two distinct sections by a nearly central ridge. The medial surface has slightly more area than the lateral surface and it concave, whereas the lateral surface is convex. A cnemial crest is absent (Nesbitt, 2011), and there is a distinct 'lip' posteriorly on the lateral portion of the head. The posterior portion of the distal end possesses a dorsoventrally oriented groove (Nesbitt, 2011: char. 337-1) for articulation with the astragalus. There is some damage to the medial condyle of the distal end in UCMP 25887. Overall there are few noticeable differences in the distal ends of UCMP 25887 and UCMP 25877 other than size. However, the proximal end in UCMP 25877 is much more expanded medially and has a distinct dorsal notch on the dorsolateral surface. There are two other gracile tibiae in the *Placerias* Quarry collection; UCMP 25896 (Figure 12e-g) is a left tibia from grid CH1, and UCMP 25894 is a left tibia from grid CH2 that was figured by Long & Murry (1995:fig. 84).

Fibula

UCMP 25802 from grid C67M is gracile compared to other fibulae in the *Placerias* Quarry collection and, as preserved, matches much of the material of *Calyptosuchus wellesi*. Long & Murry (1995) also assigned this element to *Calyptosuchus wellesi*. The specimen represents the proximal end of a left fibula. The iliofibularis trochanter is broken off. There is a small tubercle on the medial side of the shaft. Long & Murry (1995:84) state that "the diagonal ridge, so prominently exhibited along the medial fibular shaft of *Desmatosuchus* [*spurensis*], may not have been present in [*Calyptosuchus*] *wellesi*." However, UCMP 25802 is not complete enough to evaluate this claim.

Astragalus

There are many astragali in the *Placerias* Quarry collection, but none fits the gracile tibiae in the collection that probably represent *Calyptosuchus wellesi*. Long & Murry (1995) figured and assigned a right astragalus from grid CF2 to *Calyptosuchus wellesi* (UCMP 34485); however, this specimen is currently on loan to another researcher and I was unable to examine it. Nonetheless, Long & Murry (1995) stated that they were unable to differentiate between the astragali of *Desmatosuchus* and *Calyptosuchus* and thus it is unclear how this assignment was originally made. Neither the type nor referred specimens of *Calyptosuchus wellesi* preserve the astragalus.

Calcaneum

As with the astragali there are lots of aetosaur calcanea in the collections as well, but as the calcaneum of *Desmatosuchus* is unknown, they cannot be differentiated. Long and Murry (1995:fig. 82) figured a left calcaneum (UCMP 34481) from CG1 as pertaining to *Calyptosuchus wellesi*. It is not clear what characters they used to make this assignment. UCMP 34481 is very similar to the calcaneum of *Aetosauroides scagliai* (PVL 2073) with a dorsoventrally flattened, mediolaterally expanded posterior tuber, and a deep concavity on the ventral surface of the anterior portion of the tuber. This deep concavity is sharply rimmed and also prominent in *Typothorax coccinarum* (AMNH FR 2713).

Osteoderms – The holotype of *Calyptosuchus wellesi* (UMMP 13950) preserves an articulated set of osteoderms starting with the posterior dorsal trunk series and extending back through much of the tail (Figure 13). These include trunk, lateral, and appendicular osteoderms and, importantly, they are associated with a vertebral column to aid with placement of specific rows. A significant landmark is the neural spine pushed up through the dorsal carapace, which is that

of the first caudal vertebra (Case, 1929). Accordingly I have placed it between the first and second caudal paramedians where it pushed the first paramedian anteriorly and displaced the second paramedian posteriorly (Figures 13-14). UMMP 13950 was thoroughly described by Case (1932) and is not in need of a full redescription.

Referred specimens from the St. Johns, Arizona area (Blue Hills, *Placerias* Quarry) provide more details regarding the mid-dorsal region as well as the ventral trunk osteoderms. Cervical osteoderms are currently unknown for *Calyptosuchus wellesi*. The cervical lateral plates assigned by Long and Ballew (1985) to *Calyptosuchus wellesi* that were reportedly characteristic of the genus (Long and Murry, 1995) actually belong to a paratypothoracin aetosaur, most likely *Tecovasuchus* (Parker, 2005; Heckert et al, 2007).

Paramedian Osteoderms

Trunk Series

The holotype of *Calyptosuchus wellesi* (UMMP 13950) preserves the last four presacral paramedians of the right side and the last two of the left side as well as the two sets that would have been situated over the sacrum (Figures 13-14). The osteoderms bear strongly raised anterior bars with anterolateral projections, sigmoidal lateral and straight medial margins. The dorsal eminence is a broad, low pyramidal structure that contacts and slightly overhangs the posterior plate margin. The boss is slightly situated medially on the osteoderm surface. A strongly developed pattern of pits and elongate grooves and ridges radiates from the position of the eminence. This ornamentation strongly differs from that of *Stagonolepis robertsoni* (NHMUK 4789a) and *Stagonolepis olenkae* (ZPAL AbIII 570/1) where the radiating grooves and ridges are more anastomosing. *C. wellesi* also lacks the elongate parallel grooves and ridges found in *Aetosauroides scagliai* (PFV 2073). Furthermore, the posteromedial corners of the paramedians

are flat and ornamented, lacking the distinct raised triangular boss of *Scutarx deltatylus* (PEFO 34616) or the triangular unornamented area of *Adamanasuchus eisenhardtae* (PEFO 34638). The lateral edge here is slightly indented for a short triangular process of the lateral osteoderm, but is not deeply "cut-off" as in typothoracines such as *Paratypothorax* sp. (PEFO 3004) or as in *Adamanasuchus eisenhardtae* (PEFO 34638).

Isolated osteoderms from the *Placerias* Quarry (Figures 15a-k) demonstrate that at least some of the dorsal trunk paramedians had a weakly developed ventral strut (e.g., UCMP 136744; Figures 15b, d, e), an anterolateral projection (e.g., UCMP 126846; Figure 15f), "scalloping" of the medial portion of the anterior bar (e.g., UCMP 136744, UCMP 126844, UCMP 126801; Figures 15 g-h, j), and a distinct anteromedial projection (UCMP 136744, UCMP 126844, MNA V2930; UCMP 126801; Figures 15g-j). Some of the osteoderms (e.g., UCMP 136744; Figure 15c-e) are strongly flexed ventrally. Osteoderms from smaller, presumably less mature, individuals have dorsal eminences in the form of elongate keels rather than blunt pyramidal bosses. This is similar to the condition in smaller sized taxa such as *Aetosaurus ferratus* (Schoch, 2007) and *Aetosauroides scagliai* (PVL 2073).

Closer to the end of the tail the paramedian osteoderms become longer than wide with strong pyramidal dorsal eminences (e.g, UCMP 126801; Figures 15j-k). Even more distally, the bosses become reduced and blunter, but the osteoderms thicken significantly and in some cases start to fuse to each other (e.g., UCMP 136744; Figures 16a-d). This is very similar to the condition in *Scutarx deltatylus* (PEFO 34045).

Lateral Osteoderms

The lateral osteoderms from the ninth dorsal trunk row (of 16 total) through the 16th caudal rows (of approximately 40 according to Schoch, 2007 for *Aetosaurus ferratus*) are present

and well-preserved in the holotype (UMMP 13950). Thus, the positions of isolated lateral osteoderms with matching anatomy can be placed with confidence. Aetosaurian lateral osteoderms are roughly square to rectangular with a pronounced dorsal eminence or boss (Heckert & Lucas, 2000). Typically the osteoderms are flexed to some degree, divided into two 'flanges' (dorsal and lateral or ventral) by the eminence (Long and Ballew, 1985; Parker, 2007). Importantly, all of the lateral osteoderms in UMMP 13950 have more rectangular dorsal flanges, however, lateral osteoderms with strongly triangular dorsal flanges are present in the referred material of *Calyptosuchus wellesi*. These osteoderms must be from positions anterior to the ninth dorsal row. All of the lateral osteoderms have prominent anterior bars, pyramidal dorsal eminences, and a surface ornamentation of grooves and ridges radiating from the eminence.

The anteriormost lateral osteoderms of the trunk series are well represented in specimen UCMP 27225, a partial skeleton represented by osteoderms and vertebrae and collected by Charles Camp near St. Johns in 1926. They are quadrilateral in dorsal view with distinct dorsal and lateral flanges separately by an elongate keeled dorsal eminence with a pyramidal terminal end that projects just slightly beyond the posterior osteoderm margin (Figures 17a-d). The dorsal flange is distinctly triangular in dorsal view and is reduced in size compared to the lateral flange. The lateral flange appears to increase in width in more posteriorly situated osteoderms. The medial edge of the dorsal flange is strongly sigmoidal and the anterior bar is indented where the anterolateral projection of the adjacent paramedian osteoderm overlies it.

In the next positions, but still anterior to the ninth dorsal trunk row, the dorsal flanges retain their sigmoidal lateral edge, but become more quadrilateral in dorsal view (Figures 17e-f). The lateral flanges are very wide and rectangular. They are still significantly larger than the dorsal flange. The next form of lateral osteoderm occur in the 9^{th}-12^{th} dorsal trunk positions

based on comparison with the holotype (UMMP 13950) and are best represented in the *Placerias* Quarry material by left and right osteoderms (UCMP 136744; Figures 17g-j).

The dorsal eminence is larger and very hook-like. The dorsal flange is quadrilateral in dorsal view and maintains the strongly sigmoidal medial margin. The lateral flanges are still much wider than the dorsal flanges but are no longer rectangular. Instead they are strongly quadrilateral with a distinct mediolateral slant so that the anterior margin is much wider than the posterior margin. This forms a distinct anterolateral 'wing' that characterizes the osteoderms from this portion of the carapace. In posterior view the angle between the flanges is approaching 90 degrees, much more flexed than the preceding lateral osteoderms.

The sacral and anteriormost caudal lateral osteoderms are represented by a right (UCMP 78751) and two left (UCMP 136744, MNA V3744) osteoderms (Figures 17k-n). These osteoderms are reduced in overall width, the lateral flange remains larger than the dorsal flange, but only slightly and anterolateral 'wing' is no longer prominent. The dorsal eminence is still strong, but not as hook-like as the previous osteoderms.

At about the third caudal row the dorsal eminence of the lateral osteoderms becomes very rectangular, and the dorsal and lateral flanges are more equal in size. Overall the osteoderms are lengthening anteroposteriorly, corresponding with the increasing length of the caudal vertebrae. These positions are represented by two right osteoderms, UCMP 27048 from the Blue Hills area of St. Johns, and UCMP 136744 from the *Placerias* Quarry (Figures 17o-q). The dorsal eminence is taller but blunter, not hook-like. The angle of flexion between the dorsal and lateral flanges is a strong 90 degrees in these osteoderms.

Ventral Osteoderms

Ventral trunk osteoderms are best represented in UCMP 27225 (Figure 18). They are square to broadly rectangular with a strong, but narrow anterior bar. The external surface ornamentation consists of a fine pattern of grooves and ridges radiating from a central, unraised area on the osteoderm.

Appendicular Osteoderms

Numerous appendicular osteoderms are preserved close to life position in the holotype (UMMP 13950: Figure 13). They consist of small rounded to oval osteoderms with faint surface pitting. They would have been situated manly along the upper portion of the individual limbs.

DISCUSSION

Calyptosuchus wellesi has been considered one of the better known aetosaurian taxa from the American Southwest. However, it was never completely described and, whereas our knowledge of many of the other southwestern taxa (e.g., *Desmatosuchus spurensis*, *Typothorax coccinarum*) has increased because of the recovery of new specimens, hardly any new material of *Calyptosuchus* has been discovered. Several partial skeletons mentioned by Parker & Irmis (2005) and Parker & Martz (2011) including cranial material, are instead referable to a new taxon *Scutarx deltatylus* Parker (2016a, b). Thus the best sources of character information on *Calyptosuchus wellesi* are the numerous osteoderms and endoskeletal elements from the *Placerias* Quarry. Unfortunately past assignments (e.g., Long & Murry, 1995) of this material to various taxa are problematic because no methodology for assigning material is discussed. I have attempted here to use the only source of data remaining from the original excavations, the grid numbers, to look for clues regarding possible association of endoskeletal elements with the diagnostic osteoderms, however, in many cases the data are unequivocal because of the mixture of osteoderms of more than one aetosaurian taxon and because the original workers did not collect the majority of the osteoderms from the east side of the quarry.

In recent years the east side of the quarry, as well as the nearby Downs Quarry (Jacobs & Murry, 1980), has been reopened by crews from the North Carolina State Museum and Appalachian State University. Results are still forthcoming, but hopefully these sites will prove rich in associated remains of *Calyptosuchus* and help further clarify the osteology of this taxon.

Presently *Calyptosuchus wellesi* lacks discrete autapomorphies, but can be diagnosed using a unique combination of characters including the presence of a ventral strut and large posteriorly situated dorsal eminences as in typothoracisins; a strongly raised anterior bar with a 'scalloped' anterior edge and distinct anteromedial and anterolateral projections as in non-desmatosuchin desmatosuchians and in aetosaurines; a radial pattern of grooves and ridges on the dorsal paramedian osteoderms as in non-desmatosuchin aetosaurs; the lack of a raised triangular boss in the posteromedial corner of the paramedian osteoderms as in *Scutarx deltatylus*; and the lack of a smooth triangular patch of bone in the posteromedial corner of the paramedian osteoderms as in *Adamanasuchus eisenhardtae* and *Stagonolepis robertsoni*.

CONCLUSIONS

Use of quarry data from the collection of *Calyptosuchus* material from the *Placerias* Quarry of Arizona allows for hypotheses to be made regarding the assignment of non-osteoderm material to this taxon. Furthermore a previously undescribed specimen (UCMP 27225) allows for the referral of the first unambiguous skull material (dentary) to be assigned to this taxon. Although it presently has no discrete autapomorphies, *C. wellesi* can be diagnosed by a unique combination of characters. Many previous referrals of material to *Calyptosuchus* has been demonstrated to belong to other taxa instead including *Adamanasuchus eisenhardtae*, *Scutarx deltatylus*, and an undescribed Adamanian paratypothoracisin. Despite this *Calyptosuchus* is one of the most common aetosaurians in the western United States and an index taxon of the early Adamanian biozone.

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1043 **Zittel KAv. 1887–1890.** *Handbuch der Palaeontologie. 1. Abteilung: Paläozoologie, Band 3,*
1044 *Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. Druck and Verlag von R. Oldenbourg,
1045 Münich and Leipzig, 900 pp.
1046

1047

1048 Figure 1: Recovered elements of *Calyptosuchus wellesi* and *Desmatosuchus spurensis* plotted on
1049 the map of the *Placerias* Quarry. Map redrawn and modified from Camp and Welles (1956).
1050

1051 Figure 2: Partial right dentary of *Calyptosuchus wellesi* (UCMP 27225) in lateral (A), medial
1052 (B), and occlusal (C) views. Scale bar = 1cm. Arrows indicate anterior direction. Abbreviations:
1053 ds, dentary symphysis; ed, edentulous area; id, dentary infexion; mg, Meckelian groove.
1054
1055 Figure 3: Maxillary fragments possibly referable to *Calyptosuchus wellesi*. A-C, right maxilla
1056 (UCMP 195193) in lateral (A), medial (B), and occlusal (C) views. D-F, right maxilla (UCMP
1057 195194) in lateral (D), medial €, and occlusal (F) views. Scale bar equals 1 cm. Arrows indicate
1058 anterior direction. Abbreviations: al, alveolus; aof, antorbital fenestra; aofs, antorbital fossa; idp,
1059 interdental plate; na, nasal; pac, pneumatic accessory cavity; pp, palatal process of the maxilla;
1060 s.x, suture with indicated element; sh, maxillary shelf; t, tooth.
1061
1062 Figure 4: Axial and post-axial cervical vertebrae of *Calyptosuchus wellesi*. A-E, Axis (UCMP
1063 139803) in ventral (A), lateral (B), posterior (C), anterior (D), and dorsal (E) views; F, anterior
1064 cervical (UCMP 139793) in anterior view; G, anterior cervical (UCMP 139794) in posterior
1065 view; H-I, anterior cervical (UCMP 139793) in lateral (H) and ventral (I) views; J-M, posterior
1066 cervical (UCMP 139813) in anterior (J), lateral (K), ventral (L), and dorsal (M) views; N-P, mid-
1067 cervical (UCMP 78714) in lateral (N), ventral (O), and anterior (P) views. Scale bar equals 1
1068 cm. Abbreviations: diap, diapophysis; k, keel; nc, neural canal; ncs, neurocentral suture; odp,
1069 odontoid process; parp, parapophysis; prez, prezygapophyses; tb, ventral tab.
1070

Figure 5: Trunk vertebrae of *Calyptosuchus wellesi*. A-B, UCMP 139694, 10th presacral vertebra in anterior (A) and ventral (B) views; C-F, UCMP 139796, mid-trunk vertebra in left lateral (C), right lateral (D), posterior (E), and dorsal (F) views; G-H, UCMP 139702, posterior trunk vertebra in anterior (G) and lateral (H) views. Scale bar equals 1 cm. Abbreviations: acdl, anterior centrodiapophyseal lamina; ns, neural spine; parp, parapophysis; pcdl, posterior centrodiapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygapophyseal lamina; posz, postzygapophysis; prcdf, prezygapophyseal centrodiapophyseal fossa; prez, prezygapophysis; spof, spinopostzygapophseal fossa; sprf, spinoprezygapophyseal fossa; tp, transverse process; vb, ventral bar.

Figure 6: Mid-trunk vertebrae of *Calyptosuchus wellesi* (UMMP 7470). A-B, vertebra in anterior (A) and posterior (B) views. C-D, vertebra in anterior (C) and posterior (D) views. Scale bar equals 1 cm. Abbreviations: nst, neural spine table; parp, parapophysis; prdl, prezygapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygapophyseal lamina; posz, postzygapophysis; prcdf, prezygapophyseal centrodiapophyseal fossa; prez, prezygapophysis; proj, posterior projection; spof, spinopostzygapophseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina; vb, ventral bar.

Figure 7: A-D, Sacral vertebra of *Calyptosuchus wellesi* (UCMP 139785) in anterior (A), lateral (B), posterior (C), and ventral (D) views. Scale bar equals 1 cm. Abbreviations: posz, postzygapophysis; prez, prezygapophysis; proj, posterior projection; spof, spinopostzygapophseal fossa; sprf, spinoprezygapophyseal fossa; sr, sacral rib; vb, ventral bar.

Figure 8: Portion of the sacrum and vertebral column of the holotype specimen of *Calyptosuchus wellesi* (UMMP 13950) in ventral view. Abbreviations: ac, acetabulum; cdv; anterior caudal

1096 vertebra; dsv, posterior trunk vertebra; isc, left ischium; poab, postacetabular blade of the left
1097 ilium; prab, preacetabular blade of the left ilium; pu, left pubis.
1098
1099 Figure 9: Pelvic elements of *Calyptosuchus wellesi*, possibly from a single individual. A, left
1100 ilium (UCMP 25941) and ischium (UCMP 32148) in lateral view (see text about anatomic
1101 directions for the pelvic elements); B, left ilium (UCMP 25941) in medial view; C, right ilium
1102 (UCMP 25941) and ischium (UCMP 32153) in lateral view; D-G, left pubis (UCMP 32150) in
1103 lateral (D), medial (E), dorsal (F), and posterior (G) views. Scale bar equals 1 cm. Abbreviations:
1104 a.x, articular surface with specified element; ac, acetabulum; il, ilium; ip, ischiadic peduncle;
1105 poab, postacetabular blade; pp, public peduncle; prab, preacetabular blade; sac, supraacetabular
1106 crest; sr, sacral rib.
1107
1108 Figure 10: A-D, left femur of *Calyptosuchus wellesi* (UCMP 25918) in posteromedial (A);
1109 medial (B), lateral (C), and distal (D) views. Scale bar equals 1 cm. Abbreviations: ct, crista
1110 tibiofibularis; ft, fourth trochanter; gt, greater trochanter; lc, lateral condyle; mc, medial condyle.
1111
1112 Figure 11: Aetosaurian tibiae from the *Placerias* Quarry. A-C, *Desmatosuchus spurensis* left
1113 tibia (UCMP 25877) in proximal (A), posterior (B), and distal (C) views. D-F. *Calyptosuchus*
1114 *wellesi* left tibia (UCMP 25887) in proximal (D), posterior (E), and distal (F) views. Scale bar
1115 equals 1 cm.
1116
1117 Figure 12: Tibiae of *Calyptosuchus wellesi*. A-D, UCMP 25887, left tibia in posterior (A),
1118 medial (B), proximal (C), and distal (D). E-G, UCMP 25896, proximal end of left tibia in
1119 posterior (E), anterior (F), and proximal (G) views. Scale bar equals 1 cm. Arrows indicate
1120 anterior direction.
1121

Figure 13: Holotype specimen of *Calyptosuchus wellesi* (UMMP 13950) showing assigned positions of osteoderms, pelvis, and vertebral column. Modified from Case, 1932. Abbreviations: d, trunk position; sc, sacral position; cd, caudal position.

Figure 14: Close-ups of the carapace of the holotype of *Calytosuchus wellesi* (UMMP 13950) showing details of the paramedian osteoderms. Abbreviations: d, dorsal trunk row; sc, sacral row; cd, caudal row. Scale bars equal 10 cm.

Figure 15: Paramedian osteoderms of *Calyptosuchus wellesi*. A-B, UCMP 136744, left anterior dorsal trunk osteoderm in dorsal (A) and ventral (B) views; C-E, UCMP 136744, right posterior dorsal trunk osteoderm in dorsal (C), ventral (D), and anterior (E) views; F, UCMP 126846, left dorsal trunk osteoderm in dorsal view; G, UCMP 136744, left dorsal mid-trunk osteoderm in dorsal view; H, UCMP 126844, left dorsal mid-trunk osteoderm in dorsal view; I, MNA V2930, left posterior dorsal trunk osteoderm in dorsal view; J-K, left posterior mid-caudal osteoderm in dorsal (J) and posterior (K) views. Scale bar equals 1 cm. Abbreviations: ab, anterior bar; alp, anterolateral process; amp, anteromedial process; de, dorsal eminence; me, medial edge; sc, scalloped area of anterior bar; vs, ventral strut.

Figure 16: Distal caudal paramedian osteoderms of *Calyptosuchus wellesi* (UCMP 136744). A-B, Two semi-articulated sets of fused paired osteoderms in dorsal (A) and ventral (B) views; C-D, isolated osteoderm in dorsal (C) and ventral (D) views. Scale bar equals 1 cm. Abbreviations: ab, anterior bar; mls, mid-line suture.

Figure 17: Lateral osteoderms of *Calyptosuchus wellesi*. A-D, anteriormost dorsal trunk lateral osteoderms (UCMP 27225) from the left (A, C-D) and right (B) sides in dorsal view; E-F, anterior dorsal trunk lateral osteoderms (UCMP 27225) from the left (E) and right (F) sides in dorsal view; G-J, posterior dorsal trunk lateral osteoderms (UCMP 136744) from the left (G-H) and right (I-J) sides in dorsal (G, I) and posterior (H, J) views; K-N, sacral and anteriormost

caudal lateral osteoderms (UCMP 78751, K-L; UCMP 136744, M; MNA V3744, N) of the right side in dorsal (K, M-N) and posterior (L) views; O-Q, anterior-mid-caudal lateral osteoderms (UCMP 27048, O; UCMP 136744, P-Q) of the right side in dorsal (O-P) and posterior (Q) views. Scale bar equals 1 cm. Abbreviations: df, dorsal flange, lf, lateral flange.

Figure 18: Ventral and appendicular osteoderms of *Calyptosuchus wellesi*. A, UCMP 175148, ventral osteoderm in ventral view; B, UCMP 136744, ventral osteoderm in ventral view; C-N, UCMP 27225, ventral osteoderms in ventral view; O, UCMP 136744, external surface of an appendicular osteoderm. Scale bar equals 1 cm.

Figure 1(on next page)

Figure 1: Recovered elements plotted on the map of the *Placerias* Quarry.

Recovered elements of *Calyptosuchus wellesi* and *Desmatosuchus spurensis* plotted on the map of the *Placerias* Quarry. Map modified from Camp and Welles (1956).

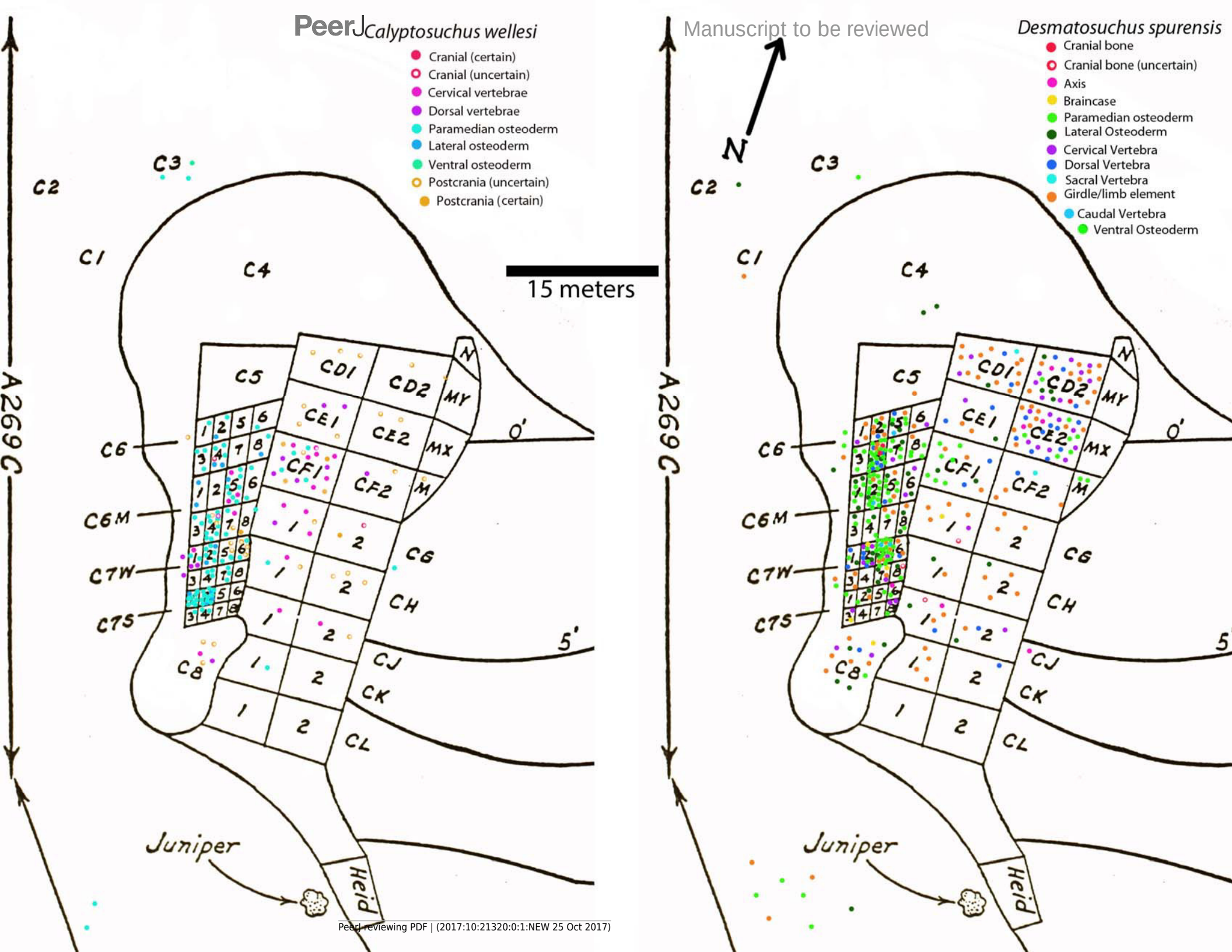

Calyptosuchus wellesi
Cranial (certain)
Cranial (uncertain)
Cervical vertebrae
Dorsal vertebrae
Paramedian osteoderm
Lateral osteoderm
Ventral osteoderm
Postcrania (uncertain)
Postcrania (certain)
15 meters
Desmatosuchus spurensis
Cranial bone
Cranial bone (uncertain)
Axis
Braincase
Paramedian osteoderm
Lateral Osteoderm
Cervical Vertebra
Dorsal Vertebra
Sacral Vertebra
Girdle/limb element
Caudal Vertebra
Ventral Osteoderm
N
A269C
C1
C2
C3
C4
C5
C6
C6M
C7W
C7S
C8
CD1
CD2
CE1
CE2
CF1
CF2
CH
CJ
CK
CL
MY
MX
M
O'
5'
Juniper
Heid

Figure 2

Partial right dentary of *Calyptosuchus wellesi*

Partial right dentary of *Calyptosuchus wellesi* (UCMP 27225) in lateral (A), medial (B), and occlusal (C) views. Scale bar = 1cm. Arrows indicate anterior direction. Abbreviations: ds, dentary symphysis; ed, edentulous area; id, dentary infexion; mg, Meckelian groove.

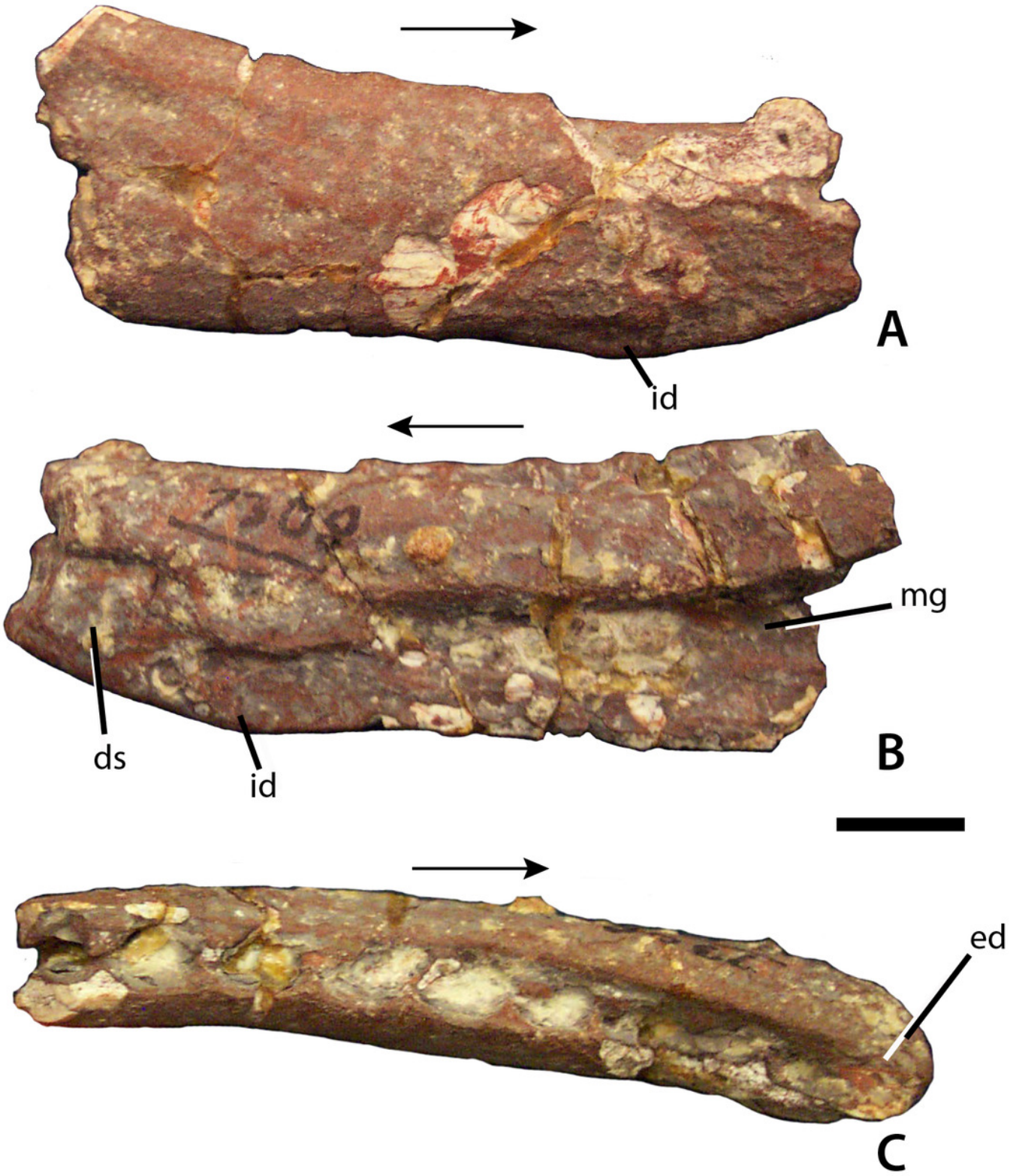

A
id
mg
ds
id
B
ed
C

Figure 3

Maxillary fragments possibly referable to *Calyptosuchus wellesi*.

Maxillary fragments possibly referable to *Calyptosuchus wellesi*. A-C, right maxilla (UCMP 195193) in lateral (A), medial (B), and occlusal (C) views. D-F, right maxilla (UCMP 195194) in lateral (D), medial (E), and occlusal (F) views. Scale bar equals 1 cm. Arrows indicate anterior direction. Abbreviations: al, alveolus; aof, antorbital fenestra; aofs, antorbital fossa; idp, interdental plate; na, nasal; pac, pneumatic accessory cavity; pp, palatal process of the maxilla; s.x, suture with indicated element; sh, maxillary shelf; t, tooth.

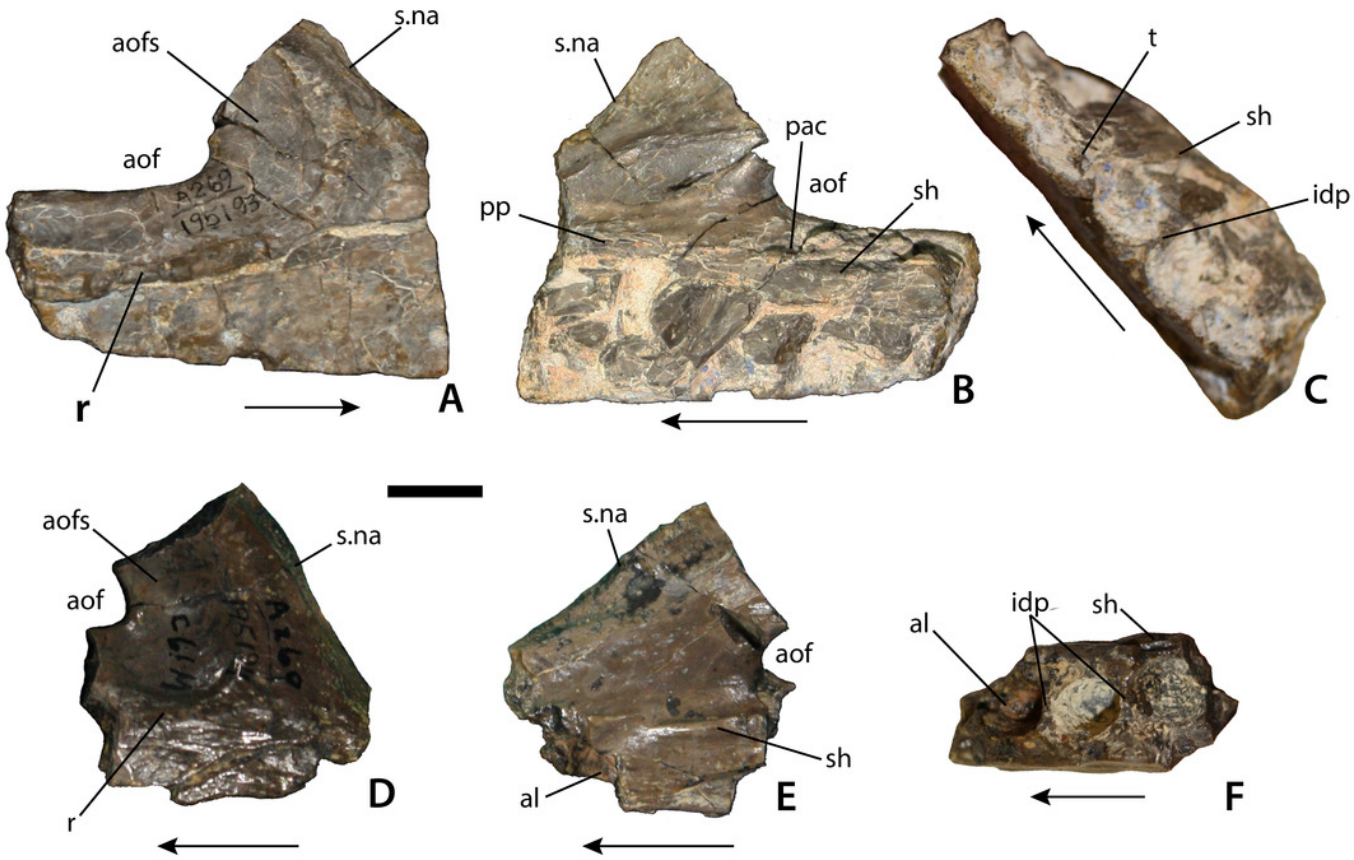


Figure 4

Axial and post-axial cervical vertebrae of *Calyptosuchus wellesi*.

Axial and post-axial cervical vertebrae of *Calyptosuchus wellesi*. A-E, Axis (UCMP 139803) in ventral (A), lateral (B), posterior (C), anterior (D), and dorsal (E) views; F, anterior cervical (UCMP 139793) in anterior view; G, anterior cervical (UCMP 139794) in posterior view; H-I, anterior cervical (UCMP 139793) in lateral (H) and ventral (I) views; J-M, posterior cervical (UCMP 139813) in anterior (J), lateral (K), ventral (L), and dorsal (M) views; N-P, mid-cervical (UCMP 78714) in lateral (N), ventral (O), and anterior (P) views. Scale bar equals 1 cm. Abbreviations: diap, diapophysis; k, keel; nc, neural canal; ncs, neurocentral suture; odp, odontoid process; parp, parapophysis; prez, prezygapophyses; tb, ventral tab.

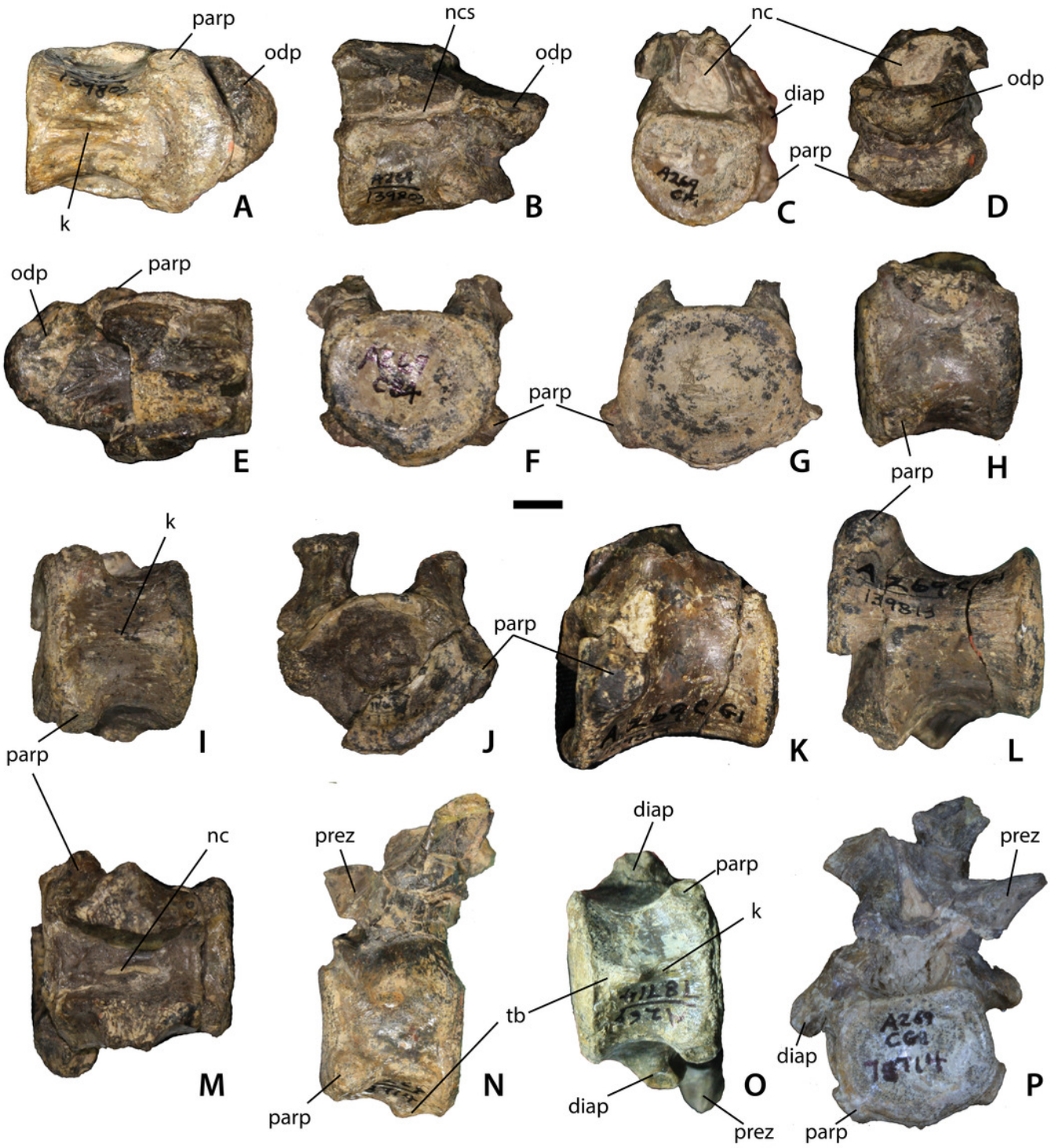

parp
odp
k
A
ncs
odp
B
nc
diap
odp
parp
C
D
odp
parp
E
parp
F
G
H
k
parp
I
parp
J
K
parp
L
nc
M
prez
parp
N
diap
parp
k
tb
diap
prez
O
prez
diap
parp
P

Figure 5

Trunk vertebrae of *Calyptosuchus wellesi*.

Trunk vertebrae of *Calyptosuchus wellesi*. A-B, UCMP 139694, 10th presacral vertebra in anterior (A) and ventral (B) views; C-F, UCMP 139796, mid-trunk vertebra in left lateral (C), right lateral (D), posterior (E), and dorsal (F) views; G-H, UCMP 139702, posterior trunk vertebra in anterior (G) and lateral (H) views. Scale bar equals 1 cm. Abbreviations: acdl, anterior centrodiapophyseal lamina; ns, neural spine; parp, parapophysis; pcdl, posterior centrodiapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygapophyseal lamina; posz, postzygapophysis; prcdf, prezygapophyseal centrodiapophyseal fossa; prez, prezygapophysis; spof, spinopostzygapophseal fossa; sprf, spinoprezygapophyseal fossa; tp, transverse process; vb, ventral bar.

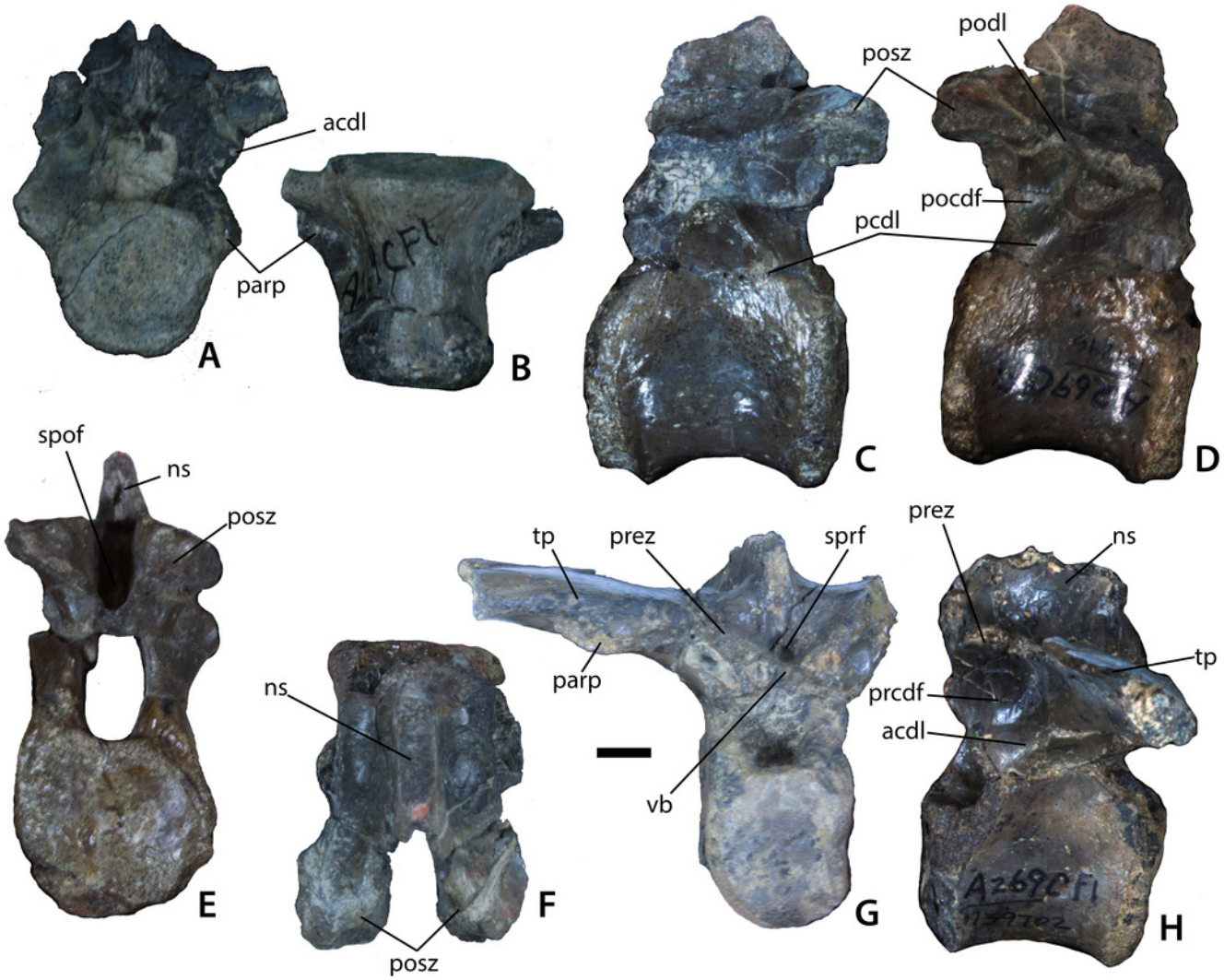

acdl
parp
A
B
podl
posz
pocdf
pcdl
C
D
spof
ns
posz
E
ns
posz
F
tp
prez
sprf
parp
vb
G
prez
ns
tp
prcdf
acdl
H

Figure 6

Mid-trunk vertebrae of *Calyptosuchus wellesi* (UMMP 7470).

Mid-trunk vertebrae of *Calyptosuchus wellesi* (UMMP 7470). A-B, vertebra in anterior (A) and posterior (B) views. C-D, vertebra in anterior (C) and posterior (D) views. Scale bar equals 1 cm. Abbreviations: nst, neural spine table; parp, parapophysis; prdl, prezygapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygapophyseal lamina; posz, postzygapophysis; prcdf, prezygapophyseal centrodiapophyseal fossa; prez, prezygapophysis; proj, posterior projection; spof, spinopostzygapophseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina; vb, ventral bar.

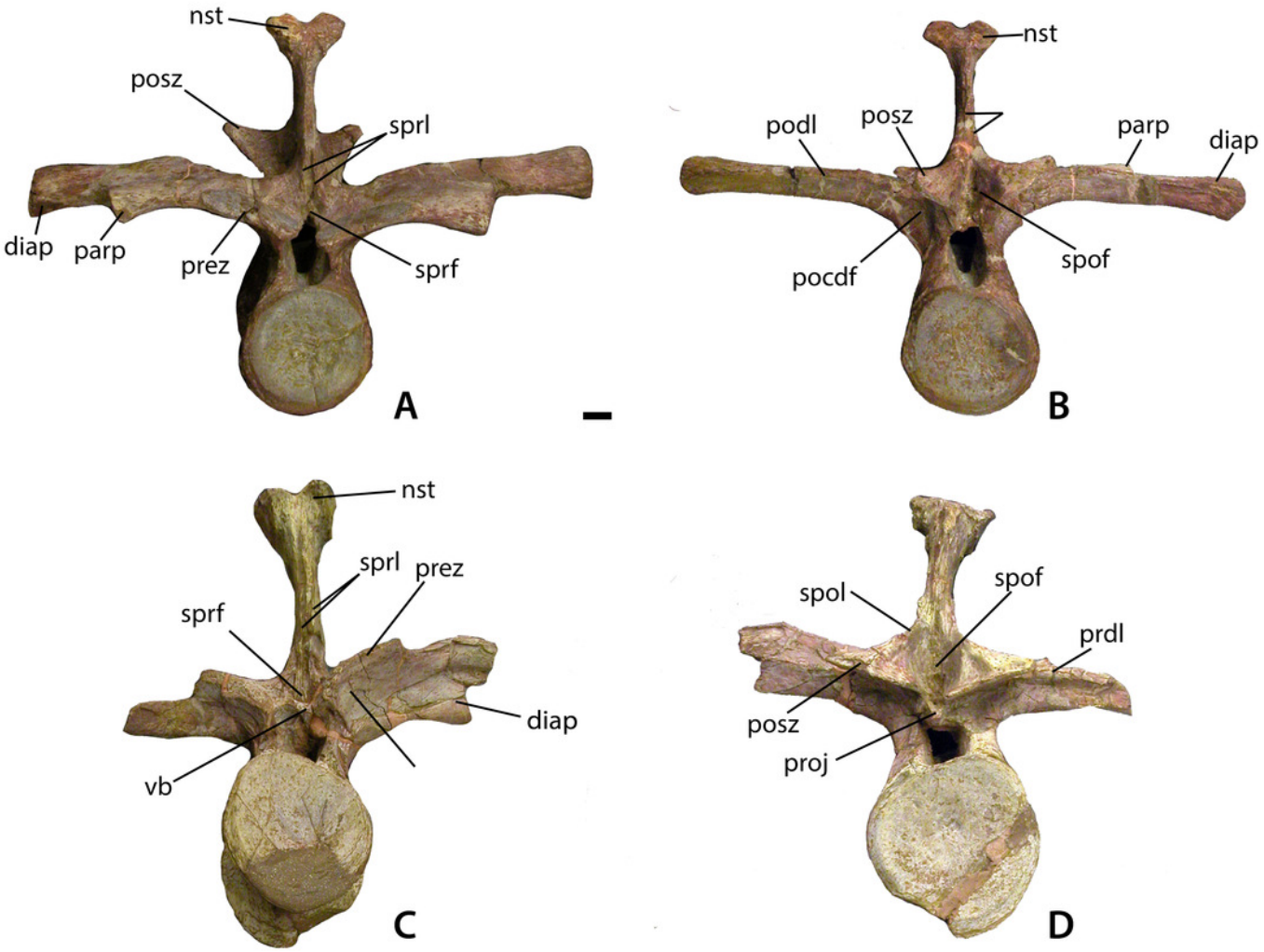

nst
posz
sprl
diap
parp
prez
sprf
A
nst
podl
posz
parp
diap
pocdf
spof
B
nst
sprl
prez
sprf
diap
vb
C
spol
spof
prdl
posz
proj
D

Figure 7

Sacral vertebra of *Calyptosuchus wellesi* (UCMP 139785)

A-D, Sacral vertebra of *Calyptosuchus wellesi* (UCMP 139785) in anterior (A), lateral (B), posterior (C), and ventral (D) views. Scale bar equals 1 cm. Abbreviations: posz, postzygapophysis; prez, prezygapophysis; proj, posterior projection; spof, spinopostzygapophseal fossa; sprf, spinoprezygapophyseal fossa; sr, sacral rib; vb, ventral bar.

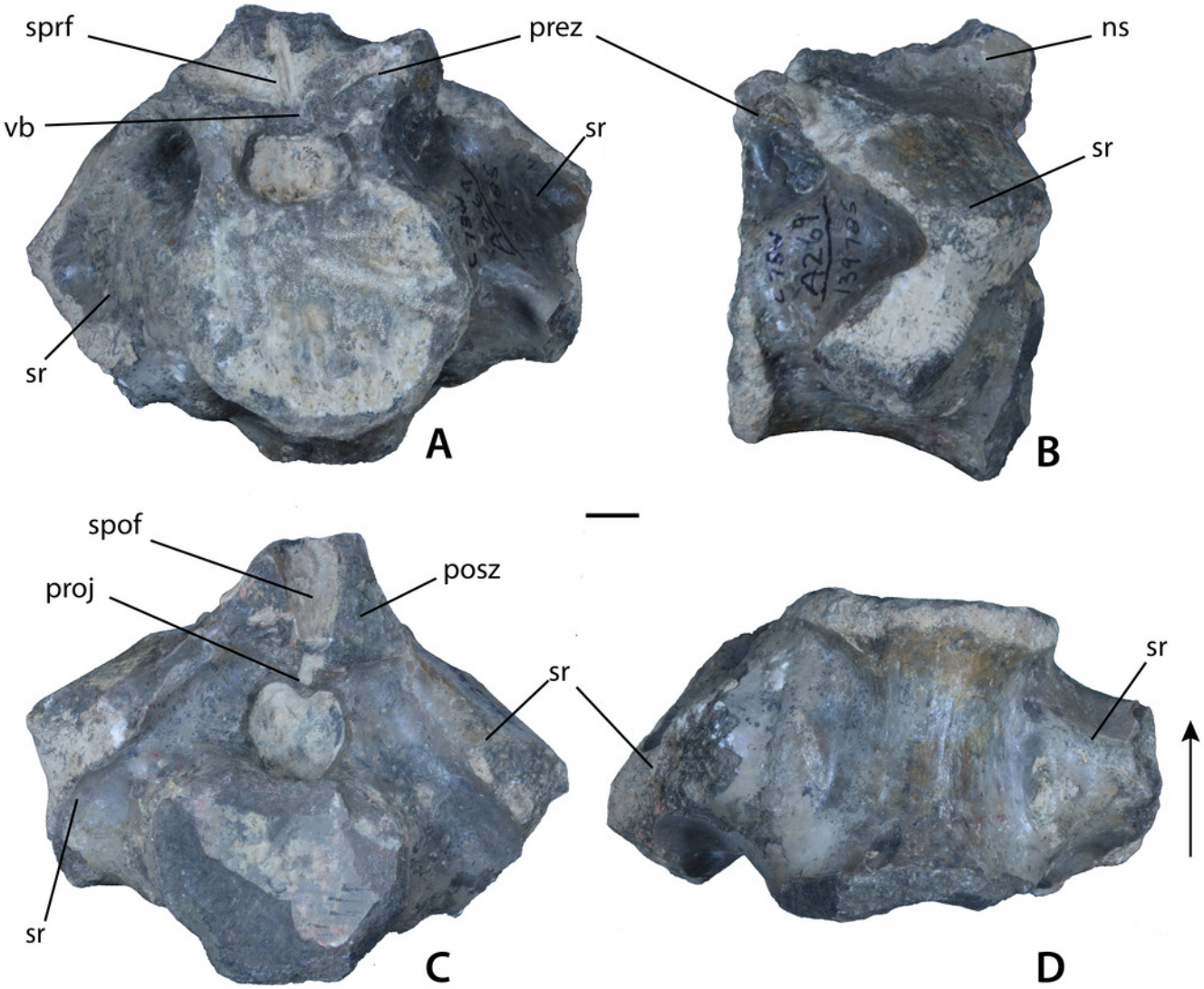


Figure 8

Portion of the sacrum and vertebral column of the holotype specimen of *Calyptosuchus wellesi*

Portion of the sacrum and vertebral column of the holotype specimen of *Calyptosuchus wellesi* (UMMP 13950) in ventral view. Abbreviations: ac, acetabulum; cdv; anterior caudal vertebra; dsv, posterior trunk vertebra; isc, left ischium; poab, postacetabular blade of the left ilium; prab, preacetabular blade of the left ilium; pu, left pubis.

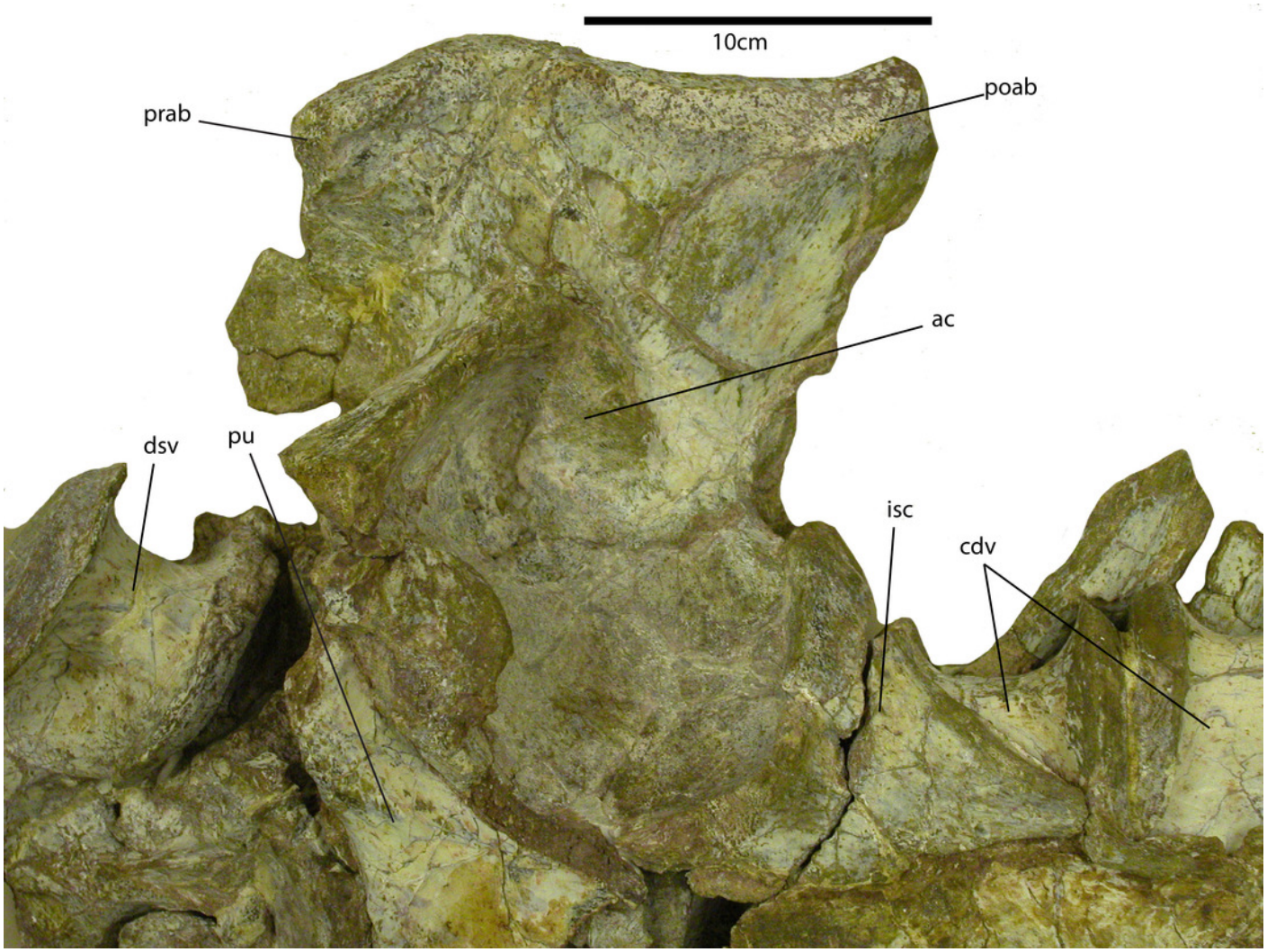


Figure 9

Pelvic elements of *Calyptosuchus wellesi*

Pelvic elements of *Calyptosuchus wellesi*, possibly from a single individual. A, left ilium (UCMP 25941) and ischium (UCMP 32148) in lateral view (see text about anatomic directions for the pelvic elements); B, left ilium (UCMP 25941) in medial view; C, right ilium (UCMP 25941) and ischium (UCMP 32153) in lateral view; D-G, left pubis (UCMP 32150) in lateral (D), medial (E), dorsal (F), and posterior (G) views. Scale bar equals 1 cm. Abbreviations: a.x, articular surface with specified element; ac, acetabulum; il, ilium; ip, ischiadic peduncle; poab, postacetabular blade; pp, public peduncle; prab, preacetabular blade; sac, supraacetabular crest; sr, sacral rib.

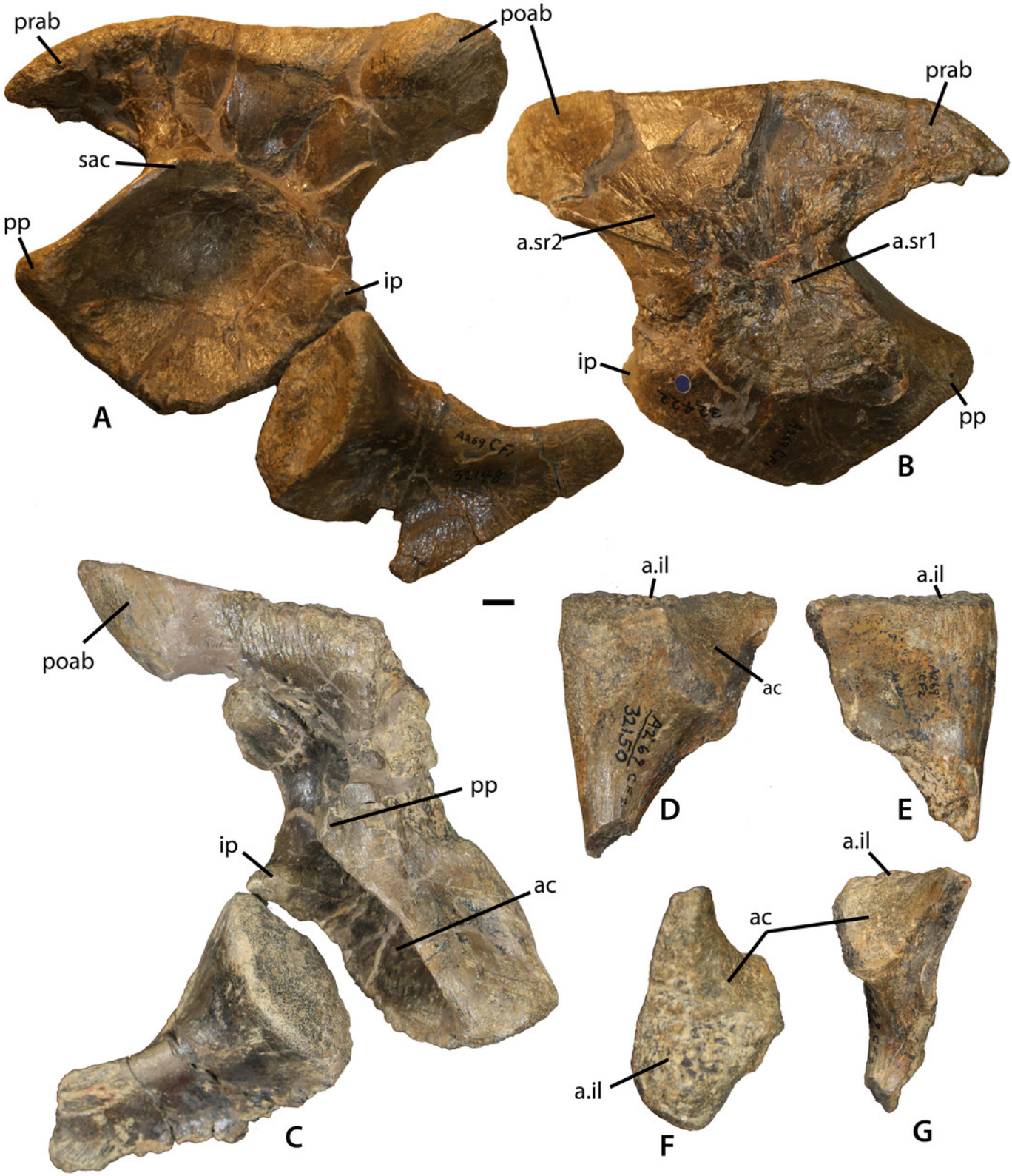

prab
poab
sac
pp
ip
A
prab
a.sr2
a.sr1
ip
pp
B
poab
pp
ip
ac
C
a.il
ac
D
a.il
E
ac
a.il
a.il
F
G

Figure 10

Left femur of *Calyptosuchus wellesi*

A-D, left femur of *Calyptosuchus wellesi* (UCMP 25918) in posteromedial (A); medial (B), lateral (C), and distal (D) views. Scale bar equals 1 cm. Abbreviations: ct, crista tibiofibularis; ft, fourth trochanter; gt, greater trochanter; lc, lateral condyle; mc, medial condyle.

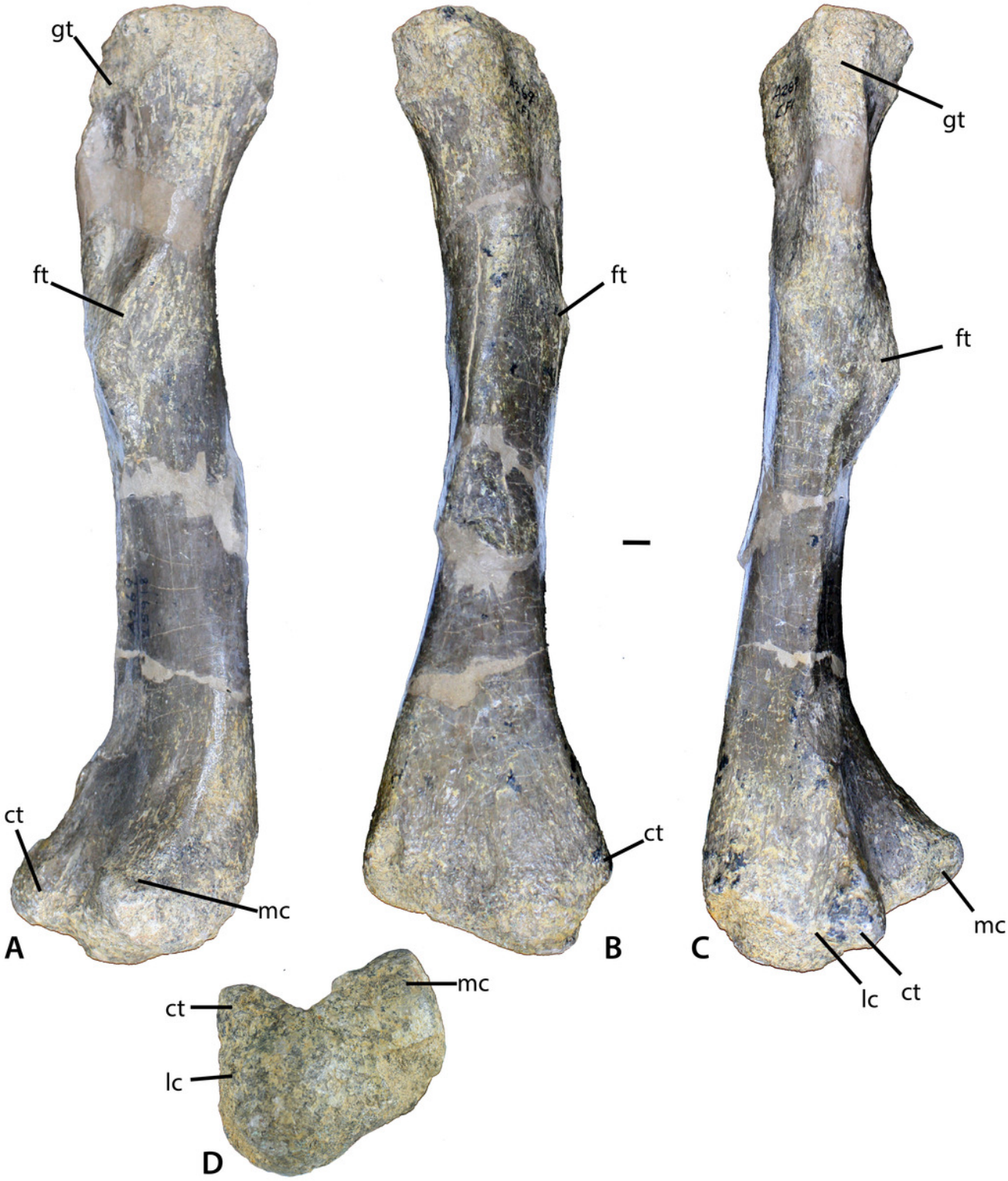

gt
ft
ct
mc
A
ft
ct
B
gt
ft
mc
lc
ct
C
mc
ct
lc
D

Figure 11

Aetosaurian tibiae from the *Placerias* Quarry.

Aetosaurian tibiae from the *Placerias* Quarry. A-C, *Desmatosuchus spurensis* left tibia (UCMP 25877) in proximal (A), posterior (B), and distal (C) views. D-F. *Calyptosuchus wellesi* left tibia (UCMP 25887) in proximal (D), posterior (E), and distal (F) views. Scale bar equals 1 cm.


A
D
B
I
E
F
C

Figure 12

Tibiae of *Calyptosuchus wellesi*.

Tibiae of *Calyptosuchus wellesi*. A-D, UCMP 25887, left tibia in posterior (A), medial (B), proximal (C), and distal (D). E-G, UCMP 25896, proximal end of left tibia in posterior (E), anterior (F), and proximal (G) views. Scale bar equals 1 cm. Arrows indicate anterior direction.

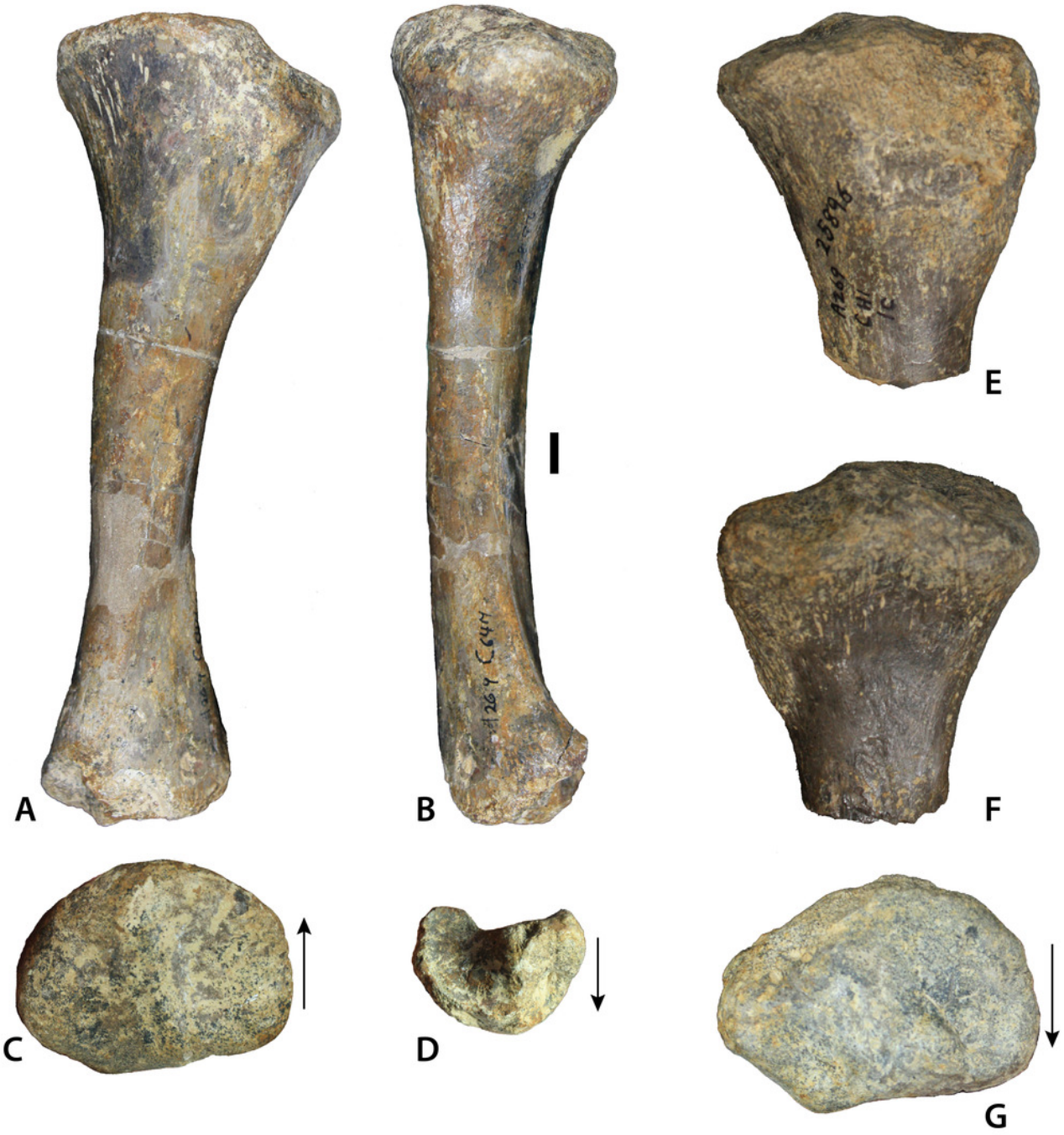

A
B
C
D
E
F
G

Figure 13

Holotype specimen of *Calyptosuchus wellesi* (UMMP 13950)

Holotype specimen of *Calyptosuchus wellesi* (UMMP 13950) showing assigned positions of osteoderms, pelvis, and vertebral column. Modified from Case, 1932. Abbreviations: d, trunk position; sc, sacral position; cd, caudal position. Figure 14: Close-ups of the carapace of the holotype of *Calytosuchus wellesi* (UMMP 13950) showing details of the paramedian osteoderms. Abbreviations: d, dorsal trunk row; sc, sacral row; cd, caudal row. Scale bars equal 10 cm.

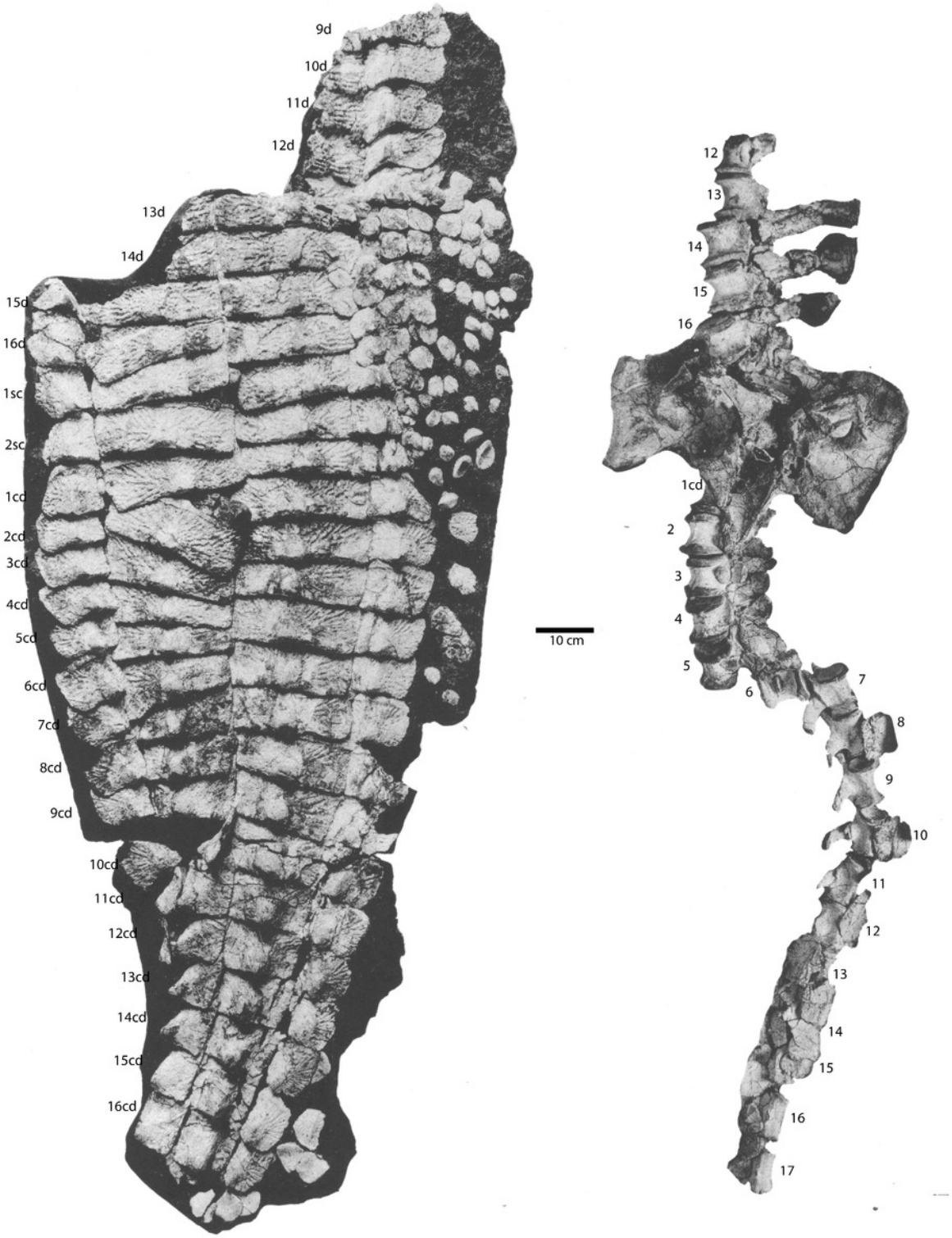
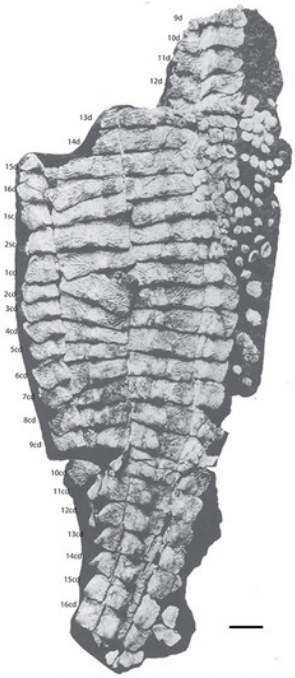

9d
10d
11d
12d
13d
14d
15d
16d
1sc
2sc
1cd
2cd
3cd
4cd
5cd
6cd
7cd
8cd
9cd
10cd
11cd
12cd
13cd
14cd
15cd
16cd
10 cm
12
13
14
15
16
1cd
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

Figure 14

Carapace of the holotype of *Calytosuchus wellesi*

Close-ups of the carapace of the holotype of *Calytosuchus wellesi* (UMMP 13950) showing details of the paramedian osteoderms. Abbreviations: d, dorsal row; sc, sacral row; cd, caudal row. Scale bars equal 10 cm.


16d
1sc
2sc
1cd
2cd
ns
3cd
4cd




1sc
2sc
1cd
2cd

Figure 15

Paramedian osteoderms of *Calyptosuchus wellesi*.

Paramedian osteoderms of *Calyptosuchus wellesi*. A-B, UCMP 136744, left anterior dorsal trunk osteoderm in dorsal (A) and ventral (B) views; C-E, UCMP 136744, right posterior dorsal trunk osteoderm in dorsal (C), ventral (D), and anterior (E) views; F, UCMP 126846, left dorsal trunk osteoderm in dorsal view; G, UCMP 136744, left dorsal mid-trunk osteoderm in dorsal view; H, UCMP 126844, left dorsal mid-trunk osteoderm in dorsal view; I, MNA V2930, left posterior dorsal trunk osteoderm in dorsal view; J-K, left posterior mid-caudal osteoderm in dorsal (J) and posterior (K) views. Scale bar equals 1 cm. Abbreviations: ab, anterior bar; alp, anterolateral process; amp, anteromedial process; de, dorsal eminence; me, medial edge; sc, scalloped area of anterior bar; vs, ventral strut.

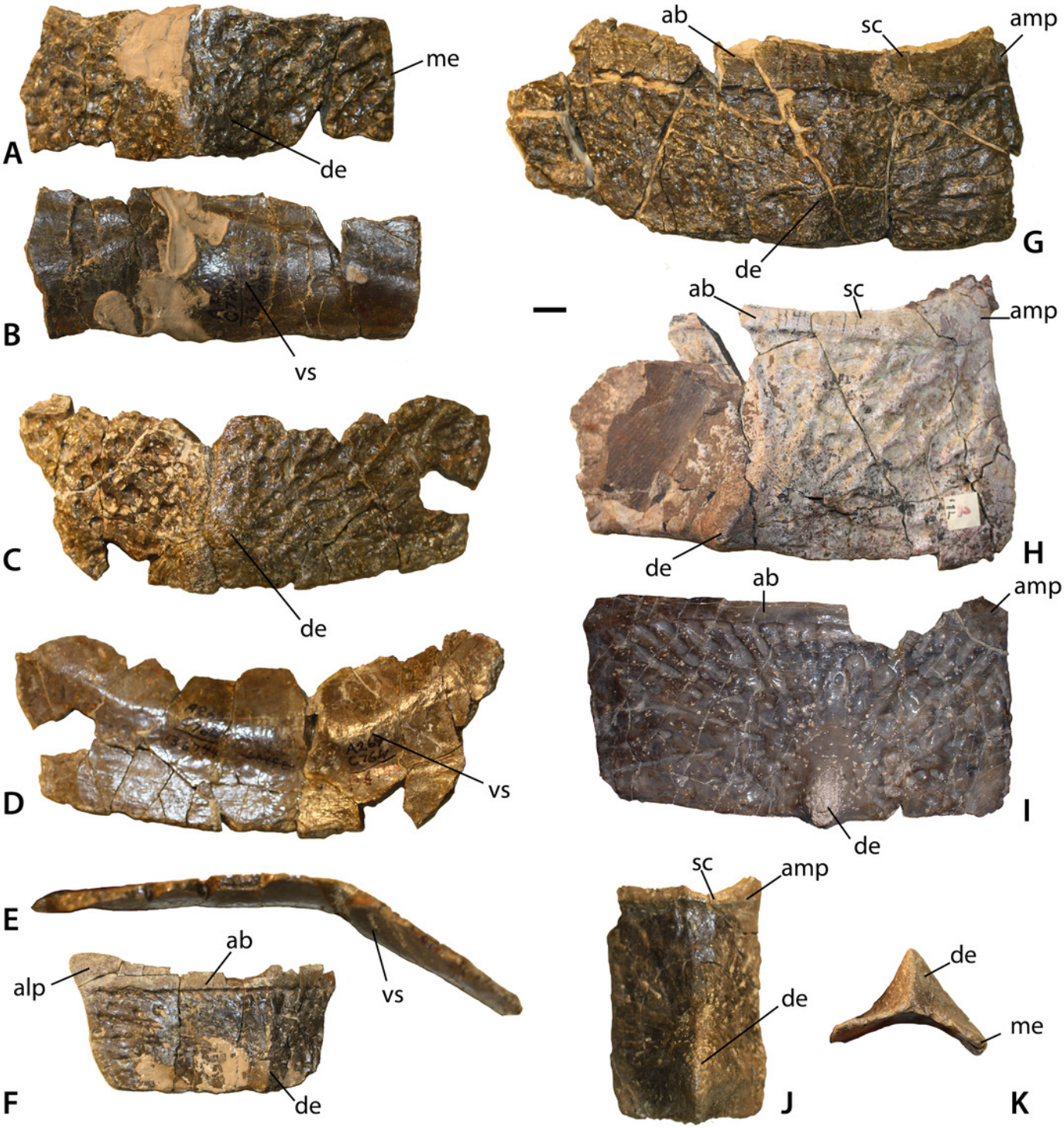

A
me
de
B
vs
C
de
D
vs
E
alp
ab
vs
F
de
G
ab
sc
amp
de
H
ab
sc
amp
de
I
ab
amp
de
J
sc
amp
de
K
de
me

Figure 16

Distal caudal paramedian osteoderms of *Calyptosuchus wellesi*

Distal caudal paramedian osteoderms of *Calyptosuchus wellesi* (UCMP 136744). A-B, Two semi-articulated sets of fused paired osteoderms in dorsal (A) and ventral (B) views; C-D, isolated osteoderm in dorsal (C) and ventral (D) views. Scale bar equals 1 cm. Abbreviations: ab, anterior bar; mls, mid-line suture.

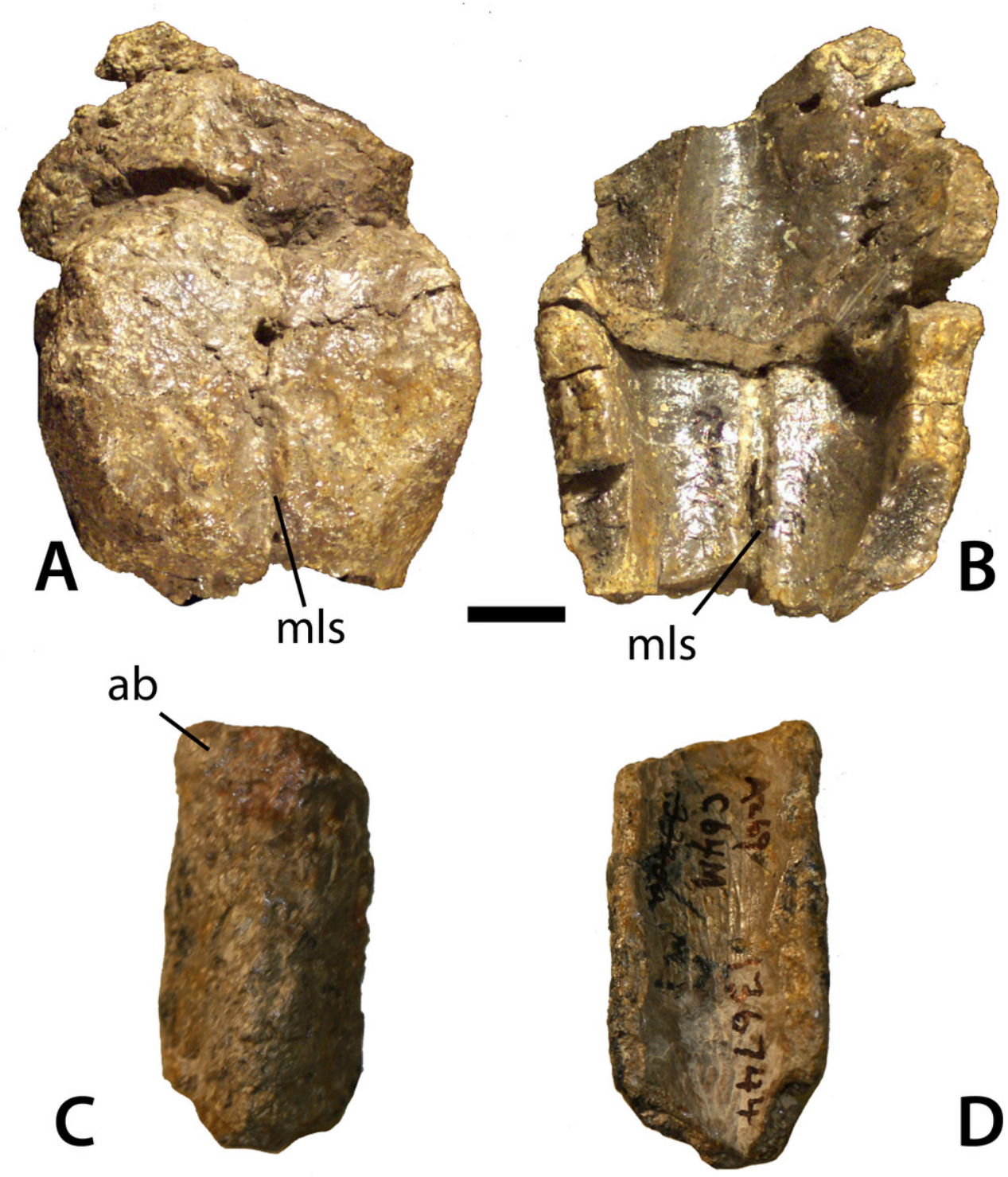

A
mls
B
mls
ab
C
D

Figure 17

Lateral osteoderms of *Calyptosuchus wellesi*.

Lateral osteoderms of *Calyptosuchus wellesi*. A-D, anteriormost dorsal trunk lateral osteoderms (UCMP 27225) from the left (A, C-D) and right (B) sides in dorsal view; E-F, anterior dorsal trunk lateral osteoderms (UCMP 27225) from the left (E) and right (F) sides in dorsal view; G-J, posterior dorsal trunk lateral osteoderms (UCMP 136744) from the left (G-H) and right (I-J) sides in dorsal (G, I) and posterior (H, J) views; K-N, sacral and anteriormost caudal lateral osteoderms (UCMP 78751, K-L; UCMP 136744, M; MNA V3744, N) of the right side in dorsal (K, M-N) and posterior (L) views; O-Q, anterior-mid-caudal lateral osteoderms (UCMP 27048, O; UCMP 136744, P-Q) of the right side in dorsal (O-P) and posterior (Q) views. Scale bar equals 1 cm. Abbreviations: df, dorsal flange, lf, lateral flange.


A
lf
df
B
lf
C
lf
df
D
lf
df
E
lf
df
F
df
lf
G
alw
lf
df
H
lf
df
I
df
alw
lf
K
df
lf
J
df
lf
alw
L
df
lf
M
df
lf
N
df
lf
O
df
lf
P
df
lf
Q
lf
df

Figure 18

Ventral and appendicular osteoderms of *Calyptosuchus wellesi*.

Ventral and appendicular osteoderms of *Calyptosuchus wellesi*. A, UCMP 175148, ventral osteoderm in ventral view; B, UCMP 136744, ventral osteoderm in ventral view; C-N, UCMP 27225, ventral osteoderms in ventral view; O, UCMP 136744, external surface of an appendicular osteoderm. Scale bar equals 1 cm.