The systematic position of the Late Jurassic alleged dinosaur *Macelognathus* (Crocodylomorpha: Sphenosuchia)

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Abstract: *Macelognathus vagans* was described by O.C. Marsh in 1884, based on a mandibular symphysis from the Upper Jurassic Morrison Formation of Wyoming. Often considered a dinosaur but later tentatively referred to the Crocodylia, its phylogenetic identity has until now been enigmatic. New material of this species from the Morrison Formation of western Colorado demonstrates its affinities with basal crocodylomorphs commonly grouped together as the Sphenosuchia, which are characterized by a gracile postcranial skeleton with erect limb posture. *Macelognathus* shares features with *Kayentasuchus* from the Lower Jurassic Kayenta Formation of Arizona and *Hallopus*, which may be from the Morrison Formation of eastern Colorado. The new material constitutes the youngest definitive occurrence of a sphenosuchian, previously known from the Late Triassic to the Middle or Late? Jurassic.

Résumé : *Macelognathus vagans* a été décrit par O.C. Marsh en 1884 à partir d'une symphyse mandibulaire provenant du Jurassique supérieur de la Formation de Morrison, du Wyoming. Les affinités de cette espèce souvent considérée comme étant un dinosaure, mais attribuée par la suite de façon incertaine aux Crocodylia, sont demeurées jusqu'à ce jour énigmatiques. Du nouveau matériel de cette espèce provenant de la Formation de Morrison de l'ouest du Colorado démontre que ses affinités avec des crocodylomorphes primitifs généralement groupés sous le nom de Sphénosuchia et caractérisés par un squelette postcrânien gracile et une posture droite. *Macelognathus* présente des caractères communs avec *Kayentasuchus*, du Jurassique inférieur de la Formation de Kayenta de l'Arizona, et *Hallopus*, possiblement de la Formation de Morrison de l'est du Colorado. Ce nouveau matériel constitue l'occurrence certaine la plus récent d'un sphénosuchien, dont l'existence certaine n'était connue auparavant que du Trias supérieur au Jurassique moyen ou ?supérieur.

Introduction

In 1884, O.C. Marsh described an incomplete mandibular symphysis from the upper Morrison Formation (Upper Jurassic) of Quarry 9 at Como Bluff, Wyoming, and erected the new binomen *Macelognathus vagans*, which he classified within the new reptilian order Macelognatha. Since its discovery, the systematic identity of *Macelognathus* has been controversial. Marsh suggested that Macelognatha was most closely allied to the Chelonia (Marsh 1884, p. 341), but subsequent authors referred *Macelognathus* to Dinosauria (Moodie 1908), to Reptilia (Gilmore 1909; Mook 1916), to Ornithischia (Simpson 1926), to Hypsilophodontidae (Huene 1956), and questionably to Crocodylia or Eosuchia (Ostrom and McIntosh 1966). Most recently, Ostrom (1971) suggested a crocodylian relationship for *Macelognathus*. Undoubtedly, assessment of

its systematic affinities was hampered by the fact that *Macelognathus vagans* was known only by the holotype — the symphysial and anterior portions of both dentaries (YPM 1415), which are unusual in being much flattened dorso-ventrally and anteriorly edentolous.

The specimens described here closely correspond in the structure of the dentaries with the holotype of *Macelognathus vagans*, and for the first time provide postcranial information critical for assessing the phylogenetic relationships of this taxon. This new material comes from the same stratigraphic unit as the holotype of *Macelognathus vagans*, the upper Morrison Formation (Brushy Basin Member, Upper Jurassic, Kimmeridgian), although from another locality, the Fruita Paleontological Area (FPA), Colorado, about 210 miles (~340 km) away. This material was collected by Callison et al. (California State University, Long Beach) during the late

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Fig. 1. Geographical position of the Fruita locality and geological section (modified from Kirkland 1994, fig. 9.2). M., Member.
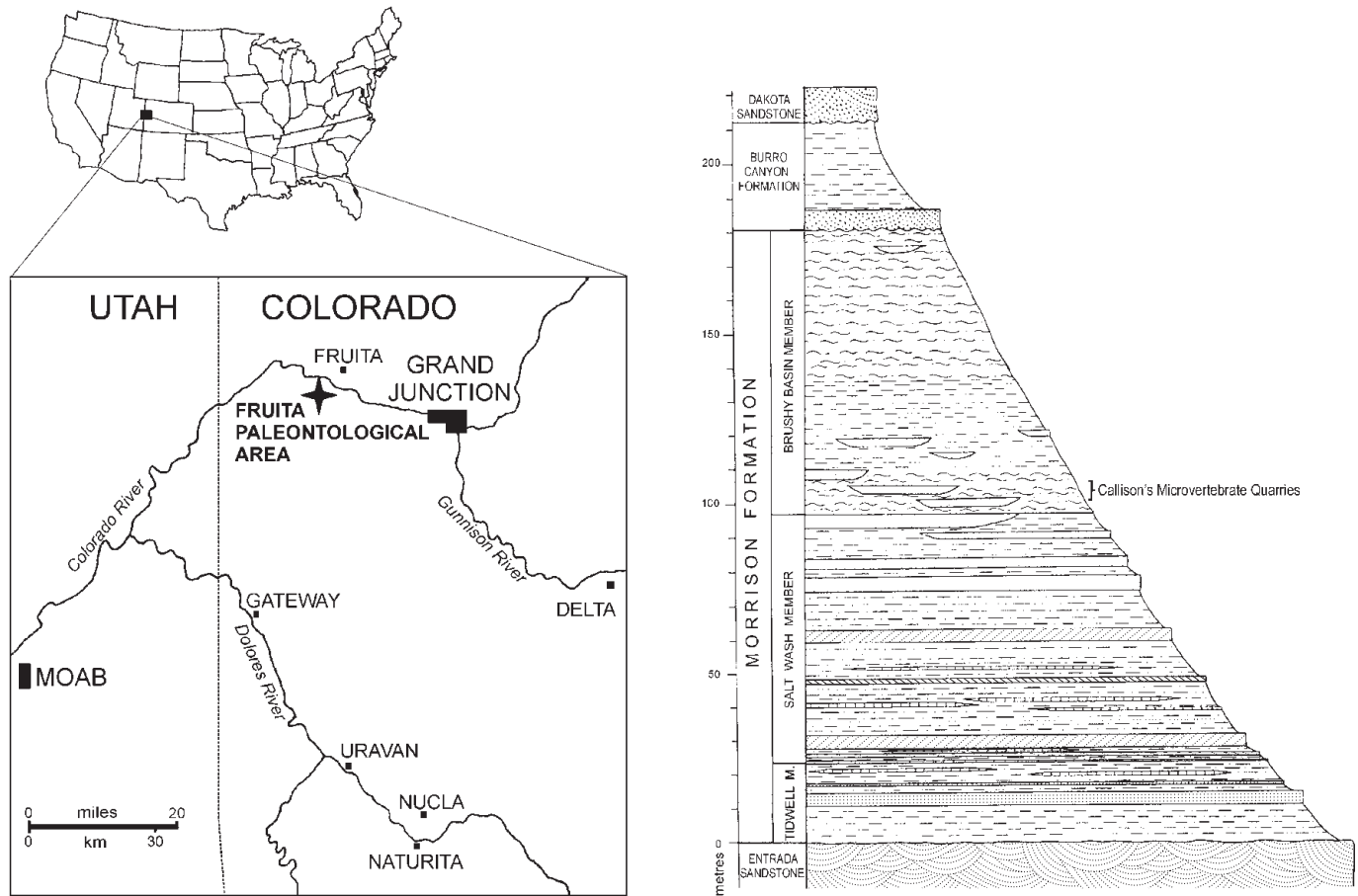
1970s and the mid-1980s from the base of the Brushy Basin Member (Engelmann and Callison 1998, p. 345; Kirkland 1994, p. 127; Fig. 1).

The FPA in Mesa County, Colorado, has long being known for its diverse and well-preserved vertebrate fauna (Rasmussen and Callison 1981*a*, 1981*b*). The many fossils collected from this area include Actinopterygii, Testudinata, Sphenodontia (*Opisthias*, *Eilenodon*), Squamata (*Paramacellodus*, *Saurillodon*, *Parviraptor*, *Dorsetisaurus*), Crocodyliformes (*Goniopholis*, "*Fruitachampsa*"), Pterosauria, Theropoda (Coelurosauria), Sauropoda (*Apatosaurus*, *Brachiosaurus*, *Camarasaurus*, *Diplodocus*), Ornithischia (*Stegosaurus*, cf. *Echinodon*), Multituberculata (*Glirodon*), Triconodonta (*Priacodon*), Symmetrodonta and Pantotheria (Foster 2003, p. 75 f).

Abbreviations

AMNH, American Museum of Natural History, New York, N.Y. USA; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; YPM, Yale University, Peabody Museum of Natural History, New Haven, Connecticut, USA.

Systematic Paleontology

Class   Archosauria Cope, 1869
Order   Crocodylomorpha Hay, 1930 sensu Walker, 1970

Family   Sphenosuchidae Haughton, 1924

The Sphenosuchia are a problematic group. It includes 14 valid taxa mostly represented by incomplete specimens that were previously placed in the "Pedeticosauria" or "Thecodontia" (Bonaparte 1972; Walker 1968, 1970, 1972). Together with the Crocodylia (Crocodyliformes, sensu Clark 1986), Sphenosuchia form the Crocodylomorpha (Walker 1968). Sphenosuchia was initially considered to comprise a series of sister-taxa of the Crocodyliformes by Benton and Clark (1988) and Parrish (1991), but later workers have differed as to whether sphenosuchians themselves constitute a para- or monophyletic group (Sereno and Wild 1992; Wu and Chatterjee 1993). Recent cladistic analysis of crocodylomorphs by Clark et al. (2000) and Sues et al. (2003) recovered a monophyletic Sphenosuchia, although support for this hypothesis was weak, and a similar analysis by Clark and Sues (2002) did not find support for this clade. The recent description of *Junggarsuchus* from China (Clark et al. 2004) was accompanied by an analysis resulting in a paraphyletic "Sphenosuchia" with this genus the sister-taxon to Crocodyliformes.

Genus *Macelognathus* Marsh, 1884
Macelognathus vagans Marsh, 1884
(Figs. 2–14)

HOLOTYPE: YPM 1415, anterior portions (including symphysis) of both dentaries. Figured by Marsh (1884, p. 341; 1897, figs. 65, 66), Ostrom (1971, fig. 1) and in Fig. 5 of this paper.

Fig. 2. Maxillae. (A) portion of left maxilla (LACM 5572/150148) lateral view; (B) and (C) portion of right maxilla (LACM 4684/133772): (B) lateral view, (C) occlusal view. ao.f, antorbital fossa; ao.fe, antorbital fenestra.
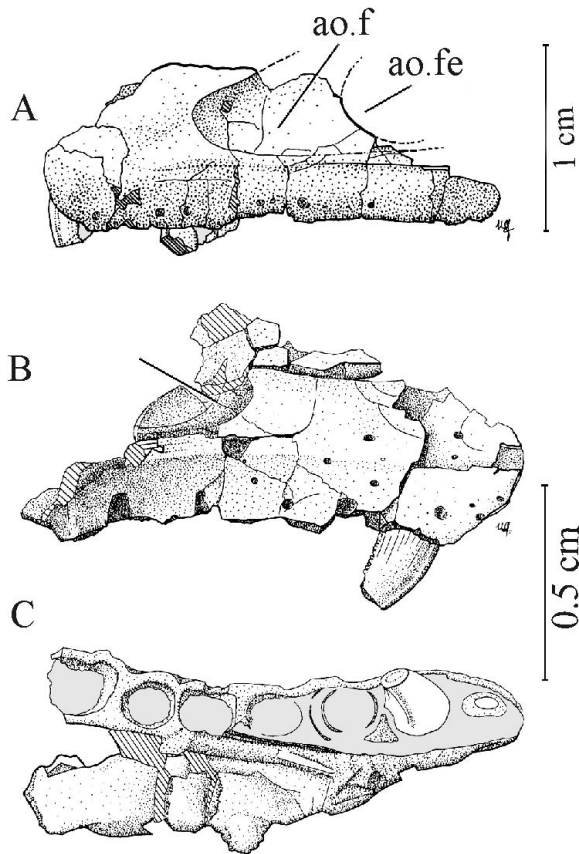

Fig. 3. Mandible (LACM 4684/133772). (A) and (B) dorsal view, (C) lateral view.
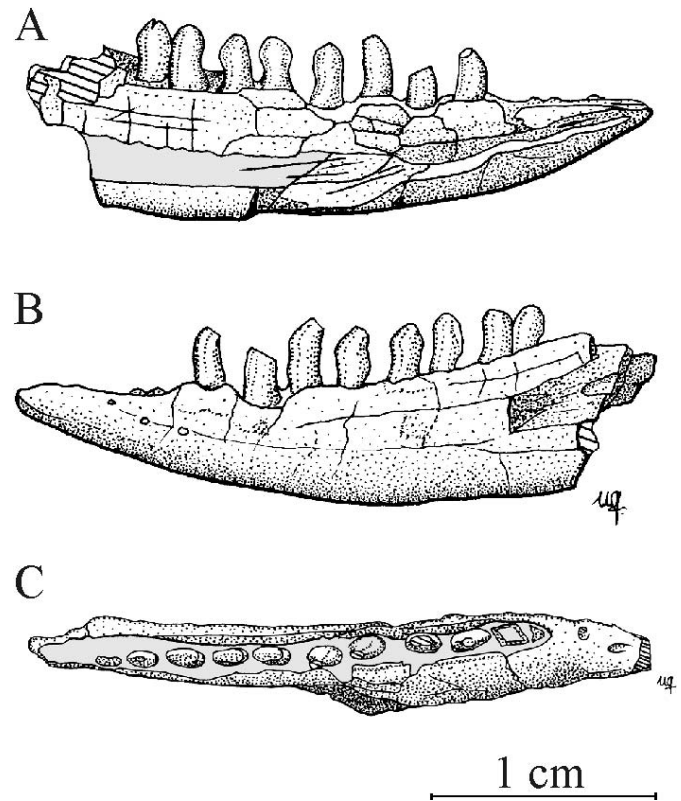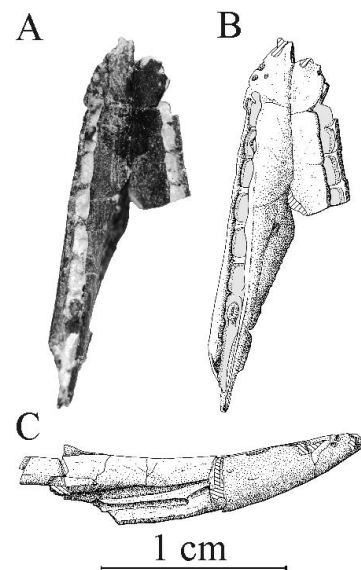

Fig. 4. Left dentary (LACM 5572/150148). (A) medial view, (B) lateral view, (C) occlusal view.

For a detailed description and taxonomic history of the holotype see Ostrom (1971).

TYPE LOCALITY: Quarry 9, SW 1/4 Section 12, Township 22N, Range 77W, Como Bluff, Albany County, Wyoming, USA.

TYPE HORIZON: Upper Brushy Basin Member, Morrison Formation, Late Jurassic, Kimmeridgian.

The new material of *Macelognathus vagans* Marsh, 1884

REFERRED SPECIMENS: The material is housed at the Natural History Museum of Los Angeles County, Los Angeles, California.

LACM 5572/150148 includes a left dentary, two dorsal vertebrae, a left ilium, the proximal half of the left femur and the distal halves of both femora, the right tibia and the distal half of the left tibia, the proximal and distal ends of the right fibula and the distal half of the left fibula, the left calcaneum, portions of metatarsals, and indeterminate fragments of bone. These elements are mostly disarticulated, although they were found together in a single small block (LACM field number 19#2). The relative proportions of the individual bones to each other and the fact that there is no duplication of elements supports their identification as of a single individual.

LACM 4684/128271, including a right femur, the proximal halves of both tibiae and the distal half of the right one, the distal half of the right fibula, the left metatarsal II and most of the left metatarsal III, the proximal half of the right metatarsal II, and the distal half of a metatarsal (possibly metatarsal III). These bones are regarded as representing a

single individual because they were found in close association and correspond in both structure and size.

LACM 4684/128272, a single left femur that, based on identical structure and size, may belong to the individual catalogued as LACM 4684/128271. LACM 4684/128272 and LACM 4684/128271 were collected from the same quarry.

LACM 5572/150211, the proximal end of the right metatarsal III and both calcanea.

LACM 4684/133772, a portion of the right maxilla, both dentaries including the symphysial region, and a fragmentary posterior portion of the cranial roof.

HORIZON AND LOCALITY: Fruita Paleontological Area, localities "Fruita General" and "Fruita Main" (Quarry 4), Mesa County, Colorado, USA; base of the Brushy Basin Member (zone 4, Foster 2003, p. 75 ff.) of the upper Morrison Formation (Upper Jurassic, Kimmeridgian). The locality LACM 4684 (LACM locality numbers are listed preceding the specimen number; e.g., LACM 4684/133772) is a general number for several quarries within a portion of the FPA, combined as "Fruita General." LACM locality number 5572 refers to George Callison's Quarry 4 ("Fruita Main"), a site contained within the area designated as locality LACM 4684. Other localities in the upper Brushy Basin Member include, for example, Dinosaur National Monument (Utah), Dry Mesa Quarry (Colorado), and Como Bluff (Quarry 9) (Wyoming); the latter is the type locality of *Macelognathus vagans*.

EMENDED DIAGNOSIS: A sphenosuchian crocodylomorph with dorsoventrally much flattened and anteriorly edentulous dentary, with heterodont dentition, and tooth crowns devoid of mesial and distal serrations; dentary lacking caniniform teeth; maxilla with laterally concave and ventrally sinuous alveolar margin; lateral longitudinal ridge above alveolar margin of maxilla; at least two enlarged anterior maxillary teeth; enlarged maxillary teeth serrated only distally; presacral vertebrae with large neural canals (almost as large as the centrum); ilium without supraacetabular crest; ventral margin of preacetabular process of ilium thickened and medially projecting; round femoral head oriented medially and separated from proximal end by a distinct neck; proximal facet of tibia distinctly slanted laterally; longitudinal groove on proximoanterior end of fibula; calcaneum with a completely flat distal surface; strong medioplantar crest on medial base of calcaneal tuber; overlapping proximal ends of metatarsals.

DESCRIPTION: In general, the individuals LACM 4684/133772, LACM 4684/128271 and 128272, LACM 5572/150211, and LACM 4684/133772 are smaller than LACM 5572/150148, which is of later ontogenetic stage, as will be discussed later in the text. For measurements see Table 1.

Cranium. A small and very fragmentary portion of the skull roof is preserved in LACM 4684/133772. It exhibits a short and weakly developed sagittal crest, which posteriorly separates the concave dorsal surfaces of the parietals. The sagittal crest joins a posteriorly concave nuchal crest that delimits the skull roof from the occipital surface.

Maxilla. An incomplete left maxilla (LACM 5572/150148) (Fig. 2A) and a portion of the right maxilla (LACM 4684/133772) (Figs. 2B, 2C) are preserved. The two maxillae are

identical in all details, except that the rostral end of the antorbital fossa of LACM 4684/133772 forms a small but deep rostral concavity. The maxilla shows no evidence of sculpturing. In lateral view, the alveolar margin is slightly concave. An irregular row of nutrient foramina extends parallel to the alveolar margin. A weak longitudinal ridge is developed dorsal to the nutrient foramina; in LACM 5572/150148, this ridge is 2–3 mm above the alveolar margin. Dorsal to this ridge, the maxilla is gently slanted medially. Only the anterior portion of the antorbital fossa is preserved. It is clearly longer than high. In LACM 5572/150148, a portion of the anterior margin of the antorbital fenestra is also preserved. This specimen retains part of its contact with the nasal. This contact is straight and encompasses the anterior margin of the antorbital fossa. Ten and seven alveoli are preserved in the maxilla of LACM 5572/150148 and LACM 4684/133772, respectively. Tooth remains are present in the anterior four and the sixth preserved alveoli of LACM 5572/150148 as well as in the first and second alveoli of LACM 4684/133772. These alveoli are separated from each other by bony septa. In LACM 5572/150148, the second preserved alveolus is larger than the others; in LACM 4684/133772, the second and third preserved alveoli are the largest. In lateral view, the anterior part of the antorbital fossa reaches the level of the septum between the third and fourth preserved alveoli in LACM 5572/150148 and the fourth and fifth preserved alveoli in LACM 4684/133772. Thus, the antorbital fossa extends anteriorly up to the level of one alveolus posterior to the largest teeth. In ventral view, the alveolar margin is weakly sinuous. The posterior portion of the bone is laterally concave and its rostral part is convex. Medially, the maxillae form a secondary palate, which is incomplete in both specimens. The teeth are labiolingually compressed and slightly recurved. They are serrated only along the distal margin; these serrations can be seen in the third preserved position in LACM 5572/150148 and the second preserved tooth in LACM 4684/133772.

Mandible. An incomplete left dentary (Fig. 3) containing the symphysial region is the only mandibular portion preserved in LACM 5572/150148. LACM 4684/133772 (Fig. 4) also includes only portions of the dentaries, including the symphysial region. As with other elements, the dentaries of these two specimens are identical in all respects, except that LACM 5572/150148 is larger (its symphysial region is 40% longer). The dentary is low with respect to its preserved length and labiolingually compressed posterior to the symphysis. The tooth rows are sub-parallel to each other, diverging only slightly from one another more posteriorly. In lateral and (or) medial view, the alveolar and ventral margins of the dentary are slightly concave and convex, respectively, tapering towards the anterior end. The lateral surface of the bone is pierced by an irregular row of nutrient foramina, which extends parallel to the alveolar margin. The symphysial region is long — about 1.4 times longer (in LACM 4684/133772) than the mandible is broad at the posterior end of the symphysis (in the holotype it is about 1.2 times longer). The rostral portion of the symphysis is edentulous. In the holotype of *Macelognathus vagans* (Fig. 5), the edentulous portion is approximately half the length of the symphysis. In the Fruita specimens, it appears to be somewhat shorter, but

Fig. 5. Mandible, holotype *of Macelognathus vagans* (YPM 1415). (A) and (D) occlusal view, (B) and (E) ventral view, (C) and (F) medial view. Drawings from Ostrom (1971, fig. 1, copyright© of the Peabody Museum of Natural History, Yale University, New Haven, Connecticut).
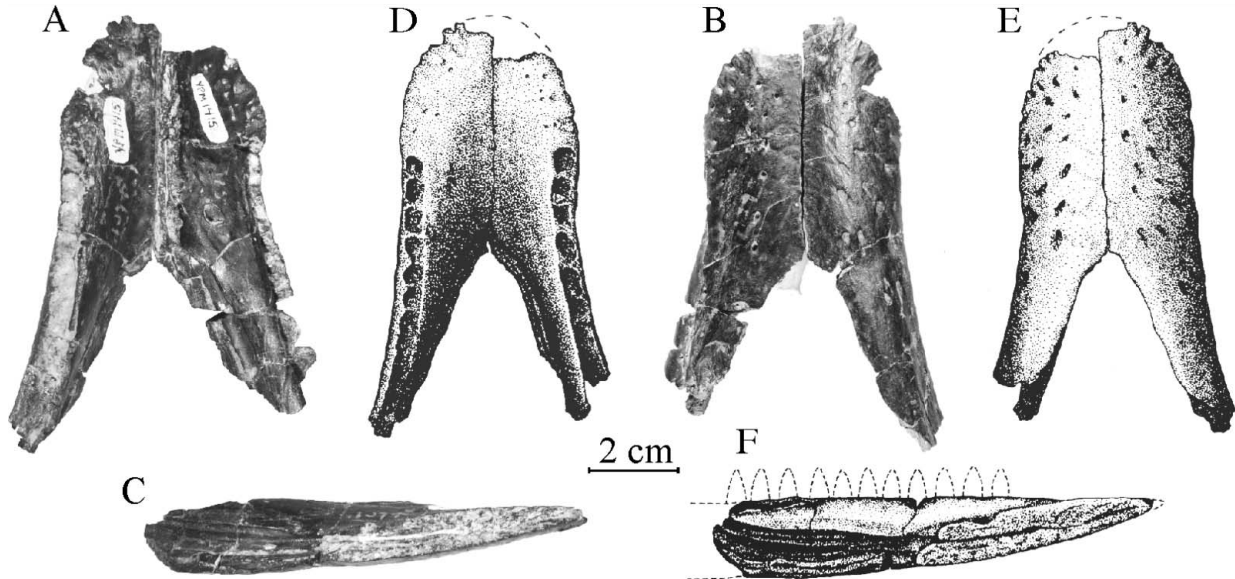

Fig. 6. Dorsal vertebrae (LACM 5572/150148). (A) and (C) lateral view, (B) posterior view.
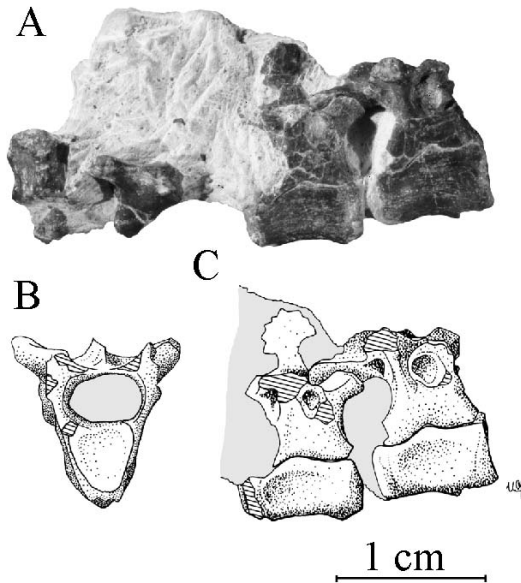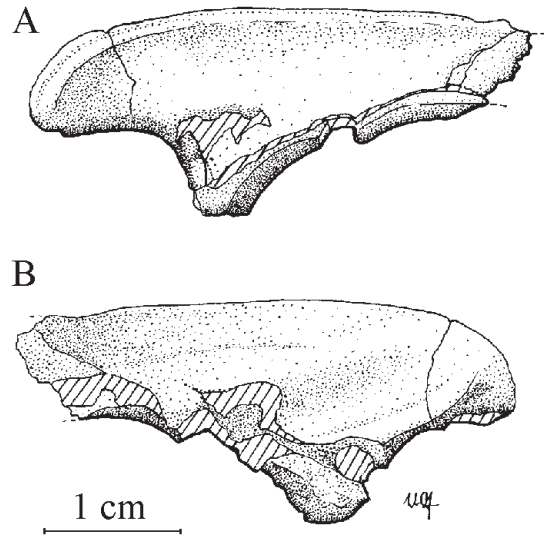

**Fig. 7.** Left ilium (LACM 5572/150148). (A) lateral view, (B) medial view.

in neither specimen is the anterior end of the symphysis well preserved. The edges of the edentulous portion of the symphysis are deeply scared by large pits. The symphysis extends posteriorly to the level of the fourth dentary tooth. The dental tooth rows are more parallel along the symphysis, and diverge slightly more posteriorly. At least 10 alveoli are preserved in LACM 5572/150148 — the intermediate eight bearing erupted teeth — and eight and four alveoli are preserved in the left and right portions of the dentary of LACM 4684/133772, respectively. The alveoli are more or less identical in size and are separated from each other by bony septa. The teeth are best preserved in LACM 5572/ 150148. They are labiolingually compressed, but the structure varies greatly along the dental row. The second to fifth dentary teeth of

LACM 5572/150148 have pointed crowns that are curved distally. The crown of the fifth dentary tooth is separated from its root by a very gentle constriction. This constriction, however, becomes well defined in the subsequent teeth, which have blunt crowns. The dentary teeth show no evidence of serrations. Along the medial surface of the dentary, a long and narrow Meckelian groove extends forward to the symphysial margin. The splenial is missing; thus, it is difficult to determine whether the splenial only approached or actually formed part of the symphysis. In the latter case, it may have made only a small contribution to the mandibular symphysis anteriorly.

Postcranium: **Vertebrae.** Although remains of at least seven vertebrae are preserved in LACM 5572/150148, only three

Fig. 8. Left femur (LACM 4684/128272). (A) and (B) anterior view, (C) and (D) lateral view, (E) and (F) medial view, (G) and (H) posterior view, with proximal and distal views. ft, fourth trochanter; lt, lesser trochanter; pi.t, possible homologue of "pseudotrochanter" in *Hallopus* (Walker 1970) and *Kayentasuchus* (Clark and Sues 2002); fi.c, fibular condyle; m.c, medial condyle.
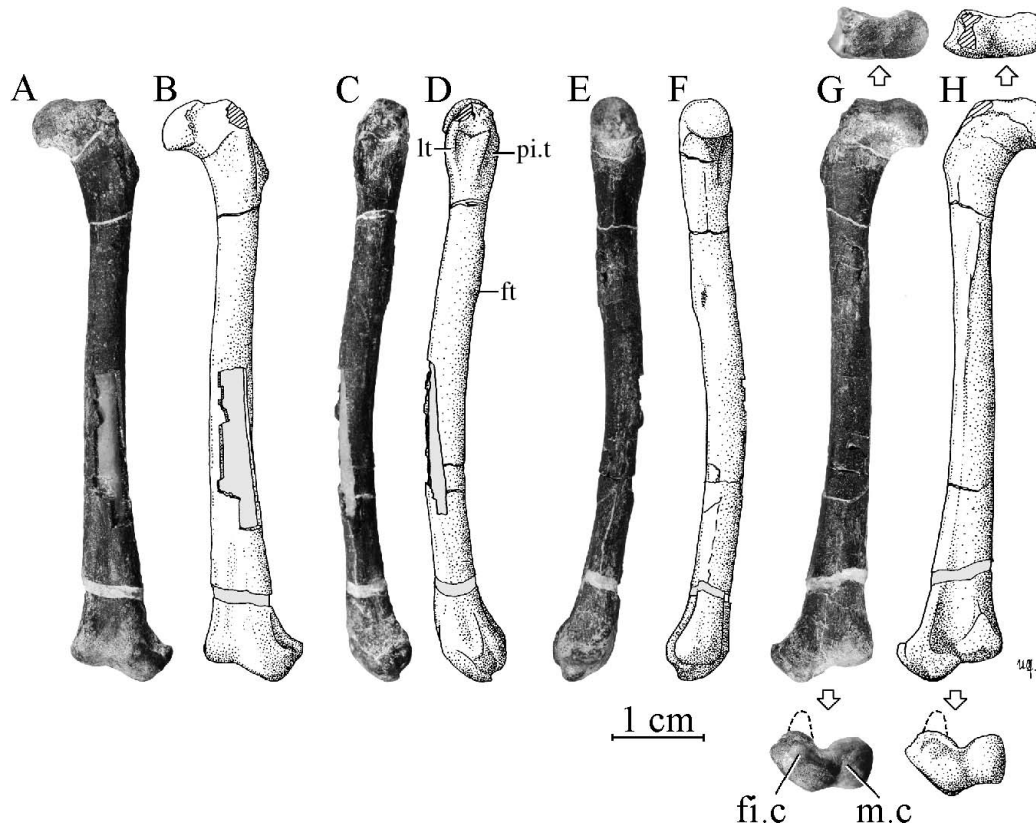
of them are informative. These vertebrae are presacrals — anterior dorsals and posterior cervicals — and, with the exception of two dorsals (Fig. 6), are disarticulated. Neurocentral sutures are visible on all of them, except for a poorly preserved vertebra that appears to be a cervical. The centra are amphicoelous and slightly concave laterally. The neural canal is very large. It is larger than the articular surface of the centrum in all preserved vertebrae. On the dorsal vertebrae, the centrum is dorsoventrally compressed. On an anterior dorsal, the ventral surface of the centrum is keeled, and its anterior half shows a broken surface that indicates the presence of a hypapophysis, although its size is indeterminate. Two more posterior dorsal vertebrae have centra that are less compressed dorsoventrally. They have tall neural arches with round parapophyses located near the base of the prezygapophyses. The more posterior of these two vertebrae has a tall neural spine; that of the other vertebra is broken. The prezygapophyses of these vertebrae are short and have nearly vertically inclined facets. The postzygapophyses project posteriorly beyond the posterior articular surface of the centrum. Infrapostzygapophysial fossae are present on these two vertebrae, the fossae on the more posterior vertebra being more pronounced.
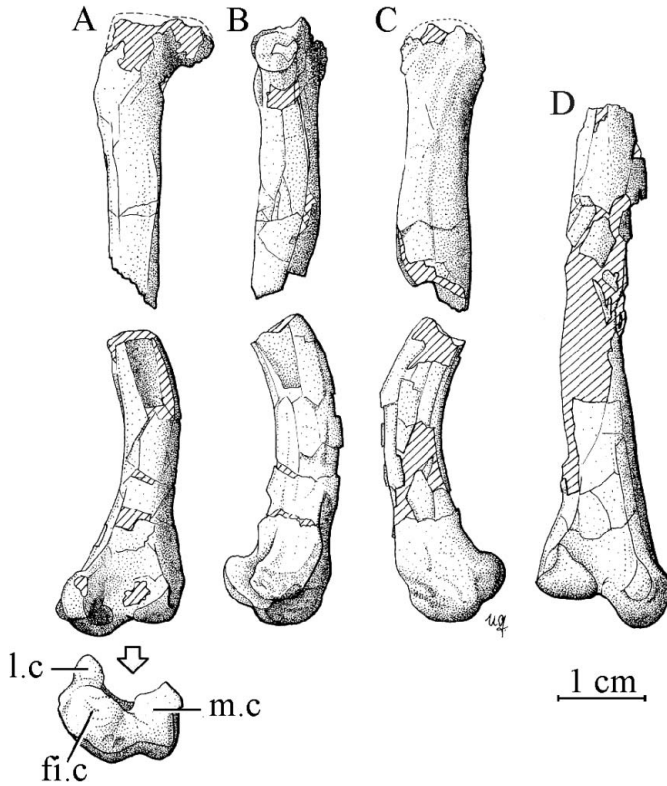
Ilium. Only the left element of LACM 5572/150148 (Fig. 7) is preserved, lacking the caudal portion of its postacetabular process. Despite its incompleteness, it is evident that the preacetabular process of the ilium is the shorter of the two processes. The ilium is anteroposteriorly long and dorsoventrally narrow, with its lateral surface longitudinally depressed. The blade is laminar, becoming thicker ventrally, more so on the preacetabular process than on the postacetabular one. In lateral view, the ventral margin of these processes is slightly concave; the acetabular wall carrying the facet is largely missing. The dorsal edge of the ilium is horizontal; near the anterior end of the preacetabular process, it curves anteroventrally to form the rounded end of the process. In dorsal view, this edge — and the bone itself — is laterally concave. The pubic peduncle is somewhat weathered but is clearly robust and transversely broad; the ischiadic peduncle is missing. Ventrally, the preacetabular process is laterally bent, unlike the straighter postacetabular process; the former is also broader than the latter. On the medial surface, the thick ventral margin of the preacetabular process flares out to define a distinct shelf that runs from the pubic peduncle anterodorsally.

Femur. LACM 5572/150148 (Fig. 9) preserves the proximal half of the left femur and the distal halves of both femora. In addition, both femora are preserved of individual LACM 4684/128271 and LACM 4684/128272 (Fig. 8), although the proximal end of the left femur and the shaft of the right femur are poorly preserved, and the shaft of the left femur exhibits postmortem deformation.

The femur is characterized by a medially oriented head, angled at approximately 90° with respect to the shaft. The head and proximal end of the femur are best preserved in the smaller LACM 4684/128271 and LACM 4684/128272. The

Fig. 9. Femora (LACM 5572/150148). (A) proximal and distal portion of left femur, posterior, and distal view; (B) proximal and distal portion of left femur, medial view; (C) proximal and distal portion of left femur, lateral view; (D) distal portion of right femur, anterior view. fi.c, fibular condyle; l.c, lateral condyle; m.c, medial condyle.

Fig. 10. Tibiae (LACM 5572/150148). Right tibia: (A) lateral view; (B) cranial view, with proximal and distal view. Distal portion of left tibia: (C) anterior view; (D) lateral view, (E) posterior view, with distal view.

dimensions of these specimens are approximately 75% those of LACM 5572/150148, the length of which can only be estimated. LACM 4684/128271 and LACM 4684/128272 show that the head is robust, round, and situated at the same level as the greater trochanter. The head is separated from the proximal end of the femur by a distinct neck; this condition is best seen in LACM 4684/128271 and LACM 4684/128272. A short trochanteric crest sharply defines the anterolateral edge of the proximal end of the femur; in LACM 4684/128271 and LACM 4684/128272, this crest extends over 17% of the bone. Laterally, on the proximal end an axial groove, bordered anteriorly by the trochanteric crest and posteriorly by another ridge, possibly served as the site of attachment of M. puboischiofemoralis internus (Sues et al. 2003). The shaft is moderately bent and anteriorly convex; it is rounded in cross-section, gradually becoming anteroposteriorly compressed more distally. Breaks in all preserved femora show that the shaft was hollow with a very thin compacta. The fourth trochanter, although preserved on the left femur of LACM 5572/150148, is more clearly visible in LACM 4684/128272. It is developed as a weak axial crest on the posterior surface, roughly on the proximal third of the bone. Along the posterior surface of the shaft in LACM 4684/128272, a weak intermuscular line extends distally from the fourth trochanter to the lateral condyle. In LACM 5572/150148, this structure is developed as a crest projecting proximally from the lateral condyle and becoming weaker towards the
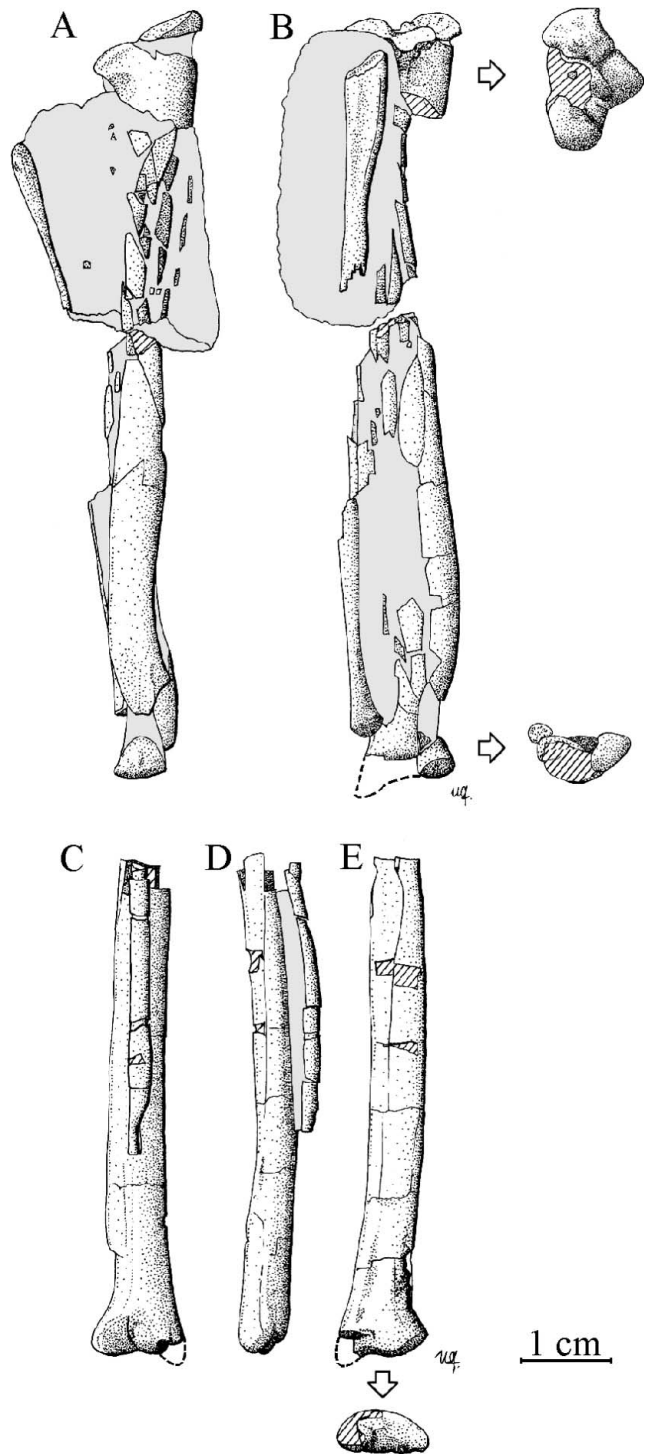
shaft. The distal end of the femur is anteroposteriorly compressed and has well-defined articular condyles. The lateral condyle protrudes posteriorly; in both LACM 4684/128271 and LACM 4684/128272, this condyle is somewhat weathered. A distinct fibular condyle is developed anterolateral to the lateral condyle; these condyles are separated by a mediolateral

Fig. 11. Proximal half of left tibia (LACM 4684/128271). (A) and (B) medial view, (C) anterior view, (D) anterolateral view, (E) lateral view, (F) and (G) posterior and proximal view.
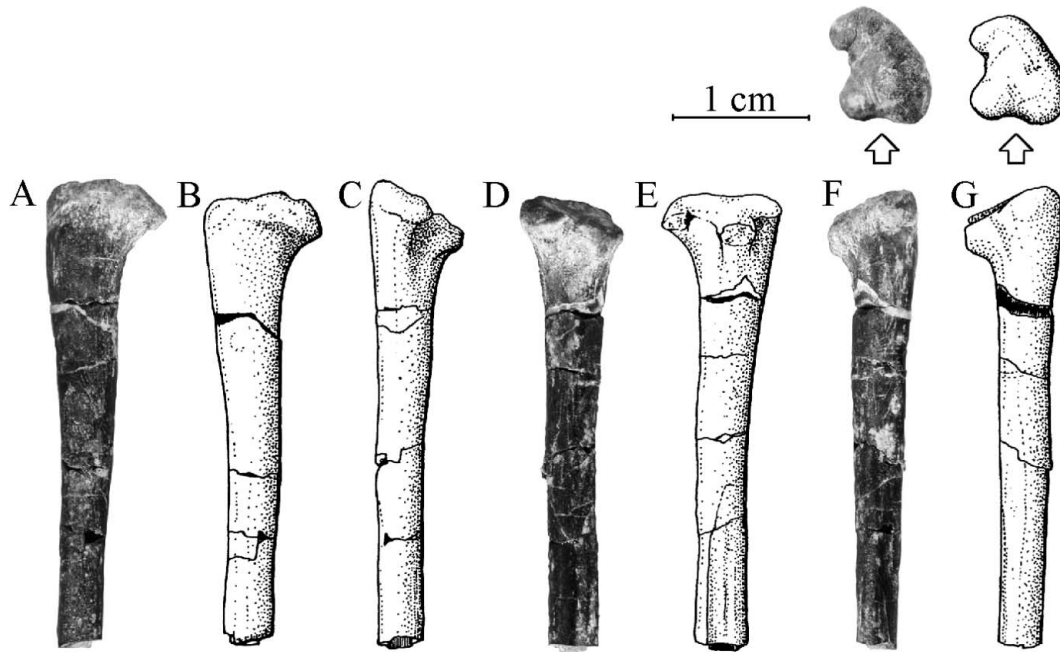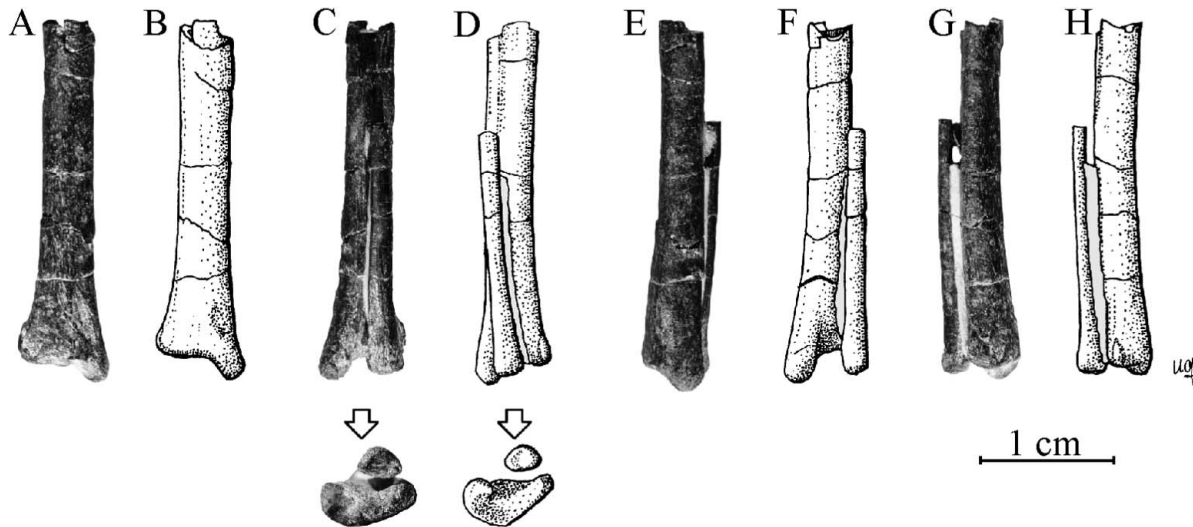

Fig. 12. Distal half of right tibia (LACM 4684/128271). (A) and (B) posterior view; (C) and (D) anterior view and distal view, (E) medial view, (F) anteromedial view, (G) and (H) lateral view.


groove. The fibular condyle projects distally far beyond the distal extension of the medial condyle. The distal articular surface of the fibular condyle has a pointed appearance, whereas that of the medial condyle is much flatter.

Tibia. The right tibia of LACM 5572/150148 (Figs. 10A, 10B) is nearly complete, although preserved in two parts that lack any contact; the distal half of its left tibia (Figs. 10C–10E) is also preserved. LACM 4684/128271 includes the distal half of the right tibia (Fig. 12) and proximal halves of both left (Fig. 11) and right tibiae; the pieces of the right do not contact. The combined lengths of the preserved portions of the left tibia of LACM 5572/150148 indicate that this bone is about 19% longer than the estimated length of the

femur. The tibia is straight and slender, lacking a fibular crest. Its proximal articular surface is strongly slanted laterally, a condition consistent with the distal protrusion of the fibular condyle of the femur. The proximal end of the tibia bears a very short, transversely broad, blunt cnemial crest, with minimal anterior development, as is best seen in LACM 4684/128271. In proximal view, the outline of the articular surface is convex medially and deeply concave laterally. The articular surface is nearly flat, with a faint central depression. Posteriorly, the proximal articular surface is subdivided by an indentation; the medial portion of the articular surface projects more than the lateral one. The mid-shaft is oval in cross-section, with a somewhat shorter transverse axis. LACM 4684/128271 exhibits a flat surface extending along

Fig. 13. Calcanea. Right calcaneum (LACM 5572/150211): (A) medial view; (B) dorsal view, (C) plantar view. Left calcaneum (LACM 5572/150148): (D) medial view; (E) dorsal view, (F) plantar view. Arrow indicates the medial crest which forms a probable tendon furrow.
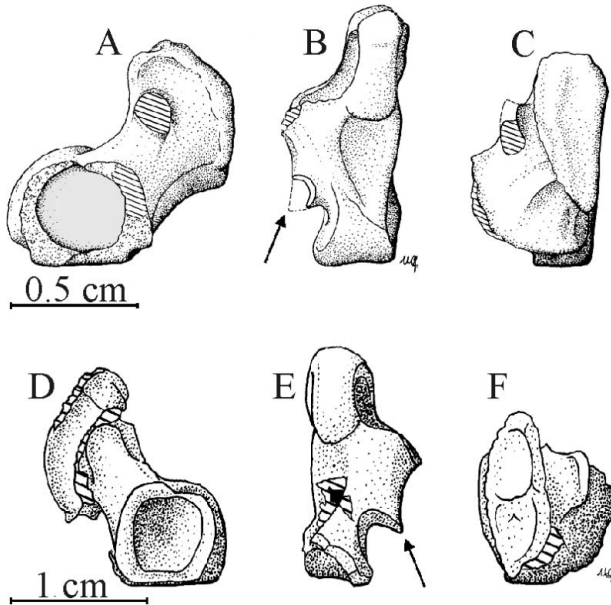
the middle third of its anterolateral aspect; this feature is not so apparent in LACM 5572/150148. The distal end is anteroposteriorly compressed, with its medial edge projecting strongly distally, a projection preserved only in LACM 4684/128271. The distal end of the tibia is anteriorly convex and posteriorly concave. The transversely elongated articular facet tapers laterally and extends proximally on the posterior surface.

Fibula. The fibula of LACM 5572/150148 is represented by distal and proximal thirds of the right element and the mid-shaft of the left one (Fig. 10). In addition, the distal half of the right fibula of LACM 4684/128271 (Fig. 12) is preserved. The fibula is a thin bone and is slightly expanded at both ends. It is anteroposteriorly compressed for most of its length and it becomes more oval towards the distal end. The posterior surface, which faces the tibia, is flattened. Although the proximal end of the fibula is missing, it is evident that a longitudinal groove runs along the anterior surface. The distal end of the fibula has a flat articular surface that is D-shaped in cross-section, with its straight border facing posteriorly. LACM 4684/128271 shows that the distal end of the fibula reaches the distal end of the tibia. The fact that the fibula of LACM 5572/150148 is situated proximal to the distal end of the tibia is regarded as an artifact of preservation.

Calcaneum. The left calcaneum of LACM 5572/150148 (Figs. 13D–13F) is about 41% longer (maximal diagonal depth including the condyle and the tuber) than the two calcanea of LACM 5572/150211 (Figs. 13A–13C), as measured on the right element (the left lacks its tuber).

The medial side of the calcaneum bears a deep hemicylindrical facet for the articulation with the astragalus. The proximoplantar margin of this facet protrudes strongly to-

wards the medial side. In proximal view, the calcaneal tuber is aligned with the condyle, projecting straight towards the plantar direction. The tuber is almost twice as tall as it is broad and carries a vertical groove on its plantar surface. A strong vertical crest protrudes medioproximally from the medial surface of the tuber, near the base of its neck. This crest defines a plantar furrow with the medial wall of the tuber that probably accommodated a ligament — probably the distal ligament of the M. flexor hallucis, which is part of the tarsal apneurosis (Brinkman 1980). In lateral view, the calcaneum is relatively flat, although a shallow, crescent-shaped depression scars the central portion of both condyle and tuber. This depression is much less visible in LACM 5572/150211 and it is mostly developed on the condylar surface. The distal surface of the condyle is completely flat.

Metatarsals. LACM 5572/150148 includes several metatarsal (mt.) fragments whose identity is difficult to determine. The general structure of these elements agrees with that of the better preserved metatarsals of LACM 4684/128271. That specimen preserves left mt. II and III (Fig. 14), articulated to one another; missing the distal end of mt. III. In addition, a disarticulated proximal half of the right mt. II and a distal half of an indeterminate metatarsal are also preserved in this specimen. In LACM 4684/150211, only a proximal end of a right metatarsal is preserved.

The metatarsals are slender and straight. The proximal ends of both metatarsals are transversely compressed and oriented along a dorsomedial-plantolateral axis. The proximal ends of these metatarsals overlap in much of their depths. In proximal view, their outlines have an hour-glass shape — compressed centrally and expanded at either end. The dorsoplantar axis of the proximal end of mt. III is somewhat longer than that of mt. II. The proximal end of the former is also more compressed mediolaterally than that of the latter. Proximally, the medial side of mt. III is slightly concave but its lateral side is flat. Although the distal end of mt. III is missing, the complete element would have been be longer than mt. II. In cross-section, the distal shafts of these metatarsals are round and oval, respectively. Metatarsal II has a ginglymous distal trochlea, which is slightly asymmetric in distal view; the lateral rim of this trochlea is deeper than the medial one.

Anatomical comparisons

The phylogenetic affinity of *Macelognathus* with the sphenosuchian crocodylomorphs is evident from a few, key features. The fully crocodyloid structure of its tarsus places it within the Suchia (see Sereno 1991), and within Suchia, the combination of a relatively well-developed antorbital fenestra with elongate, slender limb bones, and an inturned head on the femur uniquely place it among sphenosuchians (Clark et al. 2000). All of the other known features of the skeleton are consistent with a placement with sphenosuchians.

Comparisons among sphenosuchians are complicated by the fact that its monophyly is questionable, and most of the described taxa are known from incomplete skeletons; in addition, different elements often are preserved among the various known specimens. Currently recognized taxa of Sphenosuchia, either as a monophyletic group or as the para-

Table 1. Measurements (in mm) of the studied sphenosuchian material from the Fruita locality and the holotype of *Macelognathus vagans*.

(A)

	Collection No.	Greatest L	L medially	Prox W	Prox D	W caput	Prox diagonal W	Min W of shaft	Dist W	Dist D
LACM 5572/										
Femur sin dist	150148	Est. sin+dext (75)	—	—	—	—	—	—	15.0	10.9
Femur sin prox	150148	—	—	—	—	—	—	6.1	—	—
Femur dext dist	150148	—	—	—	—	—	—	(6.3)	14.3	11.4
Tibia dext prox	150148	Prox+dist (R) (89)	—	(13.7)	(12.6)	—	(16)	—	—	—
Tibia dext dist	150148	—	—	—	—	—	—	—	(11)	—
Tibia sin dist	150148	—	—	—	—	—	—	6.0	9.9	—
Fibula dext	150148	—	—	—	—	—	—	—	3.1	4.1
Fibula sin	150148	—	—	—	—	—	—	—	—	—
Ilium sin	150148	>40.1	—	—	—	—	—	—	—	—
Metatarsalia II? sin	150148	33.9	—	2.3	4.5	—	—	(2.5)	3.5	3.0
Metatarsalia III? sin	150148	—	—	—	5.5	—	—	—	—	—
Metatarsalia II? dext	150148	—	—	2.7	4.2	—	—	2.3	—	—
Metatarsalia ? dist	150148	—	—	—	—	—	—	—	3.4	2.9
LACM 4684/										
Femur sin	128272	58.7	56.7	8.8	5.5	4.5	—	4.1	10.1	(5.9)
Femur dext	128271	56.8	54.6	6.4	—	5.2	—	—	10.1	6.4
Tibia sin prox	128271	—	—	7.5	8.5	—	—	—	—	—
Tibia dext prox	128271	—	—	(8.2)	8.4	—	(9.5)	—	—	—
Tibia dext dist	128271	—	—	—	—	—	9.7	3.4	7.6	—
Fibula sin	128271	—	—	—	—	—	—	1.1	3.3	2.3
Metatarsal II or IV	128271	—	—	—	5.5	—	—	—	—	—
Metatarsal III	128271	33.9	—	4.5	2.3	—	—	(2.5)	3.5	3.0
Metatarsal ? dist half	128271	—	—	—	—	—	—	—	3.4	2.9

(B)

	D	Max. D diagonally	Max. W	H of corpus[a]	D of corpus[a]	H of tuber	W of tuber
LACM 5572/							
Calcaneum	12.7	14.7	7.8	6.3	8.6	9.4	4.8
Calcaneum dext	9.2	10.4	—	4.7	6.9	6.3	—
Calcaneum sin	—	—	—	4.9	6.9	—	—

Table 1 (concluded).

(C)	L centrum	W centrum cranially	H centrum cranially	W centrum caudally	H centrum caudally	W neural canal	H neural canal	W parapophyses	W prezygapophyses
LACM 5572/									
Dorsal vertebra 150148	8.3	4.9	5.1	—	—	4.8	3.9	(12)	7.4
Dorsal vertebra 150148	8.1	—	—	4.7	—	—	—	—	—

(D)	L sympysis
LACM 5572/	
Mandible 150148	~15
LACM 4684/	
Mandible 133772	~10
Holotype mandible **YPM 1415**	~58

Note: Estimated measurements of slightly damaged bones in parentheses. sin, sinister; dext, dexter; dist, distal portion; prox, proximal portion. D, depth; H, height; L, length; W, width; Max., maximum; Min., minimum. (R), reconstructed; Est., estimated.
[a]Without tuber.

phyletic base of Crocodylomorpha, are *Hesperosuchus agilis* Colbert, 1952 and *Parrishia mccreai* Long and Murry, 1995 (only isolated vertebrae) from the Upper Triassic Chinle Formation, southwestern USA; *Pseudhesperosuchus jacheleri* Bonaparte, 1972 from the Upper Triassic Los Colorados Formation, northwestern Argentina; *Saltoposuchus connectens* Huene, 1921 from the Upper Triassic Upper Stubensandstein, Württemberg, Germany; (*Dyoplax arenaceus* Fraas, 1867 from the Upper Triassic Schilfsandstein, Württemberg, Germany, is often listed as a sphenosuchian; it might be a crocodyliform, but the poorly preserved holotype and only known specimen of *Dyoplax arenaceus* provides no unambiguous features to suggest sphenosuchian affinities); "*Terrestrisuchus*" *gracilis* Crush, 1984 from Late Triassic fissure fillings in southwest England, but which was considered congeneric with *Saltoposuchus* by Clark (1986) and Allen (2003), but a valid taxon by Sereno and Wild (1992); the undescribed "Slickstone Crocodylian," probably *Saltoposuchus* (Parrish 1991), from the Late Triassic of the Slickstone Quarry of Embrough, UK; *Barbarenasuchus brasiliensis* Mattar, 1987 from the Upper Triassic Santa Maria Formation, southern Brazil; *Trialestes romeri* (Reig, 1963) from the Upper Triassic Ischigualasto Formation, northwestern Argentina (which is probably based on a composite type specimen; see Clark et al. 2000); *Dromicosuchus grallator* Sues, Olsen, Carter and Scott, 2003 from the Upper Triassic "Lithofacies Association II" of the Deep River basin, North Carolina, USA; *Dibothrosuchus elaphros* Simmons, 1965 (including *Dibothrosuchus xingsuenensis* Wu, 1986) from the Lower Jurassic Lower Lufeng Formation, Yunnan, China; *Clarencea gracilis* Brink, 1959, *Sphenosuchus acutus* Haughton, 1915, and *Litargosuchus leptorhynchus* Clark and Sues, 2002 from the Lower Jurassic upper Elliot Formation of South Africa (the first originally described as an ornithosuchid thecodont by Brink (1959), the latter initially identified as *Pedeticosaurus* sp. by Gow and Kitching [1988]); *Kayentasuchus walkeri* Clark and Sues, 2002 from the Lower Jurassic Kayenta Formation of Arizona, USA; *Hallopus victor* (Marsh, 1877), whose precise geographic and stratigraphic provenance remains controversial — either from the Middle Jurassic Lower Ralston Creek Formation (Parrish 1991; Norell and Storrs 1989) or from the upper member of the Upper Jurassic Morrison Formation (Ague et al. 199; Foster 2003); and *Junggarsuchus sloani* Clark, Xu, Forster and Wang, 2004 from the Middle Jurassic of China.

Sphenosuchian classification is primarily based on features of the skull because this anatomical region is best preserved in most taxa. The limited cranial information available in the new material of *Macelognathus* thus complicates comparisons to other taxa.

Skull

The maxilla of *Macelognathus* differs from that of other sphenosuchians in the presence of a lateral ridge extending dorsal and parallel to both the longitudinal row of nutrient foramina and the alveolar margin. The antorbital fossa is weakly recessed as opposed to the deeply indented fossa of *Hesperosuchus* (Clark et al. 2000). LACM 4684/ 133772 shares with *Dromicosuchus* (Sues et al. 2003), *Saltoposuchus* (Sereno and Wild 1992), and *Kayentasuchus walkeri* (Clark and Sues 2002) a conical excavation in the rostral extension

of the antorbital fossa, which is laterally concealed by the ascending wall of the maxilla. This rostral excavation perforates the maxilla in *Kayentasuchus*, but not in LACM 4684/133772. Interestingly, LACM 5572/150148 shows no evidence of this concealed rostral extension of the antorbital fossa. Nonetheless, in light of the great resemblance between LACM 5572/150148 and LACM 4684/133772, we continue to refer both specimens to the same taxon. The only two exposed maxillary tooth crowns of *Macelognathus* (one in LACM 5572/150148 and one in LACM 4684/133772) exhibit only distal serrations, unlike the maxillary teeth of most sphenosuchians (e.g., *Hesperosuchus*, *Dromicosuchus*, "*Terrestrisuchus*"), which have both mesial and distal serrations (Clark and Sues 2002); dental serrations appear to be absent in *Kayentasuchus* (Clark and Sues 2002).
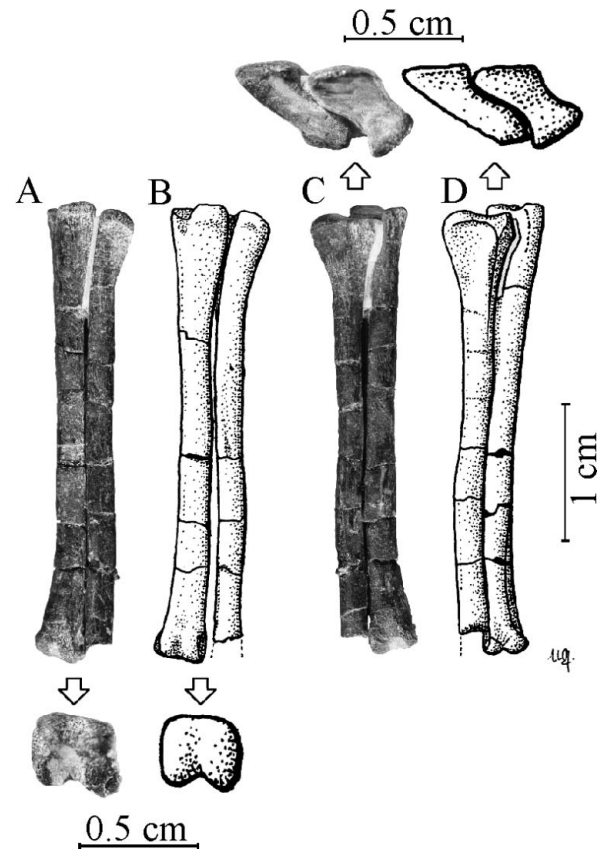
Dentary

The dentary is the only known bone of the holotype of *Macelognathus vagans*. Unfortunately, all teeth are missing in both dentaries of the holotype — only the alveoli are preserved. The dentary of the holotype and those of the Fruita specimens are morphologically identical and share the following characteristics: symphysial region long, with edentulous rostral portion; dentary low and laterally compressed posterior to the symphysis; symphysis extending back to level of fourth dentary tooth; tooth rows sub-parallel, diverging only slightly from one another more posteriorly; tooth rows extending more or less parallel along the symphysis but diverging slightly more posteriorly; in lateral view, alveolar and ventral margins slightly concave and convex, respectively, tapering towards anterior end; lateral surface of the bone pierced by irregular row of nutrient foramina, parallel to the alveolar margin; and edges of edentulous portion of symphysis deeply scared by large pits.

The only differences between the holotype of *Macelognathus vagans* and the Fruita specimens are the considerably larger size of the former and the relative length of the symphysis — the length of the symphysis in the holotype is about 5 cm, about 1.5 cm in LACM 5572–150148, and about 1 cm in LACM 4684–133772. Given the fact that the Fruita specimens represent juveniles, it is reasonable to assume that these differences represent ontogenetic changes and that all specimens belong to the same taxon.

Like in most other sphenosuchians, with the exception of *Hesperosuchus*, the symphysial portion of the dentary is low in lateral view. Dental serrations are also typical of sphenosuchians and their absence in the mandibular teeth of *Macelognathus* appears to be shared only by *Kayentasuchus* (Clark and Sues 2002). The lack of mandibular caniniforms also contrasts *Macelognathus* from most other known sphenosuchians (e.g., *Dibothrosuchus*, *Dromicosuchus*, *Hesperosuchus*, *Litargosuchus*, *Sphenosuchus*), although the new taxon shares this condition with *Kayentasuchus* and "*Terrestrisuchus*." The dentaries of *Macelognathus* and *Kayentasuchus* also share the presence of a long symphysis; the symphysis is much shorter in *Sphenosuchus*, *Dibothrosuchus*, and *Dromicosuchus*, but it is quite long in *Hesperosuchus* and *Pseudhesperosuchus*, even if not nearly as long as in *Macelognathus*. Perhaps the most salient similarity between *Macelognathus* and *Kayentasuchus* is the presence of an edentulous anterior portion of the dentary, a feature apparently unique to these two sphenosuchians.

Fig. 14. Left metatarsal II and III (LACM 4684/128271). (A) and (B) dorsal view, with distal view; (C) and (D) plantar view, with proximal view.

Yet, the degree of heterodonty seen in the dentary of *Macelognathus* seems more pronounced than in *Kayentasuchus* or in any other known member of the group.

Ilium

There exists only limited comparative information about this bone. The sphenosuchian ilium is generally of low profile, like in *Macelognathus*. The latter, however, differs from other sphenosuchian ilia by lacking a distinct supraacetabular crest, which is present in *Dibothrosuchus*, *Dromicosuchus*, *Kayentasuchus*, and "*Terrestrisuchus*." Even if slightly damaged, a supraacetabular ridge also seems to be lacking in *Hallopus*. Unlike in "*Terrestrisuchus*," the ventral margin of the preacetabular process of *Macelognathus* lacks a deep concave posterior indentation. Furthermore, the medial crest that projects from the preacetabular process has not been reported in any other taxon.

Femur

Unlike other crocodylomorphs, at least some sphenosuchians have femoral heads that are set at an approximately right angle with the shaft, suggesting a fully upright (erect) posture. In *Macelognathus*, the femoral head is not only set in this position but it is also round, medially oriented at a 90° angle to the shaft, and separated from the shaft by a distinct neck. The head of most other sphenosuchians (e.g., *Dromicosuchus*, *Hesperosuchus*, *Pseudhesperosuchus*, "*Terrestrisuchus*") is anteroposteriorly compressed. *Kayentasuchus* and perhaps

Hallopus, where the proximal portion of the femur is only preserved as an impression in the holotype of *H. victor*, apparently share the ball-shaped condition of the femoral head of *Macelognathus*. The femoral head is also twisted anteromedially in *Hesperosuchus*, *Pseudhesperosuchus*, *Dromicosuchus*, *Dibothrosuchus*, *Saltoposuchus*, and "*Terrestrisuchus*" (probably based on juvenile specimens of *Saltoposuchus*; Allen 2003); the medially in-turned head of *Kayentasuchus*, and perhaps *Hallopus*, approaches more closely the condition in *Macelognathus*. The degree of medial inflection of the femoral head in *Kayentasuchus*, however, does not reach the condition of *Macelognathus*, where the femoral head faces directly medially at an almost right angle. Nonetheless, the distinct neck that separates the head from the remainder of the femur in *Macelognathus* seems to be absent in all other sphenosuchians; *Kayentasuchus* at most has only an incipient femoral neck.

Tibia

Varying degrees of lateral slanting of the proximal end are typical of sphenosuchian tibiae. The marked degree seen in *Macelognathus* is more similar to that of *Sphenosuchus* than to that of *Dromicosuchus* and *Pseudohesperosuchus*. The tibia in *Macelognathus* is inferred to be longer than the femur, unlike in *Dromicosuchus*.

Fibula

The longitudinal groove centered on the lateral side of the proximal end of the fibula of *Macelognathus* appears to be unique among sphenosuchians; this feature has not been described for *Hesperosuchus*, *Pseudhesperosuchus*, *Sphenosuchus*, or *Kayentasuchus*. *Dromicosuchus* contrasts with the condition of *Macelognathus* in having a lateral ridge on the proximal end of the fibula, which is also the case in crocodyliformes.

Calcaneum

The completely flattened distal end of the condyle of the calcaneum of *Macelognathus* seems to be shared only by *Hallopus*; in *Dromicosuchus*, the end is flattened but not to the extent as in the latter taxa. The vertical crest on the medial base of the calcaneal tuber is unique to *Macelognathus*, although the medial side of the calcaneal tuber in the only known specimen of *Hallopus* is still buried in the matrix, preventing determination of this condition. However, the calcaneum of *Hallopus* appears narrower mediolaterally than that of *Macelognathus*.

Metatarsals

The metatarsals of *Macelognathus* are much slender than those in *Dromicosuchus*, resembling more those of *Hallopus*.

Discussion

The holotype dentary of *Macelognathus vagans*, as well as the new material described here, come from the Upper Jurassic Brushy Basin Member of the Morrison Formation, although the holotype is somewhat younger. The latter comes from Como Bluff, Wyoming, Reed's Quarry 9, which stratigraphically belongs to "zone 5" as opposed to the underlying "zone 4," the stratigraphic level of the FPA, Colo-

rado (Foster 2003, p. 88). However, the paleoenvironment of these two localities was inferred to be similar. Whereas the type locality is attributed to a "Type 1 Pond," a near-channel pond and fine splays environment, the FPA (at least the quarry 4) is considered to belong to the "Type 2 Pond" environment, with near-channel ponds and fine-grained splays (Foster 2003, table 2).

Although identical in structure, the holotype dentaries of *Macelognathus vagans* are clearly larger than the specimens found in the FPA. This can be explained by the fact that specimen LACM 5572/150148 can be identified as a juvenile individual because of the open neurocentral sutures on all of its preserved vertebrae. No vertebrae are preserved in the other small specimens LACM 4684/128272 and 128271, LACM 5572/150211, and LACM 4684/133772.

Besides *Macelognathus*, there are two sphenosuchian taxa, *Hallopus* and *Kayentasuchus*, that seem to be morphologically closest to the new material described in this paper.

The diagnostic features of the holotype dentaries of *Macelognathus*, which are also present in the referred specimens, are the edentulous anterior part of the dentary, the long symphysis, and the considerable dorsoventral flattening of the dentaries towards anterior. These characters are also shared by *Kayentasuchus walkeri*. However, *Kayentasuchus* is distinguished from the material referred here to *Macelognathus* in several mandibular and postcranial features, such as the absence of dental serrations, the presence of a supraacetabular ridge on the ilium, and a less distinct and less medially oriented femoral neck. In addition, *Kayentasuchus* is known only from the Lower Jurassic Kayenta Formation of Arizona.

The stratigraphic and geographic origin of *Hallopus victor*; as noted earlier in the text, still remain uncertain. If the holotype of *Hallopus victor* really comes from the Morrison Formation, its stratigraphic range would correspond to that of *Macelognathus*. Unfortunately, no cranial remains are known of *Hallopus*. There are similarities in some postcranial characters, but the holotype of *Hallopus victor* is so poorly preserved that comparisons between these two taxa are difficult. Like *Macelognathus*, *Hallopus* seems to lack the supraacetabular crest on the ilium. However, in the only known specimen of *Hallopus*, both ends of the tibia are poorly preserved and the proximal portion of the femur is only preserved as an impression. However, the femoral head appears to be ball-shaped and oriented relatively medially, even if not as directly medially as in *Macelognathus*. The calcaneum differs in being mediolaterally much more narrower in *Hallopus* than in *Macelognathus* from the FPA. Unfortunately, the absence or presence of the unusual feature on the calcaneum of *Macelognathus* from the FPA, the remarkable probably tendinous crest on the medial base of the calcaneal tuber cannot be verified in *Hallopus*, because this part of the calcaneum is still embedded in the matrix. Thus, *Hallopus* cannot be fully compared with *Macelognathus* at the present time, and *Macelognathus* may yet prove to be a subjective junior synonym of *Hallopus*.

Conclusions

On the basis of this new sphenosuchian material from the FPA it is possible for the first time to identify the enigmatic

taxon *Macelognathus vagans*, formerly usually referred to dinosaurs, as a sphenosuchian crocodylomorph; this assessment supports its identification by Ostrom (1971) who identified *Macelognathus* as a possible "crocodilian."

The new material of *Macelognathus vagans* also augments our knowledge of the diversity of sphenosuchians. In addition, the new material from the Upper Jurassic Morrison Formation of the FPA extends the known stratigraphic range of sphenosuchians (if they are indeed a monophyletic group) into the latest Jurassic. The fossil record of this group was previously considered to extend from the Late Triassic to the Middle or Late? Jurassic of North and South America, Africa, Europe, and Asia (Clark and Sues 2002). The Late Jurassic record was in dispute because of uncertainty regarding the precise geographic and stratigraphic origin of *Hallopus victor*.

Several new features unique for *Macelognathus* are described, indicating that this taxon is distinct from other sphenosuchian taxa.

Acknowledgments

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