

Leidyosuchus (Crocodylia: Alligatoroidea) from the Upper Cretaceous Kaiparowits Formation (late Campanian) of Utah, USA

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Several crocodyliform lineages inhabited the Western Interior Basin of North America during the late Campanian (Late Cretaceous), with alligatoroids in the Kaiparowits Formation of southern Utah exhibiting exceptional diversity within this setting. A partial skeleton of a previously unknown alligatoroid taxon from the Kaiparowits Formation may represent the fifth alligatoroid and sixth crocodyliform lineage from this unit. The fossil includes the lower jaws, numerous osteoderms, vertebrae, ribs, and a humerus. The lower jaw is generally long and slender, and the dentary features 22 alveoli with conical, non-globidont teeth. The splenial contributes to the posterior quarter of the mandibular symphysis, which extends posteriorly to the level of alveolus 8, and the dorsal process of the surangular is forked around the terminal alveolus. Dorsal midline osteoderms are square. This combination of character states identifies the Kaiparowits taxon as the sister taxon of the early alligatoroid *Leidyosuchus canadensis* from the Late Cretaceous of Alberta, the first verified report of the *Leidyosuchus* (sensu stricto) lineage from the southern Western Interior Basin. This phylogenetic placement is consistent with at least occasional faunal exchanges between northern and southern parts of the Western Interior Basin during the late Campanian, as noted for other reptile clades.

INTRODUCTION

The late Campanian (Late Cretaceous) was a time of notable taxonomic diversity for crocodyliforms in the Western Interior Basin of North America, particularly in comparison to the diversity of crocodyliforms in contemporary North American faunas. In the well-sampled Dinosaur Park Formation of Alberta, at least three distinct species co-existed—the alligatoroids *Leidyosuchus canadensis*, *Stangerochampsia mccabei* (likely including *Albertochampsia langstoni*), and a possible third taxon known only from dentaries (Brochu 1999, Wu 2005)—and up to four are known from the Fruitland and Kirtland formations of New Mexico: the putative goniopholidid neosuchian *Denazinosuchus kirtlandicus*, and the alligatoroids *Brachychampsia montana* and *Deinosuchus hatcheri*, as well as a third possible alligatoroid (Lucas et al. 2006). Even within this context, species diversity within the Kaiparowits Formation of southern Utah—up to five previously reported taxa—is truly remarkable in the number of represented lineages.

The Kaiparowits Formation preserves sediments deposited in a non-marine setting between 76.5 and 74.5 Ma (Roberts et al. 2013), with an increasingly well-sampled vertebrate assemblage, particularly from the lower half of the formation. The crocodyliforms of this formation were recently reviewed by Irmis and colleagues (2013), who noted the presence of a basal neosuchian (possibly closely related to *Denazinosuchus*) as well as at least three alligatoroids: *Brachychampsia* sp., *Deinosuchus hatcheri*, and an unnamed alligatoroid (hereafter referred to as “Taxon A”) lacking globidont dentition. Subsequent fieldwork recovered multiple specimens of a fourth alligatoroid taxon (“Taxon B”) with distinct cranial, appendicular, and osteoderm morphology (Irmis, Sertich and

Titus, *personal communication*, February, 2013). Importantly, with the exception of *Deinosuchus hatcheri*, these previously recovered taxa from the southern part of the Western Interior Basin (WIB) are distinct from penecontemporaneous forms to the north, although they belong to clades with more cosmopolitan distributions.

Here, we report on a hitherto unknown species of alligatoroid from the Kaiparowits Formation that represents the fifth alligatoroid and sixth crocodyliform taxon from this unit. Furthermore, the specimen is closely allied with *Leidyosuchus canadensis* from Alberta, linking another late Campanian alligatoroid of the southern WIB to those of the northern WIB.

Institutional abbreviations

RAM, Raymond M. Alf Museum of Paleontology, Claremont, California, USA; **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **RTMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP**, Laboratory of Vertebrate Palaeontology, University of Alberta, Edmonton, Alberta, Canada; **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA; **UMNH**, Natural History Museum of Utah, Salt Lake City, Utah, USA.

SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin 1789 sensu Benton and Clark 1988
ALLIGATOROIDEA Gray 1844 sensu Norell et al. 1994
Leidyosuchus Lambe 1907

Emended diagnosis—Alligatoroid characterized by a unique combination of features including square dorsal midline osteoderms (shared with *Mecistops*, *Crocodylus* spp. excepting *C. pigotti*, *Osteolamius*, and globidontans excluding

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Brachychampsa and *Tsoabichi*), dentary with alveoli 13 and 14 the largest immediately posterior to alveolus 4 (shared with *Procaimanoidea*, *Arambourgia*, and *Alligator* excepting *A. prenasalis*), and a spur of the surangular bordering the lingual edge of the terminal alveolus (shared with *Borealosuchus sternbergii*, *Caiman crocodilus* and *C. yacare*, Tomistominae, and Gavialidae). Other characteristics may define the clade *Leidyosuchus*, but cannot be evaluated with currently known material from the clade.

Leidyosuchus sp.

Diagnosis—*Leidyosuchus* sp. is differentiated from *L. canadensis* in having a narrow symphyseal region of the lower jaw (width:length ratio <0.3) as well as having a rounded termination of the angular above foramen intermandibularis caudalis.

Referred material—RAM 14527, partial skeleton including partial lower jaws, left humerus, cervical rib, dorsal rib, cervical vertebra, dorsal vertebrae, and numerous osteoderms.

Locality—RAM V201017, Grand Staircase-Escalante National Monument, Garfield County, Utah, USA. Detailed locality data are on file at RAM and are available to qualified investigators upon request.

Horizon—Upper portion of the middle unit of the Kaiparowits Formation, 17 m above an ash bed tentatively correlated to ash KBC-109, which has been dated to 75.51 ± 0.15 Ma (late Campanian; Roberts et al. 2005, 2013). The specimen was disarticulated but closely associated across a 3 m² area, at the base of an indurated tabular sandstone with abundant plant fragments and clay clasts. Associated specimens included lepisosteid actinopterygian scales, unionid bivalve molluscs, and a testudinean humerus.

Comments—Because the material is relatively incomplete, we refrain from naming a new species at this point in time.

Description

Lower jaws—This description of RAM 14527 is based upon the more complete, and completely-prepared right ramus of the mandible unless otherwise indicated. In overall profile, the lower jaw (Fig. 1) is long and slender as compared to most known alligatoroids.

The dentary has a maximum length of 354 mm, measured from the anterior end to the posterior end of the process bounding the dorsum of the external mandibular fenestra. This places the specimen in the same general size range as the largest specimens of *Leidyosuchus canadensis* (Table 1; Wu et al. 2001). In lateral view (Fig. 1C, D), the dorsal margin is strongly convex in the interval containing alveoli 3 through 5, strongly concave at alveoli 6 through 10, and convex again

to approximately alveolus 15. In dorsal view (Fig. 1E, F), the splenial-dentary suture is fairly straight along its entire length. The dentary forms nearly the entirety of the dorsal margin of the external mandibular fenestra, and at least the proximal quarter of the ventral margin. The external mandibular fenestra is roughly triangular, with the dorsal border the longest (Fig. 1C, D). In greatest dimensions, the fenestra is 50 mm long by 22 mm tall.

The dentary of RAM 14527 possesses 23 alveoli and 12 *in-situ* teeth; a number of loose teeth with roots were also recovered in association with the specimen. Teeth are conical, slightly lingually curved, and range from 4.5 mm to 15.8 mm long (excluding the root). None of the teeth, even those in more posterior positions, approach the bulbous morphology observed in *Brachychampsa*, other globidontans, or hylaeochampsids (Norell et al. 1994; Brochu 1999; Delfino et al., 2008; Ösi 2008). Each tooth has a subtle carina, and parallel, subdued striations converge on the apex of each tooth. In dorsal view, the first three teeth are distinctly separated and unequal in size, with the first only slightly projecting anteriorly, consistent with other crocodylians. Alveoli 3 and 4 are closely spaced, nearly equal in size, and separated by only a thin lamina, effectively making the alveoli confluent, as in *Diplocynodon* spp., *Deinosuchus riograndensis*, *Borealosuchus* spp., and *L. canadensis* (Brochu 1999, Brochu et al. 2012). Based on alveolar diameter, the largest teeth are presumably in alveoli 3 and 4 and 13 and 14. Enlarged teeth in the latter two positions are characteristic of some basal alligatoroids, such as *L. canadensis* and *Alligator*, among others (Brochu 2004); subsequent alveoli are progressively smaller in all of these taxa. The posterior three teeth in the dentary are similar in size and shape to those located in the concavity of the symphysis, representing another trait of basal alligatoroids (Wu et al. 2001). A very subtle depression medial to alveoli 9 and 10 may represent an occlusal pit, but no other obvious pits are evident elsewhere along the dentary, nor do occlusal grooves occur on the lateral surface.

The symphysis extends to alveolus 8 (Fig. 1F), with only the posterior 20% of the symphysis composed of the splenial, as in some *Borealosuchus* spp. and *L. canadensis*, among many other crocodylians (Wu et al. 2001). In medial view, the symphysis is oval (99 mm long and 27 mm tall; Fig. 1A, B). In dorsal view, the symphyseal region of the jaw is elongate, with a subtle narrowing centered at the seventh alveolus. Including both splenial and dentary, the minimum width of the right ramus of the mandible at the symphysis is 27 mm, and the maximum width is 29 mm. Overall, the symphyseal region in RAM 14527 is relatively longer and narrower than seen in specimens of *L. canadensis*, but approximately the

► **Figure 1A–H.** Lower jaws of *Leidyosuchus* sp., RAM 14527, scale bar=10 cm. **A, B.** Right lower jaw in medial view. **C, D.** Same in lateral view. **E, F.** Same in dorsal view. **G, H.** Detail of left lower jaw in medial view. Abbreviations: **a**, angular; **afio**, anterior foramen intermandibularis oralis; **d**, dentary; **dsym**, dentary portion of symphysis; **emf**, external mandibular fenestra; **fic**, foramen intermandibularis caudalis; **sa**, surangular; **scor**, sutural surface for coronoid; **sp**, splenial; **span**, sutural surface for splenial on angular; **psym**, splenial portion of symphysis. Numbers indicate dental positions, and dashed lines indicate sutural contacts with missing elements.

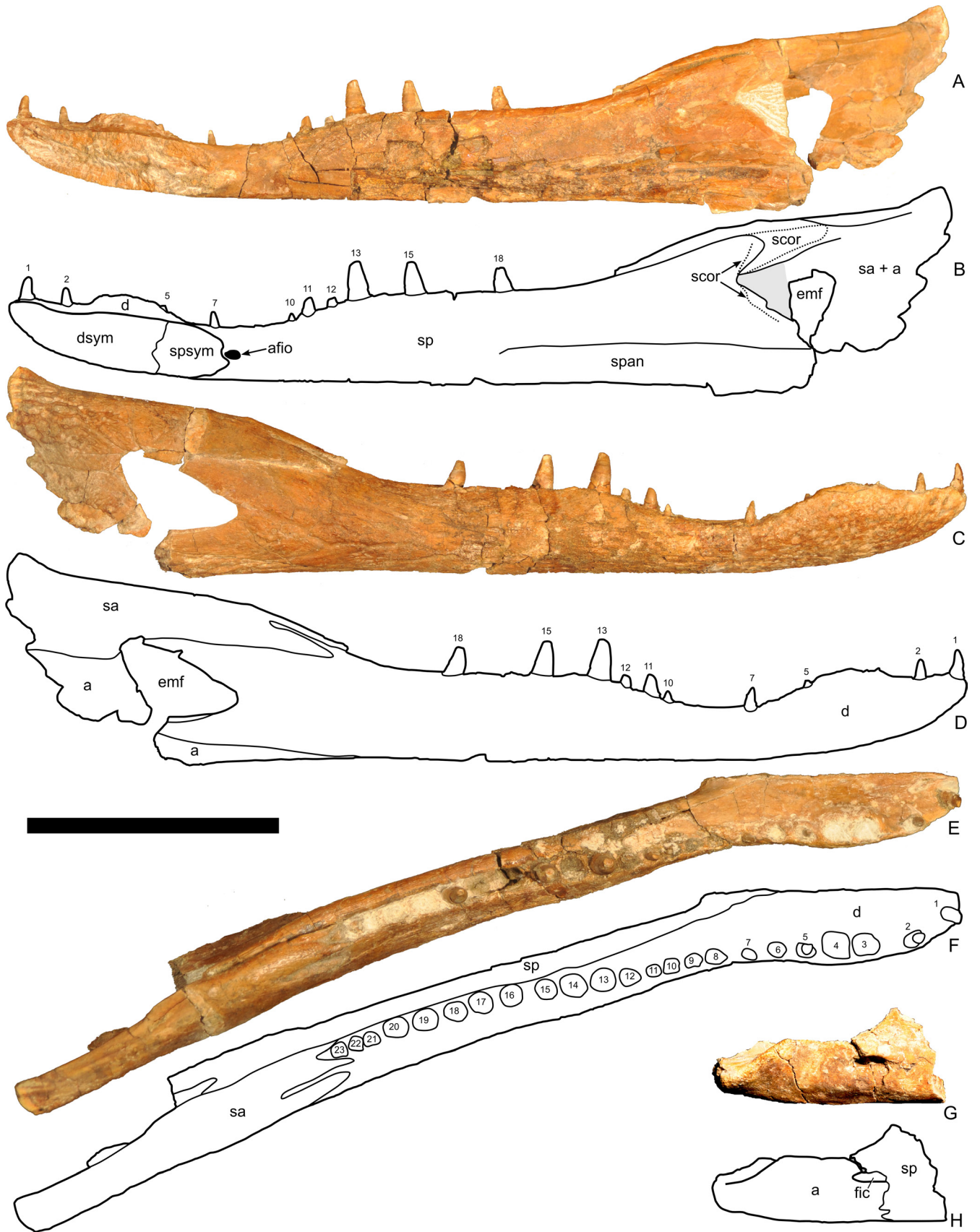


Table 1. Measurements of mandibular symphysis in RAM 14527 and *Leidyosuchus canadensis* (RTMP specimens), in millimeters. All measurements for the latter were taken from scaled photographs. Width is maximum medio-lateral dimension in dorsal view; height is maximum dorso-ventral dimension in medial view. Ratios are indicated by W:L (width:length) and H:L (height:length).

Specimen	Length	Width	Height	W:L	H:L
RAM 14527	99	29	27	0.29	0.27
RTMP 81.16.181	81	42	22	0.52	0.35
RTMP 81.16.216	71	39	24	0.55	0.34
RTMP 86.221.1	81	47	—	0.58	—

same height (Table 1).

Viewed dorsally, the splenial is 228 mm in maximum anteroposterior length. In relation to neighboring bones, its posterior end extends to the middle of the surangular and its anterior end terminates at alveolus 6 (Fig. 1E, F), similar to the condition in *L. canadensis* and *Borealosuchus* spp. (Wu et al. 2001). The width of the splenial remains nearly consistent throughout the element, tapering only at its contribution to the mandibular symphysis. A distinct anterior foramen intermandibularis oralis opens just posterior to the symphysis (Fig. 1B). The presence of a foramen intermandibularis medius and posterior foramina intermandibularis oralis cannot be evaluated in RAM 14527, because these areas are fractured or missing. The splenial contributes broadly to the medial wall of alveoli 13 through 22. The splenial contributes 22 mm to the mandibular symphysis and extends at least 60 mm past the terminal alveolus (the posterodorsal-most part of the process is broken). In medial view, the dorsal margin of the splenial has a sinuous profile similar to that of the dentary. At its posteroventral-most extent, the splenial forms the entire anterior and most of the dorsal margin of foramen intermandibularis caudalis, bluntly abutting the angular dorsal to the foramen and articulating along a sinuous suture ventral to the foramen (Fig. 1G, H). *Leidyosuchus canadensis* has previously been scored as having an acute termination of the angular against the splenial in this region (Brochu et al. 2012). The posterodorsal portion of the splenial is widely notched to conform to the bounds of the internal mandibular fenestra, with a scar for attachment of the coronoid (Fig. 1A, B).

In lateral view, the angular makes up the posteroventral portion of the ramus of the mandible, as well as much of the ventral border of the external mandibular fenestra (Fig. 1C, D). The angular and dentary contributions to the margin parallel each other, with the angular medial to the dentary. In medial view, the angular forms the ventral and posterior margins of the fenestra intermandibularis caudalis. In ventral view, the angular inserts between the splenial and dentary. The posterior end of the angular is not preserved.

The surangular forms the posterodorsal margin of the lower jaw, as preserved in RAM 14527 (Fig. 1C, D). The greater portion of the dorsal margin is gently concave, with a slight convexity at the posterior quarter. The surangular forms the posterodorsal corner of the external mandibular fenestra, and the bone is deepest posterior to that opening, with a relatively straight contact with the angular. The dorsal process is slightly longer than the ventral process of the surangular, and the two are separated by a deep and narrow gap that exposes the dentary beneath. The dorsal process is forked around the terminal alveolus, so that a “spur” of the surangular borders part of the dentary tooth row (Fig. 1E, F). A similar condition is observed in *L. canadensis* (RTMP 81.16.181, UALVP 40594), *Borealosuchus sternbergii*, crocodylids and others, but not in globidontans such as *Brachychampsa* spp. (Brochu et al. 2012). The entire lateral surface of the surangular is sculptured along its preserved extent (Fig. 1C), although the texture along the anterior portion is much less distinct than that on the posterior portion.

Axial skeleton—The parapophyses of the most complete vertebra are located on the lateral surface of the centrum and it is therefore identified as a cervical vertebra (Fig. 2A–C). The centrum is strongly procoelous, with a prominent and anteroventrally projecting hypopophysis, as seen in other eusuchians. The centrum is 33 mm long and 17 mm tall by 18 mm wide on its cranial articular surface, and the neurocentral sutures are fully closed. The neural canal is stretched dorsoventrally (14 mm tall by 10 mm wide), reflected similarly in a dorsoventrally elongated neural arch. The mediolaterally elongate (15 mm wide by 9 mm long) postzygapophyses face ventrolaterally. The articular surfaces of the diapophyses are triangular and project posteroventrally. Fragmentary dorsal vertebrae do not preserve any noteworthy morphology.

One partial cervical rib and one right dorsal rib from approximately the middle of the series (based on comparison with *Borealosuchus*; Erickson 1976) are preserved. In the dorsal rib (Fig. 2D), the capitulum is longer than the tuberculum, with 43 mm separating the ends of the two. The distal end of the rib is missing.

Appendicular skeleton—A single left humerus (Fig. 2L), which lacks the proximal end and most of the deltopectoral crest, has a preserved length of 167 mm. Its distal end is 44 mm wide, and the diameter and circumference at midshaft are 20 and 74 mm, respectively. The deltopectoral crest extends for approximately the proximal third of the humeral shaft. The bone is robust, similar to humeri in most other crocodylians (including *Leidyosuchus canadensis*), but this robusticity differs from the much more slender humerus seen in *Borealosuchus* spp. (Brochu 1997). The medial condyle on the distal end is bulbous and more prominent than the lateral condyle. The lateral surface of the lateral condyle is flattened.

Osteoderms—All of the osteoderms (Fig. 2E–K) are thin and lack an anterior process (unlike non-alligatoroids such as *Borealosuchus*). They can be divided into four morphotypes based on their shape in dorsal view: square ($n = 18$), triangular

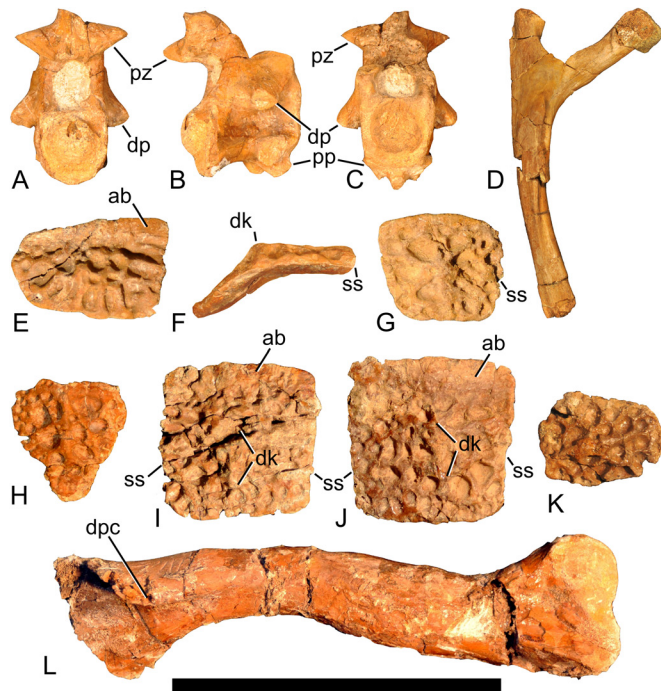


Figure 2A–L. Postcrania of *Leidyosuchus* sp., RAM 14527, scale bar=10 cm. **A–C**, mid-cervical vertebra. **A**. Vertebra in posterior view. **B**. Same in right lateral view. **C**. Same in anterior view. **D**. Rib in cranial view. **E–K**. Osteoderms in dorsal view. The sole exception is **F**, which is a posterior view of the osteoderm shown in **E**. **L**. Left humerus in ventral view (proximal end to right). Abbreviations: **ab**, anterior bar; **dk**, dorsal keel; **dp**, diapophysis; **dpc**, deltopectoral crest; **pp**, parapophysis; **pz**, postzygapophysis; **ss**, sutural surface.

($n = 5$), rounded ($n = 5$), and rectangular ($n = 3$). There are no osteoderms comparable in morphology to ventral positions as described for *Diplocynodon*, *Borealosuchus* or *L. canadensis* (Brochu 1997, Irmis et al. 2013); i.e., with a combination of extremely enlarged anterior bars and well-defined sutures. Because many other osteoderm positions are not preserved in RAM 14527, we cannot make a firm statement on presence or absence of ventral osteoderms. Life positions of osteoderms were inferred from comparisons with extant and fossil taxa.

Square osteoderms (Fig. 2I, J) are the largest and most abundant elements in the sample (up to 55 mm in maximum width), and we interpret them as representing the dorsal midline (or immediately lateral to the midline) position. These osteoderms tend to have subdued anteroposterior dorsal keels, gentle dorsoventral arching, a short and smooth anterior bar on the dorsal surface (< 20 percent of total osteoderm length), and irregularly-sized but closely spaced pits up to 8 mm. Finely-detailed sutures occur on the medial and lateral borders. Slightly smaller osteoderms are more trapezoidal (Fig. 2G), with slight arching, smaller pits, no keeling, and sutures on only one edge. These may represent more laterally-positioned osteoderms.

A rectangular osteoderm morphotype (Fig. 2E, F) is

strongly arched and generally keeled, with pits ranging from circular to oval (~4 mm average diameter). The anterior bar tapers in width across the diameter of the osteoderms, and sutures are only on the medial border. These osteoderms are interpreted to occupy anterolateral positions from the dorsal surface.

Triangular osteoderms (Fig. 2H) show subdued keeling and arching, and range from 25 to 30 mm in maximum length. Pits are relatively large, measuring 8 mm in maximum diameter. Rounded osteoderms (Fig. 2K) lack keeling, arching, and sutures, and average 30 mm in maximum diameter. In the absence of sutures or anterior bars, both triangular and rounded osteoderms are interpreted as originating from lateral positions on the body or the proximal parts of the limbs.

PHYLOGENETIC ANALYSIS

In order to better elucidate its relationships among Eusuchia, RAM 14527 was entered into the matrix of Brochu et al. (2012); we were able to score the specimen for 20 of 179 characters (11%). The scoring for character 62 (spur of surangular bordering lingual edge of dentary tooth row) in *L. canadensis* was changed from absent (1) to present (0), based on RTMP 81.16.181 and UALVP 40594. Codings for *Diplocynodon deponiae*, *D. elavericus*, and *D. ungeri* were adapted from Delfino and Smith (2012). The matrix (Table 1S) was analyzed using a traditional search in TNT 1.1 (Goloboff et al. 2008), with 1,000 replicates using Tree Bisection Reconnection (TBR), saving 1,000 trees per replication, and *Bernissartia* as the outgroup. Characters were unordered.

A total of 23,040 equally parsimonious trees of 685 steps each were recovered (consistency index = 0.335; retention index = 0.802), placing RAM 14527 within Alligatoroidea as the sister taxon of *L. canadensis* (Fig. 3, Fig. 1S). Two extra steps were required to collapse RAM 14527 to a polytomy at the base of Alligatoroidea, and four extra steps were required to collapse RAM 14527 to the base of Crocodylia. RAM 14527 and *L. canadensis* are united by three unambiguous synapomorphies, including square dorsal midline osteoderms, a dentary with alveoli 13 and 14 the largest alveoli in succession posterior to alveolus 4, and a spur of the surangular bordering the lingual edge of the terminal alveolus. All of these features are found individually in other crocodylians, but no other taxa besides *L. canadensis* and RAM 14527 possess this exact combination. An additional five steps were required to force RAM 14527 as the sister taxon to *Borealosuchus*.

DISCUSSION

A combination of synapomorphies identified in the phylogenetic analysis confirms a sister relationship between RAM 14527 and *Leidyosuchus canadensis*, but differences in the proportions of the symphyseal region (Table 1) as well as in the shape of the termination of the angular above foramen intermandibularis caudalis suggest that they are probably distinct species. We tentatively assign RAM 14527 to *Leidyosuchus* sp., but choose not to erect a new species

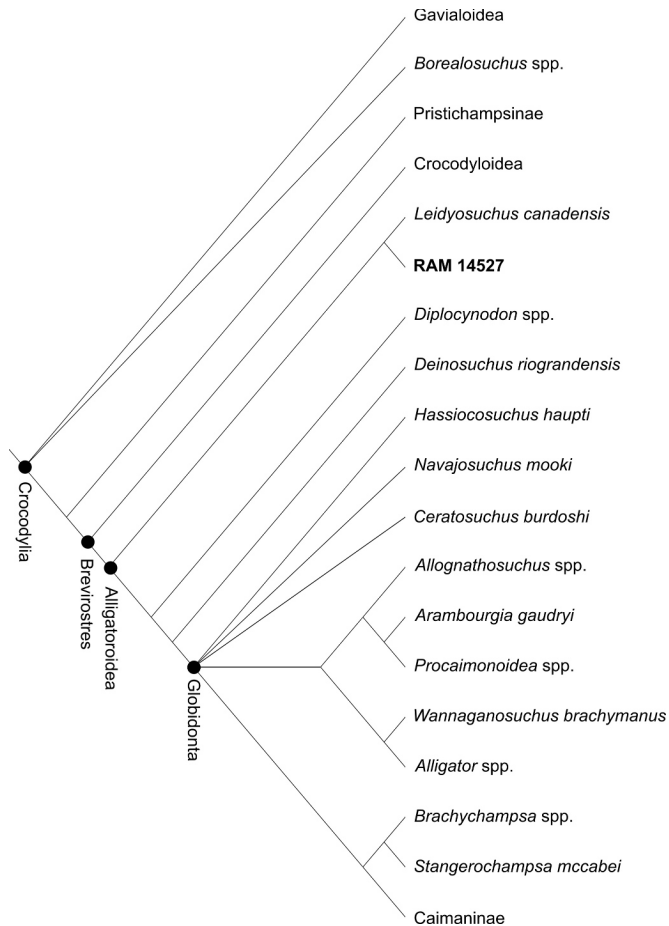


Figure 3. Strict consensus of 3,072 most parsimonious trees from phylogenetic analysis of Crocodylia, including RAM 14527 (consistency index equals 0.335; retention index equals 0.802). Some clades have been collapsed from species-level operational taxonomic units to conserve space (Gavialoidea, Pristichampsinae, Crocodyloidea, *Borealosuchus*, *Diplocynodon*, *Allognathosuchus*, *Procaimonoidea*, *Alligator*, *Brachychampsa*, and *Caimaninae*); similarly, non-crocodylian outgroup taxa are not shown (*Bernisartia*, *Allodaposuchus*, *Acynodon*, *Hylaeochampsa*, and *Iharkutosuchus*). A complete version, with all taxa shown, is contained in Figure 1S.

in the absence of more complete cranial material from the Kaiparowits Formation. Although numerous isolated teeth and osteoderms from the Kaiparowits Formation and other locales in the southern WIB (Western Interior Basin) have been previously assigned to *Leidyosuchus* (summarized in Irmis et al. 2013), these morphotypes are common across Eusuchia and such referrals are not warranted (Brochu 1997, Irmis et al. 2013). Thus, RAM 14527 is the first confirmed report of *Leidyosuchus* from the southern WIB.

Relative to other alligatoroids reported from the Kaiparowits Formation (Irmis et al., 2013), RAM 14527 is undoubtedly a separate taxon. The dorsoventrally thin osteoderms are definitively different from the inflated osteoderms known from

Deinosuchus hatcheri, and the conical teeth along the length of the dentary and mandibular morphology (including a narrower mandible with splenial participating in the symphysis) are unlike *Brachychampsa* sp. A third, non-globidontan alligatoroid (“Taxon A”; UMNH VP 19268 and possibly UCMP 150283) has a shorter mandibular symphysis and more rounded profile at its anterior end (Irmis et al. 2013) as compared to RAM 14527. A fourth, as yet undescribed alligatoroid (“Taxon B”), also has a shorter mandibular symphysis and restricted sculpturing on the posterolateral corner of the surangular, among other features (Sertich and Titus *personal communication*, February, 2013). Thus, RAM 14527 may suggest that there are a minimum of five alligatoroids in the Kaiparowits Formation: the greatest fossil diversity of this clade in any single North American stratigraphic unit. Because RAM 14527 comes from a higher part of the section than do most other specimens from the Kaiparowits Formation (Roberts et al. 2013), additional work is needed to determine if this taxon, and other taxa from this formation, in turn, are restricted to particular levels in the formation or particular depositional environments.

Undoubtedly, most species of the Kaiparowits Formation are endemic to the southern WIB, and overall differences between the northern and southern faunal assemblages in the WIB are well-supported (Lehman 2001, Gates et al. 2010). Nonetheless, an inferred sister taxon relationship between RAM 14527 from Utah and *L. canadensis* from Alberta implies at least occasional faunal exchanges between North and South. Similar cosmopolitan occurrences of other alligatoroids, including *Deinosuchus hatcheri* and brachychampsids (Irmis et al. 2013) provide additional confirmation within the clade. This is consistent with patterns noted for some other clades (e.g., hadrosaurs and ceratopsids; Gates and Sampson 2007, Sampson et al. 2010), and indicates more complexity in late Campanian biogeography than a simple north-south split (Gates et al. 2010).

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SUPPLEMENTARY INFORMATION

Character list for phylogenetic analysis (see Table 1S). All characters were taken directly from Brochu et al. (2012); that paper provides complete details on sources for characters. The list is reproduced here for the convenience of the reader.

- (1) Ventral tubercle of proatlas more than one-half (0); or no more than one half (1) the width of the dorsal crest.
- (2) Fused proatlas boomerang-shaped (0); strap-shaped (1); or massive and block-shaped (2).
- (3) Proatlas with prominent anterior process (0); or lacks anterior process (1).
- (4) Proatlas has tall dorsal keel (0); or lacks tall dorsal keel; dorsal side smooth (1).

- (5) Atlas intercentrum wedge-shaped in lateral view, with insignificant parapophyseal processes (0); or plate-shaped in lateral view, with prominent parapophyseal processes at maturity (1).
- (6) Dorsal margin of atlantal rib generally smooth with modest dorsal process (0); or with prominent process (1).
- (7) Atlantal ribs without (0); or with (1) very thin medial laminae at anterior end.
- (8) Atlantal ribs lack (0); or possess (1) large articular facets at anterior ends for each other.
- (9) Axial rib tuberculum wide, with broad dorsal tip (0); or narrow, with acute dorsal tip (1).
- (10) Axial rib tuberculum contacts diapophysis late in ontogeny, if at all (0); or early in ontogeny (1).
- (11) Anterior half of axis neural spine oriented horizontally (0); or slopes anteriorly (1).
- (12) Axis neural spine crested (0); or not crested (1).
- (13) Posterior half of axis neural spine wide (0); or narrow (1).
- (14) Axis neural arch lacks (0); or possesses (1) a lateral process (diapophysis).
- (15) Axial hypapophysis located toward the center of centrum (0); or toward the anterior end of centrum (1).
- (16) Axial hypapophysis without (0); or with (1) deep fork.
- (17) Hypapophyseal keels present on eleventh vertebra behind atlas (0); twelfth vertebra behind atlas (1); or tenth vertebra behind atlas (2).
- (18) Third cervical vertebra (first postaxial) with prominent hypapophysis (0); or lacks prominent hypapophysis (1).
- (19) Neural spine on third cervical long, dorsal tip at least half the length of the centrum without the cotyle (0); or short, dorsal tip acute and less than half the length of the centrum without the cotyle (1).
- (20) Cervical and anterior dorsal centra lack (0); or bear (1) deep pits on the ventral surface of the centrum.
- (21) Presacral centra amphicoelous (0); or procoelous (1).
- (22) Anterior sacral rib capitulum projects far anteriorly of tuberculum and is broadly visible in dorsal view (0); or anterior margins of tuberculum and capitulum nearly in same plane, and capitulum largely obscured dorsally (1).
- (23) Scapular blade flares dorsally at maturity (0); or sides of scapular blade sub-parallel; minimal dorsal flare at maturity (1).
- (24) Deltoid crest of scapula very thin at maturity, with sharp margin (0); or very wide at maturity, with broad margin (1).
- (25) Scapulocoracoid synchondrosis closes very late in ontogeny (0); or relatively early in ontogeny (1).
- (26) Scapulocoracoid facet anterior to glenoid fossa uniformly narrow (0); or broad immediately anterior to glenoid fossa, and tapering anteriorly (1).
- (27) Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0); or emerges abruptly from proximal end of humerus and is obviously concave (1).
- (28) *M. teres major* and *M. dorsalis scapulae* insert separately on humerus; scars can be distinguished dorsal to deltopectoral crest (0); or insert with common tendon; single insertion scar (1).
- (29) Olecranon process of ulna narrow and sub-angular (0); or wide and rounded (1).
- (30) Distal extremity of ulna expanded transversely with respect to long axis of bone; maximum width equivalent to that of proximal extremity (0); or proximal extremity considerably wider than distal extremity (1).
- (31) Interclavicle flat along length, without dorsoventral flexure (0); or with moderate dorsoventral flexure (1); or with severe dorsoventral flexure (2).
- (32) Anterior end of interclavicle flat (0); or rod-like (1).
- (33) Iliac anterior process prominent (0); or virtually absent (1).
- (34) Dorsal margin of iliac blade rounded with smooth border (0); or rounded, with modest dorsal indentation (1); or rounded, with strong dorsal indentation (wasp-waisted) (2); or narrow, with dorsal indentation (3); or rounded with smooth border; posterior tip of blade very deep (4).
- (35) Supraacetabular crest narrow (0); or broad (1).
- (36) Limb bones relatively robust, and hind limb much longer than forelimb at maturity (0); or limb bones very long and slender (1).
- (37) *M. caudofemoralis* with single head (0); or with double head (1).
- (38) Dorsal osteoderms not keeled (0); or keeled (1).
- (39) Dorsal midline osteoderms rectangular (0); or nearly square (1).
- (40) Four (0); six (1); eight (2); or ten (3) contiguous dorsal osteoderms per row at maturity.
- (41) Nuchal shield grades continuously into dorsal shield (0); or differentiated from dorsal shield, with four nuchal osteoderms (1); or differentiated from dorsal shield and six nuchal osteoderms with four central and two lateral (2); or differentiated from dorsal shield, with eight nuchal osteoderms in two parallel rows (3).
- (42) Ventral armor absent (0); or present and comprising single ventral osteoderms (1); or present and comprising paired ventral ossifications that suture together (2).
- (43) Anterior margin of dorsal midline osteoderms with anterior process (0); or smooth, without process (1).
- (44) Ventral scales have (0); or lack (1) follicle gland pores.
- (45) Ventral collar scales not enlarged relative to other ventral scales (0); or in a single enlarged row (1); or

- in two parallel enlarged rows (2).
- (46) Median pelvic keel scales form two parallel rows along most of tail length (0); or form single row along tail (1); or merge with lateral keel scales (2).
- (47) Alveoli for dentary teeth 3 and 4 nearly same size and confluent (0); or fourth alveolus larger than third, and alveoli are separated (1).
- (48) Anterior dentary teeth strongly procumbent (0); or project anterodorsally (1).
- (49) Dentary symphysis extends to fourth or fifth alveolus (0); or sixth through eighth alveolus (1); or behind eighth alveolus (2).
- (50) Dentary gently curved (0); deeply curved (1); or linear (2) between fourth and tenth alveoli.
- (51) Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14; (1) 13 or 14 and a series behind it; (2) 11 or 12; or (3) no differentiation; or (4) behind 14.
- (52) Splenial with anterior perforation for mandibular ramus of cranial nerve V (0); or lacks anterior perforation for mandibular ramus of cranial nerve V (1).
- (53) Mandibular ramus of cranial nerve V exits splenial anteriorly only (0); or splenial has singular perforation for mandibular ramus of cranial nerve V posteriorly (1); or splenial has double perforation for mandibular ramus of cranial nerve V posteriorly (2).
- (54) Splenial participates in mandibular symphysis; splenial symphysis adjacent to no more than five dentary alveoli (0); or splenial excluded from mandibular symphysis; anterior tip of splenial passes ventral to Meckelian groove (1); or splenial excluded from mandibular symphysis; anterior tip of splenial passes dorsal to Meckelian groove (2); or deep splenial symphysis, longer than five dentary alveoli; splenial forms wide 'V' within symphysis (3); or deep splenial symphysis, longer than five dentary alveoli; splenial constricted within symphysis and forms narrow V (4).
- (55) Coronoid bounds posterior half of foramen intermandibularis medius (0); or completely surrounds foramen intermandibularis medius at maturity (1); or obliterates foramen intermandibularis medius at maturity (2).
- (56) Superior edge of coronoid slopes strongly anteriorly (0); or almost horizontal (1).
- (57) Inferior process of coronoid laps strongly over inner surface of Meckelian fossa (0); or remains largely on medial surface of mandible (1).
- (58) Coronoid imperforate (0); or with perforation posterior to foramen intermandibularis medius (1).
- (59) Process of splenial separates angular and coronoid (0); or no splenial process between angular and coronoid (1).
- (60) Angular-surangular suture contacts external mandibular fenestra at posterior angle at maturity (0); or passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1).
- (61) Anterior processes of surangular unequal (0); or sub-equal to equal (1).
- (62) Surangular with spur bordering the dentary tooth row lingually for at least one alveolus length (0); or lacking such spur (1).
- (63) External mandibular fenestra absent (0); or present (1); or present and very large; most of foramen intermandibularis caudalis visible in lateral view (2).
- (64) Surangular-dentary suture intersects external mandibular fenestra anterior to posterodorsal corner (0); or at posterodorsal corner (1).
- (65) Angular extends dorsally toward or beyond anterior end of foramen intermandibularis caudalis; anterior tip acute (0); or does not extend dorsally beyond anterior end of foramen intermandibularis caudalis; anterior tip very blunt (1).
- (66) Surangular-angular suture lingually meets articular at ventral tip (0); or dorsal to tip (1).
- (67) Surangular continues to dorsal tip of lateral wall of glenoid fossa (0); or truncated and not continuing dorsally (1).
- (68) Articular-surangular suture simple (0); or articular bears anterior lamina dorsal to lingual foramen (1); or articular bears anterior lamina ventral to lingual foramen (2); or bears laminae above and below foramen (3).
- (69) Lingual foramen for articular artery and alveolar nerve perforates surangular entirely (0); or perforates surangular/angular suture (1).
- (70) Foramen aerum at extreme lingual margin of retroarticular process (0); or set in from margin of retroarticular process (1).
- (71) Retroarticular process projects posteriorly (0); or projects posterodorsally (1).
- (72) Surangular extends to posterior end of retroarticular process (0); or pinched off anterior to tip of retroarticular process (1).
- (73) Surangular-articular suture oriented anteroposteriorly (0); or bowed strongly laterally (1) within glenoid fossa.
- (74) Sulcus between articular and surangular (0); or articular flush against surangular (1).
- (75) Dorsal projection of hyoid cornu flat (0); or rodlike (1).
- (76) Dorsal projection of hyoid cornu narrow, with parallel sides (0); or flared (1).
- (77) Lingual osmoregulatory pores small (0); or large (1).
- (78) Tongue with (0); or without (1) keratinized surface.
- (79) Teeth and alveoli of maxilla and/or dentary circular in cross-section (0); or posterior teeth laterally compressed (1); or all teeth compressed (2).
- (80) Maxillary and dentary teeth with smooth carinae (0); or serrated (1).
- (81) Naris projects anterodorsally (0); or dorsally (1).

- (82) External naris bisected by nasals (0); or nasals contact external naris, but do not bisect it (1); or nasals excluded, at least externally, from naris; nasals and premaxillae still in contact (2); or nasals and premaxillae not in contact (3).
- (83) Naris circular or keyhole-shaped (0); or wider than long (1); or anteroposteriorly long and prominently teardrop-shaped (2).
- (84) External naris of reproductively mature males remains similar to that of females (0); or develops bony excrescence (ghara) (1).
- (85) External naris opens flush with dorsal surface of premaxillae (0); or circumscribed by thin crest (1).
- (86) Premaxillary surface lateral to naris smooth (0); or with deep notch lateral to naris (1).
- (87) Premaxilla has five teeth (0); or four teeth (1) early in post-hatching ontogeny.
- (88) Incisive foramen small, less than half the greatest width of premaxillae (0); or large, more than half the greatest width of premaxillae (1); or large, and intersects premaxillary-maxillary suture (2).
- (89) Incisive foramen completely situated far from premaxillary tooth row, at the level of the second or third alveolus (0); or abuts premaxillary tooth row (1); or projects between first premaxillary teeth (2).
- (90) Dorsal premaxillary processes short, not extending beyond third maxillary alveolus (0); or long, extending beyond third maxillary alveolus (1).
- (91) Dentary tooth 4 occludes in notch between premaxilla and maxilla early in ontogeny (0); or occludes in a pit between premaxilla and maxilla; no notch early in ontogeny (1).
- (92) All dentary teeth occlude lingual to maxillary teeth (0); or occlusion pit between seventh and eight maxillary teeth; all other dentary teeth occlude lingually (1); or dentary teeth occlude in line with maxillary tooth row (2).
- (93) Largest maxillary alveolus is 3 (0); 5 (1); 4 (2); 4 and 5 are same size (3); 6 (4); or maxillary teeth homodont (5); or maxillary alveoli gradually increase in diameter posteriorly toward penultimate alveolus (6).
- (94) Maxillary tooth row curved medially or linear (0); or curves laterally broadly (1) posterior to first six maxillary alveoli.
- (95) Dorsal surface of rostrum curves smoothly (0); or bears medial dorsal boss (1).
- (96) Canthi rostralii absent or very modest (0); or very prominent (1) at maturity.
- (97) Preorbital ridges absent or very modest (0); or very prominent (1) at maturity.
- (98) Vomer entirely obscured by premaxilla and maxilla (0); or exposed on palate at premaxillary-maxillary suture (1).
- (99) Vomer entirely obscured by maxillae and palatines (0); or exposed on palate between palatines (1).
- (100) Surface of maxilla within narial canal imperforate (0); or with a linear array of pits (1).
- (101) Medial jugal foramen small (0); or very large (1).
- (102) Maxillary foramen for palatine ramus of cranial nerve V small or not present (0); or very large (1).
- (103) Ectopterygoid abuts maxillary tooth row (0); or maxilla broadly separates ectopterygoid from maxillary tooth row (1).
- (104) Maxilla terminates in palatal view anterior to lower temporal bar (0); or comprises part of the lower temporal bar (1).
- (105) Penultimate maxillary alveolus less than (0); or more than (1) twice the diameter of the last maxillary alveolus.
- (106) Prefrontal dorsal surface smooth adjacent to orbital rim (0); or bearing discrete knoblike processes (1).
- (107) Dorsal half of prefrontal pillar narrow (0); or expanded anteroposteriorly (1).
- (108) Medial process of prefrontal pillar expanded dorsoventrally (0); or anteroposteriorly (1).
- (109) Prefrontal pillar solid (0); or with large pneumatic recess (1).
- (110) Medial process of prefrontal pillar wide (0); or constricted (1) at base.
- (111) Maxilla has linear medial margin adjacent to suborbital fenestra (0); or bears broad shelf extending into fenestra, making lateral margin concave (1).
- (112) Anterior face of palatine process rounded or pointed anteriorly (0); or notched anteriorly (1).
- (113) Anterior ectopterygoid process tapers to a point (0); or forked (1).
- (114) Palatine process extends (0); or does not extend (1) significantly beyond anterior end of suborbital fenestra.
- (115) Palatine process generally broad anteriorly (0); or in form of thin wedge (1).
- (116) Lateral edges of palatines smooth anteriorly (0); or with lateral process projecting from palatines into suborbital fenestrae (1).
- (117) Palatine-ptyergoid suture nearly at (0); or far from (1) posterior angle of suborbital fenestra.
- (118) Pterygoid ramus of ectopterygoid straight, posterolateral margin of suborbital fenestra linear (0); or ramus bowed, posterolateral margin of fenestra concave (1).
- (119) Lateral edges of palatines parallel posteriorly (0); or flare posteriorly, producing shelf (1).
- (120) Anterior border of the choana is comprised of the palatines (0); or choana entirely surrounded by pterygoids (1).
- (121) Choana projects posteroventrally (0); or anteroventrally (1) at maturity.
- (122) Pterygoid surface lateral and anterior to internal choana flush with choanal margin (0); or pushed inward anterolateral to choanal aperture (1); or

- pushed inward around choana to form neck surrounding aperture (2); or everted from flat surface to form neck surrounding aperture (3).
- (123) Posterior rim of internal choana not deeply notched (0); or deeply notched (1).
- (124) Internal choana not septate (0); or with septum that remains recessed within choana (1); or with septum that projects out of choana (2).
- (125) Ectopterygoid-pterygoid flexure disappears during ontogeny (0); or remains throughout ontogeny (1).
- (126) Ectopterygoid extends (0); or does not extend (1) to posterior tip of lateral pterygoid flange at maturity.
- (127) Lacrimal makes broad contact with nasal; no posterior process of maxilla (0); or maxilla with posterior process within lacrimal (1); or maxilla with posterior process between lacrimal and prefrontal (2).
- (128) Prefrontals separated by frontals and nasals (0); or prefrontals meet medially (1).
- (129) Lacrimal longer than prefrontal (0); or prefrontal longer than lacrimal (1); or lacrimal and prefrontal both elongate and nearly the same length (2).
- (130) Ectopterygoid extends along medial face of postorbital bar (0); or stops abruptly ventral to postorbital bar (1).
- (131) Postorbital bar massive (0); or slender (1).
- (132) Postorbital bar bears process that is prominent, dorsoventrally broad, and divisible into two spines (0); or bears process that is short and generally not prominent (1).
- (133) Ventral margin of postorbital bar flush with lateral jugal surface (0); or inset from lateral jugal surface (1).
- (134) Postorbital bar continuous with anterolateral edge of skull table (0); or inset (1).
- (135) Margin of orbit flush with skull surface (0); or dorsal edges of orbits upturned (1); or orbital margin telescoped (2).
- (136) Ventral margin of orbit circular (0); or with prominent notch (1).
- (137) Palpebral forms from single ossification (0); or from multiple ossifications (1).
- (138) Quadratojugal spine prominent at maturity (0); or greatly reduced or absent at maturity (1).
- (139) Quadratojugal spine low, near posterior angle of infratemporal fenestra (0); or high, between posterior and superior angles of infratemporal fenestra (1).
- (140) Quadratojugal forms posterior angle of infratemporal fenestra (0); or jugal forms posterior angle of infratemporal fenestra (1); or quadratojugal-jugal suture lies at posterior angle of infratemporal fenestra (2).
- (141) Postorbital neither contacts quadrate nor quadratojugal medially (0); or contacts quadratojugal, but not quadrate, medially (1); or contacts quadrate and quadratojugal at dorsal angle of infratemporal fenestra (2); or contacts quadratojugal with significant descending process (3).
- (142) Quadratojugal bears long anterior process along lower temporal bar (0); or bears modest process, or none at all, along lower temporal bar (1).
- (143) Quadratojugal extends to superior angle of infratemporal fenestra (0); or does not extend to superior angle of infratemporal fenestra; quadrate participates in fenestra (1).
- (144) Postorbital-squamosal suture oriented ventrally (0); or passes medially (1) ventral to skull table.
- (145) Dorsal and ventral rims of squamosal groove for external ear valve musculature parallel (0); or squamosal groove flares anteriorly (1).
- (146) Squamosal-quadrate suture extends dorsally along posterior margin of external auditory meatus (0); or extends only to posteroventral corner of external auditory meatus (1).
- (147) Posterior margin of otic aperture smooth (0); or bowed (1).
- (148) Frontoparietal suture deeply within supratemporal fenestra; frontal prevents broad contact between postorbital and parietal (0); or suture makes modest entry into supratemporal fenestra at maturity; postorbital and parietal in broad contact (1); or suture on skull table entirely (2).
- (149) Frontoparietal suture concavoconvex (0); or linear (1) between supratemporal fenestrae.
- (150) Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0); or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity (1); or supratemporal fenestra closes during ontogeny (2).
- (151) Shallow fossa at anteromedial corner of supratemporal fenestra or no such fossa (0); anteromedial corner of supratemporal fenestra smooth (1).
- (152) Medial parietal wall of supratemporal fenestra imperforate (0); or bearing foramina (1).
- (153) Parietal and squamosal widely separated by quadrate on posterior wall of supratemporal fenestra (0); or parietal and squamosal approach each other on posterior wall of supratemporal fenestra without actually making contact (1); or parietal and squamosal meet along posterior wall of supratemporal fenestra (2).
- (154) Skull table surface slopes ventrally from sagittal axis (0); or planar (1) at maturity.
- (155) Posterolateral margin of squamosal horizontal or nearly so (0); or upturned to form a discrete horn (1).
- (156) Mature skull table with broad curvature; short posterolateral squamosal rami along paroccipital process or with nearly horizontal sides (0); or significant posterolateral squamosal rami along paroccipital process (1).
- (157) Squamosal does not extend (0); or extends (1) ventrolaterally to lateral extent of paroccipital process.
- (158) Supraoccipital exposure on dorsal skull table small (0); absent (1); large (2); or large such that parietal

- is excluded from posterior edge of table (3).
- (159) Anterior foramen for palatine ramus of cranial nerve VII ventrolateral (0); or ventral (1) to basisphenoid rostrum.
- (160) Sulcus on anterior braincase wall lateral to basisphenoid rostrum (0); or braincase wall lateral to basisphenoid rostrum smooth; no sulcus (1).
- (161) Basisphenoid not exposed extensively (0); or exposed extensively (1) on braincase wall anterior to trigeminal foramen.
- (162) Extensive exposure of prootic on external braincase wall (0); or prootic largely obscured by quadrate and laterosphenoid externally (1).
- (163) Laterosphenoid bridge comprised entirely of laterosphenoid (0); or with ascending process or palatine (1).
- (164) Capitate process of laterosphenoid oriented laterally (0); or anteroposteriorly (1) toward midline.
- (165) Parietal with recess communicating with pneumatic system (0); or solid, without recess (1).
- (166) Significant ventral quadrate process on lateral braincase wall (0); or quadrate-ptyergoid suture linear from basisphenoid exposure to trigeminal foramen (1).
- (167) Lateral carotid foramen opens lateral (0); or dorsal (1) to basisphenoid at maturity.
- (168) External surface of basioccipital ventral to occipital condyle oriented posteroventrally (0); or posteriorly (1) at maturity.
- (169) Posterior pterygoid processes tall and prominent (0); or small and project posteroventrally (1); or small and project posteriorly (2).
- (170) Basisphenoid thin (0); or anteroposteriorly wide (1) ventral to basioccipital.
- (171) Basisphenoid not broadly exposed ventral to basioccipital at maturity; pterygoid short ventral to median eustachian opening (0); or basisphenoid exposed as broad sheet ventral to basioccipital at maturity; pterygoid tall ventral to median eustachian opening (1).
- (172) Exoccipital with very prominent boss on paroccipital process; process lateral to cranioquadrate opening short (0); or exoccipital with small or no boss on paroccipital process; process lateral to cranioquadrate opening long (1).
- (173) Lateral eustachian canals open dorsal (0); or lateral (1) to medial eustachian canal.
- (174) Exoccipitals terminate dorsal to basioccipital tubera (0); or send robust process ventrally and participate in basioccipital tubera (1); or send slender process ventrally to basioccipital tubera (2).
- (175) Quadrate foramen aerum on mediodorsal angle (0); or on dorsal surface (1) of quadrate.
- (176) Quadrate foramen aereum is small (0); comparatively large (1); or absent (2) at maturity.
- (177) Quadrate lacks (0); or bears (1) prominent, medio-laterally thin crest on dorsal surface of ramus.
- (178) Attachment scar for posterior mandibular adductor muscle on ventral surface of quadrate ramus forms modest crests (0); or prominent knob (1).
- (179) Quadrate with small, ventrally-reflected medial hemicondyle (0); or with small medial hemicondyle; dorsal notch for foramen aerum (1); or with prominent dorsal projection between hemicondyles (2); or with expanded medial hemicondyle (3).

A downloadable version of the character matrix in TNT format is available at:

<http://dx.doi.org/10.6084/m9.figshare.921655>

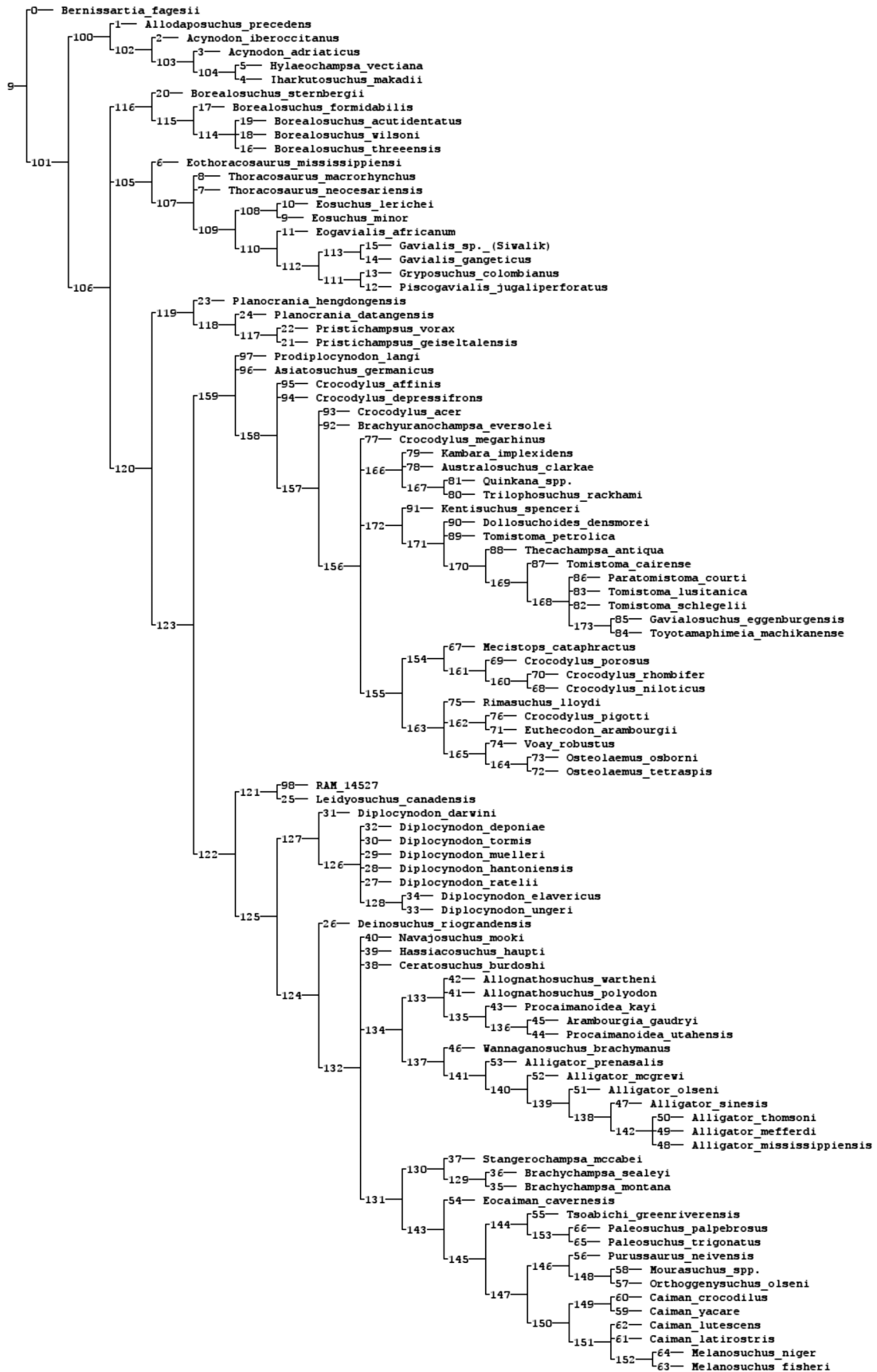


Figure 18. Strict consensus tree from phylogenetic analysis of Crocodylia.

80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100 101 102 103 104 105 106 107 108 109 110 111 112 113 114 115 116 117 118 119 120 121 122 123 124 125 126 127 128 129 130 131 132 133 134 135 136 137 138 139 140 141 142 143 144 145 146 147 148 149 150 151 152 153 154 155 156 157 158 159 160 161 162 163 164 165 166 167 168 169 170 171 172 173 174 175 176 177 178 179

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